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Address all correspondence to

The Managing Editor, *Pachyderm*
PO Box 68200–00200
Nairobi, Kenya
Email: pachydermeditor@gmail.com
Website: http://www.iucn.org/african_elephant
http://pachydermjournal.org

Cover caption: African savannah elephant calf (*Loxodonta africana)*, Samburu National Reserve, Kenya.

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CHAIR REPORTS

African Elephant Specialist Group Chair report
Rapport du Groupe de Spécialistes de l'Eléphant d'Afrique

Benson Okita-Ouma[1] and Rob Slotow[2], co-Chairs/Présidents

[1]Director, Wyss Academy for Nature, East Africa Hub, PO Box 18, Nanyuki 10400, Kenya
[2]Oppenheimer Fellow in Functional Biodiversity, School of Life Sciences, University of Kwazulu-Natal, Pietermaritzburg, 3209, South Africa

email contacts: okitaben@gmail.com; slotow@ukzn.ac.za

Introduction

The past year has been one of significant progress and renewed engagement for the IUCN–SSC African Elephant Specialist Group (AfESG) (hereafter 'Group'). Against a backdrop of persistent conservation challenges—ranging from habitat fragmentation and escalating human-elephant conflict (HEC) to debates over sustainable use, the Group has remained steadfast in its mission to provide rigorous, science-based guidance for the conservation of African elephants across their range. With two distinct species, the African forest elephant (*Loxodonta cyclotis*) and the African savannah elephant (*Loxodonta africana*) recognized and listed separately on the IUCN Red List, the need for species-specific data and coordinated action has never been greater.

In this context, the updated African Elephant status report will stand as a flagship achievement. These comprehensive assessments of both forest and savannah elephant populations represent the most authoritative updates on population trends, threats, and distribution to date. The reports draw from hundreds of survey records, reflect wide-ranging engagement with partners and range States, and directly feed into critical platforms such as the African Elephant Database (AED),

Introduction

Ces douze derniers mois ont été prolifiques pour le Groupe de Spécialistes de l'Éléphant d'Afrique (GSEAf) de l'UICN CSE, avec des progrès importants réalisés et un engagement renouvelé de la part de ses membres. Face aux défis qui sillonnent le monde de la conservation – fragmentation des habitats, montée des conflits humains-éléphants (CHE), débats autour d'une utilisation durable des éléphants – le groupe de spécialistes est resté fidèle à sa mission de fournir des orientations rigoureuses et fondées sur la science pour la préservation des éléphants sur leur aire de répartition en Afrique. Compte tenu de l'existence de deux espèces distinctes reconnues par la Liste rouge de la CITES et répertoriées séparément (l'éléphant de forêt *Loxodonta cyclotis* et l'éléphant de savane *Loxodonta africana*), jamais le besoin de recueillir des données spécifiques à chaque espèce et de mener des actions coordonnées n'a été plus important.

Dans ce contexte, la mise à jour du rapport de situation de l'éléphant d'Afrique constituera un aboutissement majeur. Ces évaluations exhaustives des deux populations d'éléphants d'Afrique représentent à ce jour la référence qui fait autorité en matière de tendances démographiques, de répartition des populations et de menaces relatives à ces espèces. Réaliser ces rapports – qui reflètent un engagement profond avec les partenaires et les États de l'aire de the IUCN Red List, the Green Status of Species assessments, and CITES processes. The AfESG's collaborative role in facilitating and validating this work is a core part of our mandate, ensuring that conservation policy is grounded in credible, standardized data.

Beyond population status and trends, the AfESG has also made significant strides in addressing complex issues shaping the future of elephant conservation. The Green Status assessments of both forest and savannah elephants will provide a forward-looking framework for measuring species recovery, ecological functionality, and the effectiveness of ongoing conservation action. These assessments will help stakeholders move beyond extinction risk towards a deeper understanding of what it will take to restore healthy, resilient elephant populations across Africa's diverse landscapes.

At the same time, the Group has launched a pioneering, policy-oriented initiative through its *Sustainable Use* task force, to navigate one of the most polarizing debates in African elephant conservation. By facilitating structured dialogue, synthesizing evidence, and integrating community perspectives, this process seeks to move beyond entrenched positions and identify areas of shared understanding that can support more effective collective action.

Meanwhile, the *Human-Elephant Conflict and Coexistence* working group (HECx WG) is revising the longstanding Decision Support System, a toolbox for HEC mitigation, updating it with current best practices and resources to better support practitioners and communities navigating the realities of living with elephants.

These efforts demonstrate the AfESG's commitment to providing strategic and evidence-based leadership while fostering inclusive processes that value collaboration, local knowledge, and long-term sustainability. As we prepare for CITES CoP20 and the official launch of the 2023 and 2024 African elephant status reports for forest and savannah elephants, respectively, we remain dedicated to supporting the recovery and coexistence of both the African elephant species through partnerships, science-based research and open dialogue.

répartition – demande de puiser dans des centaines de recensements documentés, et ils alimentent des plateformes incontournables telles que la Base de données sur l'éléphant d'Afrique (BDEA), la Liste rouge de l'UICN, les évaluations du Statut vert des espèces et les processus de la CITES. Le rôle collaboratif du GSEAf dans la facilitation et la validation de ce travail est au cœur de notre mission, laquelle consiste à garantir que les politiques de la conservation reposent sur des données crédibles et standardisées.

Hormis ces activités relatives aux tendances démographiques et à l'état des populations, le groupe de spécialistes a effectué de grandes avancées dans le traitement des problématiques complexes qui détermineront l'avenir de la conservation des éléphants. L'évaluation du Statut vert des éléphants de forêt et de savane fournira un cadre prospectif afin d'estimer le rétablissement des espèces, la fonctionnalité écologique et l'efficacité des mesures de conservation en cours. Ce processus permettra aux parties prenantes de penser au-delà du risque d'extinction et d'avoir une meilleure appréhension des éléments nécessaires au rétablissement de populations en bonne santé et résilientes dans les divers paysages africains.

Dans le même temps, le groupe de spécialistes a été à l'origine d'une initiative axée sur la prise de décisions politiques par l'intermédiaire de son équipe spéciale dédiée à *l'utilisation durable*, qui vise à aiguiller l'un des débats les plus clivants de la conservation de l'éléphant d'Afrique. Par la facilitation d'un dialogue structuré, et par la synthèse des données probantes en la matière et l'intégration des points de vue des communautés, ce processus s'attache à transcender les positions figées et à identifier les zones de compréhension mutuelle susceptibles d'encourager une action collective plus efficace.

Par ailleurs, le groupe de travail sur *les conflits humain-éléphants et leur coexistence* procède actuellement à la révision de l'historique Système de soutien à la prise de décision – un ensemble d'outils destinés à l'atténuation des CHE – afin de l'enrichir des bonnes pratiques et des ressources actuelles, permettant ainsi d'aider les praticiens et les communautés qui doivent composer au quotidien avec les réalités de la coexistence avec les éléphants.

Ces efforts reflètent l'engagement du GSEAf à fournir un leadership stratégique et fondé sur des données probantes, tout en encourageant des processus inclusifs qui valorisent la collaboration, le savoir local et la durabilité à long terme. Alors que nous nous

Updated African Elephant Status Report: Forest and Savannah populations and range

Over the past year, the AfESG has made outstanding progress in compiling the 2023 and 2024 African Elephant status reports for both forest and savannah elephants, reinforcing our commitment to delivering the most robust and current data to inform conservation and policy decisions. These reports not only represent the culmination of extensive collaboration with range States, technical experts, and conservation partners, but also serve as a vital cornerstone for guiding targeted action to secure the future of both species.

The African Forest Elephant status report has now been finalized and is in the process of being published as an official IUCN document. It identifies 22 countries where forest elephants occur and includes data from 252 survey records, of which 150 were systematic surveys, greatly enhancing the confidence and credibility of the estimates. This effort underscores the continued relevance and impact of rigorous population monitoring, with results already presented at key forums, including the African Elephant range States dialogue in Maun, Botswana.

Simultaneously, the Savannah Elephant status report is advancing through its final internal review phase. Data consolidation has been completed across all 22 range States, with input from 257 zones, most of which reflect systematically collected survey data. One of the most significant highlights is the inclusion of results from the 2022 KAZA Transfrontier aerial survey, which estimated nearly 228,000 elephants in the KAZA region, demonstrating the scale and potential of transboundary conservation efforts. Final drafting is underway, with plans to launch both reports at the CITES CoP20 in Uzbekistan taking place from 24 November to 5 December 2025.

These reports exemplify the power of collaborative science and monitoring that are central to efforts in continuous updating of the AED from which these reports are drawn, and which feed into informing CITES processes. They reflect the collective commitment of stakeholders across Africa and beyond to ensuring that tournons vers la CdP20 de la CITES et le lancement officiel des rapports de situation de l'éléphant de forêt 2023 et de l'éléphant de savane 2024, nous restons centrés sur le rétablissement et la coexistence des deux espèces grâce aux partenariats, aux recherches scientifiques et au dialogue.

Mise à jour du rapport de situation de l'éléphant d'Afrique : aire de répartition et population de l'éléphant de forêt et l'éléphant de savane

L'année dernière, le GSEAf a réalisé des progrès remarquables dans l'élaboration des rapports de l'éléphant d'Afrique 2023 et 2024 pour les deux espèces, renforçant ainsi notre engagement à livrer les données les plus solides et les plus actuelles possibles pour aider la conservation et les décisions politiques en la matière. Non seulement ces comptes-rendus représentent l'aboutissement d'une vaste collaboration avec les États de l'aire de répartition, les experts techniques et les partenaires de la conservation, mais ils sont également une étape vitale pour orienter des actions ciblées visant à assurer l'avenir des deux espèces.

Le rapport de situation de l'éléphant de forêt d'Afrique, désormais finalisé et sur le point d'être publié en tant que document officiel de l'UICN, identifie 22 pays dans lesquels vivent les éléphants de forêt et comprend des données issues de 252 recensements, dont 150 relevés systématiques, ce qui accroît considérablement la fiabilité et la crédibilité des estimations. Ces efforts soulignent la pertinence et l'impact constants d'un suivi des populations rigoureux, dont les résultats ont déjà été présentés lors d'événements décisifs, notamment la rencontre entre les États de l'aire de répartition de l'éléphant d'Afrique à Maun, au Botswana.

En parallèle, le rapport de situation de l'éléphant de savane est en phase finale d'examen en interne. La consolidation des données a été réalisée dans les 22 États de l'aire de répartition, avec des informations issues de 257 régions, dont la plupart font preuve d'une collecte de données systématique. L'un des éléments les plus marquants est l'intégration des résultats du recensement aérien effectué par la zone de conservation transfrontalière du Kavango-Zambèze (KAZA) en 2022, dont l'estimation compte près de 228 000 éléphants dans cette région, ce qui montre l'ampleur et le potentiel des efforts transfrontaliers. La decisions on elephant conservation are guided by credible, up-to-date, and transparent information. At the heart of this process is the *Data Review WG*, whose members have played a pivotal role in compiling, reviewing, and validating the data and findings, thereby ensuring scientific rigour and legitimacy in all outputs.

Assessing the Green Status of African forest and savannah elephants

In parallel with status assessments, the AfESG has been actively leading progress on the IUCN Green Status of Species assessments for both forest and savannah elephants. This initiative represents a transformative shift in focus towards understanding not only how far these species are from extinction but also understanding (and fostering) full ecological recovery. It reflects a shift from crisis response to proactive restoration and resilience-building.

The Green Status assessment for forest elephants is nearing completion and provides a comprehensive evaluation of species' recovery across their range in Central and West Africa. Based on the 2023 Forest Elephant status report, this assessment takes into account habitat integrity, the effectiveness of protection measures, connectivity among populations, and reductions in illegal killing. It presents a forward looking perspective of recovery scenarios under various conservation strategies, providing vital insights to guide future conservation investments and action.

The final components of the savannah elephant report are expected to be completed and made available in November 2025, by the IUCN publications committee. Preparations are currently underway to conduct the Green Status of Species assessment for the savannah elephant. This next phase will be critical in evaluating the species' recovery potential, current and future range occupancy, population viability, and the effectiveness of conservation measures, particularly those aimed at mitigating HEC and enhancing coexistence.

Although the status report is still being finalized, a savannah elephant Green Status of Species team of AfESG is in place and preliminary data and expert input are already being synthesized to version définitive sera achevée sous peu, et il est prévu de publier les deux rapports lors de la CdP20 de la CITES, qui se tiendra du 24 novembre au 5 décembre en Ouzbékistan.

Ces comptes-rendus sont le parfait exemple de la puissance de la collaboration, tant scientifique qu'au niveau des suivis – des composantes essentielles à la mise à jour constante de la BDEA. En alimentant les processus informatifs de la CITES, ils reflètent l'engagement collectif des acteurs de la protection des éléphants en Afrique (et au-delà) à garantir que les décisions dans le domaine de la conservation soient guidées par des informations crédibles, actuelles et transparentes. Au cœur de ce processus se trouve le *groupe de travail sur l'examen des données*, dont les membres ont joué un rôle central dans la compilation, l'examen et la validation des données et des conclusions, assurant ainsi la rigueur et la légitimité scientifiques de l'ensemble des résultats.

Évaluation du Statut vert des éléphants de forêt et de savane

En parallèle, le GSEAf continue d'accompagner les démarches en vue de l'évaluation du Statut vert des espèces pour les éléphants de forêt et de savane. Cette initiative représente une étape clé pour comprendre, non seulement, le degré de menace d'extinction encourue par ces espèces, mais également leur place sur le chemin du rétablissement écologique total. Signe qu'une transition est en cours, c'est désormais le rétablissement proactif et le renforcement de la capacité de résistance qui prennent le pas sur la réaction aux crises.

L'évaluation du Statut vert des éléphants de forêt est en cours d'achèvement et fournit une évaluation exhaustive du rétablissement de l'espèce dans son aire de répartition du centre et de l'ouest de l'Afrique. En mobilisant les données du rapport de situation de l'éléphant de forêt, cette évaluation prend en considération l'intégrité des habitats, l'efficacité des mesures de protection, la connectivité entre les populations et la baisse des abattages illégaux. Elle offre une vision prospective des scénarios de rétablissement suivant différentes stratégies de conservation, en produisant des perspectives déterminantes qui permettront de guider les investissements et les actions de conservation à venir.

Comme les derniers éléments du rapport de situation d'éléphant de savane étaient attendus pour support a rigorous, evidence-based assessment. This process will draw on the experience gained from the forest elephant Green Status assessment and will be undertaken in close collaboration with the IUCN's Green Status of Species team.

By integrating these insights, the AfESG is helping to redefine what successful conservation looks like, beyond simply avoiding extinction, towards restoring elephants as functional components of healthy ecosystems. The results of these assessments will not only inform the global community but will also provide practical tools for range States and conservation practitioners to prioritize and measure progress.

Navigating the debate: AfESG's collaborative approach to sustainable use of African Elephants

In response to longstanding divisions in the global conservation community, the AfESG has taken a proactive and inclusive approach to the debate on sustainable use. Recognizing that polarized positions on this issue have often hindered collective action, the *Sustainable Use* task force (SUTF) has embarked on a policy-oriented process designed to pilot a new model of collaboration, one grounded in mutual respect, evidence-based dialogue, and transparency.

This initiative is not about resolving all disagreements. Rather, it is about creating space for understanding, acknowledging diverse experiences and values, and exploring potential areas of convergence. By incorporating structured mental modelling, systematic evidence synthesis, and participatory insights from community-level stakeholders, the task force has developed a process that enables honest reflection and shared learning, as shown in Figure 1.

Participants have worked to articulate their underlying assumptions and values, examine the current evidence base, and identify key uncertainties. This has fostered a more nuanced understanding of the factors shaping differing views on the sustainable use of African elephants and allowed for the identification of research gaps and priorities. Importantly, the process also highlights how deeply moral values and lived experience

septembre 2025, les préparatifs de l'évaluation du Statut vert des éléphants de savane ont été entrepris. Cette nouvelle phase sera cruciale pour estimer le potentiel de rétablissement de l'espèce, son occupation actuelle et future de l'aire de répartition, la viabilité de la population et l'efficacité des mesures de conservation, en particulier celles visant à atténuer les conflits humains-éléphants et à améliorer leur coexistence.

Bien que le rapport de situation soit en cours de finalisation, une équipe du GSEAf dédiée au Statut vert des espèces est déjà en place, et les données préliminaires ainsi que les résultats des experts sont en train d'être synthétisés afin de permettre une évaluation rigoureuse et fondée sur des données probantes. Ce processus s'appuiera sur l'expérience acquise lors de l'évaluation du Statut vert de l'éléphant de forêt et sera mené en étroite collaboration avec l'équipe de l'UICN chargée de l'évaluation du Statut vert des espèces.

Par l'intégration de ces perspectives, le GSEAf aide à redéfinir l'image d'une conservation réussie et qui aspire, au-delà de la simple prévention contre l'extinction, à réinstaurer les éléphants en tant que composantes fonctionnelles d'écosystèmes sains. Les résultats de ces évaluations n'auront pas pour seul rôle d'informer la communauté mondiale, ils fourniront en outre des outils pratiques aux États de l'aire de répartition et aux professionnels de la conservation afin d'établir des priorités et de mesurer les progrès accomplis.

Le GSEAf adopte une approche collaborative dans le débat de l'utilisation durable des éléphants d'Afrique

En réponse aux divisions historiques existant au sein de la conservation mondiale, le GSEAf a adopté une approche proactive et inclusive dans le débat sur l'utilisation durable des éléphants. Reconnaissant que les clivages sur ce sujet ont souvent entravé l'action collective, l'équipe spéciale *utilisation durable* a initié un processus fondé sur la prise de décisions politiques et qui vise de nouveaux modèles de collaboration, ancrés dans le respect mutuel et le dialogue construit, et s'appuyant sur les données probantes et la transparence.

Cette initiative n'a pas pour vocation de résoudre tous les désaccords, mais elle s'attache à créer un

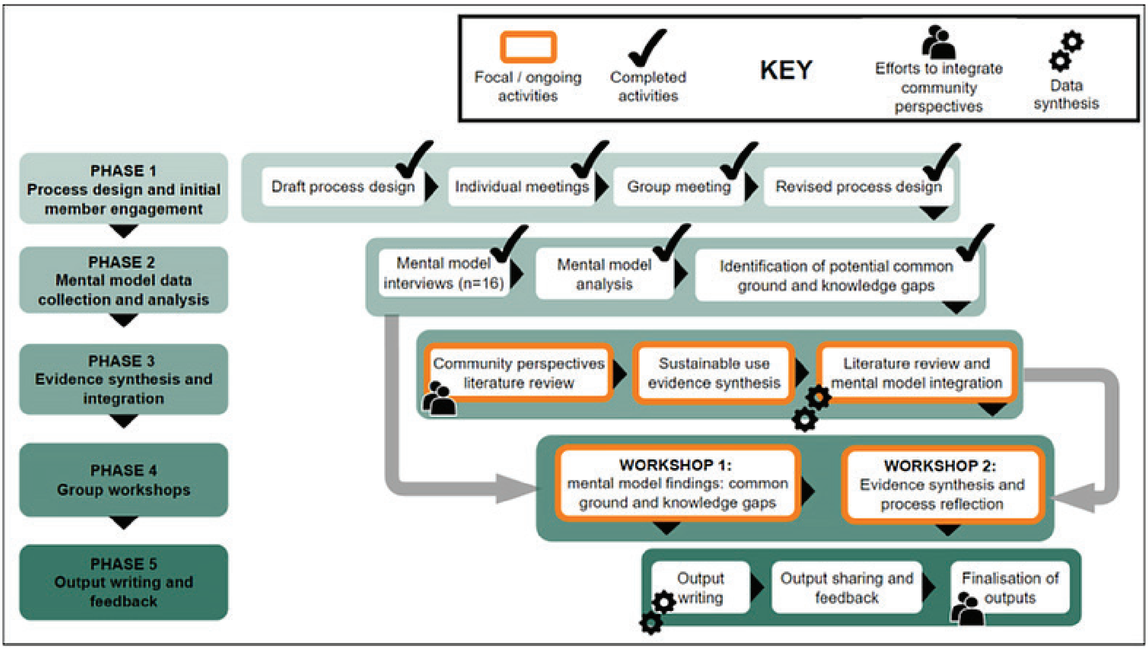

Figure 1. Multi-phase collaborative process integrating mental models and evidence synthesis (Source: Facilitation Team)

Graphique 1. Processus collaboratif multiphase intégrant des modèles mentaux et des synthèses de données probantes (source : équipe *facilitation*)

influence perceptions of what is effective, ethical, and appropriate in elephant conservation.

The anticipated outputs of this initiative, including a final process report, literature reviews, and a draft framework for capturing community perspectives, will be shared with the wider AfESG for input and refinement. This approach is already demonstrating value not only in reframing entrenched debates but also in establishing a replicable model for addressing other complex conservation challenges involving iconic species.

Figure 1 illustrates a five-phase structured approach for integrating diverse stakeholder perspectives into sustainable use assessments, with a particular emphasis on incorporating community knowledge and expert evidence.

Update on the revision of the AfESG Human-Elephant Conflict Decision Support System

In another important development, the AfESG has launched a major revision of the HEC Decision Support System (HEC DSS), a widely used tool originally developed to help practitioners manage

espace pour la compréhension, la reconnaissance des différentes expériences et valeurs de chacun, et l'exploration des potentiels points de convergence. En intégrant modélisation mentale structurée, synthèse systématique des données probantes et vision participative des acteurs issus des communautés locales, l'équipe dédiée a développé un processus permettant une réflexion honnête et un apprentissage partagé, comme illustré dans l'image ci-dessous.

Les participants ont travaillé à articuler les valeurs et les postulats qui sous-tendent leur pensée, à étudier la base de preuves actuelles et à identifier les principales incertitudes. Cela a facilité une compréhension plus nuancée des facteurs à l'origine des divers points de vue en la matière, la détection des lacunes de la recherche, et la définition des priorités sur ce thème. Il faut noter que le processus a également mis en exergue combien les valeurs morales et l'expérience vécue influencent fortement la perception de ce qui est efficace, éthique et approprié dans le domaine de la conservation des éléphants.

Les premiers résultats de ce projet, dont un compte-rendu final sur l'évolution du processus, l'examen de la littérature disponible sur le sujet et un cadre provisoire visant à recueillir les perspectives des communautés, and mitigate HEC effectively. Building on its strong foundation, the update seeks to modernize the DSS to reflect current best practices, incorporate new tools, and improve usability for a broader range of stakeholders.

Led by the original author, Richard Hoare, a longstanding member of AfESG and supported by a dedicated team of the *Human Elephant Coexistence* working group (HECx WG) members and consultants, the revision process has been designed to be collaborative and inclusive. Feedback from the HECxWG has guided improvements to content structure, clarity, and functionality. The updated DSS will also incorporate new resources, such as the Save the Elephants' Human Elephant Co-existence Toolbox and the IUCN SSC Human-Wildlife Conflict Guidelines, ensuring users can access the latest thinking and innovations in the field.

When complete, the revised DSS will serve as a central resource for practitioners, policymakers, and community leaders working across Africa. It will provide accessible, evidence-based guidance tailored to diverse contexts, supporting efforts to reduce conflict and foster coexistence. Contributors who play a significant role in content development and peer review will be acknowledged, underscoring the collaborative spirit of the revision process.

Report of the 78th Standing Committee Meeting (CITES)

The AfESG's ongoing engagement at the international policy level was exemplified through its active participation in the 78th Meeting of the CITES Standing Committee (SC78) held in Geneva, Switzerland. The Group was represented by Dr Kathleen Gobush, AfESG's CITES Focal Point, and contributed its technical expertise and conservation insights to discussions directly relevant to African elephants.

The SC78 was particularly pivotal as it was the last regular Standing Committee meeting before the 20th Conference of the Parties (CoP20). During the meeting, the AfESG was invited to provide an update on the conservation status, trends, and management strategies for African elephants, aligning with CITES Resolution Conf. 10.10.

seront partagés avec l'ensemble des membres du GSEAf, afin qu'ils offrent leurs retours et propositions d'amélioration. Cette approche démontre déjà son intérêt dans le fait de recadrer un débat aux arguments tranchés, et d'établir un modèle reproductible sur d'autres défis complexes de la conservation impliquant des espèces emblématiques.

Ce schéma illustre une approche structurée en cinq phases visant à inclure les différents points de vue des parties prenantes dans l'évaluation de l'utilisation durable, avec un accent particulier porté sur l'intégration du savoir communautaire et des données probantes fournies par les experts.

Des nouvelles de la révision du système de soutien à la prise de décision sur les conflits humains-éléphants

Le GSEAf est à l'origine d'une importante initiative avec la révision du système de soutien à la prise de décision sur les conflits humains-éléphants, une ressource largement utilisée et initialement développée en vue d'aider les praticiens de la conservation à gérer et à atténuer de façon efficace les conflits humains-éléphants. La mise à jour, en s'appuyant sur les bases solides du dispositif, tend à moderniser le système afin de refléter les bonnes pratiques actuelles, d'incorporer les nouveaux outils et d'en améliorer l'ergonomie pour l'ensemble des parties prenantes.

Piloté par son auteur original, Richard Hoare (membre de longue date du GSEAf), avec l'aide d'une équipe dédiée composée de membres du groupe de travail sur la *coexistence humains-éléphants* et de consultants, le processus de révision a été conçu pour être collaboratif et inclusif. Les commentaires de ce groupe ont orienté les améliorations apportées à la structure, la clarté et la fonctionnalité du contenu. Le système de soutien à la prise de décision intégrera également de nouveaux éléments, tels que la boîte à outils pour la coexistence humains-éléphants proposée par Save the Elephants et les lignes directrices de l'UICN CSE sur les conflits entre les humains et la faune sauvage, afin de garantir aux utilisateurs un accès aux dernières réflexions et innovations sur le terrain.

Une fois revu, le dispositif servira de ressource principale aux praticiens de la conservation, aux décideurs et aux responsables communautaires qui travaillent sur le continent africain. Il fournira des orientations accessibles et fondées sur des données

Additional agenda items covered during the session included assessments of National Ivory Action Plans, proposed changes to ETIS methodology, and ongoing discussions on taxonomy and nomenclature. Contributions by the AfESG ensured that African elephant conservation remained grounded in robust data and aligned with best practices, further reinforcing its value as a technical partner within the CITES framework.

In this issue

Leading the research section, Ruijs et al's. paper investigates the use of olfactory cues to redirect elephants along paths in the Makgadikgadi Pans/ Boteti River area of Botswana, which is notable in that the authors draw attention to the negative results obtained. It is important to continue exploring non-invasive management strategies that may enable us to communicate to elephants where high-risk areas are in a changing landscape. Can elephants be persuaded to follow one path rather than another using olfactory cues? Further studies are encouraged (see pp. 43–52).

Dunham's paper expands on his research published in Vol. 65/2024, which examined the importance of drought-related mortality among non-adult elephants in Gonarezhou NP. Following the 1992 drought, female herds in subsequent years consisted mainly of adult females, with few immatures. Among the survivors, immature females outnumbered immature males significantly. The models Dunham presents and analyses demonstrate that a low proportion of immature males within female herds can lead to a notable decrease in adult male recruitment, persisting for approximately 16 years after a drought. This resulted in a decline in the number of adult bulls in the population during that period, and due to bull mortality surpassing recruitment. (pp. 53–71).

There are several HEC related manuscripts in this issue. *Transition and conflict: patterns and drivers of human–elephant conflict in a changing pastoral landscape of northern Kenya* is the focus of Leneuiyian et al.'s research in a predominantly pastoralist landscape in a semi-arid/arid environment. As pastoral communities navigate the complex transition from nomadic

probantes, adaptées aux différents contextes et qui viennent soutenir les actions visant à réduire les conflits et à promouvoir la coexistence. Les contributeurs qui jouent un rôle de poids dans le développement du contenu et l'examen par les pairs seront reconnus, en accord avec l'esprit collaboratif de ce processus de révision.

Compte-rendu de la 78e réunion du Comité permanent de la CITES

L'engagement constant du GSEAf au niveau des politiques internationales a été illustré par la participation active du groupe à la 78e session du Comité permanent de la CITES, qui s'est tenue à Genève, en Suisse. Représenté par Dr Kathleen Gobush, le point focal du groupe à la CITES, le GSEAf a partagé son expertise technique et ses connaissances approfondies en matière de conservation lors de discussions directement liées aux éléphants d'Afrique.

Cette 78e session était particulièrement cruciale puisqu'elle constituait la dernière séance ordinaire du Comité avant la 20e Conférence des Parties (CdP20). Le GSEAf y a été invité à faire le point sur les statuts de conservation et les approches de gestion des éléphants d'Afrique, conformément à la Résolution Conf. 10,10 de la CITES.

Parmi les autres sujets à l'ordre du jour figurait l'évaluation des plans d'action nationaux pour l'ivoire, les propositions d'amendement de la méthodologie ETIS et des discussions sur la taxonomie et la nomenclature. Les contributions du GSEAf ont permis de garantir que la conservation de l'éléphant d'Afrique demeure ancrée dans des données solides et soit conforme aux bonnes pratiques, renforçant d'autant plus la valeur du groupe en tant que partenaire technique au sein du cadre de la CITES.

Dans ce volume

Dans la section dédiée à la recherche, l'article par Vera Ruijs et al. étudie l'usage de signaux olfactifs pour rediriger les éléphants en direction de certains passages, dans la région du Pan de Makgadikgadi et de la rivière Boteti au Botswana. Point intéressant : les auteurs soulignent les résultats négatifs obtenus lors de cette expérience. Ce type de stratégies de gestion non invasives, qui pourraient nous aider à transmettre aux éléphants l'emplacement des zones à haut risque dans un paysage en mutation constante, doivent traditions to agro-pastoral livelihoods, driven by climate pressures, land use change, and cultural evolution, new dynamics of conflict are emerging. The author's findings and anecdotal accounts from informal interviews demonstrate that these intersecting transitions amplify the risks of HEC. The authors propose adapting conservation planning to irreversible transitions towards agro-pastoralism by designating corridors and seasonal zoning; strengthening institutional responsiveness through expanded ranger patrols and alert; and embedding local knowledge in coexistence strategies via stakeholder forums that balance biodiversity and livelihood priorities, (pp. 85–100).

Another complex HEC situation is examined in Hill et al.'s paper from Murchison Falls NP, Uganda, presenting engaging and original data on elephant movements, resulting in intensive snaring pressure (in 32% of the observed elephants). The data were obtained from GPS collars fitted to elephants, from surveys of crop-raiding incidents in farmland bordering the Park, and from ground observations of elephants in the PA and surrounds, describing a comprehensive picture of elephant conservation issues in the wider conservation area. Unresolved land tenure, community distrust, and evictions further complicate elephant management outside the Park. The authors recommend prioritising protection within Murchison Falls NP, fencing the northern and eastern boundaries, and strengthening community engagement through transparency and trust-building (pp. 111–127).

Weinmann et al.'s manuscript addresses HEC within the context of mitigation strategies that focus on the palatability of certain crops to elephants. The authors consider factors such as crop suitability for specific soils and rainfall conditions, socio-cultural contexts, and the importance of assessing this suitability when designing effective mitigation strategies, and challenges and the benefits of transitioning to non-palatable crops, emphasizing critical considerations such as market access and training. (pp. 128–141).

To balance the demands of expanding human populations with the needs of wildlife, governments have been placed under increased pressure to implement successful coexistence

continuer à être explorées. Peuvent-ils être poussés à emprunter un passage plutôt qu'un autre, grâce à des signaux olfactifs ? Nous encourageons des recherches supplémentaires en ce sens (voir pages. 43 à 52).

Dans son article, Kevin M Dunham développe sa recherche parue dans le volume n° 65 de *Pachyderm*, qui traite de la mortalité liée à la sécheresse parmi les éléphants juvéniles dans le parc national de Gonarezhou. Après l'épisode de 1992, il a été identifié que les hardes de femelles étaient formées principalement de femelles adultes et de quelques juvéniles. Chez les éléphants survivants, le nombre de femelles juvéniles dépassait de loin des mâles non adultes. Les modèles présentés et analysés par l'auteur montrent qu'une faible proportion de mâles juvéniles au sein d'un groupe de femelles est susceptible d'entraîner une baisse notable du recrutement de mâles adultes – une situation qui peut se poursuivre pendant environ seize années. Cette configuration a conduit à un déclin du nombre d'adultes mâles dans la population pendant cette période, dû à une mortalité de cette classe d'âge plus importante que leur recrutement. (pages 53 à 71).

Par ailleurs, plusieurs réflexions portent sur les conflits humains-éléphants dans ce numéro. Kennedy Leneuiyian et al., dans leur recherche intitulée *Transition and conflict: patterns and drivers of human–elephant conflict in a changing pastoral landscape of northern Kenya* (« Transition et conflits : modèles et facteurs de conflits humains-éléphants dans un paysage pastoral en mutation au nord du Kenya »), se concentrent sur les heurts, dans le paysage à prédominance pastorale d'un environnement semi-aride à aride. Alors que les communautés, en raison de la pression climatique, des changements dans l'utilisation des terres et de l'évolution culturelle, éprouvent les complexités de la transition entre traditions nomades et mode de vie semi-pastoral, de nouvelles dynamiques de conflits apparaissent. Les conclusions de Leneuiyian et al. ainsi que des entretiens avec les intéressés montrent que ces transitions interconnectées amplifient les risques de conflits humains-éléphants. Les auteurs proposent d'adapter les plans de conservation aux transitions irréversibles vers l'agropastoralisme en désignant des corridors et des zonages saisonniers, en renforçant la réponse institutionnelle grâce à l'extension des patrouilles et des alertes émises par les rangers, et en intégrant le savoir local dans les stratégies de coexistence afin d'équilibrer les priorités entre biodiversité et moyens de subsistance (pages 85 à 100).

management strategies, and honeybees have proven to be one of the more effective deterrents elsewhere in African range States. However, Tempe et al.'s study in the Chobe NP, northern Botswana, which trialled bee recordings, has so far proven limited in its efficacy. This study demonstrates the value of conducting behavioural trials on specific elephant populations under local conditions to gauge reactions to differing deterrents before investing in mitigation (pp. 191–196).

An intriguing paper by Paterson in the history section introduces *Pachyderm* readers to the artwork, storytelling, and mythology of the San people, highlighting their harmonious relationship with elephants. To explore this connection, the paper compares and analyses various behavioural contexts that link the San to elephants, as depicted in 17 of the rock art sites (chosen for Pachyderm) of the Cederberg region. Most researchers believe that these paintings, which remain visible on the rocks of Cederberg, were created within the last 7,000 years. Additionally, many of the paintings featuring elephants, eland, and lines of dancing people are estimated to be at least 1,500 years old. (pp. 142–165)

Parker presents a history paper on the role of tusks and how variation in shape influences their use as male fighting weapons from observations and historical measures of tusk shape. If all elephants, including females, of both *Loxodonta africana* and *Elephas maximus* lived to maturity without breaking or damaging their tusks through use and wear (nor so many died of untimely deaths), would elephant tusks grow into curved helicoid tusk forms (much like a corkscrew)? This can only be satisfactorily answered when the shapes and lengths of the extinct elephantids' tusks are put into population perspectives related to sex and age. It is an interesting paper in the history section, combining philosophical thought with decades of scientifically based observation (pp. 166–176).

Acknowledgements

We extend our deepest gratitude to all members of the AfESG who have contributed their time, expertise, and passion across our various task

Joanna Hill et al. se penchent sur une situation similaire dans le parc national de Murchison Falls en Ouganda et présentent des données intéressantes et originales sur les déplacements des éléphants, ainsi que sur l'intense pression exercée sur eux par les pièges (des blessures ont été constatées sur 32 % des individus suivis). Ces données ont été obtenues à partir de colliers GPS placés sur les éléphants, de relevés des incidents de pillages des cultures dans les fermes en périphérie du parc et d'observations de terrain dans la zone protégée et ses alentours, le tout permettant de produire une vue d'ensemble des difficultés liées à la conservation dans cette région. Les problématiques non résolues relatives au foncier, au manque de confiance des communautés et aux expulsions, compliquent d'autant plus la gestion des éléphants en dehors du parc. Les auteurs recommandent de prioriser la protection au sein du parc national, d'ériger des clôtures aux limites nord et est de la zone protégée et de renforcer l'engagement des communautés par la transparence et l'établissement de liens de confiance. (pages 111 à 127).

Le manuscrit de Sophia Weinmann et al. aborde les aspects majeurs des conflits, ainsi que les stratégies de réduction de l'appétence des cultures pour les éléphants. Il s'agit notamment d'étudier la pertinence de cultures alternatives selon le type de sol, le taux de précipitations et les contextes socioculturels. L'importance d'évaluer ces caractéristiques dans la mise en place des stratégies d'atténuation est par ailleurs soulevée, de même que les défis afférents et les bénéfices d'une transition vers des cultures non-appétantes, y compris les notions 128 à 141).

L'objectif visant à équilibrer les demandes des populations humaines en pleine expansion et les besoins des espèces sauvages a soumis les gouvernements à une pression constante afin qu'ils mettent en œuvre des stratégies de gestion efficaces en termes de coexistence – l'installation de ruches s'est notamment avérée l'un des moyens de dissuasion les plus performants dans d'autres pays africains de l'aire de répartition. Toutefois, l'étude de Tempe et al., effectuée dans le parc national de Chobe au nord du Botswana et qui s'est attachée à enregistrer les bourdonnements des abeilles, s'est, pour l'instant, révélée peu probante. Cette recherche montre l'intérêt de conduire des essais comportementaux sur place et sur des populations d'éléphants spécifiques dans le but de jauger leurs réactions aux divers moyens de dissuasion, avant tout investissement dans des

forces and working groups—especially the Data Review working group. Their dedication has been instrumental in advancing the Group's mission during a period of ambitious and multifaceted activity.

We also acknowledge with appreciation the generous financial support provided by our partners: the European Union through the CITES MIKE Project, the Paul G. Allen Family Foundation/Vulcan Inc., Save the Elephants, the International Fund for Animal Welfare, WWF–US, WWF–International, the US Fish and Wildlife Service, the African Elephant Conservation Fund, and the Wyss Academy for Nature. Their investment enables the work that underpins this report and supports broader conservation activities across the continent.

Finally, we offer heartfelt thanks to the AfESG Secretariat team, Mohammed Yahya, Rose Mayienda, and Rachel Sharon, whose extraordinary commitment, coordination, and professionalism have made this progress possible. Their behind-the-scenes efforts, logistical support, and thoughtful facilitation have helped to weave together a highly productive and forward-looking year for the AfESG.

méthodes d'atténuation des conflits humains-éléphants. (pages 191 à 196).

Il faut également noter un article fascinant écrit par Andrew Paterson, figurant dans notre section *Histoire*, et qui fait découvrir aux lecteurs de pachyderm l'art, les récits et les mythes du peuple San, en soulignant la relation harmonieuse qu'ils entretiennent avec les éléphants. Afin d'explorer cette connexion, Paterson compare et analyse divers contextes comportementaux qui lient les San aux éléphants, tels que représentés dans 17 des sites d'art rupestre (choisis pour Pachyderm) de la région du Cederberg. La plupart des chercheurs considèrent que ces peintures, toujours visibles, ont été réalisées au cours des 7 000 dernières années. En outre, nombre de celles qui dépeignent des éléphants, des oryx et des rangées de danseurs, dateraient d'au moins 1 500 ans. (pages 142 à 165).

Ian SC Parker, pour sa part, présente un article s'appuyant sur des observations et des mesures historiques de défenses d'éléphant, et explorant leur rôle et la façon dont la variation dans leur forme influence leur usage, par les mâles, en tant qu'armes. Si tous les éléphants, y compris les femelles, des deux espèces *Loxodonta africana* et *Elephas maximus* vivaient jusqu'à l'âge adulte sans casse ni dommages infligés à leurs défenses du fait de leur utilisation et de l'usure (et si peu d'entre eux mouraient prématurément), leurs défenses pousseraient-elles en suivant une forme hélicoïdale courbée (comme celle d'un tire-bouchon) ? On ne peut répondre à cette question de manière satisfaisante qu'en replaçant la forme et la longueur des défenses des éléphantidés disparus dans le contexte démographique lié au sexe et à l'âge. Cet article intéressant est présenté dans la section *Histoire* de notre volume, en combinant imagination philosophique et plusieurs décennies d'observations scientifiques (pages 166 à 176).

Remerciements

Nous exprimons notre profonde gratitude aux membres du GSEAf, qui ont consacré leur temps, leur expertise et leur passion au service de nos différents groupes de travail et équipes spéciales, et tout particulièrement au groupe de travail sur l'examen des données. Leur dévouement a grandement contribué à faire avancer les missions du groupe de spécialistes dans une période d'activités ambitieuses et variées.

Nous tenons également à remercier nos partenaires pour leur généreux soutien financier : l'Union européenne par le biais du projet MIKE de la CITES, la Fondation Paul G. Allen Family/Vulcan Inc., Save the Elephants, le Fonds international pour la protection des animaux (IFAW), WWF États-Unis et WWF International, le département américain Fish and Wildlife, le Fonds pour la conservation de l'éléphant d'Afrique et Wyss Academy for Nature. Leurs investissements ont permis de réaliser les travaux sur lesquels s'appuie ce compte-rendu et soutiennent des activités de conservation plus larges sur le continent africain.

Enfin, nous adressons nos remerciements les plus sincères à l'équipe du secrétariat du GSEAf, Mohammed Yahya, Rose Mayienda, and Rachel Sharon, dont l'engagement, la coordination et le professionnalisme extraordinaires ont rendu ces progrès possibles. Leurs efforts en coulisses, leur soutien logistique et leur attention portée à faciliter toute situation ont aidé à construire une année très productive pour le GSEAf, et tournée vers l'avenir.

African Rhino Specialist Group Chair report
Rapport du Groupe de Spécialistes du Rhinocéros d'Afrique

David Balfour[1] (Chair/Président) and Sam M Ferreira[2] (Scientific Officer)*

[1]Independent conservation ecologist; Research Associate: Zoology Department, Nelson Mandela University, Gqeberha, South Africa
[2]Scientific Services, SANParks, Skukuza, South Africa; Department of Conservation and Marine Sciences, Cape Peninsula University of Technology, South Africa

*corresponding email: environ1@mweb.co.za

Dave/OrcID: 0000-0002-4613-4069
Sam/OrcID: 0000-0001-6924-1150

Introduction

Through its mission statement, the IUCN/SSC African Rhino Specialist Group (AfRSG) envisions thriving wild populations of both species of African rhinoceroses (rhinos)—*Diceros bicornis* (black rhino) and *Ceratotherium simum* (white rhino)—that are not only ecologically viable but also widely valued by people. To realise this vision, the AfRSG works to guide and facilitate the conservation of rhinos across their natural range. Increasingly, however, expectations are expanding and there is growing recognition that rhino conservation should also contribute to the broader well-being of people who share landscapes with these iconic species.

In early 2025, the AfRSG published the *African Rhino Conservation Framework* (ARCF), which provides a strategic framing for future conservation actions (Balfour et al. 2025a). The ARCF emphasises the need to integrate ecological management, safety and security for rhinos and people, the disruption of organised wildlife crime, and our evolving understanding of the dynamics of rhino horn markets, into planning and conservation action for rhinos. It recognises the importance of increasing equity of all stakeholders, and of promoting diverse perspectives on the value of rhinos in society. These interconnected elements serve as the six strategic pillars that collectively underpin the guidance for effective and inclusive rhino conservation in future.

Introduction

Le Groupe de spécialiste du Rhinocéros d'Afrique (GSRAf) de la CSE de l'UICN, dans sa déclaration de mission, projette sa vision pour les rhinocéros d'Afrique noirs (*Diceros bicornis*) et blancs *Ceratotherium simum*) : des populations épanouies dans leur environnement, viables dans leur écosystème, et hautement estimées du monde qui les entoure. À ces fins, le GSRAf travaille à orienter et à faciliter la conservation des rhinocéros dans leur aire de répartition naturelle. Les attentes en ce sens sont toujours plus fortes, tout comme l'est la conscience que ce domaine devrait également contribuer au bien-être général des personnes qui partagent leur habitat avec ces espèces emblématiques.

En début d'année 2025, le GSRAf a publié le guide African Rhino Conservation Framework (ARCF–Plan de conservation des rhinocéros d'Afrique), qui fournit un cadre stratégique pour les futures actions de conservation (Balfour et al. 2025a). L'ARCF insiste sur la nécessité d'intégrer, au cœur des plans et des mesures de protection, la gestion écologique, la sécurité et la sûreté des animaux comme des habitants, la lutte contre le crime organisé lié aux espèces sauvages, ainsi que notre compréhension progressive des dynamiques du marché de la corne de rhinocéros. Ce cadre reconnait l'importance d'accroître l'équité entre toutes les parties prenantes, et de promouvoir la diversité des points de vue quant à la valeur des rhinocéros dans la société. Ces éléments interdépendants constituent les six piliers stratégiques qui, ensemble, soutiendront les futures orientations en

Achieving progress across these pillars requires a range of enabling conditions. These include flexible and sustained funding mechanisms, governance systems that are legitimate, devolved and collaborative, and a strong technical capacity to support evidence-based decision-making. The framework recognises that conservation must be rooted not only in sound ecological principles but also in respect for human rights, thereby promoting a more people-centred approach. It positions rhino conservation within a broader social context, where long-term success depends on acknowledging and responding to the needs, voices and rights of those who live alongside rhinos. Importantly, the framework is designed to be adaptive and dynamic. It acknowledges that conservation is not static, and that strategies must evolve as ecological realities and social expectations change.

This report reflects on progress made in achieving the AfRSG's objectives and considers the alignment of ongoing efforts with evolving societal expectations.

Planning rhino conservation

The 15th members' meeting of the AfRSG, held from 23 February to 2 March 2025 at Bonamanzi Game Reserve in KwaZulu-Natal, marked a significant moment of collective reflection, technical exchange, and strategic alignment among African and international rhino conservation stakeholders. The meeting brought together government representatives, conservation scientists, managers, NGOs, and private custodians to assess progress, share innovations, and refine the AfRSG's future focus. While "Proceedings of the meeting" are in preparation, this reflection provides a brief overview of key themes and outcomes.

As is tradition, the meeting opened with rhino range State "Country Reports" contributing to the preparation of the African Rhino Status Report for CITES 20th Conference of the Parties (CoP20 [1]). These updates captured the range of national

[1]The 20th meeting of the Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES CoP20) will be held in Samarkand, Uzbekistan, from 24 November to 5 December 2025

vue d'une conservation efficace et inclusive.

Certaines conditions sont nécessaires à la mise en œuvre de ces axes de progression, tels que des mécanismes de financement souples et durables, des systèmes de gouvernance légitimes, décentralisés et collaboratifs, ainsi qu'une forte capacité technique permettant de prendre des décisions reposant sur des données probantes. L'ARCF établit que la conservation doit, certes, s'ancrer dans de solides principes écologiques, mais également dans le respect des droits de l'homme – une approche, en somme, davantage axée sur l'humain. Il s'agit donc de placer la conservation des rhinocéros au cœur d'un contexte social plus large, dans lequel la réussite sur le long terme dépend de la reconnaissance des besoins, des opinions et des droits de ceux qui vivent auprès des rhinocéros, et de la réponse qui leur est apportée. Il est important de noter que l'ARCF a été conçu pour être dynamique et présenter une capacité d'adaptation. Il soutient une conservation non figée et des stratégies évoluant au fil des mutations des réalités écologiques et des attentes sociales.

Nous restituons ici les progrès accomplis dans le cadre des objectifs fixés par le GSRAf et nous examinons dans quelle mesure les efforts actuels sont en adéquation avec l'évolution des attentes de la société.

Les temps forts de la conservation des rhinocéros

La 15e réunion du GSRAf, qui s'est tenue du 23 février au 2 mars 2025 dans la réserve de Bonamanzi dans le KwaZulu-Natal, a marqué un temps important de réflexion collective, de dialogues techniques et d'alignement stratégique entre les différents acteurs africains et internationaux de la conservation des rhinocéros. Représentants de gouvernements, scientifiques et responsables de la conservation, ONG et gérants d'organismes privés s'y sont réunis afin d'évaluer les progrès réalisés, d'échanger sur leurs procédés innovants et de redéfinir les futurs objectifs du GSRAf. Le procès-verbal de la réunion étant en cours de rédaction, nous présentons ici une vue d'ensemble de l'issue des discussions et des thèmes abordés.

Conformément à la tradition, la rencontre a débuté par les comptes-rendus nationaux des États de l'aire de répartition du rhinocéros, qui contribueront à l'élaboration du rapport de situation pour la 20e contexts and highlighted conservation successes, poaching threats, law enforcement challenges, and adaptive responses across range states. These shared insights set the tone for the week.

The programme spanned a wide range of interconnected themes. Technical sessions addressed global conservation trends, the effectiveness of anti-poaching interventions, disruption of organised crime, and lessons from Asia. Finance was a central concern, with workshops exploring emerging mechanisms to improve the sustainability and impact of rhino conservation funding, especially security and anti-poaching. Parallel sessions on fragmented habitats and community relevance underscored the importance of socially grounded approaches, especially where local custodianship, tenure models, and meta-population dynamics intersect with conservation goals.

Knowledge exchange was enriched through structured techniques such as buzz groups, brainwriting, feedback circles, and World Café dialogues. These participatory methods encouraged inclusive reflection on performance factors, indigenous and local community expectations, reintroduction models, and climate adaptation. Technological innovation also featured prominently, with sessions exploring the potential of artificial intelligence, remote sensing, and spatial forecasting to support rhino protection and management.

In-depth discussions on genetic health, population viability, and One Plan approaches for rhinos highlighted the need for integration between in situ and ex situ strategies. A reflection on the outcomes of the "genetics bootcamp" held earlier in the year (see below) and scenario-based discussions on translocations and range expansion helped refine conservation guidance and will likely inform the revision of IUCN rhino translocation guidelines. Parallel sessions on governance, values, and stakeholder communication further reinforced the AfRSG's commitment to inclusive, science-based, and adaptive conservation.

The Members' Only session provided an opportunity for internal discussion on governance updates, financial and scientific reporting, and working group feedback. The AfRSG's emphasis on building trust,

Conférence des parties (CdP20[1]) de la CITES. Ces informations ont permis de jauger les contextes locaux et de mettre en lumière les progrès réalisés, les menaces liées au braconnage, les défis de la lutte contre la criminalité et les moyens mis en œuvre par les États pour y répondre – des perspectives qui ont donné le ton pour cette semaine d'échanges.

Le programme de l'événement couvrait un ensemble de thématiques interconnectées. Les sessions techniques ont porté sur divers sujets : les tendances mondiales en matière de conservation, l'efficacité des interventions anti-braconnage, la lutte contre le crime organisé et certains enseignements venus du continent asiatique. Au centre des préoccupations, les problématiques de financement ont été abordées lors d'ateliers visant à explorer les mécanismes émergents afin d'améliorer la durabilité et l'impact du financement de la conservation, notamment la sécurité et la lutte contre le braconnage. Des séances parallèles sur la fragmentation des habitats et l'intérêt de la conservation pour les communautés ont souligné l'importance d'approches socialement ancrées, particulièrement lorsque la gestion au niveau local, les modèles fonciers et les dynamiques de métapopulations croisent les objectifs de conservation.

Des dispositifs structurés – ateliers de travail en petits groupes, sessions d'échange d'idées sur papier, cercles de retour sur expérience et discussions suivant le concept de World café – ont aidé au partage de connaissances. Ces méthodes participatives ont encouragé une réflexion inclusive sur les facteurs de performance, les attentes des communautés locales et autochtones, les modèles de réintroduction et l'adaptation au changement climatique. La part belle a également été faite aux innovations techniques, lors de sessions consacrées au potentiel de l'intelligence artificielle, de la télédétection et des prévisions géospatiales comme outils venant servir la conservation des rhinocéros.

La nécessité d'une intégration mutuelle des stratégies in situ et ex-situ a été mise en évidence grâce à des échanges approfondis abordant la santé génétique, la viabilité des populations et les approches de planification intégrée de la conservation («One

[1]La 20e session de la Conférence des Parties à la Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction (CdP20 de la CITES) se tiendra à Samarkand, Uzbekistan, du24 novembre au 5 décembre 2025

strengthening coordination, and sharpening strategic focus through its revised task forces and working groups was affirmed (see below). Final discussions addressed emerging controversies and clarified communication priorities.

The 15th AfRSG members' meeting reaffirmed the AfRSG's role in promoting open dialogue, peer-to-peer learning, and a shared commitment to strategic priorities. The meeting significantly strengthened the collective foundation for achieving long-term conservation outcomes for both black and white rhinos.

The AfRSG also faces notable operational challenges. The loss of financial support from the USF&WS following the United States government's 'Stop Work Order' has required the AfRSG to curtail several of its core activities while alternative funding sources are sought. To sustain essential functions, the AfRSG has drawn more heavily on a range of funding sources—though these are often less certain and may not provide the long-term stability required for the AfRSG to meet its continental mandate. In the short term, the financial burden has been partially eased by funds reallocated from the resignation of the Programme Officer and recruitment for this key position has been postponed until a more stable financial outlook is secured.

In the interim, this situation has placed considerable additional demand on the time and energies of the Scientific Officer and the Chair as they assume responsibilities previously handled by the Programme Officer. The redistribution of duties has contributed to short-term constraints in the AfRSG's internal operations, including a temporary lapse in the maintenance of platforms such as WeNaturalist, and to a lesser extent, our engagement with the IUCN's online systems.

Despite these challenges, the AfRSG remains committed to fulfilling its mandate. Members continue to work collaboratively to maintain essential functions, secure alternative support, and ensure continuity in delivering strategic conservation guidance. The AfRSG recognises the need for strengthened financial resilience and is actively pursuing pathways to restore its full operational capacity in the service of African rhino conservation.

Plan »). Le bilan du « genetics bootcamp », organisé en février de cette année (voir détails ci-dessous), puis des discussions basées sur des scénarios de translocations et d'accroissement des aires de répartition, ont permis de redéfinir les orientations de la conservation, sur lesquelles la révision des directives de l'UICN en matière de réintroductions de rhinocéros pourra s'appuyer. Des sessions parallèles portant sur la gouvernance, les valeurs et la communication avec les différents acteurs du secteur ont renforcé l'engagement du GSRAf envers une conservation inclusive, fondée sur la science et adaptative.

Les dernières informations au sujet de la gouvernance, des rapports financiers et scientifiques ainsi que les conclusions des groupes de travail ont pu être échangées lors de la séance « réservée aux membres ». Le GSRAf a affirmé sa volonté profonde d'instaurer un climat de confiance, de renforcer la coordination et de préciser les priorités stratégiques grâce à des équipes spéciales et des groupes de travail redéfinis. L'évènement s'est achevé sur la question des nouvelles controverses émergeant dans le domaine de la conservation, et les priorités en matière de communication ont été clarifiées.

Lors de cette 15e réunion des membres, le rôle du GSRAf a été réaffirmé – celui d'un groupe qui favorise un dialogue ouvert, ainsi que l'apprentissage entre pairs et un engagement commun envers les priorités stratégiques. La rencontre a considérablement renforcé les bases collectives nécessaires à l'obtention de résultats sur le long terme.

D'autre part, le GSRAf est confronté à des défis opérationnels de taille. Suite à la perte du soutien financier venu du département américain Fish and Wildlife (USF&WS) émanant de la décision « Stop Work Order » émise par le gouvernement des États-Unis, le GSRAf a été contraint de restreindre plusieurs de ses activités principales, le temps de considérer des alternatives de financement. Les membres ont dû recourir à d'autres sources de revenus, lesquels ne garantissent toutefois pas le même niveau de sécurité ni la stabilité sur le temps long que requiert l'atteinte des objectifs dans le cadre du mandat continental du GSRAf. À court terme, la charge financière a été partiellement allégée par la réaffectation des fonds issus de la démission du responsable de programme, poste central pour lequel le recrutement est reporté jusqu'à ce que de meilleures perspectives de stabilité financière soient assurées.

Cette situation a sollicité un engagement

Guiding rhino conservation

Following the 15th members' meeting of the AfRSG, the structure of its technical and advisory bodies was revised to better align with emerging priorities in rhino conservation. This led to the establishment of eight task forces (TFs) and three working groups (WGs), each with a focused mandate to address specific challenges across the conservation spectrum. Although the Chair is currently reviewing these arrangements, considering funding constraints, the thematic orientation of each group remains strategically aligned with the AfRSG's mission.

TF1: Leadership Process is responsible for guiding the procedures for appointing chairs and ensuring effective succession planning. This includes developing transparent criteria and mechanisms to oversee leadership transitions and maintain institutional continuity.

TF2: Population Rating Systems is finalising the AfRSG's system for evaluating rhino populations. This rating tool is critical for standardising site assessments and guiding conservation investment according to ecological performance, risk, and strategic value.

TF3: Tracking Systems for Rhinos focuses on the application of various transmitter technologies for rhino monitoring. The task force is evaluating both the technical potential and practical limitations of this system, including deployment feasibility, data reliability, and animal welfare considerations.

TF4: Rhino Conservation Integration aims to strengthen the implementation of national and global rhino conservation frameworks. It works to enhance collaboration and communication among stakeholders and elevate the visibility and practical utility of the ARCF.

TF5: Rhino Reintroduction and Ex Situ Integration provides guidance on the integration of ex-situ populations into in-situ recovery efforts. The task force is developing risk-based frameworks for reintroduction and translocation, and assessing when insurance populations are warranted to safeguard against demographic or environmental shocks.

TF6: Review of Rhino Introduction Guidelines critically assesses existing IUCN introduction guidelines, to ensure their continued relevance and scientific rigour in guiding future

supplémentaire considérable en temps et en énergie au responsable scientifique et au président du GSRAf, qui assument désormais les responsabilités du responsable de programme. La redistribution des tâches a contribué à l'émergence de certaines difficultés de courte durée au sein des opérations internes du GSRAf, notamment une interruption temporaire de la maintenance de plateformes telles que WeNaturalist, et, dans une moindre mesure, de notre implication dans les systèmes en ligne de l'UICN.

Malgré ces difficultés, le GSRAf est déterminé à remplir sa mission. Les membres poursuivent leur travail en commun afin de maintenir les fonctions essentielles du groupe, d'obtenir un soutien financier alternatif et d'assurer la continuité en fournissant des orientations stratégiques. Le GSRAf est conscient du besoin de renforcer sa résilience financière et recherche activement les moyens de rétablir sa pleine capacité opérationnelle au service de la conservation des rhinocéros d'Afrique.

Une conservation organisée et pilotée

Suite à la 15e réunion du GSRAf, la structure des comités techniques et consultatifs a été révisée dans l'objectif de montrer un meilleur alignement avec les nouvelles priorités de la conservation des rhinocéros. Huit équipes spéciales et trois groupes de travail ont été créés, chacun porteur d'un mandat précis afin de relever les défis spécifiques de ce domaine. Malgré les contraintes de financement actuelles, qui exigent une refonte de ces prérogatives par le président, les orientations thématiques de chaque groupe restent cohérentes, d'un point de vue stratégique, avec la mission du GSRAf.

L'équipe spéciale n° 1 *Processus directionnel*, doit guider les procédures de nomination du président et garantir une planification efficace pour la succession à ce poste, grâce à la mise en place de critères et de mécanismes transparents afin de superviser les transitions de la présidence et de maintenir la continuité institutionnelle.

L'équipe spéciale n° 2 *Système d'évaluation des populations* finalise actuellement le système d'évaluation des populations de rhinocéros mis au point par le GSRAf. Cet outil essentiel vise à standardiser l'évaluation des sites et à orienter les investissements en matière de conservation, selon les performances écologiques, les risques et la valeur reintroductions.

TF7: Rhino Funding Futures addresses the alignment between conservation funding and measurable outcomes. It is also working to mitigate risks posed by funding instability—such as recent reductions from major donors—and to promote financial resilience through diversification of funding streams.

TF8: Economics Underpinning Rhino Conservation explores the economic context of rhino conservation, including socioeconomic drivers, benefit distribution, and the structure of both legal and illegal rhino horn markets. This work supports informed, ethical, and economically viable conservation strategies.

In addition to the TFs, the AfRSG maintains three WGs with cross-cutting responsibilities.

WG1: Governance assists the chair with the governance and operational functions of the AfRSG. It monitors capacity development opportunities.

WG2: Rhino Management concentrates on ecological and technical dimensions of rhino conservation, including metapopulation structure, genetic integrity, partnerships, protection measures, and range expansion. It plays a key role in curating and disseminating best practices.

WG3: Communication and Public Support supports strategic communication to build broad-based public and stakeholder understanding of, and support for, rhino conservation and law enforcement. It aligns with IUCN communication principles and connects the AfRSG to broader outreach efforts.

Together, these TFs and WGs reflect a coordinated, science-based, and adaptive framework to advance rhino conservation across Africa. Their thematic focus enables the AfRSG to respond effectively to ecological, socio-political, and economic challenges, while maintaining alignment with global conservation standards and local stakeholder needs.

Enhancing rhino conservation

In February 2025, the Secretariat of the AfRSG convened a focused workshop in Pretoria, supported by Save the Rhino International Inc., to compile preliminary guidelines for black rhino (*Diceros bicornis*) genetic conservation.

stratégique des projets.

L'équipe spéciale n° 3 *Systèmes de suivi des rhinocéros* travaille sur l'application de diverses technologies d'émetteurs pour le suivi des rhinocéros. Elle en évalue le potentiel technique et les limites pratiques, dont la faisabilité du déploiement de tels équipements, la fiabilité des données collectées et la prise en considération du bien-être des animaux.

L'équipe spéciale n° 4 *Intégration de la conservation des rhinocéros* vise à renforcer la mise en œuvre de cadres nationaux et internationaux. Elle s'attache à améliorer la collaboration et la communication parmi les différents acteurs et à accroître la visibilité de l'ACRF et son utilité dans la pratique.

L'équipe spéciale n° 5 *Réintroduction et intégration ex-situ des rhinocéros* fournit des conseils en matière d'intégration de populations ex-situ au sein d'opérations de rétablissement in situ. Elle développe des cadres fondés sur les risques pour la réintroduction et la translocation de rhinocéros, et étudie si les situations requièrent de constituer des populations de réserve comme garde-fou contre le choc démographique ou environnemental.

L'équipe spéciale n° 6 *Examen des lignes directrices relatives* à l'introduction de rhinocéros évalue d'un point de vue critique les directives actuelles de l'UICN en matière d'introduction, afin de garantir une pertinence et une rigueur scientifique constantes dans l'accompagnement des futures réintroductions.

L'équipe spéciale n° 7 *L'avenir du financement de la conservation des rhinocéros* examine l'adéquation entre financement de la conservation et résultats quantifiables. Elle travaille également à atténuer les risques posés par l'instabilité des financements, tels que les récentes coupes opérées par des acteurs majeurs, et à promouvoir la résilience économique par le biais de la diversification des canaux de soutien.

L'équipe spéciale n° 8 *Fondements économiques de la conservation des rhinocéros* explore le contexte économique de la conservation, dont les facteurs socio-économiques, la répartition des bénéfices obtenus, et la structure des marchés de cornes de rhinocéros, légaux comme illégaux. Ce travail vient soutenir des stratégies de conservation éclairées, éthiques et économiquement viables.

En parallèle, le GSRAf maintient trois groupes de travail aux prérogatives transversales.

Le groupe de travail n° 1 *Gouvernance* assiste le président dans ses fonctions relatives à l'opérationnel et à la gouvernance au sein du GSRAf. Ce groupe étudie

The workshop brought together 20 specialists—including geneticists, conservation leaders, and rhino practitioners—to develop a "straw dog" framework addressing two critical areas: 1) informed decision making for the movement and assembly of black rhinos across Africa; and 2) the genetic monitoring required to support and evaluate translocations and population management at the continental scale. These guidelines are intended to support coordinated, science-based conservation among range States.

Black rhinos remain Critically Endangered (Emslie 2020), and their long-term survival depends on maintaining both demographically viable and genetically diverse populations. Genetic diversity underpins population adaptability and resilience to environmental change. However, historical overharvesting (almost entirely illegal), habitat loss, and population fragmentation have led to genetic erosion and the extinction of some genetic lineages (Moodley et al. 2017). Admixture and founder effects from earlier interventions further highlight the need for genetically informed decision-making.

Genomic analyses suggest nine historic subspecies (Moodley and Robovský 2025), of which only five likely persist. Subspecies used by the IUCN, such as *D. b. minor*, *D. b. bicornis*, and *D. b. michaeli*, are among those still represented in current populations, though many are small, isolated, and vulnerable to inbreeding and genetic drift. Effective conservation requires taking guidance from black rhino ecological dynamics and selecting appropriate founders for reintroductions, ensuring ecological suitability, and maximizing genetic diversity while respecting social compatibility and natural demographics.

Active interventions—including carefully planned translocations that simulate dispersal dynamics and ongoing genetic monitoring—are essential management for small or fragmented populations. In contrast, well-connected populations may be managed by promoting natural dispersal and maintaining habitat integrity. Conservation strategies must seek to avoid repeating past mistakes that compromised genetic integrity and instead adopt adaptive, evidence-based approaches. Interventions should minimise risk while supporting natural age and sex structures.

les opportunités de développement des capacités.

Le groupe de travail n° 2 *Gestion des rhinocéros* se concentre sur les dimensions écologiques et techniques de la conservation, dont la structure des métapopulations, l'intégrité génétique, les partenariats, les mesures de protection et l'accroissement de l'aire de répartition. Il joue un rôle majeur dans la sélection et la diffusion des bonnes pratiques.

Le groupe de travail n° 3 *Communication et soutien du public* est en charge des stratégies de communication visant à sensibiliser le grand public et les acteurs de la protection du rhinocéros, et à encourager leur soutien en faveur de la conservation et de la lutte contre la criminalité. Il adopte les principes de communication de l'UICN et permet au GSRAf d'étendre la portée de ses efforts de sensibilisation.

Ces onze équipes représentent un dispositif qui s'appuie sur la coordination, les bases scientifiques et l'adaptabilité pour faire avancer la conservation des rhinocéros sur tout le continent africain. Leur thématique propre permet au GSRAf de répondre de façon efficace aux défis écologiques, sociopolitiques et économiques, tout en maintenant une ligne en accord avec les normes mondiales de la conservation et les besoins des parties prenantes locales.

Une conservation renforcée par la science

En février 2025, le secrétariat du GSRAf, avec le soutien de Save The Rhino International Inc., a organisé un atelier thématique à Prétoria afin de préparer les orientations préliminaires de la conservation génétique des rhinocéros noirs (*Diceros bicornis*). Vingt spécialistes – généticiens, responsables et praticiens de la conservation des rhinocéros – y ont participé et avaient pour objectif d'élaborer un cadre provisoire qui aborde deux sujets cruciaux : 1) la prise de décision éclairée en ce qui a trait au déplacement et au rassemblement des rhinocéros noirs d'Afrique ; et 2) le suivi génétique qui s'impose pour évaluer et aider la gestion des populations et les translocations à l'échelle du continent. Ces lignes directrices visent à soutenir une conservation coordonnée et fondée sur des données scientifiques entre les pays de l'aire de répartition.

Le rhinocéros noir demeure en danger critique d'extinction (Emslie 2020) et sa survie sur le long terme dépend du maintien de populations viables sur le plan démographique et diversifiées sur le plan génétique – une diversité de laquelle découle

Ultimately, maintaining black rhino genetic diversity demands strategic planning that integrates ecological, demographic, and practical considerations. These include habitat suitability, source population availability, and management readiness. By embedding genetic objectives within broader conservation frameworks, and supporting natural evolutionary processes alongside managed interventions, conservationists can enhance population resilience and secure the species' long-term future in the wild.

Achieving rhino conservation

Over the past year, the AfRSG has made significant contributions to rhino conservation at both regional and global scales. These efforts reflect the Group's ongoing commitment to supporting scientifically grounded, collaborative, and adaptive strategies that secure viable rhino populations across Africa. Several recent engagements highlight the AfRSG's influence in guiding policy, management, and planning for rhino conservation in line with IUCN best practices.

A notable development was the acquisition of the 2,000 Southern White rhinos on the Platinum Rhino property by the NGO, African Parks, followed by the preparation of a rewilding framework. The AfRSG reviewed this framework, which aims to re-establish multiple viable populations across Africa. While the overall vision is commendable, the Group advised that a more flexible and pragmatic implementation approach would strengthen the initiative—especially where former Southern and functionally extinct Northern white rhino ranges are prioritised. The AfRSG also emphasised the importance of engaging with African range states to identify suitable release areas and the value of reducing breeding intensity at the original facility to avoid over-dependence on captive-origin individuals.

In Zambia, the AfRSG provided technical guidance for reintroducing black rhinos into Kafue National Park. Interim recommendations support the use of *D. b. minor* from the North Luangwa region as the primary founder stock, with additional genetic input from KwaZulu-Natal and Zimbabwe to enhance population diversity. However, further decisions regarding

leur capacité d'adaptation et leur résilience face aux changements environnementaux. Toutefois, les prélèvements historiques excessifs (illégaux pour la plupart), la perte d'habitat et la fragmentation des populations ont entraîné une érosion génétique et l'extinction de certains lignages génétiques (Moodley et al. 2017). Le brassage génétique et les effets fondateurs résultant de certaines interventions passées mettent d'autant plus en lumière la nécessité de tenir compte des connaissances en génétique avant toute prise de décision.

Les analyses génomiques suggèrent l'existence de neuf sous-espèces (Moodley and Robovský 2025), desquelles cinq seulement semblent avoir survécu. Les sous-espèces reconnues par l'UICN, telles que *D. b. minor*, *D. b. bicornis*, et *D. b michaeli*, font partie de celles toujours représentées à ce jour, bien que nombre d'entre elles appartiennent à des populations de petite taille, isolées et vulnérables en matière de consanguinité et de dérive génétique. Une conservation efficace requiert de s'inspirer des dynamiques écologiques des rhinocéros noirs et de sélectionner les fondateurs adéquats pour opérer des réintroductions, afin de garantir l'adéquation écologique et d'optimiser la diversité génétique tout en respectant la compatibilité sociale et la démographie naturelle.

Des interventions actives – dont des translocations planifiées avec soin qui simulent les dynamiques de dispersion, et le suivi génétique en cours – sont essentielles à la gestion des populations de petite taille ou fragmentées. À l'inverse, pour celles qui sont bien connectées entre elles, favoriser la dispersion naturelle et préserver l'intégrité des habitats peuvent être des méthodes de choix. Les stratégies de conservation, plutôt que de répéter les erreurs passées ayant compromis l'intégrité génétique, se doivent d'adopter des approches adaptatives et basées sur des données probantes. Minimiser les risques est un pré requis lors des interventions, tout en respectant les structures naturelles d'âge et de sexe.

En définitive, le maintien d'une diversité génétique chez les rhinocéros noirs exige une planification stratégique qui intègre des considérations écologiques, démographiques et pratiques, telles que des habitats appropriés, la disponibilité de populations sources et un système de gestion opérationnel. En incluant les objectifs génétiques dans les programmes de conservation plus généraux et en soutenant, en parallèle d'interventions bien gérées, les processus naturels de l'évolution, les acteurs de la protection peuvent admixture will await the outcomes of the dedicated genetic workshop that was scheduled for February 2025 (see above). This approach exemplifies the Group's commitment to cautious, evidence-based management that ensures both genetic integrity and long-term adaptability.

In Ethiopia, the AfRSG Chair and Scientific Officer engaged with the national Wildlife Authority to assess the potential for black rhino recovery. Discussions revisited historical records and acknowledged the possibility of re-establishing rhinos in their former ranges. However, the likely absence of local genetic variants elsewhere poses a constraint, necessitating careful consideration of reintroduction strategies and genetic provenance.

The AfRSG Chair collaborated with South African stakeholders—including provincial Rhino Management Groups (RMGs), national coordinators, and South African National Biodiversity Institute (SANBI)—to address systemic breakdowns in the consolidation of national rhino population data. Accurate, defensible estimates are essential for conservation planning and international reporting. The Chair reaffirmed support for rebuilding these processes through stronger coordination and inclusivity, including the formal involvement of SANBI to enhance technical oversight.

Regionally, the Chair also participated in the South African Development Community (SADC) Transfrontier Conservation Area (TFCA) meeting to promote integrated approaches to rhino conservation that transcend administrative boundaries. Such engagement is critical for advancing the concept of robust metapopulation management across southern and eastern Africa, allowing for more dynamic and adaptive management of rhinos across fragmented and diverse landscapes.

The AfRSG supported Ezemvelo KZN Wildlife and assessed the risks of extended boma confinement for black rhinos awaiting translocation. The assessment focused on welfare, health, behavioural, and fitness concerns for the rhinos, emphasizing that confinement beyond four months increases physiological and psychological stress, reduces ecological fitness, and may compromise post-release survival. The report highlights the need for proactive planning, contingency measures, and renforcer la résilience des populations et assurer l'avenir à long terme des espèces en milieu sauvage.

Les progrès réalisés

Au cours de l'année écoulée, le GSRAf a été à l'origine de contributions significatives, tant au niveau régional que mondial. Ces efforts reflètent la volonté constante du groupe à soutenir des stratégies fondées sur la science, collaboratives, adaptatives, et qui garantissent la viabilité des populations de rhinocéros en Afrique. Plusieurs engagements récents mettent en lumière l'influence du GSRAf quant aux orientations politiques, à la gestion et la planification de la conservation, en adéquation avec les bonnes pratiques de l'UICN.

Il faut citer le cas notable de l'acquisition des 2 000 rhinocéros blancs du Sud sur la propriété Platinum Rhino par l'ONG African Parks, suivie d'un plan de réintroduction en pleine nature. Ce dernier, qui vise à rétablir de multiples populations viables sur le continent africain, a été examiné par le GSRAf. Bien que le projet, dans son ensemble, soit louable, le groupe de spécialistes a estimé que l'initiative se verrait renforcée par une approche plus souple et pragmatique dans sa mise en œuvre – particulièrement lorsque les anciens habitats du rhinocéros blanc du Sud, et du – désormais éteint – rhinocéros blanc du nord, sont ciblés. Le GSRAf a également souligné, d'une part, l'importance de collaborer avec les États de l'aire de répartition afin d'identifier des zones de réimplantation adéquates, et d'autre part, l'intérêt de réduire l'intensité de reproduction au sein des installations d'origine pour éviter une dépendance excessive à l'égard des individus issus d'élevages en captivité.

En Zambie, le GSRAf a fourni un accompagnement technique pour la réintroduction de rhinocéros noirs dans le parc national de Kafue. Les recommandations provisoires préconisent l'emploi de *D. b. minor* de la région de North Luangwa comme stock fondateur, avec un apport génétique d'individus issus du KwaZulu-Natal et du Zimbabwe afin d'accroître la diversité de population. Toutefois, il faudra attendre les résultats de l'atelier dédié à ce sujet, qui s'est tenu en février 2025 (voir plus haut) avant de prendre d'autres décisions relatives au brassage génétique. Cette approche illustre l'engagement du groupe de spécialistes à défendre une gestion prudente et fondée sur des données probantes, qui garantisse l'intégrité génétique et l'adaptabilité sur le long terme.

En Éthiopie, le président et le responsable adaptive management, urging that bomas be used strategically and only for as long as necessary to support successful reintroduction.

Collectively, these initiatives underscore the AfRSG's central role in shaping the future of African rhino conservation. Through technical advice, policy engagement, and cross-boundary collaboration, the Group continues to contribute meaningfully to the global effort to secure the long-term survival of both black and white rhinoceroses.

Supporting rhino conservation

The AfRSG continues to play a critical technical role in supporting the implementation of CITES *Resolution Conf. 9.14 (Rev. CoP19)*, which mandates reporting on the conservation status and trade in rhino specimens. Ahead of CoP20, the AfRSG, in collaboration with TRAFFIC and the Asian Rhino Specialist Group (AsRSG), provided consolidated scientific input to guide evidence-based decision-making. However, reduced and uncertain funding significantly constrained the breadth and depth of these contributions.

For the CITES-mandated rhino status report, the AfRSG Secretariat secured partial funding, allowing it to meet a reduced set of reporting requirements, as specified by the CITES Secretariat. The final report focused only on selected elements of paragraphs 7 and 8 of the resolution, covering rhino conservation status, trade, stock management, illegal killings, and enforcement challenges. The AfRSG led the consultation efforts across 21 African range States to gather critical data, but was unable to fully address two key areas: conservation management strategies and efforts to reduce illegal demand. These omissions—directly linked to funding constraints—may limit the ability of Parties at CoP20 to assess the complete picture of rhino conservation needs and risks.

In parallel, the AfRSG provided input on two CITES listing proposals (Proposals 9[2] and 10[3]

[2]https://cites.org/sites/default/files/documents/E-CoP20-Prop-09.pdf

[3]https://cites.org/sites/default/files/documents/COP/20/prop/E-CoP20-Prop-10.pdf

scientifique du GSRAf ont travaillé avec les autorités nationales en charge de la vie sauvage pour évaluer le potentiel de rétablissement des rhinocéros noirs. Les discussions ont permis de revenir sur les données historiques et de reconnaître la possibilité d'un tel rétablissement dans l'aire de répartition antérieure. Cependant, la probable inexistence de variantes génétiques locales dans d'autres zones représente une contrainte qui demande de considérer avec prudence les stratégies de réintroduction et la provenance génétique.

Le président du GSRAf a collaboré avec des parties prenantes sud-africaines – dont des groupes de gestion des rhinocéros des provinces (« Rhino Management Groups »), des coordinateurs nationaux et l'institut sud-africain pour la biodiversité (« South African National Biodiversity Institute » – SANBI) – afin de remédier aux défaillances systémiques dans la consolidation des données nationales sur les populations de rhinocéros. Des estimations précises et défendables sont essentielles pour la planification et les comptes-rendus internationaux. Le président a réaffirmé son soutien à la refonte de ces processus grâce à une coordination et une inclusivité plus solides, dont la participation officielle du SANBI pour améliorer la supervision technique.

Au niveau régional, le président a également participé à la réunion de la communauté de développement sud-africaine (« South African Development Community » – SADC) sur la zone de conservation transfrontalière (« Transfrontier Conservation Area » – TFCA) afin de promouvoir des approches intégrées qui dépassent les frontières administratives. Un tel engagement est crucial pour faire progresser le concept d'une gestion robuste des métapopulations en Afrique méridionale et orientale, qui permette une prise en charge des rhinocéros plus dynamique et adaptative, dans des paysages diversifiés et fragmentés.

Le GSRAf a assisté Ezemvelo KZN Wildlife dans l'évaluation des risques d'un confinement prolongé en boma pour les rhinocéros noirs en attente de translocation. Les thèmes du bien-être des animaux, de leur santé, de leur comportement ainsi que de leur condition physique étaient au cœur des interrogations, qui ont mis en lumière qu'une durée de confinement excédant les quatre mois augmentait le stress physiologique et psychologique, réduisait les performances écologiques, et pouvait compromettre la survie après la remise en liberté. Le rapport souligne qu'il est impératif de développer une planification for CoP20), following a request from TRAFFIC. This included expert commentary on Namibia's proposed amendment to the annotation for its *C. s. simum* population (Southern white rhino) and its proposed transfer of *D. b. bicornis* (South-western black rhino) from Appendix I to Appendix II. The AfRSG consolidated perspectives from its membership to offer balanced, technically grounded guidance to support the decision-making process.

The Group also made substantial contributions to the CITES Rhinoceros Enforcement task force meeting in May 2025. Presentations from the AfRSG and AsRSG provided an overview of poaching and trafficking trends, enforcement responses, and underlying socio-political drivers. Poaching rates have declined since 2015 but remain concentrated in South Africa and Namibia. Enforcement challenges persist, particularly in carcass detection, judicial inefficiencies, and cross-border coordination. The AfRSG highlighted both biological and governance priorities—including the role of rewilding, habitat fragmentation, adaptive genetics, and shifting societal expectations as articulated in the Kigali Call to Action (IUCN SSC and Secretariat 2022).

Despite these strong technical contributions, the AfRSG's capacity to respond to CITES processes is increasingly undermined by financial shortfalls. Reduced support has delayed the replacement of key staff, forced reliance on voluntary contributions, and constrained follow-through on essential tasks such as platform maintenance and data coordination. These limitations not only affect the quality and timeliness of inputs to CITES but also reduce the AfRSG's ability to support Parties in implementing recommendations on the ground.

In summary, while the AfRSG remains a trusted source of scientific advice and coordination within the CITES framework, the effectiveness and comprehensiveness of its contributions are at risk without renewed and sustained funding. Continued support is essential to ensure that rhino conservation decisions at the international level are informed by robust, timely, and inclusive science.

proactive, des mesures d'urgence et une gestion adaptative, et recommande vivement que les bomas soient utilisés de façon stratégique et sans dépasser la durée nécessaire afin de garantir le succès de la réintroduction.

Collectivement, ces initiatives marquent le rôle central joué par le GSRAf dans l'avenir de la conservation des rhinocéros africain. Par ses conseils techniques, son engagement dans les politiques mises en place et sa collaboration transfrontalière, le groupe de spécialistes poursuit son importante contribution à l'effort mondial pour assurer la survie à long terme des rhinocéros noirs et blancs.

Une conservation en besoin de soutien

Le GSRAf continue de jouer un rôle technique essentiel dans la mise en œuvre de la *Resolution Conf. 9.14 (Rev. CdP19)* de la CITES, qui impose d'établir un compte-rendu sur le statut de conservation et le commerce des rhinocéros. En amont de la CdP20, le GSRAf, en collaboration avec TRAFFIC et le groupe de Spécialistes du Rhinocéros d'Asie (GRSAs), a fourni une synthèse de contributions scientifiques solides afin de guider la prise de décision basée sur des données probantes. Cependant, l'incertitude et la réduction des financements a conséquemment contraint l'ampleur des dites contributions.

En ce qui concerne le rapport de situation, un financement partiel a été obtenu par le secrétariat du GSRAf, permettant de répondre à un nombre restreint d'obligations relatives aux comptes-rendus, tel que spécifié par la CITES. Le document final a uniquement ciblé certains éléments sélectionnés des paragraphes 7 et 8 de la résolution, couvrant le statut de conservation des rhinocéros, le commerce, la gestion des stocks, l'abattage illégal et les défis de la lutte contre la fraude en la matière. Le GSRAf a mené des consultations auprès de 21 pays africains de l'aire de répartition afin de collecter des données essentielles, mais n'a pas été en mesure d'aborder deux sujets d'importance : les stratégies de gestion de la conservation et les efforts mis en place dans le but de réduire la demande de corne d'origine illégale. Ces omissions, directement liées au manque de financement, pourraient limiter la capacité des parties à réaliser une évaluation exhaustive des besoins de la conservation lors de la CdP20.

En parallèle, le GSRAf a contribué à deux propositions d'amendement des annexes de la CITES

Informing rhino conservation

The AfRSG plays a central role in guiding evidence-based rhino conservation across the continent. The ARCF (Balfour et al. 2025a) provides strategic direction for achieving thriving rhino populations valued by African people. The framework promotes adaptive, integrated approaches that align ecological needs with socio-political realities.

Recent research published in Oryx (Ferreira et al. 2025a) shows how such guidance translates into measurable outcomes. African rhino populations have shown signs of recovery since the Covid-19 pandemic, with poaching rates staying below the critical 3.5% threshold and an average population growth of 2.9% annually from 2020 to 2023. However, localised increases in poaching remain a concern. These findings support the AfRSG's message: effective conservation depends on maintaining low poaching levels, mitigating habitat loss, and tailoring responses to specific contexts.

Rewilding offers a complementary strategy by restoring rhinos to historical or suitable habitats, strengthening their ecological roles and increasing biodiversity (Ferreira et al. 2025b). Principles for successful rewilding include habitat suitability, minimising health and environmental risks, and addressing social and political complexities. This includes using reintroductions, repatriations, and managed breeding to meet specific goals, while also integrating zoo and captive-bred rhinos through adaptive management. Such efforts require strong communication to build public and political support as well as transparent governance to align stakeholders.

International translocations are regulated under CITES, which classifies black and most white rhinos under Appendix I, allowing only non-commercial imports. Southern white rhinos in Namibia, Eswatini, and South Africa are listed under Appendix II, enabling commercial trade under specific conditions. However, inconsistencies and interpretive gaps in CITES rules can hinder implementation and spark disagreements among parties (Ferreira et al. 2025c).

The AfRSG strives to demonstrate leadership in conservation science through its sustained commitment to constructive, evidence-based debate. This intellectual engagement—spanning

(propositions 9[2] et 10[3] pour la CdP20), à la demande de TRAFFIC. Elles concernent les commentaires de spécialistes sur des propositions émises par la Namibie et visant à, d'une part, amender l'annotation de sa population de C. s. simum (le rhinocéros blanc du Sud) et, d'autre part, à transférer D. b. bicornis (le rhinocéros noir du Sud-Ouest) de l'Annexe I à l'Annexe II. Le GSRAf a recueilli les points de vue de ses membres afin d'établir des recommandations techniques et nuancées qui soutiennent le processus décisionnel.

Il a également contribué de façon substantielle à la réunion de l'équipe spéciale de la CITES en charge de la lutte contre la fraude relative aux rhinocéros, qui s'est tenue en mai 2025. Les présentations effectuées par le GSRAf et le GSRAs ont donné un aperçu des tendances actuelles du braconnage et du trafic, des mesures de luttes contre ces délits et des causes sociopolitiques sous-jacentes. Les taux de braconnage sont en baisse depuis 2015 mais demeurent concentrés en Afrique du Sud et en Namibie. Les défis de la lutte contre cette criminalité sont toujours présents, particulièrement en ce qui concerne la détection des carcasses, l'inefficacité de la justice et la coordination transfrontalière. Le GSRAf a mis en avant les priorités liées à la biologie et à la gouvernance, dont le rôle du réensauvagement, de la fragmentation des habitats, de la génétique adaptative et de l'évolution des attentes sociétales, comme cela a été clairement exprimé dans l'Appel à l'action de Kigali (secrétariat et SCE de l'UICN, 2022).

Malgré ces contributions techniques de poids, la capacité du GSRAf à se conformer aux processus de la CITES se voit de plus en plus compromise par la perte de moyens financiers, qui a également eu pour effet de retarder le remplacement de membres clé du personnel, de contraindre à dépendre des participations bénévoles et de limiter notre suivi sur des tâches essentielles, telles que la maintenance des plateformes et la coordination des données. Non seulement la qualité et la rapidité de notre travail effectué pour la CITES en sont affectées, mais les ressources déployées pour soutenir les parties dans la mise en place de recommandations sur le terrain sont réduites.

En somme, bien que le GSRAf demeure une source fiable en matière de conseil scientifique et de

[2] https://cites.org/sites/default/files/documents/E-CoP20-Prop-09.pdf
[3] https://cites.org/sites/default/files/documents/COP/20/prop/E-CoP20-Prop-10.pdf

ecological interpretation, technological innovation, and policy relevance—underscores the Group's critical role in refining and grounding rhino conservation within robust scientific frameworks. Across diverse and sometimes controversial issues, the AfRSG maintains a clear emphasis on rigour, transparency, and the continual re-evaluation of assumptions considering emerging evidence.

One example of this is the AfRSG's engagement in the recent debate on long-term trends in rhino horn morphology. A paper by Wilson et al. (2022) used image-based analyses from museum collections to suggest a decline in relative horn length across five rhino species, attributing this to possible selective pressures from historical hunting or poaching. While the authors framed these results as exploratory and emphasized the novel use of digital datasets, AfRSG members published a critical response highlighting methodological limitations—particularly the limited and biased sample size, the over-representation of zoo specimens, and insufficient control for confounding variables such as age, sex, and environmental variation (Ferreira et al. 2024a). While Wilson et al. (2024) acknowledged these concerns and clarified that their original conclusions were cautiously framed, the exchange exemplified the AfRSG's commitment to refining scientific narratives and ensuring that conservation messaging remains grounded in statistical and ecological rigour.

Similarly, the AfRSG has responded critically—but constructively—to the proposed use of radioisotope horn infusions as a radical deterrent to rhino horn trafficking. Proponents argue that inserting trace amounts of radioactive material into rhino horns could make them easier to detect and less desirable on illegal markets. However, the AfRSG's analysis balances this potential with concerns about ethical and environmental risks, legal implications, and unintended market consequences, such as driving up horn value through perceived scarcity. The AfRSG emphasizes that such technologies, while innovative, should not be seen as standalone solutions but rather as potential support tools embedded within broader conservation frameworks that include habitat management, anti-poaching strategies, and stakeholder coordination dans le cadre de la CITES, l'efficacité et la portée de ses contributions sont à risque sans renouvellement de ses financements sur la durée. Il est pourtant essentiel qu'un tel soutien soit assuré sur le long terme afin de garantir que les décisions au niveau international aient une assise scientifique robuste, au fait des dernières avancées et inclusive.

Une conservation éclairée

Le GSRAf joue un rôle déterminant dans la conservation des rhinocéros à l'échelle du continent africain, pour maintenir une approche fondée sur des données probantes. L'ACRF (Balfour et al. 2025a) fournit un plan de route stratégique qui vise à établir des populations de rhinocéros épanouies et estimées à leur juste valeur par les peuples africains. Il encourage des pratiques adaptatives et intégrées qui concilient les nécessités écologiques et les besoins sociopolitiques.

De récentes recherches publiées dans la revue *Oryx* (Ferreira et al. 2025a) exposent la façon dont ces orientations se traduisent en résultats mesurables. Les rhinocéros d'Afrique montrent des signes de rétablissement depuis la pandémie de Covid-19, avec des taux de braconnage en deçà du seuil critique de 3,5 % et une croissance moyenne des populations de 2,9 % chaque année entre 2020 et 2023. Certaines régions connaissent cependant d'inquiétantes hausses de cas de braconnage. Ces conclusions vont dans le sens du message véhiculé par le GSRAf, qui assure qu'une conservation efficace dépend du maintien de faibles taux de braconnage, de l'atténuation de la perte des habitats et de l'adaptation des actions à la spécificité des contextes.

Le réensauvagement offre une stratégie complémentaire en réintégrant les rhinocéros dans des habitats historiques ou appropriés, ce qui renforce leur rôle écologique et accroît la biodiversité (Ferreira et al. 2025b). Les principes qui prévalent à la réussite de ces opérations sont ceux d'un habitat adéquat, de risques sanitaires et environnementaux réduits au maximum, et de complexités sociales et politiques abordées en amont. Cela se traduit par le recours aux réintroductions, aux rapatriements et aux programmes de reproduction suivant des objectifs spécifiques, tout en intégrant des rhinocéros élevés en zoos et en captivité par le biais d'une prise en charge adaptative. De tels efforts requièrent de solides campagnes de communication afin d'obtenir un soutien fort de la part des politiques et du public, engagement (Ferreira et al. 2025d).

Ecological debates have also drawn critical reflection from AfRSG members. Sky et al. (2024) reported that black rhino diet composition shifts in response to vegetation productivity, suggesting that acacias—commonly considered preferred browse—may function as fallback foods. This challenges long-standing assumptions about black rhino dietary selectivity and implies a link between foraging flexibility and reproductive output. In response, AfRSG foraging experts initiated a meta-analysis of existing dietary studies and argued that these findings should be interpreted within a more ecologically robust framework. They advocate for applying Owen-Smith's (2004) model of functional heterogeneity, which categorizes forage into optimal, staple, reserve, and buffer resources. This typology better reflects the adaptive strategies large herbivores employ to cope with spatiotemporal variability in resource availability and helps clarify how shifts in diet composition relate to ecological function and population dynamics.

Together, these examples reflect the AfRSG's core ethos: that constructive scientific debate is not only necessary to question assumptions and refine methodologies but is also essential to improving the credibility and impact of conservation practice. Whether scrutinising emerging technologies, reassessing ecological interpretations, or challenging prevailing narratives, the AfRSG promotes a culture of open, critical inquiry. This ongoing process of reflection and exchange fosters adaptive learning and helps ensure that rhino conservation remains anchored in sound ecological theory, local context, and interdisciplinary collaboration. In a landscape where conservation science is increasingly expected to deliver rapid and visible solutions, such deliberative rigour is indispensable for long-term resilience and success.

Recent peer-reviewed contributions by AfRSG members further demonstrate this commitment to evidence-based conservation. These works advance both conceptual thinking and practical tools across ecological, social, and governance domains. Collectively, they highlight the importance of learning from real-world implementation, engaging constructively with diverse stakeholders, and continuously re-

ainsi qu'une gouvernance transparente pour accorder les parties prenantes.

Les translocations internationales sont soumises aux règles de la CITES, qui classe les rhinocéros noirs – et la plupart des rhinocéros blancs – sous l'Annexe I n'autorisant que les importations non commerciales. Les rhinocéros blancs du Sud en Namibie, en Eswatini et en Afrique du Sud sont inscrits à l'Annexe II qui autorise le commerce sous certaines conditions spécifiques. Cependant, certaines incohérences et lacunes d'interprétation dans la réglementation de la CITES peuvent entraver la mise en place de telles opérations et susciter des désaccords entre les parties (Ferreira et al. 2025c).

Le GSRAf s'attache à montrer la voie en matière de science de la conservation par son implication constante dans un débat constructif et fondé sur la preuve. Cet engagement intellectuel, qui couvre autant l'interprétation écologique et l'innovation technologique que la pertinence des politiques mises en place, souligne le rôle crucial du groupe de spécialistes dans l'amélioration de la conservation et son ancrage dans des cadres scientifiques solides. Sur un ensemble de thèmes variés et parfois sujets à controverse, le GSRAf maintient une ligne claire empreinte de rigueur, de transparence et de réévaluation permanente des hypothèses à la lumière des nouvelles preuves ayant vu le jour.

Un des exemples illustrant cette exigence peut s'observer dans l'engagement du GSRAf dans le débat récent autour des tendances sur le long terme de la morphologie des cornes de rhinocéros. Wilson et al. (2022) ont exploité des analyses d'imagerie tirées de collections de musées qui suggèrent un déclin de la longueur relative des cornes de cinq espèces de rhinocéros, attribuant ce constat à de potentielles pressions sélectives dues à la chasse ou au braconnage. Bien que les auteurs aient décrit ces résultats comme exploratoires et qu'ils aient insisté sur la nouveauté que constituait l'utilisation de données numériques, les membres du GSRAf ont publié une réponse critique mettant en évidence certaines limites méthodologiques – particulièrement le fait d'avoir usé d'un échantillon biaisé et restreint, la surreprésentation de spécimens provenant de zoos et le manque de prise en compte du risque d'erreur lié à des variables telles que l'âge, le sexe et les variations environnementales (Ferreira et al. 2024a). Wilson et al. (2024) ont reconnu la validité de ces éléments et ont précisé que leurs conclusions initiales avaient evaluating and improving conservation strategies for species like rhinos in an ever-changing world.

A key theme is the importance of locally grounded, inclusive conservation models. Muntifering et al. (2025) present over a decade of experience from northwest Namibia, showing that sustained reductions in black rhino poaching—by more than 90%—can be achieved through participatory ranger programmes rooted in local values rather than militarised enforcement. Their findings highlight the ethical, social, and ecological efficiency of co-designed interventions that align protection efforts with community priorities. Similarly, Lopes-Lima et al. (2025) proposed a stakeholder-driven framework for applying eDNA technology in Africa. Their Namibian case study illustrates how empowering local institutions and integrating cultural context into monitoring can enhance biodiversity data collection and relevance for decision-making.

Complementing these social innovations are advances in applied ecological tools. Curk et al. (2024) modelled the early detection of poisoning events using GPS-tracked vultures, demonstrating how targeted investment in animal-borne sensors can mitigate mass mortality risks. Their work contributes practical, cost-effective guidance for designing sentinel-based surveillance systems in support of scavenger conservation.

From a species-specific intervention perspective, Kuiper et al. (2025) provided robust empirical evidence that dehorning rhinos significantly reduces poaching risk, achieving a 78% decline in poaching incidents with a fraction of typical enforcement budgets. Their multi-site analysis stresses the importance of reducing poacher incentives, though also cautions that dehorning must be accompanied by ongoing security and strategic implementation to remain effective.

At a broader landscape scale, Naidoo et al. (2025) proposed a theory of change (ToC) for conserving ecological connectivity, emphasising the need for context-sensitive approaches that integrate ecological and socioeconomic systems. Their synthesis across continents offers insights into leveraging science to inform landscape-level planning that benefits both biodiversity and human well-being.

Further, emerging work on wildlife health and governance reinforces the need for institutional

été formulées avec prudence. Cet échange illustre l'engagement du GSRAf dans l'amélioration des récits scientifiques et son rôle de garant d'un message ancré dans une rigueur statistique et écologique.

Par ailleurs, le GSRAf a répondu de façon critique, mais constructive, à la proposition d'injecter des isotopes radioactifs dans les cornes de rhinocéros comme technique de dissuasion radicale à l'égard des trafiquants. Les partisans de cette initiative affirment que de petites quantités de substance radioactive insérées à l'état de traces dans les cornes pourraient rendre ces dernières plus détectables et moins désirables sur le marché illégal. Cependant, l'analyse du GSRAf confronte les effets positifs de ce potentiel avec les inquiétudes liées aux risques environnementaux et éthiques, les implications judiciaires et les conséquences involontaires que ces actions pourraient avoir sur le marché, telles que la hausse de la valeur de la corne due à la perception de rareté qu'elle véhiculerait. Le GSRAf souligne le fait que ce type de technologie, bien qu'innovante, ne saurait représenter une solution à elle seule, mais devrait être considérée comme un outil de soutien potentiel au sein de cadres de conservation plus larges qui incluent la gestion des habitats, les stratégies de lutte contre le braconnage et l'engagement des parties prenantes (Ferreira et al. 2025d).

Des discussions autour de l'écologie ont également suscité une réflexion critique de la part des membres du GSRAf. Sky et al. (2024) ont rapporté que la composition du régime alimentaire des rhinocéros noirs changeait en fonction de la productivité de la végétation, ce qui suggère que l'acacia, communément considéré comme leur végétal de prédilection, pouvait servir d'alimentation de secours. Ces données viennent contrecarrer des hypothèses établies de longue date sur la sélectivité alimentaire des rhinocéros noirs, et impliquent qu'il y aurait un lien entre flexibilité alimentaire et reproduction. En réponse, les experts en alimentation du GSRAf ont mené une méta-analyse des études existantes sur le sujet et ont fait valoir le fait que ces résultats devraient être interprétés au cœur d'un cadre plus robuste sur le plan écologique. Ils plaident en faveur de l'application du modèle d'hétérogénéité fonctionnelle d'Owen-Smith (2004), qui classe les végétaux fourragers en catégories de ressources « optimales », « stable », « de réserve » et « tampon ». Cette typologie reflète les stratégies adaptatives déployées par les grands herbivores afin de pallier la variabilité spatiotemporelle dans la disponibilité des strengthening. Zayas et al. (2025) introduce a systematic wildlife health programme assessment tool piloted in Asia and Africa, identifying actionable gaps in disease detection, information systems, and capacity building. Their work offers a model for aligning health and conservation objectives in wildlife-rich but resource-limited countries.

Critical examinations of global conservation governance, particularly CITES, also feature prominently. 't Sas-Rolfes et al. (2025a) critiqued CITES as a rigid prohibition regime vulnerable to political manipulation. Their institutional diagnostics suggest that enhancing transparency and aligning incentive structures are crucial for reform. This is echoed by Challender et al. (2025), who developed a refined species-level ToC to improve CITES implementation by embedding it within local socio-ecological contexts and better integrating it with other multilateral environmental agreements.

Complementary reviews by Hiller and 't Sas-Rolfes (2025) and Challender et al. (2024) question the proportionality of trade restrictions and trophy hunting bans, calling for a nuanced, evidence-based wildlife trade policy. They highlight the unintended consequences of such regulations on rural livelihoods, conservation funding, and species outcomes, especially in southern Africa, where sustainable use models are embedded in national strategies.

In synthesis, these contributions reflect a growing shift towards integrated, adaptive, and context-responsive conservation approaches. By combining social engagement, technological innovation, ecological modelling, and institutional reform, members continue to advance a scientifically rigorous and socially attuned conservation agenda that responds to both urgent threats and long-term sustainability goals.

Members of the IUCN SSC African Rhino Specialist Group (AfRSG) also made substantial scientific contributions to *Rhinos of the World: Ecology, Conservation and Management* (Melletti et al. 2025), offering a wide-ranging and integrated synthesis of rhinoceros biology, conservation history, and future outlooks. Their chapters reflect both the depth of empirical research, and the pragmatic lessons derived from decades of hands-on conservation work across Africa.

ressources, et aide à clarifier en quoi les modifications dans la composition des régimes alimentaires sont en lien avec la fonction écologique et les dynamiques de population.

Tous ces exemples traduisent les valeurs fondamentales du GRSAf : non seulement un débat scientifique constructif est nécessaire pour remettre en question les hypothèses et perfectionner les méthodologies, mais il est également essentiel à l'amélioration de la crédibilité et de l'impact des pratiques de conservation. Qu'il s'agisse d'observer les technologies émergentes, de réévaluer les interprétations écologiques ou de questionner les récits dominants, le GSRAf promeut la culture d'une analyse critique et transparente. Ce processus continu de réflexion et d'échange encourage un apprentissage adaptatif et participe à garantir que la conservation des rhinocéros s'appuie sur une base théorique valable, des contextes locaux et une collaboration interdisciplinaire. Dans un paysage qui, de plus en plus, attend de la science de la conservation qu'elle livre des solutions rapides et visibles, une telle rigueur délibérative est indispensable pour assurer la résilience et de bons résultats sur le long terme.

Cet engagement s'observe par ailleurs grâce aux récentes revues par des pairs effectuées par des membres du GSRAf. Ces travaux font progresser la pensée conceptuelle comme les outils pratiques dans les domaines de l'écologie, du social et de la gouvernance. Collectivement, ils soulignent l'importance d'un apprentissage basé sur l'application sur le terrain, d'échanges constructifs avec différents acteurs et de réévaluations et améliorations perpétuelles des stratégies de conservation pour des espèces telles que les rhinocéros, dans un monde en constante mutation.

Un des thèmes clés est la portée de modèles de conservation inclusifs et ancrés localement. Muntifering et al. (2025) présentent une expérience de plus de dix ans dans le nord-ouest de la Namibie, montrant qu'une réduction durable et substantielle (de plus de 90 %) du braconnage des rhinocéros noirs peut être obtenue par des programmes participatifs, incluant les rangers et ancrés dans les valeurs locales, plutôt que par une répression militarisée. Leurs conclusions décrivent l'efficacité éthique, sociale et écologique d'interventions construites en collaboration et qui alignent les efforts de protection sur les priorités des communautés. Sur le même plan, Lopes-Lima et al. (2025) proposent un cadre piloté par les acteurs concernés pour mettre en application la technologie

Key contributions addressed both black and white rhinos. Shaw et al. (2025) documented the black rhino's continental decline to a low of 2,354 individuals in 1995 and its partial recovery to 6,487 by 2022. Their chapter highlights the varying national conservation approaches and the central role of coordinated action through the AfRSG. The account by Balfour et al. (2025b) on the white rhino details the divergent trajectories of the northern and southern subspecies. The near extinction of the northern white rhino, juxtaposed with the southern subspecies' recovery to 16,801 individuals by 2022, provides critical insights into governance, management innovation, and socio-political context.

Goodman et al. (2025) reviewed major conservation trends, emphasizing the transition from reactive to planned rhino management using capture techniques, range expansion guided by harvest theory, and private land conservation. They also examined the role of policy frameworks and innovative partnerships in sustaining rhino populations. The threat posed by poaching, and its changing dynamics over time, is explored in detail by 't Sas-Rolfes et al. (2025b), who traced two major poaching waves and highlighted how corruption, enforcement capacity, and community involvement shape outcomes.

Vigne et al. (2025a) further contextualised these threats by analysing the international horn trade. They traced centuries of rhino horn demand across cultures and regions and reflected on the modern criminal networks enabling trafficking. Their work raises important questions about the viability of regulated trade and the political will required to balance human development and rhino protection.

Several chapters contributed foundational biological knowledge. Shrader et al. (2025a) and Shrader et al. (2025b) provided detailed accounts of the life histories, ecological roles, and distribution of black and white rhinos, while Moodley and Robovský (2025) offered a comprehensive review of rhinoceros phylogeny and taxonomy, integrating molecular and morphological data to refine subspecies classifications.

von Houwald et al. (2025) underscored the role of ex situ conservation in supporting species survival. They reflected on the coordinated management of captive populations and the value

d'ADNe (ADN environnemental) en Afrique. Leur étude de cas namibienne illustre combien laisser l'initiative aux institutions locales et intégrer le contexte culturel dans le suivi des animaux peut améliorer la collecte de données sur la biodiversité et la pertinence de la prise de décision.

Ces innovations sociales, mises en place conjointement, représentent des avancées sur le plan des outils écologiques appliqués. Curk et al. (2024), pour leur part, sont parvenus à l'aide de vautours équipés de GPS, à modéliser la détection précoce des empoisonnements, ce qui montre combien un investissement ciblé dans des capteurs portés par les animaux peut atténuer les risques de mortalité de masse. Leurs travaux offrent des conseils pratiques et efficaces en termes de coût pour la conception de systèmes de surveillance sentinelle en soutien de la conservation des animaux charognards.

Du point de vue des interventions spécifiques à certaines espèces, Kuiper et al. (2025) fournissent une preuve empirique solide démontrant que le décornage des rhinocéros réduit nettement le risque de braconnage, jusqu'à atteindre une baisse de 78 % de ce type d'incidents en ne mobilisant qu'une fraction du budget généralement alloué à ce secteur. Leur analyse multisite met en exergue l'importance de restreindre les facteurs incitatifs à l'égard des braconniers, tout en précisant que l'opération de décornage doit s'effectuer dans un cadre sécuritaire constant et suivre un plan stratégique afin de montrer son efficacité.

Sur une échelle plus large, Naidoo et al. (2025) proposent une théorie du changement pour conserver la connectivité écologique, et insistent sur le besoin d'approches contextuelles qui intègrent les systèmes écologiques et socioéconomiques. Leur synthèse, nourrie d'informations issues de plusieurs continents, offre des perspectives sur la manière de tirer parti de la science afin d'éclairer les plans de conservation au niveau du paysage, qui bénéficie à la biodiversité comme au bien-être de l'humain.

D'autre part, les nouveaux travaux de Zayas et al. (2025) sur la santé des espèces sauvages et la gouvernance confirment qu'un renforcement des institutions est nécessaire. Zayas et al. y présentent un outil d'évaluation systématique de la santé des espèces sauvages, piloté en Asie et en Afrique et qui identifie les lacunes concrètes dans les domaines de la détection des maladies, des systèmes d'information et du développement des compétences. Leur travail offre un modèle permettant d'aligner les objectifs de santé et de of the One Plan Approach in linking in situ and ex situ efforts—particularly critical given the ongoing threats of habitat loss and genetic erosion.

Collectively, these contributions reflect the breadth of expertise within the AfRSG network and underscore the group's ongoing leadership in rhino conservation science. Their collaborative engagement in this volume not only advances global understanding of rhinoceros conservation but also equips future practitioners and policymakers with the knowledge needed to sustain rhinos in complex socio-ecological landscapes.

Translating rhino conservation

One of the AfRSG's core functions is to provide a structured platform for constructive debate, knowledge exchange, and the exploration of emerging ideas in rhino conservation. In the past year, webinars have proven to be an effective and accessible tool for convening a geographically dispersed network of experts, researchers, and conservation practitioners. These virtual engagements have enabled timely discussions on novel innovations, emerging policy directions, and scientific uncertainties.

A prominent topic featured in recent webinars was the Rhinomics initiative[4]—a privately driven venture in South Africa aiming to create a traceable mechanism for the legal stockpiling and domestic trade of rhino horn. The initiative rests on a national-scale infrastructure comprising a centralized vault, a secure digital inventory system, and a logistics network for storage and transport. Participants discussed the initiative's potential to generate additional revenue for rhino custodians, while also raising critical questions about governance, traceability, and alignment with international trade restrictions.

The Rhisotope Project[5], developed by the University of the Witwatersrand in partnership with the International Atomic Energy Agency, was another topic of extensive dialogue. This initiative involves inserting small, non-lethal

[4]See https://eia-international.org/wp-content/uploads/EIA_US_SA_Rhino_report_0125_FINAL.pdf for a critique

[5]https://rhisotope.org/

conservation dans des pays riches en espèces sauvages, mais disposant de ressources limitées.

La gouvernance de la conservation à l'échelle mondiale fait également l'objet d'un examen critique, notamment au sein de la CITES. 't Sas-Rolfes et al. (2025a) qualifient cette dernière de régime de prohibition rigide et vulnérable aux manipulations politiques. Leur diagnostic institutionnel suggère que le renforcement de la transparence et l'harmonisation des structures incitatives sont cruciaux pour engager un processus de réforme. Ce point de vue est repris par Challender et al. (2025), qui proposent une théorie du changement améliorée visant une meilleure mise en œuvre de la Convention par son intégration au sein des contextes socioécologiques et en l'associant mieux aux accords environnementaux multilatéraux existants.

Des articles complémentaires par Hiller et 't Sas-Rolfes (2025) et Challender et al. (2024) interrogent la proportionnalité des restrictions liées au commerce et à l'interdiction des chasses aux trophées, et plaident en faveur d'une politique de commerce des espèces sauvages nuancée et fondée sur des données probantes. Ils mettent en exergue les conséquences involontaires de telles réglementations sur les moyens de subsistance des communautés rurales, le financement de la conservation et les résultantes pour les espèces – particulièrement en Afrique australe où les modèles d'utilisation durable sont au cœur des stratégies nationales.

En résumé, ces différentes contributions reflètent un fort basculement en direction d'approches intégrées, évolutives et adaptées au contexte. En alliant engagement social, innovations technologiques, modélisation écologique et réforme institutionnelle, les membres poursuivent leur ambition d'établir une rigueur scientifique et une conservation consciente de l'environnement social – une vision qui réponde à la fois à l'urgence des menaces et aux objectifs de durabilité sur le long terme.

Les membres du GSRAf (de la CSE UICN) ont également effectué d'importantes contributions scientifiques à l'ouvrage *Rhinos of the World: Ecology, conservation and management* par Melletti et al. (2025), qui offre une vaste synthèse transversale couvrant la biologie des rhinocéros, l'histoire de leur conservation et les perspectives futures. Leurs chapitres reflètent la profondeur de la recherche empirique et les enseignements pragmatiques tirés de décennies de conservation sur le terrain en Afrique.

Par ailleurs, des éléments essentiels relatifs aux rhinocéros noirs et blancs ont été apportés au travail quantities of radioactive isotopes into live rhino horns to enhance detectability at border checkpoints using existing radiation detection infrastructure. While acknowledging the project's innovation and potential enforcement applications, webinar participants critically assessed its underlying assumptions—particularly the paradox of asserting no biological risk to rhinos while relying on perceived human health concerns to deter illicit trade. Concerns were also raised about public messaging, ethical implications, and unintended consequences.

Ecological science also featured in the webinars, with one session focusing on diet switching in eastern black rhinos and its relationship to reproductive performance (see Sky et al. 2024). Members debated the degree to which dietary flexibility is an adaptive response versus an ecological constraint, and how nutritional ecology may inform site-level management to support population growth.

Finally, participants received an update on Kenya's Rhino Range Expansion initiative (KRRE)[6], a coordinated effort led by the Association of Private and Community Land Rhino Sanctuaries (APLRS) in collaboration with the Kenya Wildlife Service (KWS). The strategy aims to create a connected network of rhino conservation landscapes, particularly in the Laikipia and Samburu landscape, enhancing both metapopulation management and long-term resilience.

These webinars demonstrate the AfRSG's commitment to fostering transparent, evidence-informed dialogue. By integrating diverse perspectives across scientific, technical, and policy domains, the webinar platform continues to play a critical role in strengthening collective problem-solving and adaptive conservation planning.

Effective communication remains central to the AfRSG's mandate of promoting evidence-based conservation and stakeholder engagement. Over the past year, the AfRSG maintained an active WhatsApp platform that enabled timely coordination and information sharing among members. Although this platform became less

[6] https://rhinorecoveryfund.org/project/development-of-laikipia-rhino-range-expansion-management-plan-and-implementation-strategy/

de Shaw et al. (2025), qui ont documenté le déclin des populations de rhinocéros noirs d'Afrique – qui ne comptaient plus que 2 354 individus en 1995 – et leur rétablissement partiel à 6 487 représentants de l'espèce en 2022. On peut y lire les différentes approches nationales de la conservation, ainsi que le rôle central de l'action coordonnée par l'intermédiaire du GSRAf. Balfour et al. (2025b) détaillent dans leur article les trajectoires divergentes des sous-espèces du Nord et du Sud. La quasi-extinction du rhinocéros blanc du Nord, ajoutée au rétablissement de la sous-espèce du Sud, qui comptait 16 801 individus en 2022, fournit des informations cruciales dans les domaines de la gouvernance, des innovations en matière de gestion et de contexte sociopolitique.

Goodman et al. (2025) ont analysé les principales tendances de la conservation, en s'intéressant à la transition d'une gestion réactive des rhinocéros vers une gestion planifiée, grâce à l'utilisation de techniques de capture, à l'extension des aires de répartition guidée par la théorie du prélèvement, et aux terres de conservation privées. Ils ont également étudié le rôle des cadres politiques et des partenariats d'innovation dans l'accompagnement des populations de rhinocéros. Par ailleurs, la menace du braconnage et ses dynamiques mouvantes sont explorées en détail par 't Sas-Rolfes et al. (2025b), qui retracent l'historique de deux vagues majeures de ce type de pratiques et soulignent combien la corruption, les moyens de répression et l'implication des communautés affectent les résultats à cet égard.

Vigne et al. (2025a) poursuivent ces perspectives par leur analyse du commerce international de corne de rhinocéros. Ils passent en revue des siècles de demande de corne à travers différentes cultures et régions, et étendent leur réflexion aux réseaux criminels modernes qui permettent ce trafic. Ce travail soulève d'importantes questions relatives à la viabilité d'un commerce réglementé et quant à la volonté politique nécessaire afin de trouver un équilibre entre développement humain et protection des rhinocéros.

Plusieurs chapitres s'attachent à fournir des bases de connaissance en matière de biologie. Shrader et al. (2025a) et Shrader et al. (2025b) produisent des descriptions détaillées des cycles biologiques, du rôle écologique et de la distribution des rhinocéros noirs et blancs, tandis que Moodley et Robovský (2025) offrent une étude approfondie de la phylogénie et la taxonomie de ces espèces, en intégrant des données moléculaires et morphologiques afin d'affiner les classifications des sous-espèces.

active following reduced support from the USFWS at the beginning of 2025, the Chair and Scientific Officer continued to play a visible role in external communication. They responded to multiple media inquiries, including those related to the status of black rhinos in Chad, and proactively engaged with national and international officials—particularly within SADC member states.

On World Rhino Day 2024, the Scientific Officer contributed to the global discourse on rhino conservation by providing an international population update as part of celebrations organized by Save the Rhino International. This event offered a platform to communicate current progress and challenges facing rhino conservation to a broader audience.

In addition to public engagement, the AfRSG has identified targeted communication as a strategic priority through a detailed stakeholder analysis (Vigne et al. 2025). A stakeholder analysis identified 68 groups, most of which play key roles in rhino conservation. The findings highlight the need for tailored communication strategies that promote active participation, responsive engagement, or informed observation, depending on stakeholder relevance.

Achieving this level of engagement will require diversified strategies, including tailored messaging and interactive dialogue that responds to the specific roles, needs, and expectations of each stakeholder type. By doing so, the AfRSG can build mutual understanding and foster shared responsibility for African rhino conservation across its diverse network of collaborators.

Assessing Rhino Conservation

The AfRSG delivered strong performance during the 2024–2025 period, with meaningful progress toward its 2021–2025 strategic objectives as outlined in the *Species: Annual Report of the IUCN Species Survival Commission and Secretariat 2024–2025* (Balfour 2025). Of 31 targets, most were either achieved or on track, particularly in population data collection, policy guidance, and scientific engagement. Rhino population monitoring was strengthened, with annual data now compiled and feeding into IUCN reporting. Planning milestones included

Von Houwald et al. (2025), de leur côté, soulignent le rôle de la conservation ex-situ dans la survie des espèces, en analysant la gestion coordonnée de populations captives et la valeur que représente l'approche One Plan pour lier des opérations in situ et ex-situ, particulièrement importantes compte tenu des risques actuels de perte d'habitat et d'érosion génétique.

Tous ces travaux reflètent l'étendue de l'expertise au sein du réseau du GSRAf, et soulignent le leadership constant du groupe dans la dimension scientifique de la conservation des rhinocéros. Non seulement leur collaboration dans ce volume de *Pachyderm* fait progresser la compréhension globale de la conservation des rhinocéros, mais il équipe également les futurs praticiens et décideurs politiques de la connaissance nécessaire au soutien de ces animaux dans des paysages socioécologiques complexes.

Une conservation nourrie par les échanges

L'une des fonctions principales du GSRAf est de fournir une plateforme structurée pour ouvrir la voie à des débats constructifs, à l'échange de savoirs et à l'exploration d'idées émergentes dans le domaine. L'année dernière, les webinaires ont représenté un outil efficace et accessible afin de réunir un réseau d'experts, de chercheurs et de praticiens de la conservation du monde entier. Ces rencontres virtuelles ont permis la tenue de discussions abordant les innovations récentes, les orientations politiques naissantes et certaines incertitudes scientifiques.

L'un des thèmes phares des derniers webinaires relevait de l'initiative Rhinomics[4], un projet ambitieux porté par une entreprise privée sud-africaine et qui vise à créer un mécanisme traçable pour l'entreposage légal et le commerce intérieur de corne de rhinocéros. La proposition repose sur une infrastructure à l'échelle nationale qui comprend un coffre-fort centralisé, un système d'inventaire numérique sécurisé et un réseau logistique pour l'entreposage et le transport. Les participants à la réunion ont abordé le revenu supplémentaire potentiel pour les personnes en charge des rhinocéros, tout en évoquant les questions critiques de gouvernance, de traçabilité et d'alignement avec les restrictions commerciales en vigueur au niveau

[4]Consulter la page https://eia-international.org/wp-content/uploads/EIA_US_SA_Rhino_report_0125_FINAL.pdf pour lire une critique

the release of the *ARCF 2025–2035* (Balfour et al. 2025a) and a Green List assessment for black rhino (Ferreira et al. 2024b).

The AfRSG contributed to national planning efforts, supported multiple reintroduction initiatives, and continued promoting genetic and metapopulation strategies. Despite reduced funding, the Secretariat remained functional, and new leadership appointments ensured continuity. Communication channels remained active through timely media responses and a functional WhatsApp group. The Group maintained strong member engagement, with productive meetings and active working groups. While challenges remain in sustainable financing and community involvement, the AfRSG continues to provide critical leadership, strategic guidance, and scientific input to secure the future of Africa's rhinos in line with IUCN SSC priorities (Balfour 2025).

The status of African rhinos

The AfRSG played a key role in contributing to the report on *African and Asian Rhinoceroses – Status, Conservation and Trade* to CITES CoP20 as per *Resolution Conf. 9.14 (Rev. CoP19)* (Ferreira et al. 2025e). By the end of 2024, Africa was home to an estimated 22,540 rhinoceroses, comprising 6,788 black rhinos (*D. bicornis*) and 15,752 white rhinos (*C. simum*). These figures are broadly consistent with those reported to CITES CoP19 in 2022 (Ferreira et al. 2022), indicating modest population stability. However, species-specific trends diverge: black rhino numbers have increased by 5.2% since 2023, while white rhinos declined by 11.2% over the same period. These dynamics reflect both gains in Eastern (*D. b. michaeli*) and South-central black rhino (*D. b. minor*) numbers and losses in South-western black (*D. b. bicornis*) and Southern white rhinos (*C. s. simum*).

Despite recent declines in poaching incidents—516 were recorded in 2024, down from 540 in 2021—the average annual poaching rate across Africa was 2.15%, the lowest since 2011. Yet, localised increases in poaching, particularly in early 2025, raise concern. South Africa accounted for 81.4% of all poaching cases, and black rhino losses varied across subspecies.

international.

Le projet Rhisotope[5], développé par l'université du Witwatersrand en partenariat avec l'Agence internationale de l'énergie atomique, a lui aussi fait l'objet d'un dialogue approfondi. Cette initiative repose sur l'insertion d'isotopes radioactifs en quantités faibles et non létales au sein des cornes de rhinocéros vivants afin qu'elles soient mieux repérées aux postes de douanes, grâce aux infrastructures existantes de détection des rayonnements radioactifs. Les participants au webinaire, tout en reconnaissant le caractère innovant du projet et ses applications possibles pour lutter contre le commerce illégal, en ont évalué de façon critique les conséquences potentielles, notamment le paradoxe qui consiste à affirmer l'absence de risques pour les rhinocéros tout en s'appuyant sur des dispositifs visant à empêcher la dissémination de produits à risque pour la santé humaine. Les problématiques autour des messages à destination du public, des implications éthiques et des impacts involontaires ont également été soulevées.

La science de l'écologie s'est, par ailleurs, invitée lors des webinaires, avec une session consacrée au changement de régime alimentaire du rhinocéros noir de l'Est et le lien avec ses performances reproductives (voir Sky et al. 2024). Les membres ont débattu de la mesure dans laquelle la flexibilité alimentaire représente une réponse adaptative plutôt qu'une contrainte écologique, et de quels moyens l'écologie nutritionnelle dispose-t-elle pour éclairer la gestion sur site afin de soutenir la croissance des populations.

Enfin, les participants ont reçu des nouvelles de l'initiative Kenya's Rhino Range Expansion (KRRE)[6], une action conjointe menée par l'association Private and Community Land Rhino Sanctuaries (APLRS), en collaboration avec le département en charge des espèces sauvages du Kenya. L'objectif est de créer un réseau connecté de zones de conservation des rhinocéros, particulièrement dans les environnements de Laikipia et de Samburu, en favorisant la gestion des métapopulations et la résilience à long terme.

Ces rencontres virtuelles montrent l'engagement du GSRAf à encourager un dialogue transparent et s'appuyant sur les données probantes disponibles. En intégrant différentes perspectives dans les domaines

[5]https://rhisotope.org/

[6]https://rhinorecoveryfund.org/project/development-of-laikipia-rhino-range-expansion-management-plan-and-implementation-strategy/

Achieving stable or growing rhino populations requires maintaining poaching rates below 3.5%, with growth targets of 5% requiring rates below 1.2%. Other drivers of decline include extended droughts, policy-induced management constraints, poor reporting, and fragmented population structures that challenge genetic and demographic viability.

Illegal trade remains a critical threat. Although reported illegal trade volumes declined from prior peaks, adjustments accounting for widespread dehorning (affecting ~48% of rhinos) suggest the true scale of trade has not meaningfully diminished. Between 2021 and 2023, an estimated 1,160–1,289 horns per year entered illegal markets. Enforcement efforts led to seizures totalling 1.8 tonnes of horn across 750 cases, although inconsistencies in stockpile reporting.

Legal trade in African rhinos continues under tightly regulated conditions. Between 2022 and 2024, 276 live rhinos were translocated for conservation or commercial purposes. Rhino hunting remained limited in scale—approximately 0.05–0.91% of national populations—and generated significant conservation revenue. Case studies show that legal hunting, when well-managed, can provide vital income for protected area management and community development. Additionally, mechanisms like the World Bank's Wildlife Conservation Bond are innovating conservation finance by linking rhino population growth to investor returns.

Despite these efforts, enforcement challenges persist. Many African range States struggle with corruption, slow prosecutions, limited inter-agency coordination, and insufficient community engagement. Long-term success will depend on effective governance, intelligence-driven operations, and partnerships with local communities. Conservation strategies are evolving to address these needs. The ARCF (2025–2035) (Balfour et al. 2025) reflects this shift, integrating Indigenous Peoples and Local Communities (IPLCs), proactive security, and collaborative approaches, while initiatives like the Rhino Rewild programme seek to reintroduce genetically valuable captive and zoo-held animals into the wild.

In conclusion, while African rhino populations remain globally significant, they are under scientifiques, techniques et politiques, la plateforme de webinaires continue de jouer un rôle crucial pour renforcer la résolution collective de problèmes et la dimension adaptative des plans de conservation.

Une communication efficace demeure au cœur de la mission du GSRAf – promouvoir une conservation fondée sur des données probantes et sur l'engagement des parties prenantes. L'année dernière, le GSRAf a maintenu une communauté WhatsApp active qui a permis une coordination et un partage d'informations performants entre ses membres. Bien que ce groupe ait connu une baisse d'activité suite aux financements supprimés, début 2025, par le département américain Fish & Wildlife, le président et le responsable scientifique continuent de jouer un rôle visible dans les communications externes. Ils ont répondu à de nombreuses demandes de la part des médias, dont celles relatives au statut du rhinocéros noir au Tchad, et se sont proactivement engagés avec des représentants nationaux et internationaux, notamment au sein des États membres de la Communauté de développement d'Afrique australe (CDAA).

Dans le cadre des célébrations organisées par Save the Rhino International à l'occasion de la Journée mondiale des rhinocéros 2024, le responsable scientifique a fourni une mise à jour de la population mondiale de rhinocéros. L'événement a permis de communiquer à un public plus large les avancées et les défis actuels rencontrés par le secteur de la protection.

La communication ciblée a été identifiée par le GSRAf comme priorité stratégique, en plus de l'engagement du public, et ce à travers une analyse détaillée des différents acteurs (Vigne et al. 2025) qui a déterminé qu'il existait 68 groupes de parties prenantes, la plupart d'entre eux jouant un rôle clé dans la conservation des rhinocéros. Ces conclusions soulignent l'impératif de développer des stratégies de communication sur mesure, et qui promeuvent, selon le champ d'action des personnes impliquées, une participation active, de la réactivité ou une observation éclairée.

Atteindre ce niveau d'engagement requiert des stratégies diversifiées, dont un message adapté aux différents publics et un dialogue interactif qui réponde au rôle spécifique de chaque type de partie prenante, à ses besoins et à ses attentes. Ce faisant, le GSRAf peut bâtir une compréhension mutuelle et encourager le partage des responsabilités de la conservation des rhinocéros africains au sein de son réseau diversifié de collaborateurs.

persistent threat. Success will require sustained political commitment, improved data systems, innovative finance, and inclusive conservation models to ensure the species' survival amid ecological and socio-political change.

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La conservation des rhinocéros et ses performances

Le GSRAf a montré des performances solides au cours de la période 2024–2025, avec des progrès significatifs réalisés dans le cadre de ses objectifs stratégiques 2021–2025, détaillés dans le *Rapport annuel du secrétariat et de la commission pour la survie des espèces de l'UICN 2024–2025* (Balfour 2025). La plupart des 31 objectifs ont été atteints ou sont en cours de réalisation, notamment en ce qui concerne la collecte de données démographiques, les orientations politiques et l'engagement scientifique. Le suivi des populations a été renforcé, les données annuelles étant désormais compilées et servant de base aux rapports de l'UICN. L'une des étapes importantes résidait dans la publication du cadre *ARCF 2025–2035* (plan de conservation des rhinocéros d'Afrique 2025–2035) (Balfour et al. 2025a) et d'une évaluation de la Liste verte pour le rhinocéros noir (Ferreira et al. 2024b).

Le GSRAf a contribué à la conception de plans nationaux, a soutenu de nombreuses initiatives de réintroduction et a continué de promouvoir des stratégies génétiques et de métapopulations. Malgré la réduction de financements, le secrétariat est resté en fonction et de nouvelles nominations à des postes clés ont permis d'assurer la continuité des opérations. Les canaux de communication ont maintenu leur activité par des réponses rapides aux médias et un groupe WhatsApp. Un engagement fort des membres a été entretenu grâce à des réunions productives et des groupes de travail opérants. Si bien des défis persistent en termes de financement durable et d'implication des communautés, le GSRAf s'attache à fournir leadership, orientation stratégique et contributions scientifiques, des éléments essentiels pour garantir l'avenir des rhinocéros d'Afrique, conformément aux priorités de la CSE de l'UICN (Balfour 2025).

Le statut du rhinocéros d'Afrique

Le GSRAf a été prééminent par sa contribution au rapport «*Statut, conservation et commerce des rhinocéros d'Afrique et d'Asie*» lors de la CdP20 de la CITES, en vertu de la *Resolution Conf. 9.14 (Rev. CoP19)* (Ferreira *et al.* 2025e). Fin 2024, l'Afrique était le foyer de quelque 22 540 rhinocéros, dont 6 788 rhinocéros noirs (*D. bicornis*) et 15 752 rhinocéros blancs (*C. simum*). Ces chiffres sont globalement cohérents avec ceux communiqués en 2022 à la CdP19 de la CITES (Ferreira et al. 2022), ce qui indique une

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stabilité relative. Cependant, les tendances par espèces divergent : le nombre de rhinocéros noirs a augmenté de 5,2 % depuis 2023, tandis que les rhinocéros blancs ont décliné de 11,2 % sur la même période. Ces dynamiques reflètent à la fois des hausses chez le rhinocéros de l’Est (*D. b michaeli*) et le rhinocéros noir du Centre-Sud (*D. b. minor*) et des baisses chez le rhinocéros noir du Sud-Ouest (*D. b. bicornis*) et le rhinocéros blanc du Sud (*C. s. simum*).

Malgré une récente diminution des cas de braconnage – 516 enregistrés en 2024 contre 540 en 2021 – le taux moyen annuel de braconnage à l’échelle du continent était de 2,15 %, son plus bas niveau depuis 2011. Pourtant, des hausses localisées, notamment en début d’année 2025, sont source d’inquiétude. L’Afrique du Sud comptabilise 81,4 % des cas de braconnage, et les pertes parmi les rhinocéros noirs varient selon les sous-espèces. Obtenir des populations stables ou en augmentation nécessite de maintenir un taux de braconnage sous les 3,5 %, voire en deçà de 1,2 % pour des objectifs de croissance de 5 %. D’autres facteurs sont en cause dans le déclin des populations, tels que les épisodes de sécheresse prolongée, les contraintes de gestion induites par les politiques en vigueur, la mauvaise qualité des comptes-rendus et des structures de populations fragmentées qui mettent en difficulté la viabilité génétique et démographique.

Le commerce illégal constitue, encore et toujours, une grave menace. Bien que les volumes rapportés en matière de commerce illégal soient en baisse relativement à certaines périodes précédentes de haute intensité, les ajustements tenant compte de l’écornage généralisé (qui concerne près de 48 % des rhinocéros) suggèrent que l’ampleur réelle du commerce n’a pas connu de ralentissement significatif. Entre 2021 et 2023, on estime que 1 160 à 1 289 cornes ont fait leur entrée sur le marché illégal chaque année. Les opérations de démantèlement ont permis la saisie de 1,8 tonne de cornes lors de 750 affaires, malgré des incohérences dans les inventaires de stocks.

Le commerce légal de cornes de rhinocéros d’Afrique se poursuit, dans un cadre réglementaire strict. Entre 2022 et 2024, 276 rhinocéros vivants ont été transférés pour des raisons commerciales ou de conservation. La chasse est restée limitée – environ 0,05 à 0,91 % des populations nationales – et a généré des revenus conséquents à destination de la conservation. Comme l’ont montré plusieurs études de cas, une chasse légale et bien encadrée peut produire des ressources vitales pour la gestion des zones

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protégées et le développement des communautés. En outre, des mécanismes tels que l'Obligation en faveur de la conservation de la vie sauvage, lancé par la Banque mondiale, visent à innover dans le financement du secteur, en associant le retour sur investissement à la croissance des populations de rhinocéros.

Malgré ces efforts, les défis relatifs à la lutte contre la criminalité persistent. De nombreux États africains de l'aire de répartition du rhinocéros font face à la corruption, à la lenteur des procédures judiciaires, à une coordination limitée entre les agences et à un engagement insuffisant des communautés. Les réussites sur le long terme dépendent d'une gouvernance efficace, d'opérations qui se basent sur le renseignement et de partenariats avec les communautés locales. Les stratégies de conservation évoluent afin de répondre à ces besoins. Le plan *ARCF (2025–2035)* (Balfour et al. 2025) reflète ces changements par l'intégration des communautés locales et des peuples autochtones (CLPA), de la sécurité proactive et d'approches collaboratives, tandis que certaines initiatives telles que le programme Rhino Rewild s'attachent à réintroduire, en pleine nature, des animaux en captivité et détenus par des zoos montrant un profil génétique intéressant.

Dans l'ensemble, les rhinocéros d'Afrique sont donc nombreux, mais font face à une menace constante. En ces temps de mutations écologiques et sociopolitiques, il s'agit d'obtenir un engagement durable de la part des décideurs, des systèmes de données améliorés, des financements innovants et des modèles de conservation inclusifs afin d'atteindre des résultats et de garantir la survie des espèces.

Remerciements

Nous remercions les États de l'aire de répartition des rhinocéros d'Afrique pour leur contribution d'informations au secrétariat, qui sont utilisées dans le cadre des rapports à destination de la CITES. Le GSRAf est également reconnaissant à l'égard des organismes Save the Rhinos International (SRI) et International Rhino Foundation (IRF), au fonds pour la conservation des rhinocéros et du tigre du département américain US Fish and Wildlife (USFWS RTC), au fonds pour les espèces sauvages menacées (EWT), à WWF-Afrique du Sud, à Save the Rhino Inc. et à la fondation Oak pour leur soutien au GSRAf, au responsable scientifique, aux responsables de programme et au président, pour leurs services au groupe de spécialistes.

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Asian Rhino Specialist Group Chair report
Rapport du Groupe de Spécialistes du Rhinocéros d'Asie

Bibhab Kumar Talukdar, Chair/Président

Aaranyak, 50 Samanwoy Path (Survey), PO Beltola, Guwahati, Assam, 781028, India
email: bibhab@aaranyak.org

Asian rhino conservation has had both encouraging and disappointing news in the past twelve months.

Current status of the greater one-horned rhinos in India and Nepal

The population of greater one-horned (GOH) rhinos in Nepal, as estimated in 2021, remains at 752, since no new population estimate has been conducted since then. In India, West Bengal carried out rhino counts in Jaldapara National Park (NP) and Gorumara NP between 5 and 6 March 2025. The rhino population has increased in Jaldapara NP from 287 to 331 individuals, and in Gorumara NP, it has grown from 52 to 61 individuals. No recent estimates have been done for other rhino-habitat areas in Assam or Uttar Pradesh. According to recent data, the global wild population of GOH rhinos in India and Nepal has risen to 4,075, with 3,323 in India and 752 in Nepal. Within India, Assam has approximately 2,885 GOH rhinos, Uttar Pradesh has 46, and the remaining 392 are in West Bengal.

Since the publication of the last Chair report from the Asian Rhino Specialist Group (AsRSG) in November 2024, which covered the reporting period from October 2023 to September 2024, there have been no reported incidents of rhino poaching in both India and Nepal as of August 15, 2025. This achievement reflects the effective vigilance, intelligence gathering, and law enforcement efforts by the governments of India (GoI) and Nepal (GoN).

In November 2024, the GoI published the Species Recovery Plan for the GOH Rhino, in which the Chair of the AsRSG and fellow members contributed to the preparation of this key document, which will guide overall rhino conservation in India. For more information, see: https://www.pib.gov.in/PressReleasePage.aspx?PRID=2107821

Dans le domaine de la conservation du rhinocéros d'Asie, des nouvelles encourageantes et décevantes se sont succédées au cours des douze derniers mois.

État actuel du rhinocéros indien en Inde et au Népal

La population du rhinocéros indien au Népal n'ayant pas connu de nouvelle estimation à ce jour, le nombre de 752 individus recensés en 2021 reste d'actualité. En Inde, le Bengale occidental a conduit des décomptes de rhinocéros dans les parcs nationaux de Jaldapara et de Gorumara, les 5 et 6 mars 2025. À Jaldapara, la population de rhinocéros a vu ses effectifs augmenter de 287 à 331, et à Gorumara, de 52 à 61. Il n'y a pas eu de nouveaux recensements entrepris dans les autres zones de présence du rhinocéros de l'Assam ou de l'Uttar Pradesh. Selon des estimations récentes, la population globale de rhinocéros indiens à l'état sauvage en Inde et au Népal s'élève à 4 075 individus, dont 3 323 en Inde et 752 au Népal. En Inde, l'Assam compte environ 2 885 rhinocéros indiens et l'Uttar Pradesh, 46. Les 392 individus restants se trouvent dans le Bengale occidental.

Depuis la publication en novembre 2024 du dernier rapport du Groupe de Spécialistes du Rhinocéros d'Asie (GSRAs), qui couvre la période d'octobre 2023 à septembre 2024, aucun braconnage de rhinocéros n'a été signalé en date du 15 août 2025, ni en Inde, ni au Népal. Cette absence d'incident reflète les engagements pris par les gouvernements indiens et népalais en termes d'efficacité de surveillance, de collecte de renseignements et d'application de la loi.

En novembre 2024, le gouvernement de New Delhi a publié le Programme de rétablissement des espèces pour le rhinocéros indien (« Species Recovery Plan for the GOH Rhino »), document crucial pour accompagner la conservation du rhinocéros en Inde, et auquel le président et les membres du GSRAs

Current status of the Javan rhino

A new report by the IUCN finds that two of the world's most endangered species are still perilously close to extinction. The Javan rhino (*Rhinoceros sondaicus*) and Sumatran rhino (*Dicerorhinus sumatrensis*), (see next section).

In 2023, Indonesian authorities reported a population of 76 Javan rhinoceroses (*Rhinoceros sondaicus*) in the country. These rhinos are currently found in only one national park: Ujung Kulon NP. Camera trapping efforts in the Park are ongoing, however, no new population estimates of Javan rhinos have been released since 2023. Based on the 2023 estimate, the population has now declined by a third, from 76 animals to just 50, due to local poaching groups that killed 26 individuals, primarily males, between 2019 and 2023.

The population had been steadily, albeit slowly, increasing in recent decades, until the poaching crisis occurred; the loss is extremely disheartening.

Current status of the Sumatran Rhino

Disappointingly, estimates for the Sumatran rhino population have remained unchanged for the past three years. Currently, the wild Sumatran rhino population is believed to be between 34 and 47 individuals, as outlined in the Convention on International Trade in Endangered Species of Wild Fauna and Flora(CITES) CoP19. This report was prepared in collaboration with the AsRSG, the African Rhino Specialist Group (AfRSG) (of IUCN/SSC) and TRAFFIC International. As a result, the Sumatran rhino is considered the most threatened of all rhino species, and one of the most endangered animals in the world.

Among all rhino species, the Sumatran rhino's population numbers are the least certain. This uncertainty stems from their elusive nature, the rugged and remote terrain they inhabit, and the fact that current population estimates have not changed in three years. In the 1980s, it was estimated that the population of Sumatran rhinos ranged from 481 to 873 individuals, although some estimates suggested even lower numbers. A meeting in 1984 raised concerns about the declining population and emphasized the need for conservation efforts. By 1986, the IUCN estimated that between 425 and 800 Sumatran

ont contribué. Pour de plus amples informations, consulter la page suivante : https://www.pib.gov.in/PressReleasePage.aspx?PRID=2107821

État actuel du rhinocéros de Java

Comme le révèle un nouveau rapport de l'UICN (Union internationale pour la conservation de la nature), deux des espèces les plus menacées au monde se trouvent toujours dangereusement proches de l'extinction : le rhinocéros de Java (*Rhinoceros sondaicus*) et le rhinocéros de Sumatra (*Dicerorhinus sumatrensis*). (Voir la partie suivante)

En 2023, les autorités indonésiennes décomptaient une population de 76 rhinocéros de Java, présents dans un seul parc national, celui d'Ujung Kulon. Le suivi par piège photographique se poursuit dans le parc, même si aucune nouvelle estimation de population n'a été transmise depuis 2023.

Leur nombre aurait aujourd'hui chuté d'un tiers, après que 26 d'entre eux, principalement des mâles, ont été massacrés par des groupes de braconniers entre 2019 et 2023. Il ne resterait à l'heure actuelle que cinquante représentants de cette espèce.

La population était en hausse, bien que croissant lentement, jusqu'à cette récente tragédie – une perte extrêmement démoralisante.

État actuel du rhinocéros de Sumatra

Les estimations relatives à la population de rhinocéros de Sumatra sont décevantes, car en trois années, les chiffres n'ont pas évolué. On estime que la population actuelle compte entre 34 et 47 individus, tel que détaillé lors de la CdP19 de la CITES (Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction) dans le compte-rendu du GSRAs, préparé en collaboration avec le Groupe de Spécialistes du Rhinocéros d'Afrique (GSRAf) du CSE/UICN et TRAFFIC International. Il est donc le rhinocéros le plus menacé et l'un des animaux les plus en péril de la planète.

De toutes les espèces, le rhinocéros de Sumatra montre les chiffres les moins fiables, étant donné le terrain accidenté de leur zone d'habitat, elle-même très isolée, leur légendaire naturel insaisissable et le fait que l'estimation soit la même qu'il y a trois ans.

Dans les années 1980, la population du rhinocéros de Sumatra était estimée entre 481 et 873 individus, bien que certains relevés semblaient indiquer de plus rhinos remained.

Although recent records from southern Sumatra have been scarce, new field research indicates a hopeful situation in northern Sumatra for the species. Currently, there are 11 Sumatran rhinos in captivity: 10 at the Sumatran Rhino Sanctuary and 1 in Kelian, East Kalimantan, Indonesia. This successful captive breeding program serves as an insurance policy against total extinction.

The Sumatran rhino, the smallest of the five existing rhino species, holds the distinction of being the most evolutionarily ancient. This species represents its own genus and is known for being the hairiest and noisiest of all rhinos. Additionally, it is the closest living relative to the extinct woolly rhino (*Coelodonta antiquitatis*), which disappeared approximately 14,000 years ago, likely due to human hunting and climate change.

For further reading on all three Asian rhino species, refer to the book review in this issue of the recently published "Rhinos of the World: Ecology, Conservation and Management," edited by Mario Milleti, Bibhab Talukdar, and David Balfour, and published by Springer Nature Limited earlier this year. (pp. 221–236).

Joint AfRSG, AsRSG and TRAFFIC report to CITES CoP20

The AsRSG, AfRSG and TRAFFIC have submitted their report on African and Asian Rhinoceroses entitled: ***African and Asian Rhinoceroses–Status, Conservation and Trade***. This was commissioned by the Secretariat of CITES, pursuant to Resolution Conf. 9.14 (Rev. CoP19) for deliberations at the upcoming CITES CoP20 to be held at Samarkand, Uzbekistan, from 24 November to 5 December 2025. The report may be downloaded from https://cites.org/sites/default/files/documents/E-CoP20-084-A3.pdf

Harry Messel award

IUCN SSC awarded the Chair of AsRSG (Dr. Bibhab Kumar Talukdar) the Harry Messel Award at the 5th SSC Leaders' meeting held at Abu Dhabi in October 2024 due to his contribution to conservation efforts of the three species of Asian Rhinos.

faibles effectifs.

Une réunion en 1984 a permis de mettre au jour le déclin de cette population et la nécessité de déployer des opérations de conservations.

En 1986, l'UICN estimait qu'il ne restait que 425 à 800 individus de cette espèce.

Ce rhinocéros, le plus petit parmi les cinq espèces encore existantes, est le plus ancien sur l'échelle de l'évolution.

Il est le seul représentant de son genre, et le plus poilu et bruyant de tous les rhinocéros.

Il est également le plus proche parent du rhinocéros laineux (*Coelodonta antiquitatis*), disparu il y a environ 14 000 ans, probablement victime de la chasse par les humains et du changement climatique.

Bien que, ces dernières années, peu d'informations nous soient parvenues de la région méridionale de Sumatra, de récentes recherches de terrain indiquent que le nord de Sumatra semble prometteur pour l'espèce.

Onze rhinocéros de Sumatra vivent actuellement en captivité en Indonésie, dont dix dans le Sumatran Rhino Sanctuary et un dans le Kelian Rhino Sanctuary, dans l'est de Kalimantan.

Le programme d'élevage en captivité, qui montre son efficacité, constitue une garantie contre l'extinction totale de cette espèce.

Rapport conjoint du GSRAf, GSRAs et TRAFFIC à la CdP20 de la CITES

Le GSRAf, le GSRAs et TRAFFIC ont remis leur rapport intitulé ***Statut, conservation et commerce du rhinocéros d'Afrique et d'Asie***, commandé par le secrétariat de la CITES, en vertu de la Résolution Conf. 9.14 (Rev. CdP19), pour fournir une base aux délibérations lors de la CdP20 de la CITES qui doit se dérouler à Samarkand en Ouzbékistan du 24 novembre au 5 décembre prochains. Le rapport peut être téléchargé sur la page suivante : https://cites.org/sites/default/files/documents/E-CoP20-084-A3.pdf

Prix Harry Messel

Lors de la cinquième réunion des dirigeants de la CSE de l'UICN, qui s'est tenue à Abu Dhabi en octobre 2024, le prix Harry Messel a été décerné au président du GSRAs, Dr Bibhab Kumar Talukdar, pour sa contribution aux efforts de conservation des trois espèces de rhinocéros asiatiques.

Investigating the use of olfactory cues to redirect elephant pathways, Makgadikgadi Pans, Botswana

*Vera Ruijs[1,2], Soren Faurby[1,2], Kate E Evans[1,2,3]**

[1]Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden
[2]Gothenburg Global Biodiversity Centre, Gothenburg 40530, Sweden
[3]Elephants for Africa, Mailbox HAKb, Maun, Botswana

*corresponding author: kate@elephantsforafrica.org

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Abstract
Human-elephant conflict poses a threat to both elephants and humans. This study explored the potential of using olfactory cues on African savannah elephant pathways (*Loxodonta africana*), to divert elephants from crops and human settlements. Where selected pathways used by elephants branched, we applied a treatment of olfactory-cue-rich soil to the less frequently used side to assess whether this would influence the side the elephants used. Camera traps were placed adjacent to where the pathway split to capture which side the elephants chose. During the 62-day experiment, the camera traps recorded 1,500 sightings of elephants along seven selected pathways leading to the Boteti River in Makgadikgadi Pans National Park, Botswana. The results showed no immediate or sustained effect of the treatments on the usage of the pathways, possibly due to pre-existing olfactory cues on established pathways or the elephants' familiarity with the area. Elephants may have been drawn to the nearby Boteti River, reducing the potential impact of the treatments on the study-designated pathways. An interesting observation was that, at night, elephants exhibited a stronger preference for the pathways that, before the application of the treatments, had a higher rate of usage, possibly suggesting a stronger dependence on olfactory cues during darkness. While the application of the olfactory cues did not significantly impact how the elephants utilised the pathways, it is important to explore means by which we can communicate to elephants where high-risk areas are in a changing landscape and how to navigate these areas. This study highlights the need to better understand the factors that influence elephant movement patterns.

Additional Keywords: behavioural ecology, mitigation strategies, conservation management, sensory perception

Résumé
Les humains comme les éléphants sont menacés par les conflits qui les opposent. Dans notre étude, nous avons exploré le potentiel de l'utilisation de signaux olfactifs sur les passages empruntés par les éléphants de savane (*Loxodonta africana*) dans le but de détourner ces derniers des cultures et des zones habitées,

et de prévenir les conflits humains-éléphants. Lorsque les passages sélectionnés se divisaient, nous appliquions un traitement, composé de terre riche en signaux olfactifs, sur le côté le moins utilisé par les éléphants, afin d'évaluer si leur choix s'en trouvait influencé. Des pièges photographiques, installés près de l'embranchement, permettaient de saisir la direction choisie par les éléphants. Pendant l'expérience de 62 jours, les pièges photographiques ont enregistré 1 500 vues d'éléphants le long de sept sentiers menant à la rivière Boteti, dans le parc national du Pan de Makgadikgadi, au Botswana. Les résultats n'ont pas témoigné d'un effet immédiat ni durable du traitement sur l'utilisation des passages, peut-être en raison de signaux olfactifs préexistants sur des chemins établis, ou du fait que les éléphants connaissaient déjà la zone. Ils peuvent avoir été attirés par la proximité de la rivière Boteti, réduisant ainsi l'impact potentiel des traitements sur les zones désignées dans le cadre de l'étude. Il est intéressant d'observer que, pendant la nuit, les éléphants montraient une préférence plus marquée pour les sentiers qui, avant l'application des traitements, étaient parmi les plus empruntés. Cela suggère potentiellement une dépendance plus élevée aux signaux olfactifs dans l'obscurité. Bien que cette expérience n'ait pas eu d'impact significatif sur la manière dont les éléphants utilisent les chemins, il est important d'explorer les moyens permettant de leur communiquer l'emplacement des zones à haut risque dans un paysage en mutation, et la façon de s'orienter dans ces espaces. Cette étude met en lumière la nécessité de mieux comprendre les facteurs qui influencent les schémas de déplacement des éléphants.

Mots clés supplémentaires: écologie comportementale, stratégies d'atténuation, gestion de la conservation, perception sensorielle

Introduction

The African savannah elephant (*Loxodonta africana*) has large spatial requirements. They often cannot meet their ecological needs within protected areas (PAs), bringing them into contact and, thus, competition for resources with humans. Hence, habitat loss and human-elephant conflict (HEC) are threatening their survival (Dejene et al. 2021). Botswana is home to the largest remaining elephant population (Thouless et al. 2016), which is increasing in size and expanding into historical rangelands (Evans 2019). The expansion includes community land, with a resulting increase in HEC.

While physical barriers are useful in mitigating conflict in certain situations, they have limitations in effectively keeping elephants away from human settlements, often being damaged and requiring high maintenance (Enukwa 2017). Influencing elephant movement through olfactory cues offers an alternative that could impact elephant conservation, both in encouraging and enabling the use of wildlife corridors connecting PAs and diverting them away from cropland (Allen et al. 2021).

Studies on African wild dogs (*Lycaon pictus*) offer a compelling example of how olfactory cues can be used to manipulate wildlife movement for conservation purposes (Apps et al. 2013; Haring et al. 2023). Wild dogs, which also face significant threats from human-wildlife conflict when they venture outside PAs, have been shown to respond to the scent of dominant predators such as lions (*Panthera leo*) (Haring et al. 2023). By deploying lion scat along the boundaries of wildlife farms, researchers successfully simulated the presence of lions, significantly reducing wild dog incursions (Haring et al. 2023). This indicates that olfactory cues can alter wild dog movement patterns by increasing their perception of risk in certain areas. Such non-invasive management strategies offer a promising approach to mitigating conflicts with farmers while conserving endangered species. The success observed in wild dogs suggests that similar methods could be adapted to influence elephant movements, thus reducing HEC and promoting coexistence in shared landscapes.

Within the core of their range, elephants rely on a mental Euclidean map to navigate and locate resources (Presotto et al. 2019). In contrast, elephants tend to travel along habitual routes called elephant pathways (referred to as pathways in this manuscript) in unfamiliar areas (Presotto et al. 2019; Allen et al. 2021). Research shows that on these pathways, elephants, particularly lone bulls, rely on scent trails left by previous elephants to make informed foraging and social decisions (Von Gerhardt 2014; Allen et al. 2021). Olfaction plays a central role in the way elephants perceive and interpret their environment.

They can distinguish between food quantities (Plotnik et al. 2019), locate water sources beyond their visual range (Wood et al. 2022), and gather detailed information about other elephants from urine and dung deposits, including age, kinship, sex, and reproductive status (Poole and Moss 1989; Bates et al, 2008; Allen et al. 2021).

At times, pathways exhibit branching locations to circumvent obstacles, such as small trees or bushes, before merging back together shortly after. These branching locations often have an asymmetric usage of the pathway, with one side of the path being used more frequently than the other. This study aimed to evaluate the possibility of influencing elephant movement along these pathways by promoting increased usage of the previously less utilised side. To test this, we conducted an experiment in which we applied olfactory cues from conspecifics to the less frequented sides of the branching locations, to encourage elephant utilisation of these less used paths (Fig. 2). This allowed us to investigate the potential to manipulate elephant movement along pathways for management and mitigation purposes, as pathways could be re-directed away from crops and human settlements, thus reducing the opportunities for HEC. Allocating olfactory cues to corridors could also enhance their effectiveness in connecting PAs (Allen et al. 2021). Therefore, adding to the toolbox of mitigation strategies that local and national stakeholders can use to reduce conflict and enable coexistence (HECx) in shared landscapes. Consequently, this study's central research question is: Can African savannah elephant (*Loxodonta africana*) movement on established elephant pathways be manipulated using olfactory cues in the Makgadikgadi Pans National Park (NP)? We hypothesized that elephant movement on the pathways can be manipulated with soil treatments consisting of olfactory cues of conspecifics and that it would stimulate and increase the usage of less-used pathways.

Materials and Methods

Study area

The study was conducted between January and April 2023 in Makgadikgadi Pans NP, Botswana (Figs. 1a, b), which is located on the southwestern boundary of the Kavango Zambezi Transfrontier Conservation Area (KAZA). The area hosts a high proportion of male elephants (Evans 2019), who are known to actively utilise more peripheral areas and explore new habitats (Thouless et al. 2016; Allen et al. 2021). The resurgence of the Boteti River in 2009 after a 19-year dry period led to an increase of elephants in the area (Evans 2019). Consequently, crop raiding has become a serious issue in this region (Chamberlain 2016; Stevens 2018). In areas such as the Makgadikgadi Pans NP region, where agricultural fields are located in close proximity to a national park and to pathways leading to the river, the fields are at a higher risk of elephant foraging (Von Gerhardt et al. 2014; Songhurst et al. 2016).

Data collection

Data on pathway usage and elephant behaviour were collected using camera traps (Reconyx Hyperfire 2 Professional Covert IR Camera OD Green). A camera was set up by each of the pathway branching locations to assess which branch the elephants utilised, seven in all (Fig. 2). They were set to take three to four pictures upon triggering the sensor, with a second between each picture. Every one to two weeks, the batteries of the camera traps were replaced, and images were retrieved for data collection. We focused on elephants travelling towards the Boteti River from the east and north-east (Fig. 2a).

The data from the camera trap images were analysed to determine whether elephants travelling towards the Boteti River were on the more or the less frequented side of the pathway. The date and timestamp of when an elephant first entered the picture frame were recorded, along with the specific pathway site. Additionally, the sizes of the elephant groups were categorised as solo, pairs, or groups of three or more individuals. A ten minute gap between the last sighting of one group of elephants and the appearance of the next was considered an appropriate cut-off period to signify the start of a new group/individual elephant/pair, based on prior research in the study area where it was found that the majority of elephants in a group passed the camera trap within 10 minutes (Allen et al. 2020). Furthermore, following the findings of Allen et al. (2020), it was assumed that the first individual in a group decided the direction of travel; thus, group sightings were reduced to one data point, representing the first elephant in the group.

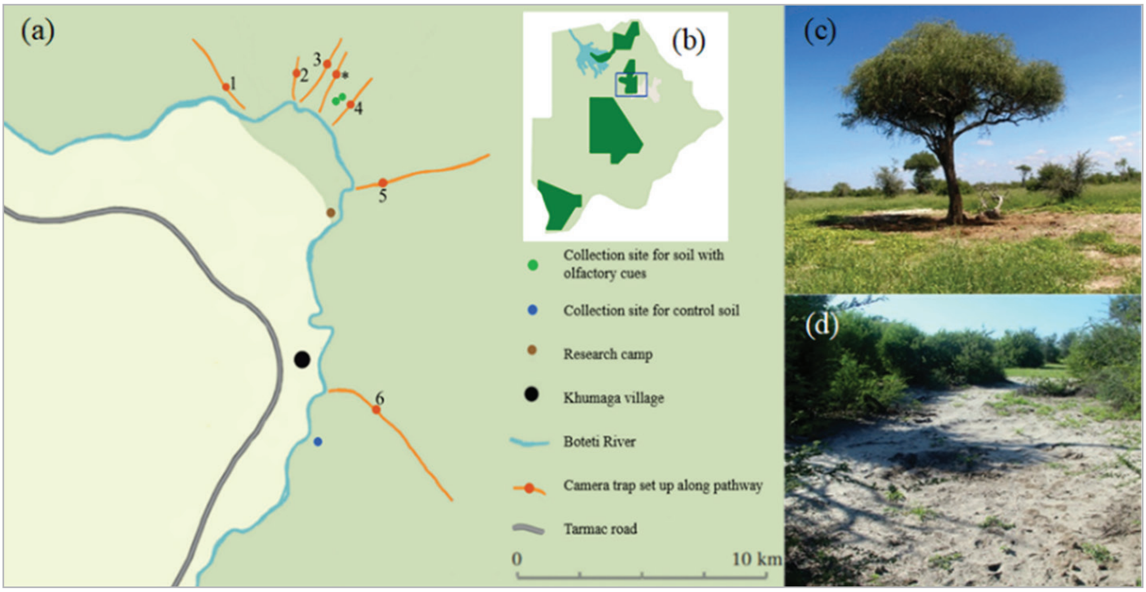

Figure 1. (a) Locations of the camera trap sites on the seven active pathways used for the experiment. The light green colour represents the Makgadikgadi Pans NP, and the light yellow represents community land. Khumaga village (black dot) is located at—20.471, 24.511 (decimal degrees). The soil for the treatments with olfactory cues was taken from two highly trafficked spots under two *Vachellia spp.* trees, indicated by green dots, and the control soil was taken from an open area of the Park, with low elephant traffic, indicated by the blue dot. The seven sites were numbered, although one of the sites (indicated by an asterisk) did not have any elephant sightings travelling in the right direction and was therefore removed from the analyses. Figure adapted from Allen et al. 2021. (b) Map of Botswana showing its national parks (dark green), the Okavango Delta (blue), and the Makgadikgadi salt pans (light grey). The Makgadikgadi Pans NP, where the experimental sites are located, is indicated with the square. (c) One of the *Vachellia spp.* trees, under which the soil was taken. (d) The open spot inside the Makgadikgadi Pans NP, from where the soil was taken for the control phase.

Experimental procedure

The experiment was set up with an interrupted time series framework, investigating whether there was an immediate or sustained effect of olfactory cues on elephant behaviour.

To establish a baseline, we conducted a control treatment using soils from an area within the Park without pathways or elephant tracks, assumed to have fewer olfactory cues (Figs. 1a, c). During the control phase (32 days), the less-used sides of the pathway were treated twice a week with the olfactory-cue-poor control soil to assess elephants' usage of the two branches of the pathway. Remote camera traps were used to collect data on elephants utilising each side of the pathway heading in the direction towards the river. In the treatment phase (30 days), olfactory-cue-rich soil was applied to the less-used pathway sides twice a week, and the elephants' usage of the pathways was assessed from the camera trap images. The olfactory-cue-rich soil was collected from well-used areas within the Park: two trees that were frequently used by elephant groups for resting in the shade (Figs. 1a, d). Under these trees, elephants were often observed urinating and defecating, meaning that these areas were rich in elephant urine and dung, making the soil samples highly concentrated with olfactory cues. To confirm the freshness of the olfactory cues in the soil, a visual assessment was made each time that soil was collected from under these trees. The visual assessment consisted, among others, of searching for footprints and fresh piles of dung that would indicate recent elephant(s) visits. Furthermore, Goodwin et al. (2012) discuss that olfactory cues from the urine of male elephants last at least three days after urination. The process of treating the pathways was repeated at seven different branching locations along distinct pathways to prevent multiple experimental sites on the same pathway (Fig. 1a).

The treatment was applied at the start of each pathway after the split, as a signal to entice the elephants to use it. It was assumed that it was sufficient to place the treatment only at the start of the pathway since we expected that once an elephant chose a pathway,

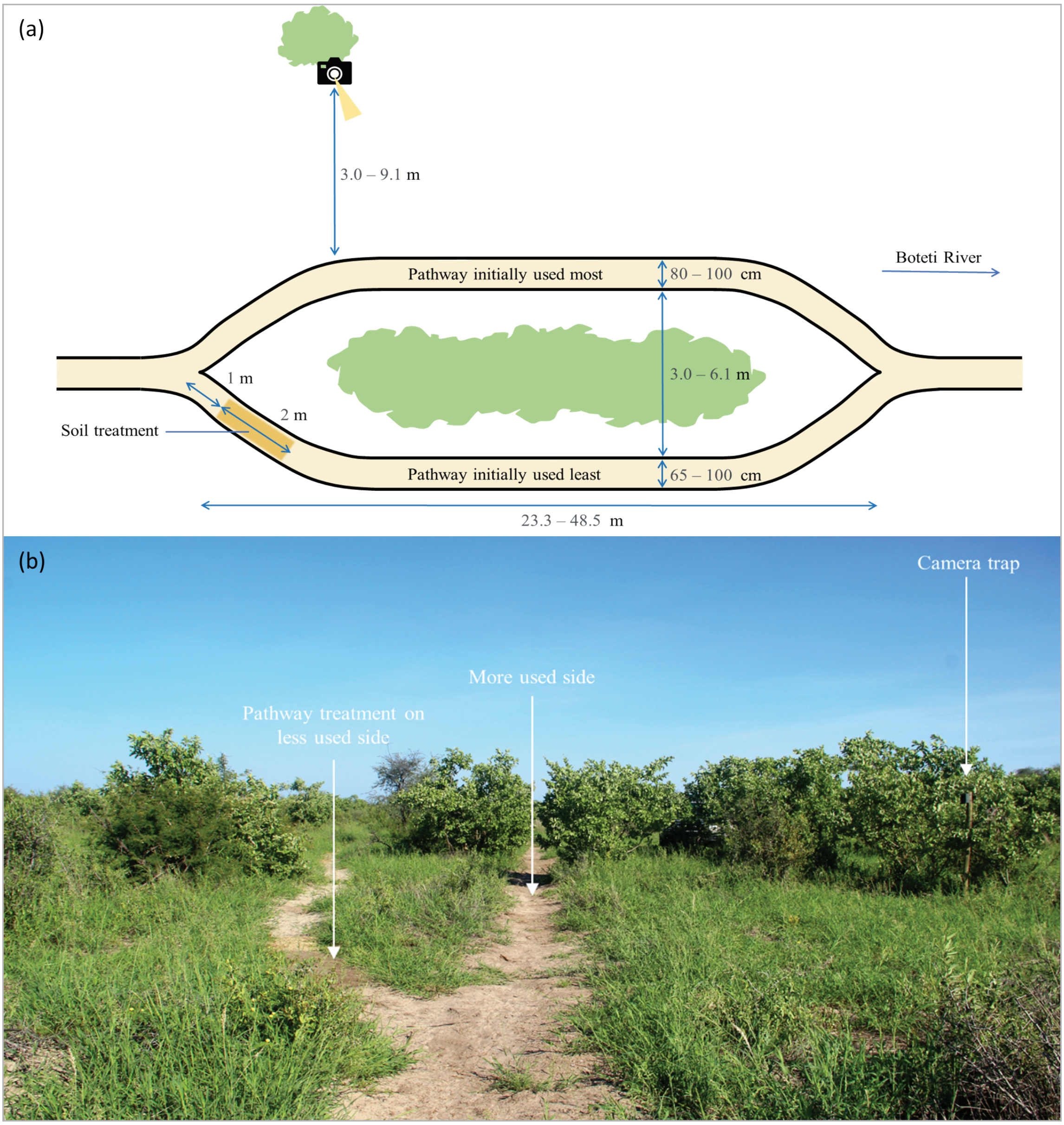

Figure 2. (a) Simplified graphic representation of the camera trap set-up and treatment on a branching location on a pathway in the Makgadikgadi Pans NP. The elephants travel in both directions on the pathways towards and from the Boteti River; the treatment was applied to assess elephants travelling towards the Boteti River. (b) Camera trap set-up at a branching location, showing the more (right) and less (left) used sides of the pathway.

they would not cross over to the other side. The treatment began 1 m above the branching location to encourage the elephants onto the path. Due to logistical constraints, the treatment could not cover the entire branch length of the pathway. Based on the stride length of elephants (average 1.8 m, range: 0.77 m–2.60 m (Hutchinson et al. 2006)), the treatments were applied for a length of 2m, spanning the entire pathway width (Fig. 2).

Statistical analyses

We were interested in predicting the probability that an elephant would choose the initially less-used pathway both before and after implementing the pathways with olfactory cue-based treatments (the intervention). So, we tested whether the probability of using the less used side was higher in the test phase than in the control phase. We analysed this using an interrupted time series framework. This type of analysis allowed us to differentiate between immediate and sustained effects. The following variables were part of the analysis: the passage of time from the beginning of the observation period (T), a variable that distinguishes observations that were made prior to the intervention from those that were made after the intervention (D) and thus the immediate effect of the intervention, and the elapsed time since the implementation of the intervention (E) and thus the sustained effect of the intervention (see also Equation 1). The dependent variable is binary and modelled using a logistic function. i.e. we were not modelling the change in observations, but rather we modelled the probability that any observation was on the least used side. Here, p is the probability that an elephant will use the less-used pathway. So, the dependent variable ln(p/(1-p)) represents the natural logarithm of the odds ratio between the probability of the event occurring (an elephant choosing the less used side), and the probability of the event not occurring (an elephant choosing the more used side). Two sets of analyses were conducted, one for each individual site and one combined, which included the site as a random effect (to account for the fact that the effect of the intervention on the elephants' decision may vary across locations). All analyses were done in R v. 4.2.2. (R Core Team 2022) and the mixed effect models were run in lme4 (v1.1.31; Bates et al. 2015).

Equation 1. Logistic regression equation for a time series model

$$ln\left(\frac{p}{1-p}\right) = b_0 + b_1T + b_2D + b_3E$$

The influence of time of day on the choice an elephant made of which pathway was also explored using the same equation with the same variables; however, the analysis was divided into one analysis solely accounting for observations made between sunrise and sunset (day), and one analysis accounting for the observations made between sunset and sunrise (night). Elephants generally rely more on olfaction than vision, but since their eyesight is moderate for mammals (Pettigrew et al. 2010), visual cues may also be relevant under adequate light conditions. Vision is slightly limited at night, and it is therefore plausible that the relative importance of olfactory cues is greater at night than during daylight hours. For this, the data were separated into observations made between sunrise and sunset, and vice versa.

Table 1. Overview of elephant sightings captured by the camera traps at the seven sites. The sightings of the excluded site (marked by * and indicated in italics) were not included in the analyses. (a) Sightings during the control and test phases are compared, as well as the sightings during the day and night. (b) An overview of the travel modes of elephants: number of elephants travelling alone, travelling with another elephant, and travelling in a group of three or more elephants. Additionally, the table shows how many individuals in groups followed the same side of the pathway as the first individual (of the group), and how many groups had differences within the group in choosing the treated or untreated side.

(a) Site	Phase:		Time of day:		Total
	Control phase	Test phase	Day	Night	
1	68	346	291	123	414
2	42	159	110	91	201
3	7	66	32	41	73
4	21	131	65	87	152
5	61	503	81	483	564
6	23	67	42	48	90
*	*0*	*6*	*4*	*2*	*6*
Total	**222**	**1,278**	**625**	**875**	**1,500**

(b) Site	Number of elephants travelling:			Number of times where individuals were in a group:		Total group sightings
	Alone	In a pair	In a group	All chose the same side	Chose different sides	
1	75	61	278	24	26	50
2	51	30	120	20	8	28
3	23	11	39	4	4	8
4	53	34	65	10	5	15
5	107	72	385	55	4	59
6	16	22	52	7	2	9
*	*1*	*4*	*1*	*0*	*1*	*1*
Total	**326**	**234**	**940**	**120**	**50**	**170**

Table 2. Summary of the model in which all sites were combined and the site was considered as a random effect. The sightings are corrected for elephants travelling in groups (i.e. group sightings are reduced to one data point).

	Estimate	Std. Error	P-value
Intercept	-1.233	0.682	0.071
Days since start (T)	-0.025	0.023	0.262
Treatment (D)	0.418	0.564	0.458
Days since treatment (E)	-0.039	0.032	0.225

Results

During the 62 days of fieldwork, the camera traps recorded 1,500 sightings of elephants on pathways leading to the Boteti River. The number of sightings varied across the seven sites, with considerably more sightings during the test phase compared to the control phase (Table 1a). Of these sightings, 625 were captured during the day, while 875 were recorded at night (Table 1a). Sites 1 and 2 had a higher number of daytime sightings, while sites 3, 4, 5, and 6 recorded more nighttime sightings. The cameras captured 326 sightings of elephants travelling alone, 234 elephants travelling in pairs, and 170 occurrences of groups of three or more elephants travelling together (Table 1b). It is important to note that the 170 group sightings may have included multiple observations of the same

Table 3. Summary of the model in which all sites were considered separately. The sightings are corrected for elephants travelling in groups. Significant value ($p < 0.05$) is indicated in bold.

	Site	Estimate	Std. Error	P-value
Intercept	1	0.728	0.608	0.231
	2	-19.870	4.286×10^3	0.996
	3	-25.570	2.069×10^5	1.000
	4	0.354	1.179	0.764
	5	-22.236	24.362	0.361
	6	-0.619	0.990	0.532
Days since start (T)	1	-0.076	0.038	**0.048**
	2	0.003	2.276×10^2	1.000
	3	0.000	1.303×10^4	1.000
	4	0.000	0.050	0.998
	5	0.642	0.787	0.414
	6	-0.049	0.105	0.642
Treatment (D)	1	1.498	0.977	0.125
	2	18.990	4.849×10^3	0.997
	3	-0.437	3.133×10^5	1.000
	4	-0.653	1.019	0.521
	5	-1.430	1.600	0.371
	6	-19.010	1.652×10^4	0.999
Days since treatment (E)	1	0.023	0.049	0.643
	2	-0.162	2.276×10^2	0.999
	3	0.004	1.493×10^4	1.000
	4	-0.080	0.071	0.263
	5	-0.688	0.789	0.384
	6	0.060	7.789×10^2	1.000

Table 4. Summary of the model in which the time of the day is considered, 'day' signifies any sighting that happened between sunrise and sunset, and 'night' signifies the time between sunset and sunrise. The sightings are corrected for elephants travelling in groups. The significant value ($p < 0.05$) is indicated in bold.

	Time of day	Estimate	Std. Error	P-value
Intercept	Day	-0.700	0.784	0.372
	Night	-2.025	0.983	**0.040**
Days since start (T)	Day	-0.037	0.032	0.249
	Night	-0.022	0.035	0.525
Treatment (D)	Day	0.686	0.761	0.367
	Night	0.536	0.890	0.547
Days since treatment (E)	Day	-0.054	0.044	0.219
	Night	-0.039	0.050	0.438

individuals. This also applies to solo travellers and pairs observed along the seven pathways during the 62-day experimental period. In some instances, not all individuals in a group chose the same side as the first (lead) elephant in the group (Table 1b). Furthermore, not all individuals in a group travelled directly along the pathway; some individuals travelled parallel to the pathway, while others were on it. The same applies to elephants travelling in pairs.

The results did not show any significant effect of the olfactory treatment on elephants' choice of pathway, analysed with all sites combined (Table 2), nor with all separately analysed sites (Table 3). With regard to the investigation into the effect of the time of day on the decision of elephants to choose the treated or untreated pathway, there were no significant immediate and/or sustained effects of the treatments (Table 4).

Discussion

The time series analyses aimed to assess the influence of introducing olfactory cues from elephant urine and dung as pathway treatments on the movement decisions elephants make. The results did not reveal any significant immediate and sustained effects of the treatments, suggesting that these olfactory cues did not alter the decision-making processes of elephants.

Although our olfactory treatment of pathways had no significant effect on which side the elephant(s) chose to travel along, given their biology and reliance on the sense of smell, it is likely that the underlying method of using olfactory cues to manipulate elephant movement may be possible. Potentially, the quality and quantity of olfactory cues introduced were insufficient to influence the elephants' choice compared to the abundance of pre-existing cues along the well-established pathways. Additional olfactory cues, such as the Boteti River's water scent, may have allowed elephants to detect the river and guide their choices more than cues from conspecifics (Wood et al. 2022). It is also possible that elephants in the area possess a deeper spatial understanding than assumed, recognising that both sides ultimately lead to the Boteti River. This familiarity with the area's pathways could render olfactory cues less influential in their decision-making process, where the experiment was undertaken.

Furthermore, elephants could be neophobic and thus potentially scared away by the addition of an introduced soil, however, research on wild Asian elephants (*Elephus maximus*) suggests they can be neophiliac-inclined (Jacobson et al. 2023), thus we do not think neophobia is a problem with this experiment. If this were a factor, it would likely reduce the use of the least used side in both the control and study period and would therefore likely not change our ability to see any potential effect of olfactory cues. Finally, the significant aversion to the less-used side of the treated pathway at night might be due to elephants relying more on their sense of smell in low-light conditions when visual perception is limited.

Future recommendations

Despite the non-significant results for immediate and sustained effects of pathway treatments, continued efforts to enhance the effectiveness of olfactory cues for conflict mitigation are crucial. This approach, based on positive chemical signalling, has the potential to create a self-reinforcing cycle where treated pathways attract and influence more elephants over time, offering a novel, sustainable mitigation method to work alongside existing strategies (Allen et al. 2021).

Alternative and stronger olfactory cues should be explored, such as using larger quantities of soil mixed with elephant dung and urine olfactory cues. Potentially, as has been done for African wild dogs, the molecular signature of the different chemicals that make up elephant urine and dung could be identified (Apps et al. 2013). The specific compound in the scent trails that elephants follow could be synthetically produced and scaled up as pathway treatments. A more pervasive application along the entire pathway, an increased frequency of cue application, and the investigation of ways to remove or mask existing cues, are worth exploring (Allen et al. 2021). Additionally, predator dung (Valenta et al. 2020) or chillis (Pozo et al. 2017) could serve as a natural deterrent to prevent elephants from travelling on the more used sides, combined with promoting the use of the initially less used sides.

Conclusion

In conclusion, this study aimed to manipulate elephant movement on established pathways using olfactory cues. However, introducing urine and dung-derived olfactory cues as pathway treatments did not have a discernible effect on elephant behaviour. Factors such as drought conditions, pre-existing olfactory cues, and elephants' familiarity with the area and the nearby location of the river, likely overshadowed the olfactory cues introduced through the treatments. Despite these results, the study emphasises the importance of persisting in finding ways to optimize the use of olfactory cues as a conflict mitigation tool. The incredible sense of smell of elephants offers the potential for effective strategies. The outcome of this study serves as a valuable foundation for future research, encouraging further exploration and refinement of the use of olfactory cues in conflict mitigation. By doing so, we can work towards sustainable and effective strategies for managing HEC and promoting HECx in communities bordering the Makgadikgadi Pans NP and similar ecosystems.

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Impact of severe drought-related mortality on the subsequent dynamics of a population of African savannah elephants

Kevin M Dunham

PO Box CH385, Chisipite, Harare, Zimbabwe
email: kmdunham@protonmail.com

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Abstract

Drought-induced mortality can significantly impact the numbers of African savannah elephants (*Loxodonta africana*) in a population, with juveniles and older adults often disproportionately represented among the elephants that die. During the severe drought in south-eastern Zimbabwe in 1992, hundreds of elephants perished, especially young elephants under eight years of age. Notably, more male juveniles than females succumbed to the drought. The impacts on the age and sex structure of an elephant population may persist for many years following such a drought period. This manuscript utilises data from frequent aerial surveys and a simple population model based on age and sex, including the unusual age and sex structure of the female herds recorded a year after the drought, to examine these impacts over a 30-year period in a population of several thousand elephants in southern Africa. Immediately after the drought, the number of elephants in female herds increased rapidly, but there was no corresponding increase in the number of elephants in bull groups. Male recruitment—when young male elephants transfer from their natal female herds to bull groups—decreased to low levels during the ~16 years following the drought. Only when males born after the drought transferred to bull groups did the predicted and observed numbers of bulls increase. Model-predicted trends in the numbers of elephants in female herds and bull groups were a credible fit with survey estimates. The number of elephants in Gonarezhou National Park increased threefold after 1993. Since 2013, the population has numbered ~11,000. This levelling off coincided with the movement of some elephants into areas bordering the Park.

Résumé

La mortalité due à la sécheresse peut avoir de lourdes répercussions sur le nombre d'éléphants de savane d'Afrique (*Loxodonta africana*), notamment chez les individus juvéniles et les adultes plus âgés, souvent surreprésentés dans le nombre de morts recensées. Lors de la sécheresse qui a frappé le sud-est du Zimbabwe en 1992 et qui a vu périr des centaines d'éléphants, un taux de mortalité particulièrement élevé a été relevé parmi les individus de moins de huit ans. Dans cette classe d'âge, les mâles ont été plus touchés que les femelles. À la suite d'une période de sécheresse, les incidences sur les structures d'âges et de sexes d'une population d'éléphants peuvent s'observer durant de nombreuses années. Cet article s'appuie sur les résultats de recensements aériens réguliers et sur un modèle démographique simple basé sur l'âge et le sexe – y compris les structures d'âge et de sexe inhabituelles relevées chez les hardes de femelles un an après l'épisode de sécheresse – afin d'étudier ces impacts sur trente ans dans une population de plusieurs milliers d'éléphants en Afrique australe. Immédiatement après la sécheresse, le nombre d'éléphants dans les hardes de femelles a rapidement augmenté, mais aucune hausse dans les groupes de mâles n'a été constatée. Pendant les seize années qui ont suivi la sécheresse, le taux de recrutement d'éléphants mâles (lorsque de jeunes individus quittent leur harde de femelles d'origine pour rejoindre des groupes de mâles) a décliné jusqu'à atteindre des niveaux faibles. Ce n'est que lorsque des mâles nés après la sécheresse ont intégré des groupes de mâles que les prévisions et les chiffres observés ont augmenté. Les tendances prévues par le modèle quant au nombre d'éléphants dans les hardes de femelles et les groupes de mâles correspondaient de manière crédible aux chiffres des estimations. Le nombre d'éléphants dans le parc national de Gonarezhou a été multiplié par trois après 1993. Depuis 2013, la population compte environ 11 000 individus. Cette stabilisation a coïncidé avec la migration de certains éléphants vers des zones adjacentes au parc de Gonarezhou.

Introduction

Drought-induced mortality can have major impacts on the numbers of African savannah elephant (*Loxodonta africana*), with juveniles and older adults often disproportionately represented among the elephants that die (Corfield 1973; Dudley et al. 2001; Lee et al. 2022). Hundreds of elephants died during the 1992 drought in south-eastern Zimbabwe, with particularly high mortality among youngsters <8 years of age (Leggett 1994), but there is no reliable estimate of the number that died. During 1993, the year after the drought, Coetsee (1996) captured >600 elephants in entire female herds in Gonarezhou National Park (Gonarezhou going forward). The age of each captured immature elephant was estimated from its recorded shoulder height using sex-specific growth curves constructed from shoulder height and age data collected during earlier culls in Gonarezhou (Dunham 2024).

The 667 elephants in 55 female herds captured during 1993 were removed from a population estimated to have included 3,000–4,000 elephants in female herds (see Fig. 7a). Hence, the captured elephants formed a sample of 17–22% of elephants in female herds. Because entire herds were caught, the captured elephants provided a representative sample of the population of females and immature males during 1993, from which the sex and age structure of the female herds could be estimated (Dunham 2024). The captured herds contained a high proportion of adult females and a low proportion of immatures.

Aerial surveys of the elephant population in Gonarezhou during 1995–2009 revealed that the estimated number of elephants in female herds increased by 7.3% per annum (Dunham 2012). The numbers of buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga burchellii*) also increased rapidly during this post-drought period. But for elephants in bull groups, the trend was different: their number was approximately constant from 1995 to 2009, but increased rapidly after 2009 (see Fig. 3).

While drought-induced mortality is immediately noticeable, it can have long-term population impacts that are less obvious. This study aimed to reveal if and how the different population trajectories of elephants in bull groups and those in female herds can be explained by the unusual age structure of the elephants that survived the drought. A simple, sex-age structured model of an elephant population was constructed to mimic the population of Gonarezhou. The model population started a year after the drought mortality and immediately after the 1993 captures, with an age structure similar to that recorded. Other model parameters were based on information from Gonarezhou or from the literature. The model population mimicked the period 1993–2022, each year increasing the population by births and reducing it by natural mortality, the recorded offtakes, and emigration. The 1993 age structure was the only parameter in the model that was unusual for an elephant population. Therefore, if the modelled population numbers are a reasonable fit to the survey estimates, this would suggest that the unusual population trends observed after the drought were likely a consequence of that age structure.

The advantage of a simple model, such as used here, is that, if the modelled population trends are a reasonable fit to the survey estimates, then it is likely that the parameters included in detail in the model and which vary annually (e.g. the sex and age structure of immatures in the model) play a major role in producing the trends. Conversely, parameters that are simply averaged for the entire run of the model (e.g. the fecundity schedule) likely play little or no role in producing the trends.

The absence of an increase in the number of elephants in bull groups prior to 2009 could perhaps be attributed to a factor such as emigration or unrecorded poaching (the latter especially so, given that the number increased rapidly after 2009, following the commencement of technical support to Park management by Frankfurt Zoological Society

(FZS)). However, any attempt to explain the observed trend in the number of elephants in bull groups after 1993 needs to commence with the unusual age structure of the female herds recorded during 1993—because these herds provided the males that were recruited to the bull groups. If emigration or poaching were significant factors in determining the observed trend, then a model incorporating these factors—and the unusual age structure—would better fit the survey estimates than a model that included just the unusual age structure. Hence, the model described above, starting with the unusual age structure, was also run assuming that some adult males were poached annually prior to 2008. The model was run several times, each time assuming that the number of poached bulls was constant between years, but varying between model runs.

After 2014, the estimated number of elephants in the female herds in Gonarezhou stopped increasing and appeared to stabilise (Fig. 3). It was not intended that the model presented here would mimic this levelling off, which is likely not related to the 1992 drought.

Methods

Study area

The study area is described briefly here, and in more detail by Dunham (2024). Gonarezhou NP lies <600 m above sea level and covers ~5,000 km^2 in south-eastern Zimbabwe, bordering Mozambique to the east (Fig. 1). The region experiences a hot wet season during November–March, a cool, dry season during April–July and a hot, dry season during August–October, and is noted for low and variable annual rainfall. Annual rainfall over the Park averages 486 mm (July–June rainfall year, n = 42 years; coefficient of variation 29%, CHIRPS records (Funk et al. 2015)). The 1992 drought followed a season of very low rainfall (annual rainfall during the 1991–1992 climate year was 157 mm, 32% of the mean). The CHIRPS records do not fully capture the impact of the 1992 drought, described by a lowveld resident as "the worst drought in living memory" (see Dunham (2024) for more details).

The Save, Runde and Mwenezi rivers dominate the area, although all rise well outside the Park. The Runde and Save are perennial, and dry season flow in the Mwenezi is controlled by water release through Manyuchi Dam, ~130 km upstream. Other rivers flow only seasonally. Elephants, drought and fire have significantly impacted the vegetation. The main vegetation types are: *Colophospermum mopane* shrubland or woodland in heavier soils; *Guibourtia conjugata* and *Combretum* dominated woodlands in sands; mixed woodland in granophyre; and riverine woodland (Cunliffe et al. 2012).

Since 2011–2012, electric fences have limited elephant movement to the north and north-west of Gonarezhou (Mandinyenya 2021) and, during 2016, the fence line was extended southwards. The Naivasha area (a wilderness area within the adjacent communal land) was included within this fenced area. Elephants are free to move from Gonarezhou to the Mahenye communal area (which includes subsistence agriculture and livestock, as well as uncultivated land), Naivasha, the Malipati Safari Area (henceforth Malipati) (a protected area) and Mozambique. Within Mozambique, adjacent to the international border, are *fazendas de bravio* (privately-owned areas intended for both wildlife conservation and hunting) totalling ~1,400 km^2. Malilangwe Wildlife Reserve (WR) lies on the northern border of Gonarezhou and since its boundary fence was completed during 2011, net movements of elephants in or out of Malilangwe WR have been limited to <5 bulls per year (B. Clegg, pers. comm., 3 January 2023).

Small numbers of elephants (<50) are also shot annually in communal areas in Zimbabwe immediately adjacent to the Park, either for problem animal control (PAC), or by trophy hunters. Prior to 2018, trophy hunting also occurred in Malipati. Some illegal hunting of wildlife occurs in the Park. A year after the 1992 drought, Coetsee (1996) captured complete female herds in Gonarezhou and translocated them elsewhere. These herds comprised 477 females of all ages, 169 males of 15 years of age or younger, and 21 males of 16 years of age or older (Dunham 2024). It is assumed here that the age and sex structure of the immatures in those herds, and the ratio of immatures to adult females, were representative of the Gonarezhou female herds during 1993.

Male and female elephants fitted with satellite collars stayed mainly within the Gonarezhou boundaries during 2009–2012 (Westhuizen 2012). The use of areas outside the Park, was mainly to the east, on the Mozambique side of the unfenced international border in the *fazendas de bravio*. Elephants

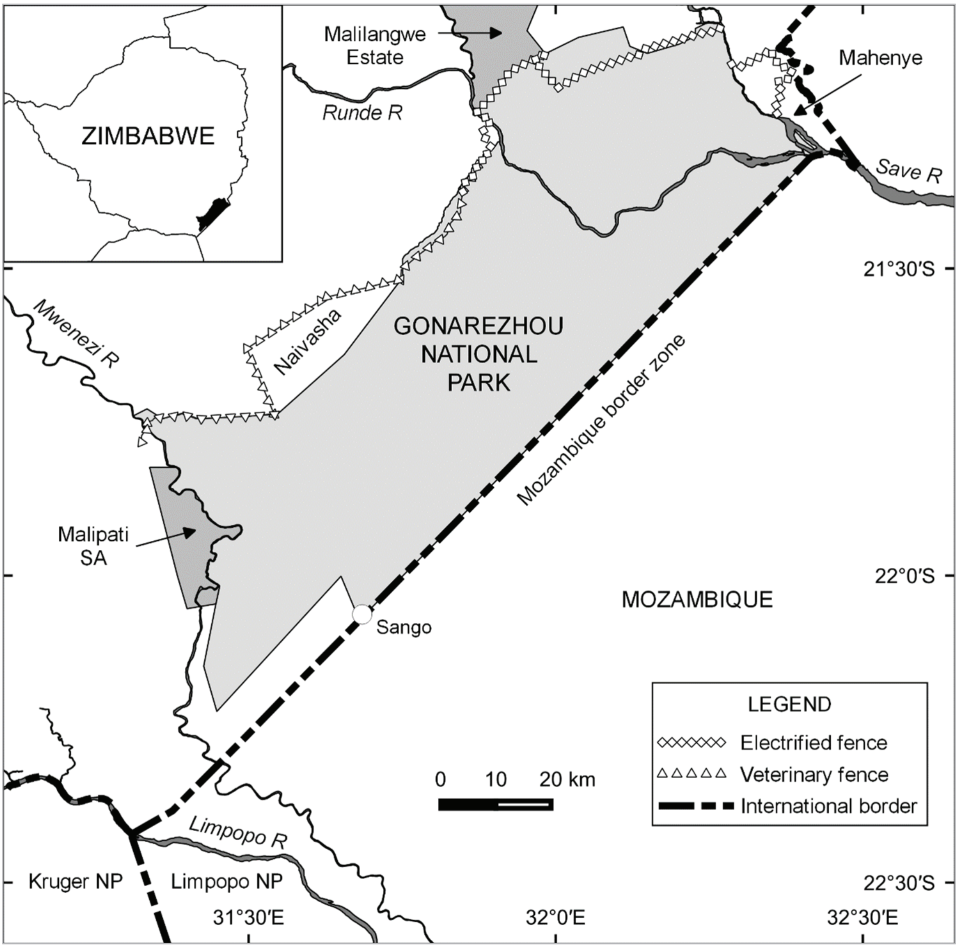

Figure 1. Gonarezhou, Kruger NP (South Africa) and Limpopo NP in Mozambique, together with the communal land between Gonarezhou and Kruger NPs, form the Great Limpopo Transfrontier Park. The insert shows the location of Gonarezhou on the south-eastern border of Zimbabwe.

occasionally move between Gonarezhou and Kruger National Park (NP), but there is no evidence that this movement is permanent and hence would constitute emigration (Sherry 1978; Henley 2013; Mandinyenya et al. 2024).

Sample surveys of the Gonarezhou elephant population

The first rigorous census of Gonarezhou elephants was carried out during 1980 and since then, similar sample aerial surveys have been undertaken regularly during the dry season. The survey methods followed those recommended for large African herbivores (Norton-Griffiths 1978). Surveys since 1995 have provided separate estimates of the number of elephants in bull groups and the number of elephants in female herds. Bull groups contained subadult and adult males, with solitary males treated as a bull group of size one. Elephants in female herds included adult females, immature elephants of both sexes and probably a few adult bulls. Elephant carcasses were also counted during the surveys. Estimating mortality from survey carcass data would be complex (Huso 2011), but the carcass ratio—the percentage of elephants seen that are dead—can provide a useful index of elephant mortality during the years preceding a survey (Douglas-Hamilton and Hillman 1981; Douglas-Hamilton and Burrill 1991). During surveys, Malipati was treated as part of Gonarezhou until 2007, but separately since 2009. Surveys since then have included the Mahenye and Naivasha areas.

Surveys during 2009, 2014 and 2022 included an area ~15 km wide of Mozambique adjacent to the international border and stretching from the Save River towards the Sango border post. This area was also surveyed in 2018 (Craig and Gibson 2018). Since 2014, the number of dead elephants in this Mozambique border zone has exceeded the number of live ones: the carcass ratio (Douglas-Hamilton and Burrill 1991) was 87–100% during 2014, 2018 and 2022.

Estimating how many elephants moved into this zone and died there depends on the duration of the period after the death of an elephant, that its carcass remains visible to a survey observer. Two trend lines were calculated for the estimated number of elephants (alive or dead) in the Mozambique border zone. A lower trend line assumed that all carcasses seen during surveys remained visible to observers during subsequent surveys; and an upper trend line assumed that all carcasses had disappeared (from the view of survey observers) by the time of the next survey, four or five years later.

When a plot of survey estimates against time suggested that it was appropriate, an exponential rate of population change per annum (*r* hat) was calculated, with 95% confidence limits (CL), using a weighted regression of natural logarithms of the survey estimates against time, with the variance of this rate of change based on the sampling variances of the survey estimates (Gasaway et al. 1986). For the variable estimates of the number of adult males in Malipati or Mahenye, an annual linear rate of population change ($\hat{g}$) was calculated. Two survey estimates were compared with a two-tailed t-test, with the null hypothesis that the population number had not changed. Other statistical tests followed Zaiontz (2025).

When a plot suggested that the rate of population change decreased with time, a logistic curve was fitted to the survey estimates. Sibly et al. (2005) suggested that, in a wide range of animal species, population regulation was generally the result of a concave relationship between the growth rate of a population and its size, in which case the theta-logistic model was more appropriate than the simple Ricker model used here. However, after a recent simulation study comparing models, Koetke et al. (2020) suggested that the Ricker model is appropriate for population survey data of species with slow life histories. It is not the intention here to compare various forms of the logistic model to determine their fit to the Gonarezhou survey data, and the Ricker logistic is used here merely to illustrate the general form of the logistic curve.

Population model

A model of an elephant population, which would mimic the real Gonarezhou population, was constructed using an MS Excel spreadsheet. The model population was divided into males and females and into 60 age classes, each representing one year (0–1,….. 59–60) and commenced immediately after the 1993 captures. The age structure of the non-adults, and the ratio of non-adult elephants to adult females, in the model at that time were proportionally the same as those observed amongst the captured elephants (Dunham 2024). The ages of the adult females could not be estimated from their shoulder heights. Hence, the age structures of the adult females and adult males <40 years of age were estimated approximately from the adult female and adult male age structures during the 1986 Gonarezhou cull (GP Sharp, unpubl. data, Gonarezhou NP files, May 2008), with each age class advanced seven years. Entire female herds and bull groups were included in this cull; hence it provided representative samples of both adult females and adult males. In the model, it was assumed that no elephants >40 years of age survived the 1992 drought. Leggett (1994) found few carcasses of elephants older than 40 years. This observation was taken as indicating that there were few elephants >40 years of age in the population immediately before the 1992 drought and that the older elephants present died during the drought. In Amboseli, Kenya, researchers also noted the high mortality for females >40 years of age during droughts (Lee et al. 2022).

In the model, each year starts at the beginning of the rainy season. The population number then increased with births. The proportion of fertile females in each age class followed the fertility versus age graph of Sherry (1975), but with ages adjusted to the schedule of Jachmann (1988). The proportion of females in each age class that gave birth annually was calculated as the proportion that were fertile divided by the mean CI, in years. This interval was assumed to be constant between years. The sex ratio at birth was assumed to be 1:1 (Sherry 1975). The elephants in each age/

sex class advanced to the next (older) age class, while the newborn elephants moved into age class 0–1.

The number of elephants in each age/sex class of the model was then reduced by any recorded deaths, such as trophy hunting or PAC in areas bordering Gonarezhou, or poaching (although there are no poaching records for 1992–2008). It was assumed that all poached elephants were males. It was further assumed that both trophy hunters and poachers would preferentially kill elephants with larger tusks, and so, in the model, the numbers of animals in the oldest age classes were reduced until the total number of reductions for each year was equal to the total recorded offtake in and around Gonarezhou that year. Information on offtakes in the Mozambique border zone is not available. In the model, it was assumed that there was negligible immigration to Gonarezhou.

Based on the survey results, it was assumed in the model that: a) some female herds emigrated to Mahenye from 2010 and to Malipati from 2015 (Fig. 5); b) some bulls emigrated to Mahenye from 2013 and to Malipati from 2017; and c) elephant movements into Naivasha were temporary and did not constitute emigration. In the model population, elephants that emigrated were removed annually, with elephants in female herds removed proportionally to their presence (in the model population).

It is reasonable to assume that the elephants in the Mozambique border zone moved there from Gonarezhou. Estimating the number of elephants that have died in the border zone during the past ~20 years depends on the mean duration of the period that an elephant carcass remains visible to a survey observer. The conservative option is to assume that all carcasses remained visible to a survey observer during subsequent surveys, and so the lower trend line (Fig. 6) was used to estimate the number of elephants emigrating annually to Mozambique from 2013. No female herds were seen in the border zone during the 2014, 2018, or 2022 surveys and the few herds seen here during earlier surveys were assumed to have returned to Gonarezhou. In the model population, it was assumed that only elephant bulls moved there from Gonarezhou.

After births and emigration, the total number of animals in the 60 x 2 age/sex classes of the model population was the predicted population number for that year, at the time when surveys are often conducted. The model population was divided into two sections: bull groups, which comprised all males older than 16 years; and breeding or female herds, which comprised males aged 1 to 16 years and all females. The model was run for 29 years, mimicking the period 1993–2022.

After surveys and at the end of the dry season, when food and water are the most limiting, the number of elephants in each age/sex class was reduced by age- and sex-specific annual mortality rates. For simplicity, the number of animals in each age/sex class was not constrained to be an integer. The Gonarezhou elephant population increased at a mean exponential rate of 6.2% annually immediately after the 1992 drought (Dunham 2012), which is a relatively high rate (Cumming 1981). Hence, it was assumed that the age and sex-specific annual mortality rates were relatively low, and the rates in the model (except that for first-year calves) were set to be identical to the mortality rates observed for South Africa's Addo elephant population, which also increased rapidly in number (Whitehouse and Kerley 2002).

First-year mortality in the model was negatively related to rainfall, as suggested by elephant carcass records from ranger patrols in Gonarezhou for 2014–2023 (GCT unpubl. data) and as noted in Amboseli (Lee et al. 2011a). If the observed rainfall during the preceding January–June was greater than the long-term mean (393 mm), the first-year mortality rate was the same as the Addo figure (6.2 %). However, if the observed rainfall was less than this mean, the first-year mortality increased by a factor that was negatively and curvilinearly related to rainfall. Hence, first-year mortality increased to 9.0% when the January–June rainfall was 300 mm, to 18.4% when it was 200 mm, and to 25.7% when the rainfall was 150 mm.

Among the elephants captured in female herds during 1993, the numbers of males in the 13–14, 14–15 and 15–16–year–age classes were similar (13, 7 and 12, respectively (Dunham 2024)). This was taken to indicate that the males left their natal female herds after their approximate sixteenth birthday. Hence, bull recruitment in any model year was defined as the number of males transferring from the 15–16–year–age class to the 16–17–year class. As they transferred between these two model age classes, males also transferred from the female herds to the bull groups. For simplicity, the age when males in the population model transferred to the bull groups coincided with their transfer between age classes, but in reality, male independence is not sudden (Lee et al. 2011b).

The real numbers of elephants in bull groups and female herds during 1993 were not known. Hence, these numbers were initially set to be 819 and 3,324, respectively, which were the 1995 survey estimates, with the constraints (for these numbers) set to be the same as the confidence limits for these estimates. The mean calving interval (CI) was also not known. It was initially set to be 4.1 years, the mean value for Gonarezhou during the early 1970s (Sherry 1975), with constraints of 2.9 and 9.1 years, which are the minimum and maximum values reported for East African elephant populations (Hanks and McIntosh 1973).

The MS Excel add-in, Solver *Evolutionary*, was used to determine the starting values (i.e. 1993) that resulted in the predicted numbers of bulls and elephants in female herds providing the closest fit to all the survey estimates for years when the Gonarezhou population was actually censused. Running the Solver add-in was equivalent to running numerous models with different starting values for the three unknowns (initial number of elephants in bull groups, initial number of elephants in female herds, and mean CI). Each model was assessed by comparing the fit of the predicted elephant numbers with the actual survey estimates. Martin's estimator (Martin 1992; Dunham 2008) was used to compare the fit of the different models. Each survey estimate was compared with the predicted population number for that year by relating the difference between the two numbers to the variance of the survey estimate. There were 12 aerial surveys of the Gonarezhou elephant population during 1995–2022, and each provided estimates of the numbers of elephants in bull groups and in female herds. Hence, the predicted population numbers were compared with 24 survey estimates for each combination of the three unknowns, 12 for bull groups and 12 for female herds. The product of the 24 comparisons gave a single 'index value', which was minimized using the Solver add-in. The robustness of this model was determined by repeating the above procedure 12 times, each time removing a different year of survey from the fit.

The Solver *Evolutionary* can find a sound solution, but not necessarily one which is optimal (Frontline Systems 2024). To increase the likelihood that Solver found a solution that was close to optimal, the default options were changed, with the convergence reduced (to 0.0000001) and the mutation rate increased (to 0.15). Solver found an identical solution even if the initial values for the three unknowns were changed, either to their minimum or maximum constraints.

Population model starting with 'normal' age structure

A revised version of the above model was run starting in 1993, with a 'normal' age structure (i.e. not affected by drought) for the population. A normal age structure was obtained by running the original model until 2093. After 100 years, all drought survivors were dead and the 2093 model age structure was determined by the fecundity and mortality schedules used in the model and assumed to be 'normal'.

This normal age structure was used as the starting (1993) age structure in another model that was, in other respects, the same as the original model with the drought-impacted age structure. The population trends from the model starting with a normal age structure were compared with both the survey estimates and the trends from the original model with the drought-impacted age structure.

Population model incorporating unrecorded poaching

The original population model, with the age structure impacted by drought, was rerun under the assumption that a certain number of adult males were poached each year from 1994 to 2007. The model was run multiple times, each time assuming a different number of poached males (1, 2, 3, 4, 5, 6, 7, 10, 15, or 20 per annum). The fit of the modelled trends to the observed trends for each scenario, as indicated by the index value, was compared to a model that assumed no adult males were poached during this period. In the model used here, poaching, trophy hunting and emigration of adult males would all have a similar impact as they all contribute to an increase in the number of adult males removed from the population each year.

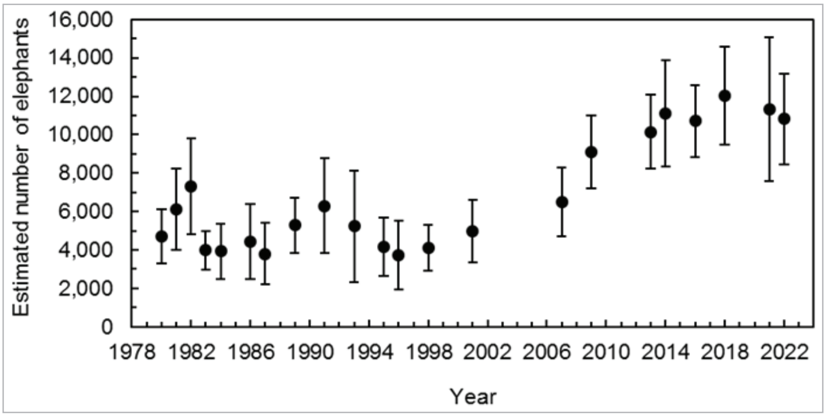

Figure 2. Temporal trend in the estimated number of elephants in Gonarezhou. Points are survey estimates with 95% CI. During 1983, 1986 and 1987, a total of >4,000 elephants were culled in response to concerns about the impact of elephants on the vegetation. A severe drought occurred in 1992, and 670 elephants were captured and translocated during 1993.

Results

Surveys of the Gonarezhou elephant population

The mean estimate of the number of all elephants in Gonarezhou increased during 1995–2018 at a mean exponential rate of 5.3% per annum (n = 10 surveys; CL 4.2 and 6.5%) (Fig. 2). But during 2013–2022, the estimated number of all elephants changed little and averaged 11,031 (n = 6 surveys), more than three times any model estimate of the number immediately after the 1993 captures (Table 1).

The mean estimate of the number of elephants in female herds increased during 1995–2018 at a mean rate of 5.7% per annum (n = 10; CL 4.4 and 7.0%) (Fig. 3). But for the entire study period, a logistic curve was a better fit to the survey estimates than an exponential curve. The apparent decline in the estimated number of elephants in female herds between 2018 and 2022 was not statistically significant (two-tailed t-test, t = 0.90, p = 0.37). Nonetheless, the last survey estimate in the time series (that for 2022) had a greater impact on the parameters of the logistic equation than other survey estimates. During 1995–2007, the number of elephants in bull groups appeared to decline, but not significantly (Fig. 4). However during 2007–2022, the number in bull groups increased exponentially, at a mean rate of 6.3% per annum.

The surveys revealed an increase in the number of elephants in Zimbabwean areas adjacent to Gonarezhou (Fig. 5). The estimated number of elephants (alive or dead) in the border zone of Mozambique also increased with time (Fig. 6). The temporal trends in the estimated numbers of all elephant carcasses and of fresh or recent carcasses in Gonarezhou gave no indication of large-scale or unusual elephant mortality in Gonarezhou during the years following the 1992 drought. The all-carcass ratio (including 'unidentified' carcasses, which are likely to have been elephant carcasses) was relatively high during the years immediately after the drought (>10% for five surveys during 1993–1998), presumably a reflection of the 1992 drought mortality. But from 2001 onwards, it averaged 5.9% (n=7, range 3.6–8.5%) and showed no significant trend (linear regression slope = -0.09, p = 0.4). From 1996 onwards, the 1+2 carcass ratio (an index of elephant mortality during the survey year) averaged 0.13% (n=12, range 0–0.39), and also showed no significant trend (slope = 0.001, p = 0.7).

Population model starting with drought-impacted age structure

Temporal trends in the numbers of elephants in bull groups and female herds modelled were within the confidence limits of all the survey estimates for the Gonarezhou population (12 estimates for elephants in female herds and 12 estimates for elephants in bull groups), except for the estimate of elephants in female herds during 2022 (Fig. 7).

The population model which predicted elephant numbers that best fit the survey estimates, started

Table 1. Estimates from aerial surveys during 1995 to 2022 of the numbers of all elephants, elephants in bull groups and elephants in female herds for Gonarezhou. CI = 95% confidence interval of estimate. Discrepancies between the estimate for all elephants and the sum of the estimates for bulls and females are usually rounding errors.

Year	All elephants		Elephants in bull groups		Elephants in female herds		Source
	Estimate	CI	Estimate	CI	Estimate	CI	
1995	4,156[a,b]	1,509	819[a]	281	3,324[a]	1,408	a Davies et al. (1996); b Douglas-Hamilton (1995) ([a,b] merged estimate)
1996	3,742	1,796	663	222	3,064	1,687	See Dunham (2012)
1998	4,132	1,198	762	274	3,369	1,169	
2001	4,987	1,637	718	228	4,272	1,623	
2007	6,516	1,790	577	213	5,939	1,778	
2009	9,123	1,902	757	195	8,366	1,892	
2013	10,151	1,922	1,145	229	9,007	1,909	See Appendix S1 of O'Connor and Shimbani (2024)
2014	11,120	2,764	1,179	372	9,940	2,741	
2016	10,715	1,878	983	195	9,734	1,867	
2018	12,046	2,555	1,489	378	10,559	2,527	Dunham and van der Westhuizen (2018); Dunham (2022)
2021	11,339	3,746	1,329	475	10,010	3,718	Dunham et al. (2022); Dunham (2022)
2022	10,812	2,371	1,810	458	9,001	2,328	Dunham (2022)

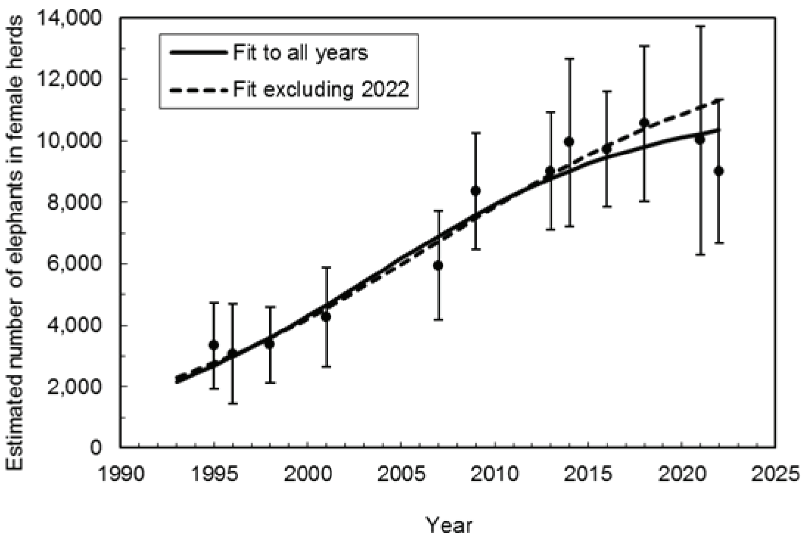

Figure 3. Temporal trend in the estimated number of elephants in female herds in Gonarezhou. Points are survey estimates with 95% CI. Lines indicate best-fit logistic curves, one fitted to all survey estimates (solid line) and the second fitted to all survey estimates except that for 2022 (dashed line). For the first line: N_0 = 2,161, r_m = 0.137 and K = 11,142. For the second curve: N_0 = 2,310, r_m = 0.113 and K = 13,317. The MS Excel add-in Solver was used to determine the N_0, r_m and K values that minimized the differences between the survey estimates and the values predicted by the equation, with each difference related to the variance of the appropriate survey estimate (Martin 1992).

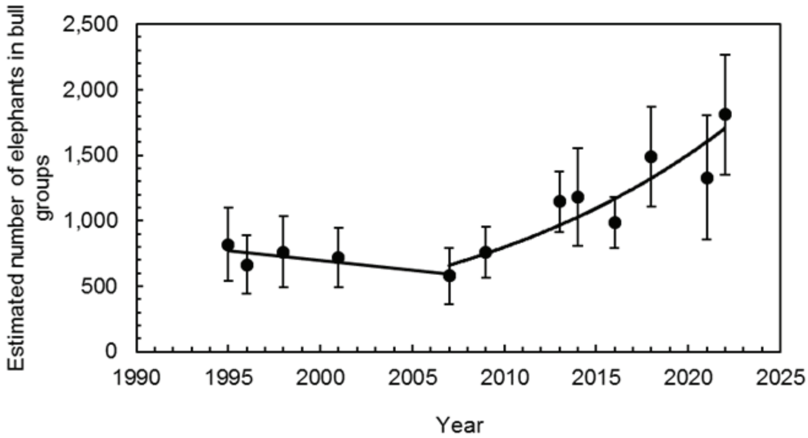

Figure 4. Temporal trend in the estimated number of elephants in bull groups in Gonarezhou. Points are survey estimates with 95% CI. Bold lines indicate the likely trends. During 1995–2007, the mean linear rate of change ($\hat{g}$) was 14 bulls per annum (CL = -37.3 and 9.3; n = 5 surveys). During 2007–2022, the number of elephants in bull groups increased at a mean exponential rate (r) of 6.3% per annum (CL = 4.2 and 8.5%; n = 8).

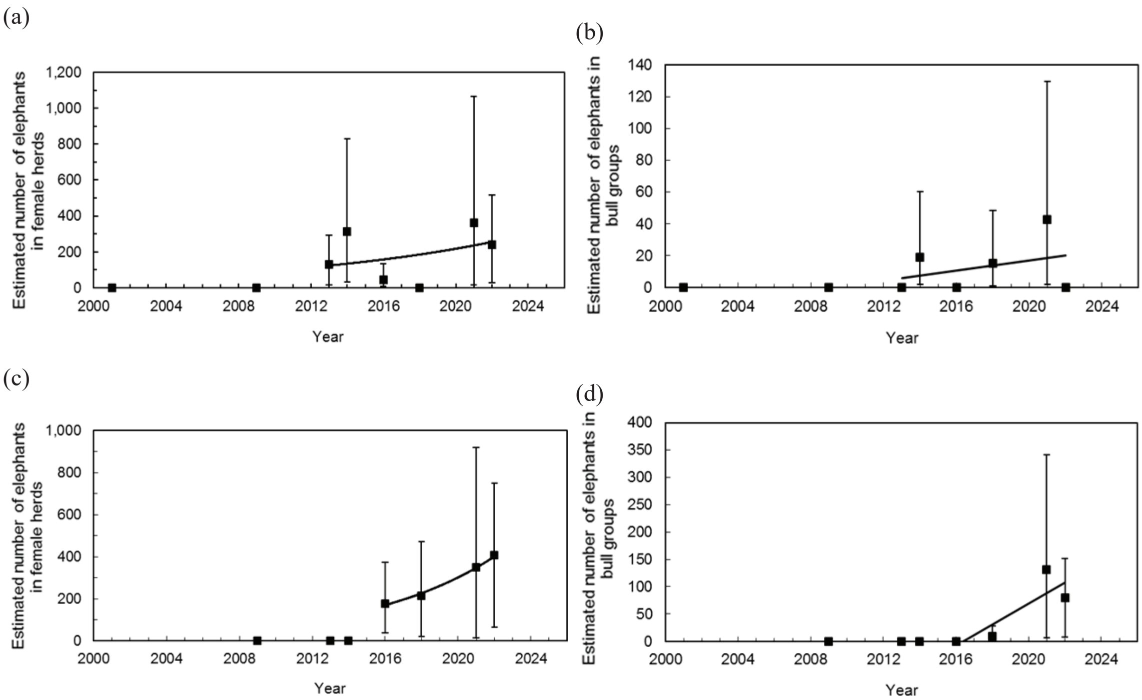

Figure 5. Temporal trends in the estimated numbers of elephants in Mahenye communal area and Malipati, which border Gonarezhou. The points are survey estimates with 95% CI: (a) female herds and (b) bulls in Mahenye; and (c) female herds and (d) bulls in Malipati. Bold lines indicate assumed trends used in the population model: exponential for female herds and linear for bulls.

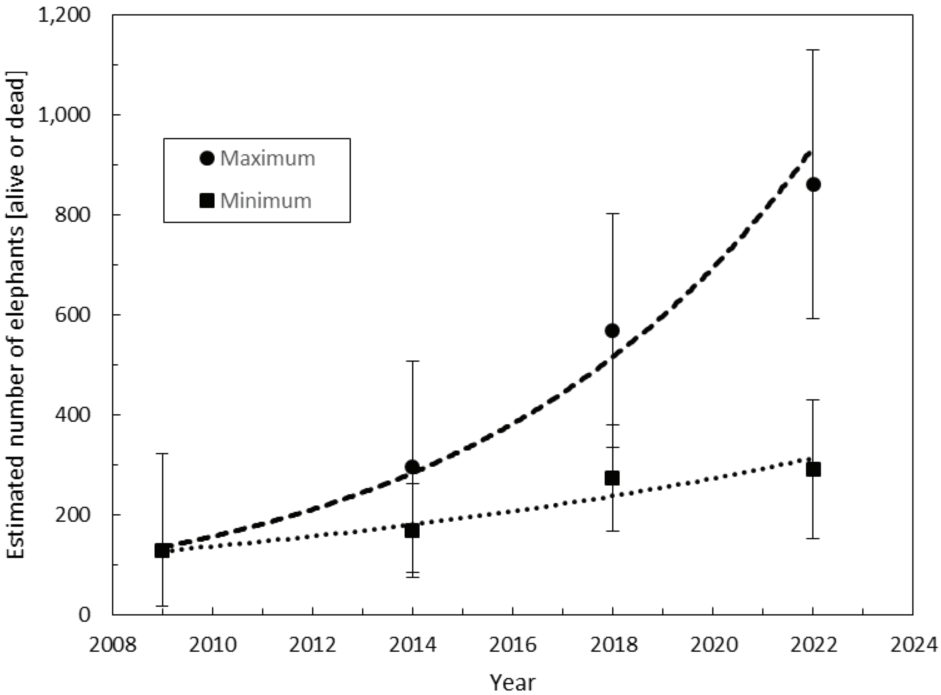

Figure 6. The temporal trend in the accumulative number of elephants estimated to have emigrated to the Mozambique border zone from Gonarezhou. Points are survey estimates with 95% CI. The lower (dotted) line is an exponential curve through estimates calculated on the assumption that all elephant carcasses seen during surveys remained available to be seen during later surveys (minimum estimates). The upper line (dashed) is an exponential curve through estimates calculated on the assumption that the elephant carcasses seen during any survey were not available to be seen during any subsequent survey (maximum estimates). For the upper line, r = 14.3% per annum (CL = 6.7 and 22.4%); and for the lower line, r = 7.0% per annum (CL = -0.8 and 15.4%).

with 2,892 elephants in female herds and 658 in bull groups after the 1993 captures and had a mean CI of 3.9 years. Even when one survey was removed from the fit, these parameters barely changed. However, the 2022 survey estimate had the most influence because that survey produced a relatively low population estimate for both elephants in female herds (less than the estimates of the four previous surveys during 2014–2021) and elephants in bull groups. (This was less than the estimates of the two previous surveys during 2018 and 2021) (Table 1).

In the model populations, the recruitment of males to the bull groups, as they transferred from the female herds, was low from 1994 until 2003 (Fig. 8) and declined further during 2004–2008, before a significant rise during 2009. Thereafter, there was generally a small increase in recruitment annually.

Population model starting with the 'normal' age structure

Temporal trends in the numbers of elephants in bull groups and female herds from a model with a normal age structure were within the confidence limits of most survey estimates, but a poorer fit (Fig. 9) than the trends from the model with the drought-impacted age structure (Fig. 7). The normal age structure model which predicted elephant numbers that best fit the survey estimates, started with 2,995 elephants in female herds and 599 in bull groups after the 1993 captures and had a mean CI of 3.1 years. Noticeably, the model trend in the number of elephants in bull groups did not show the constant or declining number observed from 1995 to 2007, but instead the modelled number increased throughout the 30 years of the model run (Fig. 9b).

Population model incorporating unrecorded poaching

For models which assumed that some adult males were poached annually between 1994 and 2007, the index value was used to compare the fit of the trends from these models to the survey estimates, with the fit for a model that assumed that no males were poached during this period. When the fit to the survey estimates for both elephants in female herds and elephants in bull groups was considered, the fit was similar whether one elephant or none was poached, but the fit declined if two or more elephants were poached (Fig. 10a). When only the fit to the survey estimates for elephants in bull groups was considered during those model runs, the fit was similar if five or fewer, or no adult males were poached; however it declined if six or more were poached. The trends produced by these models differed little from each other, whether 0, 5, 10, 15, or 20 adult males were assumed to have been poached annually (Figs 10b and c). The main difference was in the model estimate of the number of elephants in bull groups during 1993 at the start of the model, with this starting number increasing as the assumed number of poached males increased.

Discussion

Long-term effect of the 1992 drought

Temporal trends in the numbers of elephants in bull groups and female herds of a model with a drought-impacted age structure were a credible fit to the survey estimates for the Gonarezhou population during the 20 years after drought. Trends from a model with a normal age structure were a poorer fit to the observed trends and, in particular, did not reflect the observed absence of an increase in the number of elephants in bull groups from 1995 to 2007. Also, the model with the normal age structure required a notably small (implausible?) mean ICI (3.1 years) over 30 years. This compares with 3.9 years for the model with the drought-impacted age structure and, consequently, a high proportion of adult females (Dunham 2024).

Alone, the unusual age structure of the elephant female herds that survived the 1992 drought (Dunham 2024) can explain the differing observed post-drought trends for elephants in female herds and those in bull groups. No additional explanation is required, as shown by models that started with that unusual age structure, but also assumed that, during 1994–2007, a few (5 or fewer) adult males were lost annually from the Gonarezhou population (by unrecorded poaching, trophy hunting, emigration, or any combination of these), being an equally good, but no better fit to the survey estimates. This implies that the trend observed after the drought for elephants in bull groups cannot be accounted for primarily by unrecorded hunting (legal or illegal) or emigration.

The age structure of the drought survivors revealed that relatively few non-adults survived and that, among younger non-adults, males suffered greater mortality than females. This pattern of mortality due to drought has been observed elsewhere (Foley et al. 2008; Lee et al. 2022). In the absence of immigration, the only recruitment of elephants to the bull groups in any population is when males leave their natal female herds, with most leaving before they are 17 years of age (Lee et al. 2011b). At any time, annual recruitment to bull groups during the next ~16 years can usually be estimated from the number of males in each year/class, from 15 to 16 years down to 0 to 1 year. During the ~16 years after the 1992 drought, recruitment to bull groups, both in the model and likely in the real Gonarezhou population, declined until it was very low between 2003 and 2008, when recruits consisted of the few males who were aged <5 years during the drought and survived it.

When males born in Gonarezhou in 1993, (the year after the drought) left their natal female herds during 2009, there would have been a notable increase in recruitment to the bull groups. Following 2009, annual recruitment to bull groups was largely determined by the number of males born ~16 years earlier, during 1994, 1995, 1996, etc. After 2007, the estimates of elephants in bull groups in the survey increased at a similar annual rate as the number of elephants in female herds had increased 16 years earlier. With an elephant having a potential lifespan of >60 years, it will take another 30 years for the impact of the drought mortality on the young elephants in Gonarezhou to progress through the age profile of the population, as has been shown for the Amboseli elephants (Lee et al. 2022). In Gonarezhou, the gap in the male age profile resulting from drought mortality now (2025) coincides with the group aged 30–45 years old. Elephant tusk mass is proportional to age (Whyte and Hall-Martin 2018), and so the gap in this age group will impact the number of elephants with sizeable tusks available for trophy hunting around Gonarezhou.

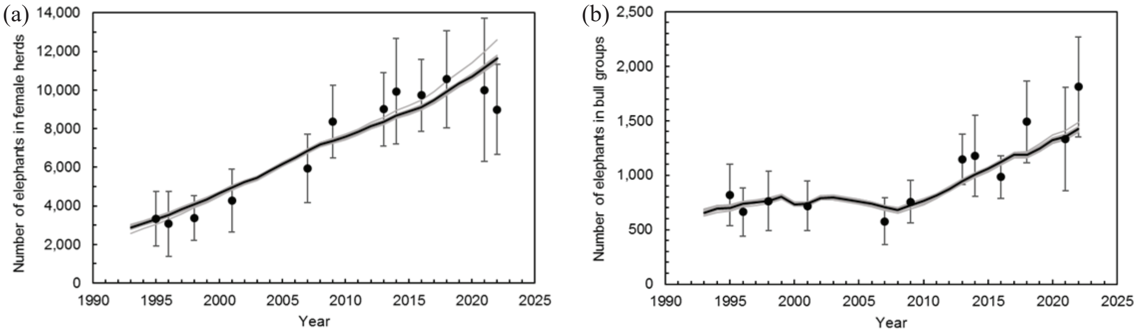

Figure 7. Temporal trends in the number of elephants in Gonarezhou: (a) elephants in female herds; (b) elephants in bull groups. Trends (lines) of a model with a drought-impacted age structure and survey estimates (points) with 95% CI are shown. Bold lines indicate the best-fit modelled trends when the model estimates are fitted to all survey estimates; and grey lines indicate the trends when the model is run 12 times, each time excluding the estimates for a different survey from the fit. The apparent grey bands are individual grey lines, most of which differ little from each other. The grey line, which diverges from the others (after 2013 for elephants in female herds and after 2019 for elephants in bull groups), is the best-fit model when the 2022 survey estimates are excluded from the fit. These models assumed that no bulls were poached during 1994–2007.

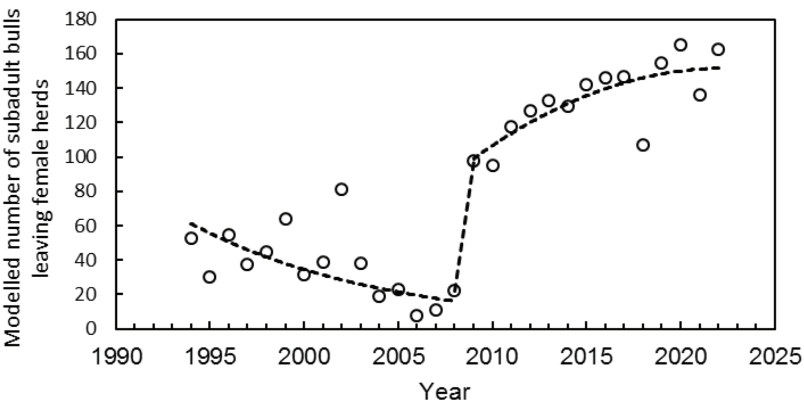

Figure 8. Temporal trend in the modelled annual recruitment of bull elephants in Gonarezhou after the 1992 drought. Recruitment occurs when males leave the female herds and transfer to the bull groups, when they are ~16 years of age. Points are not data points, but model outputs representing the number of bulls moving into the 16–17–year–old class. For illustrative purposes, the broad trend in recruitment is summarized with three (dashed) regression lines (the first a negative exponential, the second linear, and the third a two-order polynomial). Relatively low recruitment during 2018 and 2021 reflects the model-predicted high juvenile mortality during the low rainfall years when these recruits were born (2002 and 2005).

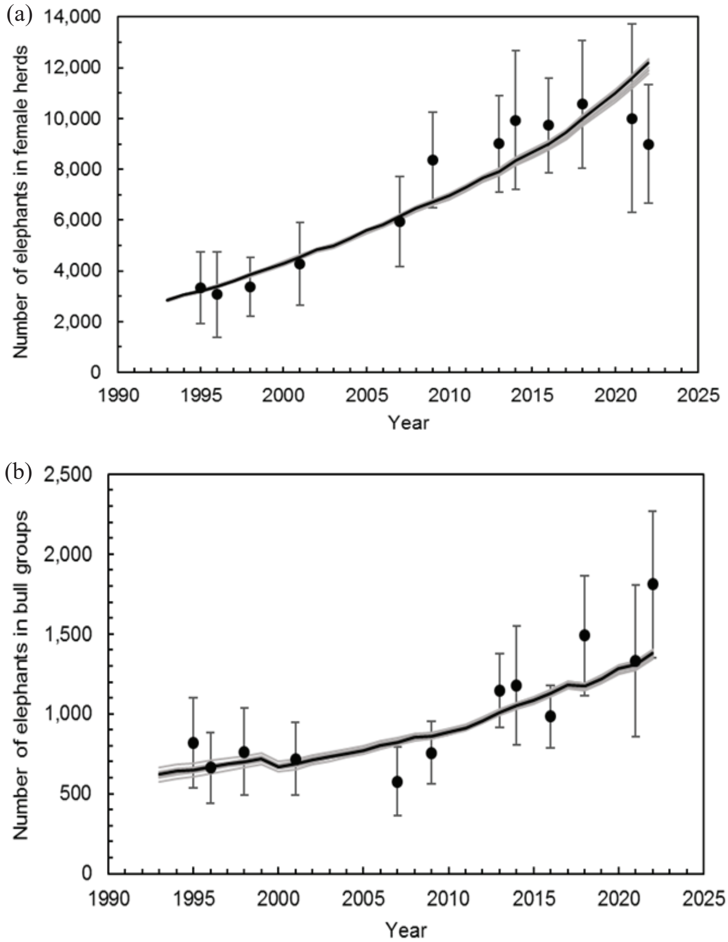

Figure 9. Temporal trends in the number of elephants in Gonarezhou: (a) elephants in female herds; (b) elephants in bull groups. Trends (lines) of a model with a normal age structure and survey estimates (points) with 95% CI are shown. Bold lines indicate the best-fit modelled trends when the model estimates are fitted to all survey estimates; and grey lines indicate the trends when the model is run 12 times, each time excluding the estimates for a different survey from the fit. The apparent grey bands are individual grey lines, most of which differ little from each other.

Trend in the number of elephants in female herds

The high rate of increase in the survey estimate of the number of elephants in female herds after the drought probably reflected the high proportion of adult females among drought survivors. But for 15 years (the approximate time for a female to reach maturity) following the drought, the proportion of adult females in the female herds would have declined, as non-adult age classes were filled by youngsters born after the drought. The rate of increase in the number of elephants in female herds decreased in both the real and model populations as a result of this changing age structure. But the rate continued to decline after that period (i.e. after 2007), as is indicated by a logistic curve being a credible fit to the survey estimates. The recorded removals from the Gonarezhou elephant population are mostly of adult males. The decline in the rate of increase of elephants in female herds within Gonarezhou revealed by the surveys is at least partly due to emigration to areas bordering the park. There were often a few elephants seen in Malipati and Mahenye, but recent movement into Malipati

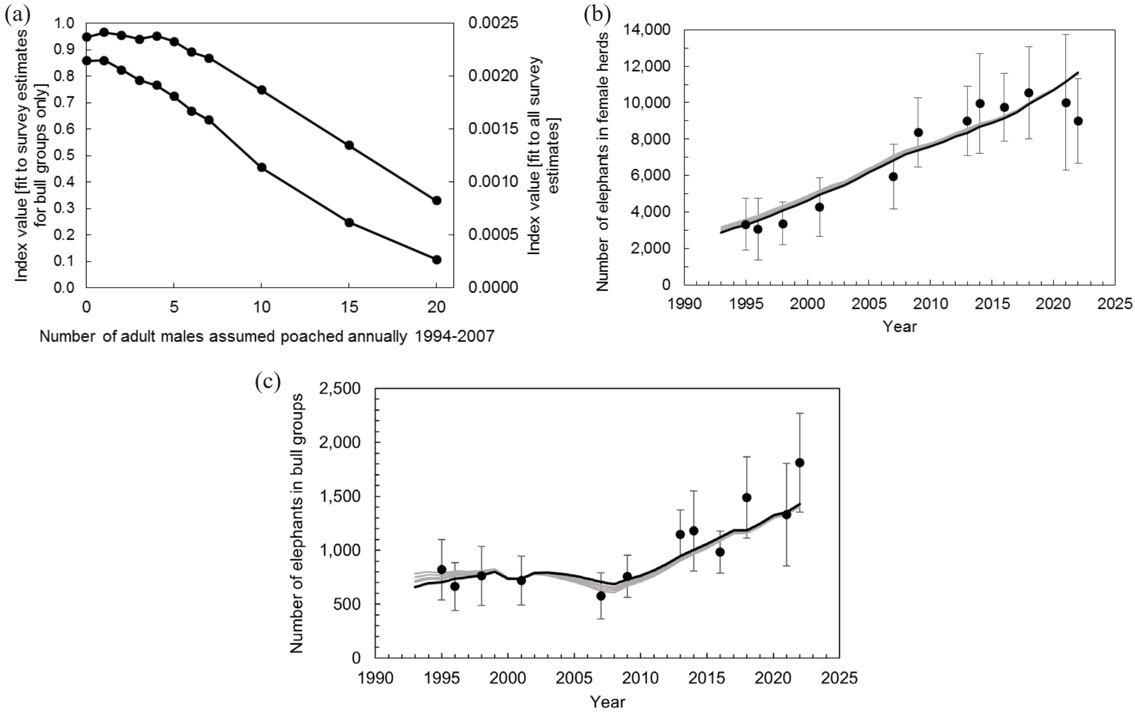

Figure 10. (a) The fit to the survey estimates of trends from models that assumed that some adult males were poached annually during 1994–2007. Each point represents a run of the model, with the indicated number of adult males assumed to have been poached. The lower line indicates the fit to all 24 survey estimates, 12 for elephants in female herds and 12 for elephants in bull groups (right scale). The upper line indicates the fit from the same model runs, to the 12 estimates only for elephants in bull groups (left scale). The greater the index value, the better the fit. The left and right scales differ and are not comparable with each other (because the left index is based on the product of 12 numbers, while the right is based on the product of 24 numbers).
Temporal trends in the number of elephants in Gonarezhou for (b) elephants in female herds and (c) elephants in bull groups. Trends from these same models (lines) and survey estimates (points) with 95% CI are shown. Bold lines indicate the best-fit modelled trends when the model estimates were fitted to all survey estimates, and it was assumed that no adult males were poached between 1994 and 2007. The grey lines indicate the trends when the model was run four times, each time assuming that 5, 10, 15, or 20 adult males were poached annually. The apparent grey band is composed of several individual grey lines (which merge), most of which differ little from each other.

has probably been encouraged by the cessation of trophy hunting there after 2017. Movements into Mahenye may have been encouraged by the establishment of a 70 km^2 wildlife area, fenced to reduce HEC, but open to Gonarezhou across the Save River.

The discrepancy between the estimate of elephants in female herds in 2022 and the predicted number is large. In the absence of any evidence of major mortality of elephants between the 2021 and 2022 surveys, or of undetected emigration, it is likely that the 2022 estimate of elephants in female herds in Gonarezhou is simply a low estimate. The planned 2025 survey should reveal whether this is the case.

Emigration at least partly accounts for the decline during the last decade in the rate of increase in the number of elephants in female herds in Gonarezhou. There appears to have been no increase in subadult or adult mortality within the Park, because the aerial surveys recorded that the carcass estimates and carcass ratio there have not increased. The surveys do record a large increase in mortality in the Mozambique border zone, but most of these dead elephants were likely adult males. The levelling off of the number of elephants in female herds may have involved changes in the female age at first conception, the inter-calving interval (ICI), or juvenile survival, or any combination of these factors. This would be in line with expectations that these parameters would change before any increase in non-anthropogenic adult mortality (Eberhardt 2002). But Gonarezhou data are not available to test for changes in these parameters. For elephant populations, a change in the ICI is an important population regulating mechanism (Hanks and McIntosh 1973).

Assumptions of model

The model is intentionally a simple one and includes various assumptions. The mean ICI was assumed to be constant for the ~30 years that the model runs simply because there is no information available for Gonarezhou to indicate if or how the interval has changed, or even what the mean interval has been since 1992. Carcass records from ranger patrols since 2014 suggest that the mortality of juvenile elephants in Gonarezhou was negatively related to rainfall, with the relationship being curvilinear, as also in Amboseli (Lee et al. 2011a). A similar relationship between first-year mortality and rainfall was assumed to apply for the duration of the model, although possibly, during the decade or so after the drought, when elephant density was relatively low, there was a weaker relationship, or none at all.

During surveys after 2009, no female herds were seen in the Mozambique border zone, but numerous elephant carcasses, indicative of the illegal killing of elephants, were observed. Given that elephant female herds are more risk-averse than bull groups (Smit et al. 2023), it was assumed in the model that, while female herds from Gonarezhou may have visited Mozambique occasionally, no female herds emigrated there. Therefore, in the model, it was assumed that all elephant carcasses seen in Mozambique were of elephant bulls. If some female herds did emigrate to Mozambique, the effect of this would be to improve the fit of the Gonarezhou model estimates of the number of elephants in female herds to the survey estimates for the years after emigration commenced.

Estimating how many elephant bulls have moved into the Mozambique border zone depends on the duration of the period after the death of an elephant that its carcass remains visible to a survey observer. In the model, it was conservatively assumed that all the carcasses remained potentially visible during subsequent surveys. But if it is assumed that, on average, a carcass remained visible to a survey observer for four years (Booth and Dunham 2016), the number of elephants estimated to have moved to Mozambique during 2009–2022 almost triples, from 291 (+/- CI 48%) (if no carcasses disappeared) to 860 (+/- 31%). If the number of bulls that moved to Mozambique was greater than assumed in the model, the effect of this would be to reduce the fit of the model estimates of the number in bull groups to the survey estimates after 2009.

The model assumed that there was no immigration into Gonarezhou; however, Kruger NP lies ~30 km south of Gonarezhou, and elephants are known to move between the two PAs, although at present there is no evidence that the moves are permanent and hence would constitute immigration/emigration (Sherry 1978; Henley et al. 2023; Mandinyenya et al. 2024). Studies of bull movements in Kruger NP and the wider ecosystem have tended to focus on adult bulls with large tusks, i.e. older individuals. If there are annual dispersal movements of younger bulls from Kruger NP northwards, the effect of this immigration would be consistent with an increase in the estimated number of bulls emigrating from Gonarezhou to Mozambique.

Management implications

Since 1993, the number of elephants in Gonarezhou has increased threefold. The mean rate of population increase of 5.3% per annum over 23 years compares with 4.1% annually in Kruger NP (Louw et al. 2021). The increase in the Gonarezhou population contrasts with the situation elsewhere in Zimbabwe (Dunham 2015) and much of Africa (Thouless et al. 2016), where poaching has caused significant population declines. The contrast with other Zimbabwean subpopulations follows the formation in Gonarezhou of a conservation partnership between the national wildlife management authority and an INGO (FZS), with resulting increases in local law enforcement capacity and in economic engagement with local households (Kuiper et al. 2023).

Since 2013, the Gonarezhou population has numbered ~11,000 elephants, with the levelling off of the population coinciding with the movement of some female herds into the Mahenye community lands and Malipati. For many years, the number of elephants in the areas bordering Gonarezhou was small, but now it is necessary to consider a larger population in Gonarezhou that includes not only the elephants in Gonarezhou, but also those in neighbouring areas, including the Mozambique border zone. At present, the Mozambique border zone acts as a sink area, where the rate of elephant mortality remains high, in contrast to the situation in Gonarezhou, which is the source. There is little cultivation or human settlement in this border zone, which suggests that the high mortality rate is not a consequence of conflict, but of the illegal killing of elephants.

Significant drought-induced mortality of non-adult elephants during 1992 resulted in female herds the following year that contained a high proportion of adult females and few immatures. Immature females significantly outnumbered immature males among the survivors (Dunham 2024). The models presented here show how a low proportion of immature males in female herds can cause a significant decline in adult male recruitment during a period of ~16 years after a drought and, therefore, a decline during that period in the number of adult bulls in the population, likely because bull mortality exceeds recruitment. Similar lag effects, induced by poaching, are probably occurring in the populations of elephants of the Sebungwe and Zambezi Valley in Zimbabwe. The estimated number of elephants in female herds in Sebungwe declined by >9,000 (79%) between 2006 and 2014 as a consequence of poaching (Dunham 2008; Dunham et al. 2015). Even if poaching has reduced or stopped, a similar magnitude decrease in annual recruitment of adult males would be expected for ~16 years after 2014.

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The recruitment pattern and inter-calving interval of the reintroduced greater one-horned rhinoceros (*Rhinoceros unicornis*) population in Manas National Park, Assam, India

Deba Kumar Dutta[1], Amal Chandra Sarmah[2], Amit Sharma[3], Bibhab K Talukdar[1], Anindya Swargowari[4]*

[1]13, Tayab Ali Bi-lane, Bishnu Rabha Path, Guwahati, Assam, 781028, India
[2]House No 38, South Sarania Road, Swahid Anil Deka Path, PO Ulubari, Guwahati, Assam, 781007, India
[3]WWF-India, Block A16, Flat No. 103, Basistha, Guwahati, Assam, 781029, India
[4]House No 18, Sonaighuli Don Bosco; PO Sawkuchi, Guwahati, Assam, 781040, India

*corresponding author: debakumerdutta@gmail.com

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Abstract

This study examines the reproductive performance and inter-calving intervals (ICI) of reintroduced greater one-horned rhinoceros (*Rhinoceros unicornis*) in Manas National Park (MNP), India, from 2012 to 2021. The Park's rhino population was previously wiped out due to poaching but has been re-established through the wild-to-wild translocations under Indian Rhino Vision 2020 (IRV2020) and rhino rehabilitation programmes. Our monitoring and analysis reveal that translocated and rehabilitated rhinos have adapted progressively to their new environment, with 35 calves born during the study period (2012–2021). We observed distinct conception patterns among translocated rhinos that conceived before translocation compared with those that conceived after their release in MNP. The average ICI interval for rehabilitated rhinos was 2.12 to 4.41 years, while for translocated rhinos it was 1.99 to 6.30 years. Study findings indicate that the average age at first calving for the first generation (F1) was 5.65 years. Our findings indicate that rehabilitated rhinos tend to calve near human presence, close to the anti-poaching camps, while translocated rhinos preferred more isolated areas. We also observed seasonal calving patterns, with most births occurring during the monsoon (May–September) season. The study highlights the importance of effective monitoring, anti-poaching measures, transboundary collaboration, habitat management and community support for the long-term conservation success of the rhino population in MNP. Our research contributes to the understanding of rhino reproductive biology in re-establishing populations and informs conservation strategies for this threatened species.

Résumé

Cette étude examine les performances reproductives et les intervalles entre les naissances du rhinocéros indien (*Rhinoceros unicornis*) réintroduit dans le parc national de Manas, en Inde, entre 2012 et 2021. Les rhinocéros y avaient été exterminés par le braconnage, mais des opérations de translocations entre populations sauvages sous le plan Indian Rhino Vision 2020, ainsi que des programmes de réhabilitation, ont permis leur retour au sein du parc. Nos suivis et analyses révèlent que les individus issus de translocation et de réhabilitation se sont progressivement adaptés à leur nouvel environnement, comme le montrent les 35 petits nés pendant la période étudiée. Des schémas de conception distincts ont pu être relevés parmi les rhinocéros issus de translocation, entre les individus ayant procréé avant la translocation et ceux ayant procréé après leur introduction dans le parc national de Manas. L'intervalle moyen entre les naissances pour les rhinocéros réhabilités était de 2,12 ans à 4,41 ans, tandis que celui des individus issus de translocation était de 1,99 an à 6,3 ans. Les résultats de notre étude indiquent que l'âge moyen de la première conception pour la génération F1 était de 5,65 ans. Ils établissent également que les rhinocéros réhabilités tendent à mettre bas à proximité des zones de présence humaine – près des camps anti-braconnage – là où les individus issus de translocation privilégient les zones plus isolées. En outre, nous avons observé des schémas de mises bas corrélées aux saisons, la plupart des naissances ayant lieu entre mai et septembre, pendant la mousson. Cette étude souligne l'importance d'un suivi efficace, de mesures antibraconnage, de la collaboration transfrontalière, de la gestion des habitats et du soutien des communautés pour assurer une conservation de la population de rhinocéros dans le parc de Mana réussie sur le long terme. Nos recherches contribuent à la compréhension de la biologie reproductive des rhinocéros dans le cadre du rétablissement des populations et éclairent les stratégies de conservation de cette espèce menacée.

Introduction

Knowledge of the recruitment rate of wild animals is important for the understanding of population dynamics and can inform conservation and management strategies to ensure the long-term survival of wildlife populations. Population dynamics in herbivorous mammals are governed by the differences between births, deaths, emigration and immigration (Fowler 1981). Vital rates such as the age at sexual maturity (ASM), conception rate, gestation length and intercalving interval (ICI) all influence fecundity, growth potential, and turnover or generation time (Gaillard et al. 1998; 2000). These factors are, in turn, largely influenced by the scaling of vital rates with body size and metabolic rates (Owen-Smith 1988). The minimum age at first conception affects the potential for the population to increase, since earlier ASM equates to longer lifetime productivity (Owen-Smith 1988). Thus, if females attain sexual maturity and start reproducing at an earlier age, the growth rate for the population will increase even if no other vital rates change.

The recruitment rate of greater one-horned rhinoceros (GOH) refers to the rate at which new individuals are added to the population through reproduction. Female GOH in the wild typically reach sexual maturity at around 5–7 years and have a gestation period of 15–16 months (Dutta 1991; Steak 2024). They give birth to a single calf and typically have an ICI of 2–3 years (Owen-Smith 1988; Steak 2024). This slow intrinsic reproductive rate, combined with habitat loss, poaching, disease, and climatic variation, all contribute to low productivity of extant populations (Fowler 1981; Gaillard et al. 1998, 2000).

The Manas National Park (MNP) is one of the pristine natural habitats of the Eastern Himalaya and had around 80–100 rhinos in the 1980s. Tragically, the entire resident GOH population of MNP was wiped out due to poaching in the early 1990s. Subsequently, the Government of Assam, with the support of WWF, the International Rhino Foundation (IRF), United States Fish and Wildlife Service (USFWS), and Bodoland Territorial Council (BTC), launched Indian Rhino Vision 2020 (IRV2020), whose aims included restoring the rhino population in MNP through translocation (Bonal et al. 2009; Dutta 2018). The 22 rhinos were translocated to MNP from Kaziranga National Park (NP) and Pobitora Wildlife Sanctuary (WS) between 2008 and 2021.

In parallel to translocation, a group of rehabilitated rhinos were also reintroduced to MNP from the Centre for Wildlife Rehabilitation and Conservation (CWRC), located near Kaziranga NP (Barman et al 2014; Dutta 2023). Rehabilitation refers to the process of rescuing, treating, and gradually reintroducing injured, orphaned, displaced, or otherwise distressed animals back into their natural habitats (Emslie et al. 2009; Barman et al. 2014). The CWRC has played a pioneering role in the rhino rehabilitation process in the North Eastern Region of India, and 20 rehabilitated rhinos were introduced to MNP from CWRC between 2006 and 2021, because MNP was considered a more suitable natural situation than the rehabilitation centre.

The aim of these translocations and rehabilitation is to re-establish a self-sustaining rhino population in MNP. Knowledge of recruitment rates is vital for assessing the health and future prospects of this newly established population. This study was undertaken to fulfil this need.

Study area

MNP is located in the northern part of the Brahmaputra valley, in the foothills of the Eastern Himalayas. The Park is located in the districts of Chirang and Baksa of Assam in north-east India and shares its borders with the Royal Manas NP of Bhutan to the north. The southern boundary of the Park is adjacent to densely populated agricultural areas and human settlements. Agriculture is the primary economic activity in these areas.

MNP has a tropical climate with an annual rainfall of 3,000–4,000 mm and average annual temperatures ranging between ~20° and 27°C. The climate can be divided into four distinct seasons: pre-monsoon (March–May), a transitional season marked by dryness, humidity and steadily increased temperatures; the monsoon season (June–September), which is the wettest and hottest time of year; retreating monsoon (October–November); and winter (December–February), when it is cold and foggy (Borthakur 1986). Humidity ranges between 70% to 80% and is highest during the monsoon and retreating monsoon seasons. The Park consists of alluvial grasslands, semi-evergreen forests, and moist and dry deciduous forests. As one of the largest north bank tributaries of the Brahmaputra River, the Manas–Beki River system provides perennial water for the Park and habitats for freshwater fish, aquatic migratory birds, and wild buffalo.

The MNP is renowned for its rich fauna and flora biodiversity, which includes, in addition to rhinos, species such as tiger (*Panthera tigris tigris*), pygmy hog (*Porcula salvania*), golden langur (*Trachypithecus geei*), hispid hare (*Caprolagus hispidus*), Bengal florican (*Houbarogsis bangalensis*), and white-winged wood duck (*Asarcornis scutulata*).

Methodology

We analysed rhino monitoring data from 1 September 2012 to 31 December 2021. During this period, rhinos were monitored by using radio-telemetry systems, comprising VHF radio collars, directional antennae (Telonics RA-14K antennae, 148–152 MHz) and a VHF radio receiver to record the data (Communication Specialists, R-1000 receiver, 148–152 MHz) (Dutta 2023). Directional compasses and windows software, Locate II and Locate III (Dutta 2018), were used to triangulate locations of rhinos. We also used camera traps to observe the rhinos in inaccessible areas. Translocated rhinos were ear-notched as per IUCN/SSC-AsRSG methods at the capture site for ease of identification. The rehabilitated rhinos did not have ear notches, so we recorded their unique body features (Fig. 1) in a Master ID file to assist their identification during monitoring (Dutta et al. 2019). The likelihood of misidentification of these individuals was minimal; however, identifying F1 generation rhinos (the offspring of translocated and rehabilitated individuals) was more challenging due to the lack of prior documentation and overlapping features.

We estimated the birth dates of calves of translocated, rehabilitated, and F1 generation females based on their first recorded sightings with newborn calves. We did not assume that the date of first calf sighting equalled the actual birth date without validation (Dutta 2018). In nearly all cases, calves were detected

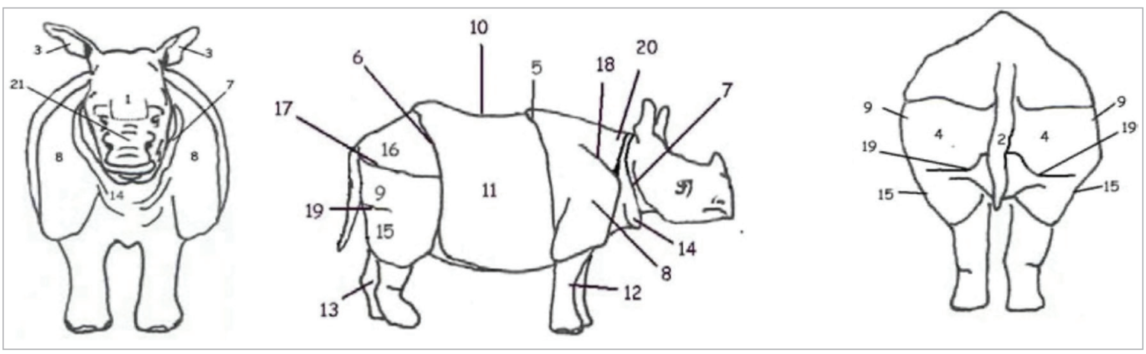

Figure 1. The unique identification features of GOH rhinoceros: 1) horn, 2) tail, 3) ear, 4) anal plate, 5) front cross fold, 6) rear cross fold, 7) neck fold, 8) shoulder plate, 9) upper right thigh plate, 10) prong (spines), 11) ribs, 12) front leg, 13) hind leg, 14) lower neck fold, 15) lower thigh plate, 16) back plate, 17) upper back corner, 18) shoulder cross fold, 19) lower back corner, 20) upper neck, 21) face.

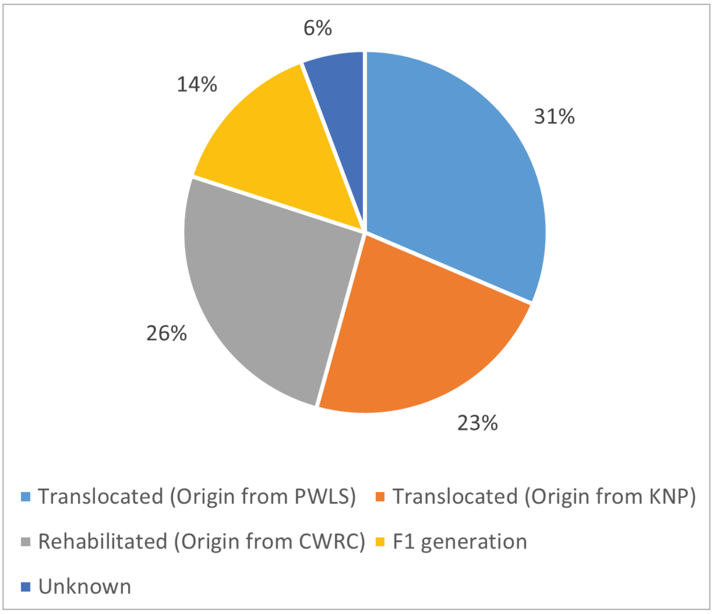

Figure 2. Proportions of the calving at Manas NP by females of different source populations.
PWLS = Pobitora WS; KNP = Kaziranga NP

within 4–5 days of birth due to the existence of rigorous, field-based monitoring protocols. Adult females—especially those close to parturition—were closely tracked, and behavioural indicators such as temporary isolation (Dutta 2018) were used to anticipate calving events. Additionally, most rehabilitated females and their F1 offspring gave birth near anti-poaching camps in open areas, improving visibility and facilitating early detection. Thus, the birth dates used to calculate female ages at first calving and ICI are based on direct, near-immediate post-birth observations.

Translocated rhinos were manually stratified into two groups (conception pre- and post-translocation), using the rhinos' estimated average gestation period of approximately 480 days based on findings of other studies (Laurie 1978; Schwarzenberger and Hermes 2023). A Chi-square test of independence was used to evaluate the association between season of birth and rhino origin (Rehabilitated, Translocated, F1, Unknown). This and all other data were analysed using Excel. Spatial data was plotted and analysed using ArcGIS 9.2 and ArcView 3.2a (ESRI 2006). A non-parametric technique, Maximum Convex Polygon (MCP) (Mohr 1947), was used to estimate overall home range size.

Results

Between September 2012 and December 2021, 35 rhino calves were born in MNP. Nine calves were born to rehabilitated rhinos, while 19 were born to translocated rhinos. Five calves were from the F1 generation, and the mothers of two rhinos born in inaccessible areas could not be identified. A total of eight translocated adult female rhinos (five from Pobitora WS and three from Kaziranga NP), four rehabilitated adult female rhinos (all from CWRC), five F1 generation female rhinos, and two unidentified adult female rhinos contributed to the growth of the rhino population in MNP during this period (Fig. 2).

Conceiving patterns of translocated females

Among translocated rhinos, adult female rhinos R3, R6, R8, R13, and R15 gave birth more than 480 days (1.314 years) after translocation and were therefore assumed to have conceived after they arrived in MNP. In contrast, rhinos R10, and R17 gave birth within 480 days of their release in MNP (R10: 261 days post-release; R17: 415 days post-release), which implies that these rhinos likely conceived in their source areas before the translocation. The translocation process did not appear to affect the pregnancy process of these two already pregnant females (Table 1).

Table 1. Translocation and birth of first calves after release of translocated female rhinos in MNP. Females giving birth less than 480 days (1.314 years) after conception were assumed to be pregnant on arrival at Manas NP.
All rhinos were captured one day prior to release in Manas NP. PWLS = Pobitora WS or KNP = Karizanga NP.

Rhino code	Origin	Estimated age at capture (years)	Estimated date of birth	Release date	Date of birth of first calf at MNP	Years to first conception at MNP	Years to birth of first calf at MNP
Females Pregnant on Arrival at Manas NP							
R10	PWLS	9	07/01/2003	09/01/2012	26/09/2012	n/a	0.71
R17	KNP	10	10/01/2002	12/01/2012	02/03/2013	n/a	1.14
Females not Pregnant on Arrival at Manas NP							
R3	PWLS	12	27/10/1998	28/12/2010	27/09/2013	1.43	2.75
R6	PWLS	10	16/01/2001	18/01/2011	14/05/2013	1.00	2.32
R8	PWLS	7	17/01/2004	18/01/2011	23/03/2013	0.86	2.18
R9	PWLS	8	08/01/2004	09/01/2012	03/04/2014	0.92	2.23
R13	KNP	11	18/01/2001	20/01/2012	27/09/2013	0.37	1.69
R15	KNP	9	10/01/2003	12/01/2012	02/11/2013	0.49	1.81

Conceiving patterns of rehabilitated females

The first-calving ages of rehabilitated female rhinos raised in MNP were estimated at 9.2 years based on their birth date during the time of rescue at Kaziranga NP, also estimated (Table 2). Manas RC = Manas Rehabilitation Centre (Popularly known as Rhino Boma area).

Conceiving patterns of F1 females born at Manas NP

The F1 generation, which represents the first filial generation resulting from an on-site mating and conception at MNP, comprised four rhinos—Ganga A, Jamuna A, Mainao A, and Mainao B—that were the offspring of rehabilitated mothers, while R3A was the only one born to a translocated mother (R3). The average age at first calving of the four F1 rhinos born to rehabilitated mothers ranged between 4.58 and 6.17 years, and R3A also calved at a comparably early age (6.25 years). Thus, all F1 females gave birth to their first offspring at a much earlier age than the rehabilitated rhinos, based on their estimated ages (range 7.85–10.61 years; Table 2).

Table 3. Age at first calving F1 generation female rhinos born in MNP

Name	Date of birth	Date of birth of first calf	Age at first calving (years)
Ganga A	04/05/2013	03/12/2017	4.58
Jamuna A	07/04/2013	07/06/2019	6.17
Mainao A	06/02/2013	07/12/2018	5.83
R3 A	14/05/2013	13/08/2019	6.25
Mainao B	12/08/2015	10/01/2021	5.42
		Average	**5.65**

Inter-calving intervals of rehabilitated rhinos

Among rehabilitated rhinos, Mainao subsequently gave birth again in 2015, 2.5 years after the birth of the fist calf. She died a natural death in 2016. Ganga gave birth again three times until 2021, with the ICI increasing from 2.21 years to 2.41 years and then 3.69 years. Jamuna gave birth again in 2017, 4.41 years after the birth of the first calf. The younger female Purabi gave birth once in the study period, in 2020. The average ICI for rehabilitated rhinos was 3.03 years (Table 4).

Table 2. Rescue history and First-calving records of rehabilitated females in Manas NP.

Rhino name	Estimated age at rescue (months)	Estimated date of birth	Date of rescue	Arrived at MRC	Released into wild at MNP	Estimated age at release into wild (years)	Date of birth of first calf at MNP	Years to conception after release	Years to first birth after release	Est. age at first calving (years)
Mainao	1	27/06/2002	28/07/2002	20/01/2006	28/11/2008	6.42	06/02/2013	2.88	4.19	10.61
Ganga	4	14/03/2004	14/07/2004	28/01/2008	27/11/2008	4.71	04/05/2013	3.12	4.43	9.14
Jamuna	6	21/01/2004	22/07/2004	28/01/2008	27/11/2008	4.85	07/04/2013	3.04	4.36	9.21
Purabi	3	27/03/2012	27/06/2012	23/09/2013	16/02/2016	3.89	02/02/2020	2.65	3.96	7.85
								Average		**9.20**

Table 4. Inter-calving intervals (ICI, values in years) of rehabilitated females at MNP.

Name	1st calf	2nd calf		3rd calf		4th calf		Date of death	Average ICI
	Date of birth	Date of birth	ICI	Date of birth	ICI	Date of birth	ICI		
Ganga A	06/02/2013	12/08/2015	2.51					2016	2.51
Jamuna A	04/05/2013	18/06/2015	2.12	15/11/2017	2.41	24/07/2021	3.69		2.74
Mainao A	07/04/2013	03/09/2017	4.41						4.41
R3 A	02/02/2020								n/a
								Overall average (n = 5)	**3.03**

Table 5. Inter-calving intervals (ICI, values in years) of translocated female rhinos at MNP

Number	1st calf	2nd calf		3rd calf		4th calf		Date of death	Average ICI
	Date of birth	Date of birth	ICI	Date of birth	ICI	Date of birth	ICI		
R3	27/09/2013	15/01/2020	6.30						6.30
R6	14/05/2013	10/05/2015	1.99	15/10/2018	3.44	04/11/2021	3.06		2.83
R8	23/03/2013							2013	n/a
R9	03/04/2014	28/04/2018	4.07	19/09/2021	3.40				3.73
R10	26/09/2012							2013	n/a
R13	27/09/2013	28/04/2018	4.58	21/10/2020	2.48				3.53
R15	02/11/2013	18/09/2017	3.88	26/08/2019	1.94	14/11/2021	2.22		2.68
R17	02/03/2013							2013	n/a
								Overall average (n = 11)	**3.40**

Inter-calving intervals of wild-to-wild translocated rhinos

Among translocated female rhinos, five individuals (R3, R6, R9, R13, and R15) gave birth to two or more calves. Three others (R8, R10 and R17) were killed by poachers following the birth of their first calf in MNP. ICI values for rhinos calving more than once ranged from 1.94 to 6.30 years, with a mean of ~3.40 years. The ICI between the first and second calf born to R3 was unusually long at 6.30 years (Table 5).

Seasonal calving patterns

The analysis revealed that there are distinct seasonal patterns in rhino reproduction in MNP. The highest number of births, 14, took place in the monsoon season. Nine births took place in the pre-monsoon period, and nine in the retreating monsoon, with only three births during the winter season.

Differences of calving patterns of translocated and rehabilitated rhinos

Two of nine births during the pre-monsoon season were from rehabilitated rhinos and seven from translocated rhinos. Out of the total of 14 births during the monsoon season, five were from rehabilitated rhinos, seven from translocated rhinos and two from F1 generations. Among the nine births in the retreating monsoon five were from translocated rhinos two from F1 generations, with two births recorded from unknown rhinos. Out of three birth records in the winter season, two were from translocated rhinos and one was from the F1 generation (Fig. 3). A chi-square test of independence (χ^2 2 = 15.05, df = 9, p = 0.089) showed that there was no significant association between the mother's origin and season of birth.

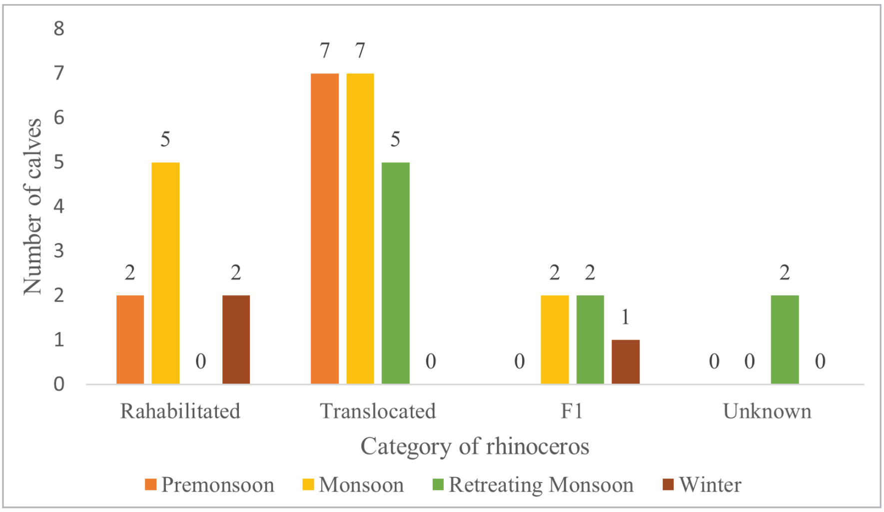

Figure 3. The calving patterns among different category of rhinos in different seasons.

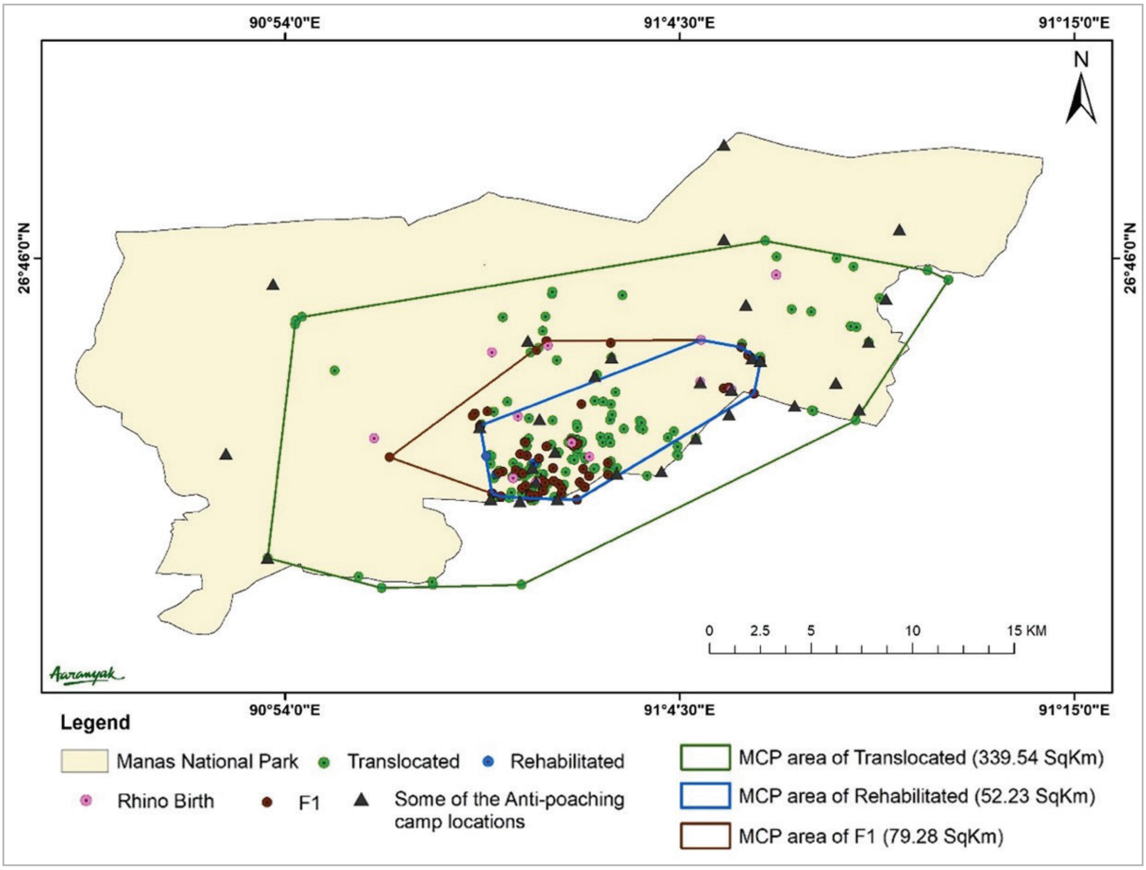

Figure 4. Overall home ranges of translocated, rehabilitated and F1 females with calving sites in MNP.

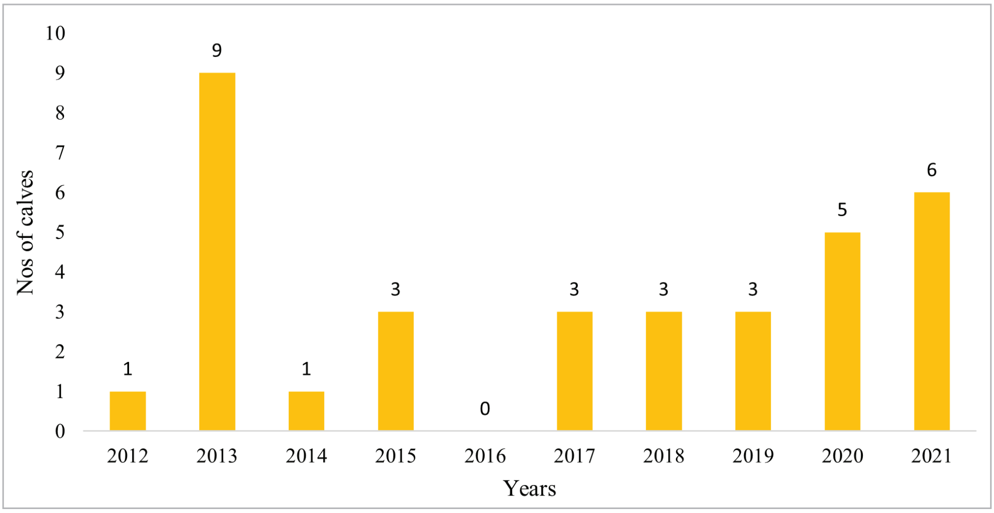

Figure 5. Numbers of calves born each year (2012–2021) Manas NP.

Spatial pattern of calving sites

Based on home range analysis, the three rhino groups—translocated, rehabilitated, and F1 generation—show overlapping yet distinct patterns of space use across MNP. Translocated rhinos occupied significantly larger areas, with an average home range of 339.54 km², often using remote and less-disturbed habitats throughout the Park. In contrast, rehabilitated rhinos had smaller home ranges averaging 52.23 km², primarily concentrated in the central and limited eastern zones of the Park. F1 individuals displayed intermediate range sizes (79.28 km²) and were largely clustered around the same core areas as the rehabilitated group (Fig. 4).

Yearly calving patterns

In 2013, nine rhino calves were born in a single year, the most ever. The number of rhino calves born in the following years declined and only one calf was born in 2014, with three in 2015, and no calves were born in 2016. In the years 2017–2019, rhino calf births increased again, with a total of three calves born each year. The number of rhino calves born increased to five in 2020 and seven in 2021. Hence calving numbers were not uniform during the period of study (Fig. 5).

Discussion

The reintroduction of rhinos in MNP is regarded as one of India's most significant conservation successes, contributing approximately 1% to the global wild rhino population, estimated at ~4,000 animals (Sharma 2022). During the period covered by this study, a total of 35 calves were born in the Park. Of these, translocated rhinos gave birth to 19 calves, rehabilitated rhinos produced nine, and F1 generation rhinos accounted for five births, while the mothers of two calves remain unidentified. This reproductive success highlights the species' ability to adapt well to both translocation and rehabilitation efforts and to new environments despite the stresses involved (Dutta 2018; Dutta 2023). While this is a commendable outcome, a closer look at the female reproductive pool and ICI dynamics suggests that the population has not yet reached its full reproductive potential.

Under average field conditions, female rhinos are expected to have their first calf before 7.5 years of age and produce one calf every 2–3 years on average. (K Adcock *in prep*) However, actual recruitment during the study period was slightly lower than expected. This shortfall was likely due to i) the rehabilitation process resulting in delayed sexual maturity in rehabilitated females; ii) poaching eliminating many adult males and some females early in the study, which limited and disrupted successful breeding; and iii) undetected calf mortality.

This study also highlights the need for a comparative assessment with source populations in Kaziranga NP and Pobitora WS to better understand reproductive rates, ICI patterns, and recruitment success under varying ecological and management conditions. Such comparisons will help inform adaptive strategies for future translocations and population reinforcement efforts.

The study identified that some females were already pregnant at the time of capture, suggesting that current capture and translocation protocols are generally well-managed to support ongoing pregnancies. However, pregnancies were not identified prior to translocation, and it is possible that early pregnancies went undetected or that foetal losses occurred in other individuals. Though translocation protocols are being adhered to, there may still be a high risk of stress-induced foetal loss in pregnant adult females. This highlights the need for improved pregnancy detection tools suitable for field use, especially in wild conditions. Assessing pregnancy status before translocation would allow for a more accurate evaluation of reproductive outcomes, including the proportion of births in relation to the number of females confirmed as pregnant at capture.

According to Milner et al. (2007) and Wittemyer et al. (2014), the poaching of breeding males can disrupt sex ratios and hinder recruitment processes in large mammal populations. This phenomenon was observed in MNP between 2012 and 2016, when all dominant adult male rhinos were killed by poachers (Dutta 2018). However, the implementation of stronger anti-poaching measures significantly improved protection, halting further male losses. In a positive development, some subadult males (R7, R14, and R18) survived and later reached sexual maturity, eventually contributing to breeding (Dutta 2023). While this marks a hopeful shift toward population recovery, it also raises concerns about potential inbreeding, particularly in a small, recovering population. If maturing males are closely related to existing females, so that male rhinos mate with mothers or related female offspring, it could lead to genetic bottlenecks and reduced genetic diversity over time. This underscores the importance of monitoring genetic relationships within the population and considering future introductions of unrelated individuals to maintain long-term genetic health.

The ICI of the two groups of rhinos showed distinct reproductive trends. Rehabilitated rhinos had a relatively consistent ICI (2.12 to 4.41 years). Their smaller home ranges (Fig. 5), which overlaps with the ranges of all dominant bulls, might contribute to this consistency. The translocated adult females' rhinos (R3, R6, R9, R13, R15) exhibited a mean ICI of 1.99 to 6.30 years, with noticeably greater variability. These rhinos typically roam more widely in the Park and tend to avoid locations with frequent human presence. Notably, R3 had an ICI exceeding six years. Following calving, R3 was observed moving further north towards the India–Bhutan border, where she stayed with her calf. Movement to these remote areas may take female rhinos outside the territories of dominant bulls, to areas where there is a low male–female sex ratio. These factors might help explain the larger ICI gap among the translocated females.

The F1 generation of rhinos has started contributing to population growth and, by the end of the study period, five F1 females had given birth, including Ganga A, Jamuna A, Mainao A, and Mainao B, all female calves from rehabilitated females, as well as R3A, the only known female calf of a translocated female (R3). The average age at first calving for these five females was around 5.65 years, showing that they reached maturity and bred at a relatively young age. Interestingly, R3A calved at 6.25 years, which is almost the same as the gap between her own birth and her mother's next calving.

There were two calves whose mothers were not identified. Since most F1 females born to rehabilitated rhinos tend to stay in areas closer to anti-poaching camps, where calf sightings are more frequent, the unidentified mothers of these calves observed in more remote, less-monitored areas of the Park are likely to be F1 females born to translocated mothers. The possibility that they were born to translocated adult females can be ruled out, as all translocated rhinos are individually identifiable by ear notches and unique ID markings. Further field monitoring and genetic analysis will be essential to confirm the maternal identity of these calves.

The study also reveals that rehabilitated female rhinos had their first calves at a later age than F1 females. This may be due to early-life captivity, stress from the rehabilitation process, delayed adaptation, and differences in nutrition and social integration. The F1 females, raised entirely in the wild, tended to mature and reproduce more naturally and quickly. The F1 generation also had more chances to mate with adult males than their mothers did. The fact that F1 females were found to reach sexual maturity and calve earlier is a positive sign, which suggests that the population is adapting well and growing in a healthy, self-sustaining way.

The results show year-on-year variations in calf births from 2013 to 2021. There was a peak of nine calves born in 2013, followed by a sharp decline in subsequent years, with only one recorded birth in 2014 and none in 2016. However, calf numbers began to recover between 2017 and 2019, with three births per year; this number increased to five in 2020 and seven in 2021. These fluctuations suggest complex ecological and biological influences. It is possible that the reproductive cycling among females was disrupted during the early years post-translocation, as individuals adjusted to their new environments. Similar trends have been documented in African rhino populations (Schwarzenberger and Hermes 2023). Additionally, the loss or temporary unavailability of mature breeding males—particularly due to poaching incidents between 2012 and 2016—as well as poaching and natural deaths of breeding females, were contributing factors to the downturn of births during this period.

Additionally, some calves may have been born but lost before detection due to early mortality or limited monitoring capacity in dense habitats. It is also possible that the initial spike in births in 2013 reflected the release of reproductively active females who had conceived either shortly before or did so soon after translocation. Overall, these fluctuations underscore the need for continuous investigation covering all the factors mentioned.

There were clear differences in calving site preferences and home range patterns among rehabilitated, translocated, and F1 rhinos in MNP. Rehabilitated females Mainao, Ganga, Jamuna, and Purabi had smaller average home ranges of approximately 52.23 km² and consistently gave birth in areas close to anti-poaching camps and zones with regular human presence. This behaviour likely reflects a degree of human imprinting from their early lives in captivity and the rehabilitation process (Barman et al. 2014). These human-inhabited areas, while more disturbed, may offer protective benefits. The presence of forest staff may reduce poaching threats, while the proximity to human activity could also deter large predators such as tigers, potentially enhancing calf survivability.

In contrast, translocated rhinos showed the largest average home ranges, covering about 339.54 km², and generally calved in remote, less-monitored locations within the Park. This calving behaviour may indicate a preference for isolation or reflect typical wild rhino behaviour, as noted in earlier studies (Dutta 2018). While such remote areas may be ecologically suitable, they could pose greater risks to calves, including exposure to predators, environmental stress, or undetected mortality due to limited surveillance and poaching. The larger spatial movement of translocated rhinos may also delay the detection of reproductive events, making monitoring more challenging.

The F1 generation rhinos, born and raised entirely in the wild, showed intermediate home range sizes averaging 79.28 km². F1 females Ganga A and Jamuna A chose calving sites that overlapped with the areas previously used by their rehabilitated mothers. This suggests potential intergenerational transmission of habitat use. Given their exposure to both wild conditions and moderate human proximity, F1 rhinos may serve as an important behavioural bridge between rehabilitated and wild translocated individuals.

Overall, these findings highlight how home range size and calving site location, influenced by rhino origin, may influence the calving patterns. Further spatial and behavioural studies, including in other rhino-bearing areas of Assam, to better inform future reintroduction efforts and adaptive habitat management strategies, are recommended.

The prime grassland habitat in Manas is currently facing the onslaught of alien invasive species (weeds) that have increased in extent due to several anthropogenic factors, including increased livestock grazing, human movement and dispersal, and uncontrolled fires Lahkar et al. (2011) and Dutta (2018). Invasive species (including *Chromolaena odorata*, *Leea asiatica*, *Ageratum conyzoides* and *Mikania spp.* along with a succession of woody species) have been observed wherever disturbances such as grazing and the creation of openings in grassland for roads, camps, bomas, etc. occur.

Wallow sites and marshes that provide green food during dry seasons are critical for rhinos and are affected by changes in flood patterns and rainfall, as well as silting. Also, there are complex hydrological changes in the ever-changing Brahmaputra River, and a changing climate affecting monsoon patterns. (Dutta

2018) These findings highlight the urgent need for a comprehensive and scientific approach to habitat management focusing on both grasslands and water bodies, alongside strengthened anti-poaching measures. Such strategies are essential for ensuring the long-term survival of rhinos in the Park. The conclusions drawn from this study are crucial for developing a robust model to predict rhino population trends and movements within MNP. Gaining a deeper understanding of reproductive timing, ICI and habitat preferences will help inform more effective conservation and management strategies to support the survival and growth of the species. The purpose of this approach is not only to advance proactive management, but also to recognize that essential habitats are vital to the persistence of rhinos.

Recommendations

This analysis reinforces the need for continued reproductive monitoring, balancing sex ratios, and targeted management to maximize calf recruitment to support long-term demographic viability in MNP. Genetic analysis of the MNP rhino population is needed to confirm the species' integrity and long-term genetic viability following losses of many males from poaching. Similar analyses to this Manas study should be undertaken in source populations in Kaziranga NP and Pobitora WS to better understand reproductive rates, ICI patterns, and recruitment success under varying ecological and management conditions across India. Such comparisons will help inform adaptive strategies for future translocations and population reinforcement efforts.

To accelerate the growth of the rhino population in MNP, additional individuals may be considered for reintroduction from donor sites such as Kaziranga NP, Orang NP and Pobitora WS. However, any future translocations should be preceded by enhanced security measures and robust monitoring systems. It is also essential to ensure that sufficient resources, both human and financial are available to support long-term protection and population stability. Additionally, it is crucial to monitor the impact of translocations/reintroductions on both reproductive success and the behavioural stability of the population.

MNP shares its northern boundary with the Royal MNP in Bhutan, and rhinos have been observed using these transboundary areas (Dutta 2018). Therefore, both India and Bhutan need to enhance cross-border collaboration to ensure the effective conservation of rhinos and other wildlife that move across the international boundary. On the southern side, MNP is bordered by densely populated human settlements. This highlights the need to strengthen community-based conservation efforts and regular awareness programs to foster coexistence and ensure long-term conservation success.

MNP authorities need to enhance anti-poaching measures, capacity building of park staff in scientific monitoring of rhinoceros, and the integration of modern technology to improve management practices. Continuous behavioural monitoring of rhinos, along with regular training of staff in both monitoring techniques and anti-poaching strategies, is essential for long-term conservation success.

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This manuscript is dedicated to Mainao (adult female rhino), Giribala (adult female rhino R8), Odangshi (adult female rhino R10) and Hainari (adult female rhino R17) and local communities living in the adjacent villages of Rajabeel and Gosaivitha (Katajhar).

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Transition and conflict: patterns and drivers of human–elephant conflict in a changing pastoral landscape of northern Kenya

Kennedy L Leneuiyia[1,2], Robert J Smith[2], Juliet M King[1,3], Christopher Thouless[1], Harry F Williams[1], George Wittemyer[1], Paul Kokiro[1], Purity Milgo[1], Giacomo D'Ammando[1]

[1]Save the Elephants, PO Box 54667, Nairobi 00200, Kenya
[2]Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK
[3]Northern Rangelands Trust, Private Bag, Isiolo 60300, Kenya

*corresponding author: kennedy@savetheelephants.org (OrcID: 0000-0002-2991-3159)

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Abstract

Human–elephant conflict (HEC) represents a major challenge for elephant conservation, as it not only fosters negative attitudes towards elephants, but also has socio-economic consequences, including loss of human lives, damage to property, and loss of livelihoods. These effects often motivate retaliatory actions against elephants, including illegal killing. While abundant research exists on the socio-economic impacts of crop raiding in agricultural areas, HEC in pastoral areas remains understudied and poorly understood as a conservation challenge. Here, we explore the nature, spatiotemporal trends, and potential drivers of HEC in 12 community conservancies of the Laikipia–Samburu ecosystem, a pastoral landscape of northern Kenya interspersed with expanding areas of agriculture. We analysed a decade of HEC records (2012–2021) and interviewed ten key informants working within community conservancies in the region. We found that HEC in our conservancies occurred throughout the study period, but different incident types peaked at different times of the year. Most HEC incidents occurred during the dry season when competition for resources increased. Incidents involving livestock and human injuries and fatalities were more spatially dispersed compared to crop raiding, which was concentrated in agricultural areas. The interviews revealed an array of issues that drive conflict, including environmental changes, socio-economic pressures affecting pastoral communities, and political motivations. Accumulated frustration due to the ongoing conflict emerged as a primary cause of increasingly negative attitudes toward elephants among the pastoral communities, leading to elephant mortalities. Understanding the underlying causes of conflict will be essential for developing effective mitigation strategies.

Résumé

Les conflits humains-éléphants (CHE) représentent un défi majeur pour le domaine de la conservation, car, non seulement ils engendrent des attitudes négatives envers ces animaux, mais ils ont également des conséquences socioéconomiques, dont la perte de vies humaines, la destruction des moyens de subsistance des habitants, et les dommages matériels. Ces effets entraînent souvent des représailles contre les éléphants, notamment des abattages illégaux. Bien que de nombreuses recherches existent sur les impacts socioéconomiques des dégâts infligés aux cultures dans les zones agricoles, les CHE dans les espaces pastoraux restent sous-étudiés et mal compris en tant que défis de la conservation. Nous explorons ici la nature des CHE, leurs tendances spatiotemporelles et leurs facteurs potentiels dans douze réserves communautaires de l'écosystème de Laikipia-Samburu, un paysage pastoral du nord du Kenya jalonné de zones agricoles en pleine expansion. Nous avons analysé l'historique des CHE entre 2012 et 2021 et interrogé dix informateurs clés qui travaillent au sein des réserves communautaires de la région. Nous avons observé que les CHE dans ces réserves se sont produits tout au long de la décennie étudiée, mais que certains types d'incidents ont atteint leur apogée sur différentes périodes de l'année. La plupart des cas se sont déroulés durant la saison sèche, lorsque s'intensifie la concurrence pour l'accès aux ressources. Les faits impliquant des blessures et des décès chez les humains et le bétail étaient plus dispersés d'un point de vue géographique que les dégâts infligés aux cultures, qui eux, se concentraient sur les zones agricoles. Les entretiens ont mis en lumière qu'un ensemble de problématiques – changement environnementaux, pressions socioéconomiques affectant les communautés pastorales, motivations politiques – sont à l'origine des conflits. Les frustrations accumulées par ces heurts qui se poursuivent et qui ont pour conséquence la mort d'éléphants, se sont révélées l'une des causes principales de l'attitude négative croissante à l'égard de ces animaux dans les communautés pastorales. La compréhension des facteurs sous-jacents des conflits constituera un élément essentiel pour l'élaboration de stratégies d'atténuation.

Introduction

Biodiversity loss is a pressing global challenge that is driven by the complex interactions between human activities and wildlife (Díaz et al. 2019). Among many exacerbating factors, human–wildlife conflict plays a significant role (Hoare et al. 2022). In Africa and Asia, human–elephant conflict (HEC) is a particular concern because it threatens the conservation of elephant populations while impacting some of the world's poorest people (Hoare 2015). The African savannah elephant (*Loxodonta africana*) is recognized as a flagship species, renowned for its iconic status in popular culture and its importance as an ecosystem engineer (Haynes 2012; Skibins et al. 2016). Despite this recognition, the species faces three imminent threats: habitat loss, poaching for ivory, and HEC (Courchamp et al. 2018). A surge in poaching resulted in severe population declines in the 1970s and 1980s (Douglas-Hamilton 1987), and a further 30% continent-wide decline between 2007 and 2015 (Schlossberg et al. 2020), while habitat loss has resulted in the species currently occupying only 17% of its former range (Wall et al. 2021). Understanding the role of HEC as an obstacle to effective elephant conservation is critical but remains a complex issue due to its combined impact on elephant population dynamics and human livelihoods.

HEC has been documented across elephant range states in Africa (Hoare 2015), where humans and elephants compete for available space, food, and water resources (Bastille-Rousseau et al. 2020). Competition over resources is exacerbated in agricultural areas, where elephants feed on both subsistence and commercial crops, with escalating conflicts often leading to human injuries and deaths, and the illegal killing of elephants (Nyumba 2017). For this reason, most HEC studies have focused on the conflict between crop-farming communities and elephants, with studies spanning from determinants of spatiotemporal patterns of crop raiding (Graham et al. 2010), drivers of crop raiding (Naha et al. 2019), and community attitudes towards crop-raiding elephants (Kiffner et al. 2021).

While extensive studies have explored crop raiding by elephants, HEC outside of agricultural areas is less well understood. This is particularly true for pastoral systems (Gadd 2005), defined as livestock-dominated systems with minimal or no crop production, which distinguishes them from agricultural (crop production) and agro-pastoral (mixed) systems (Adicha et al. 2023). With over 70% of the current elephant range outside protected areas (Blanc et al. 2007), and pastoral landscape covering approximately 43% of Africa's land area (FAO 2018), and serving as critical wildlife corridors and seasonal habitats, HEC in these systems may be more significant than commonly acknowledged. Moreover, patterns of HEC in pastoral landscapes are likely to differ from HEC in agricultural landscapes, since the former are more dynamic systems driven by both livestock and wildlife, including elephants, constantly moving in search of water and pasture (Young et al. 2005). Competition for these limited resources can fuel tensions, creating intricate and shifting challenges for coexistence and management. Such conflict may also be exacerbated by climate change, which is already affecting pastures and water distribution in semi-arid savannahs. In this study, the authors explored the nature and spatiotemporal patterns of HEC within the community wildlife conservancies of the Laikipia–Samburu ecosystem (LSE) of northern Kenya, an area where expanding agricultural land use is encroaching into traditional pastoral landscapes.

In recent years, there has been a perceived increase in HEC incidents within the LSE, resulting in a spike in the number of elephants illegally killed due to conflict (CITIES 2017). Despite the existence of a solid legal structure and political will to support elephant conservation in Kenya, information on HEC incidents remains insufficient to identify the drivers of these trends. To address this, we first examined data collected by the Kenya Wildlife Service (KWS) and by the Northern Rangelands Trust (NRT) (a membership organization run by local community wildlife conservancies), to understand the spatial and temporal distribution of HEC incidents affecting both pastoralism and agriculture in the LSE. Secondly, we identified potential drivers of HEC within this landscape through interviews with conservancy wardens, managers, and rangers.

Methodology

Study site

The study was conducted in the Laikipia–Samburu ecosystem in northern Kenya. The LSE corresponds to the drainage basin of the Ewaso Nyiro River and its tributaries (Thouless 1995) and comprises the Laikipia and Samburu sections, covering 9,500 km^2 and 21,022 km², respectively. The area is semi-arid, with wet and dry seasons alternating throughout the year. Average annual temperatures range from 16–26°C and 24–33°C (Georgiadis et al. 2007) and annual rainfall from 400–750 mm and 250–500 mm (Esilaba et al. 2007), in Laikipia and Samburu respectively. Human populations total 518,560 in Laikipia and 310,327 in Samburu, based on national census [data of 2019] (KNBS 2019), with livestock numbers (of cattle, sheep, goats, donkeys and camels) estimated at 1.35 million Laikipia and 1.49 million in Samburu as of the 2023 National Agriculture Report (KNBS 2024) Approximately 12% of the ecosystem consists of protected areas (PAs), including three IUCN Category II PAs, namely the Samburu, Shaba, and Buffalo Springs national reserves, as well as various forest reserves. The remaining areas comprises private ranches (13%), community wildlife conservancies (34%), communal pastoral land (25%), and settlements and smallholder agriculture (17%) (Ihwagi et al. 2015). We focused on the Samburu and northern Laikipia components of the ecosystem, which are characterized by various land uses, but dominated by community wildlife conservancies (Fig. 1). Community wildlife conservancies aim to harmonize wildlife conservation and livestock grazing, and generate revenues from tourism for the local communities. PAs and community conservancies in the Samburu component of the ecosystem are unfenced, except for a rhino sanctuary in Sera Conservancy, to maintain critical wildlife corridors while supporting pastoral mobility. Biodiversity in the area is uniquely adapted to the arid and semi-arid environment and includes wildlife such as beisa oryx (*Oryx beisa*), Grevy's zebra (*Equus grevyi*), pancake tortoise (*Malacochersus torneri*), African wild dog (*Lycaon pictus*), pangolin (*Smutsia temminckii*), and various primates, as well as the African savannah elephant. The LSE is home to the country's second largest elephant population, estimated at around 7,475 as per the 2021 national wildlife census (Waweru et al. 2021).

Data collection

We collated the available data on HEC incidents from 12 community conservancies in the LSE between 2012 and 2021, namely: Greater Namunyak (encompassing four sub-units: Namunyak, Kalepo, Ngilai, and Nalowuon), Il Ngwesi, Kalama, Lekurruki, Leparua, Meibae, Naibunga, Nakuprat Gotu, Nasuulu, Nkoteiya, Sera, and West Gate (Fig. 1). All conservancies are members of the NRT, except for the Greater Namunyak. The data were collected by trained scouts/rangers from multiple conservation organizations, including the KWS and the NRT. Each incident was reported by members of the local community, and scouts or rangers visited the site as soon as possible afterwards. On reaching the incident site, the observers used a standardized data collection form to record the type of conflict, time, GPS location, and wildlife species involved.

We examined a total of [556] reports. Of these, we excluded 11 records because they contained insufficient details. We analysed the temporal distribution of HEC data with respect to time of day (day or night), month, and seasonal variation in rainfall patterns (wet or dry

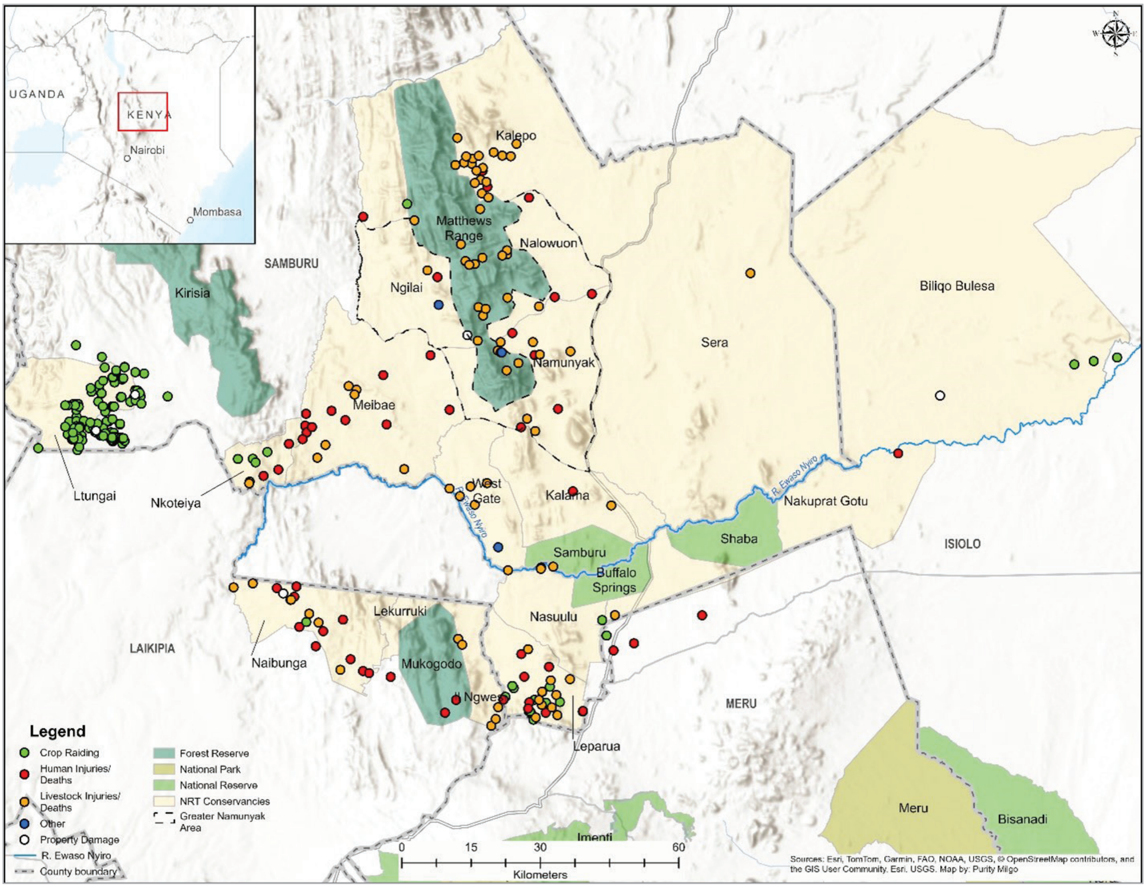

Figure 1. The Laikipia–Samburu ecosystem, showing the location of the community conservancies in which the study was conducted, and the distribution of different types of HEC incidents across the landscape. (Data source: NRT 2012–2021)

Table 1. Example of an incident report, showing information typically recorded on the standardized human–wildlife conflict data collection form.

Information collected	Example
Location name/ Conservancy	Kalama
Date/time (day/night)	20/03/2021 Day
GPS coordinates	0.6989° N, 37.6930° E
Species	Elephant
Conflict type	Human injury
Impact records	One person injured
Additional notes	One person was injured on the leg by a bull elephant as he was walking home from the market

seasons). Using rainfall gauge data from the Save the Elephants Research Camp in Samburu National Reserve, we defined the wet season as starting seven days after a cumulative rainfall of >15 mm since the end of the dry season, and the dry season as starting 30 days after the last day of rainfall since the onset of the wet season. One to two days of rainfall in two weeks of dry weather were considered insufficient to trigger the onset of the wet season. Based on these criteria, we divided our study period into wet and dry seasons.

Data analysis

We first calculated the proportion of each type of HEC incident (as defined in incident reports as crop-raiding, human injury and/or death, livestock injury and/or death, property damage, and "other") in relation to the total number of incidents recorded. We then calculated the proportion of different types of HEC incidents by time of day, month, and season. We performed multinomial logistic regression to determine whether and how temporal predictors (day/night, wet/dry season) affected the probability of occurrence of different conflict types. The inclusion of month as a predictor caused failed model convergence, and this variable was therefore excluded from this analysis. The model was fit using maximum likelihood estimation, with crop raiding as the reference outcome and wet season and daytime as reference levels for predictors. Model performance was assessed via likelihood ratio tests against a null model, with significance determined at $\alpha = 0.05$. Property damage and "other" conflict types were excluded from the model due to very small sample sizes. A further three records were excluded since information on time of day was missing. Since the sample size was small and unbalanced, with a far larger number of crop-raiding incidents recorded compared to human and livestock injuries and deaths, the modelling approach might have produced spurious coefficients and p-values. We thus also used chi-square tests of independence to investigate the association between the proportion of HEC incidents and time of day, month, and season. Quantitative analyses were performed using the nnet package in R statistical software (version 4.3.1; R Core Team, 2023). To determine the spatial distribution of HEC incidents, we identified hotspots by plotting incident locations in ArcGIS Pro using the heatmap function (with a distance radius of 30 m).

To investigate the changes in HEC over longer periods of time, we grouped the HEC incident data for two periods: 2012–2016 and 2017–2021. We structured the analysis in this manner due to likely underreporting of HEC before 2017. For example, in 2012, there were only seven incidents recorded. Although data from 2012–2016 were included in maps and in the overall calculation of proportion of conflict types over the entire study period (where sample sizes did not significantly impact interpretation), analyses of daily, seasonal, and monthly patterns of HEC incidents were restricted to the 2017–2021 period, as the underreporting of incidents before 2017 might have misrepresented the spatiotemporal distribution of different conflict types.

Community perceptions of HEC and conflict-related killing of elephants

We carried out ten semi-structured interviews with key informants. The informants comprised three community conservancy wardens, two conservancy managers, one researcher, and four NRT Security Department personnel working within the study area. While the interviewees provided valuable institutional perspectives, we acknowledge that the limited sample size may not capture the full diversity of community experiences with HEC. The interviewees were selected through purposive sampling techniques (Campbell et al. 2020), ensuring that specific individuals with valuable insights were part of the study. A pilot study was conducted to ensure the efficacy of the interview guide in gathering the necessary information (Fig. 2). Each interview lasted for approximately 35 minutes, and a distinct code was assigned to identify each of the ten interviewees (W1 to W10). Questions revolved around: (a) HEC data collection, processing and storage; (b) the motivations behind the killing of elephants; and (c) the general attitude of the community towards elephants and the conflict situation. We then carried our thematic coding of the interview transcripts using NVivo (v14), which yielded two primary themes. The first theme centred on participants' perspectives regarding drivers of HEC and the surge in conflict killings of elephants. The second theme was the intricate nature of conflicts between local communities and elephants, highlighting the social-political and economic challenges of mitigating HEC.

Results

Nature of conflict

A total of 345 HEC incidents were reported in the study area between 2012 and 2021. Of these, 55% were crop-raiding incidents (Table 1). Livestock injuries and deaths represented 26% of all incidents, while human injuries and deaths represented 16% of all incidents (Table 2). Property damage and "other" conflict types (defined as incidents for which information on conflict type was not available) represented only 3% of the incidents when combined (Table 2). After removing crop-raiding incidents from the calculations, livestock death and injury represented 58% of the remaining 155 incidents, while human death and injury represented 35%. Property damage and other conflict types combined

Interview guide

HEC

1. Do you collect data on HEC? Please share the process briefly (what type of information do you collect, is it part of a monitoring system or just ad hoc, where do you store your data – OB/datasheets/database)
2. What challenges do you encounter during the data collection process and reporting-who do you report this information to, how is this data used?
3. Are there any follow-ups after the data collection?
4. Do you think HEC has stayed the same, increased, or decreased in the past 5 and 10 Years, explain?
5. What do you think are the main drivers of HEC in your area? explain?
   a. Drought ( )
   b. Settlement in corridors ( )
   c. Grazing space ( )
   d. Water scarcity ( )
   e. Demographics change ( )
   f. Others specify………………
6. What challenges are elephants causing?
7. Is anything being done by the conservancy/authorities to reduce conflict with elephants? what do you think could be done?

Elephant mortality – conflict killing

1. When reporting elephant mortalities, how is it identified as conflict killing? How is the decision made? Any follow-ups?
2. What are the main motivations for conflict killings? Why?
3. Why do you think morans are doing shooting practice/target on elephants?
4. Do you think the communities are killing more elephants now than in the past? Why?
5. What is the general feeling in this community towards elephants and conflict situations?

Thank you so much for your time. Do you know or would you recommend any other person, warden, or conservancy manager, who you think has more information on these issues?

Figure 2. Semi-structured interview guide used to explore local data collection processes, perceptions and experiences of HEC, and responses to HEC, in the Samburu–Laikipia landscape.

Table 2. HEC incidents categorized by conflict type in the study area during 2012–2021 and showing the data for 2017–2021 that was used for statistical analysis due to the underreporting of HEC before 2017.

Conflict type	No. of incidents (2012–2021)	Proportion (%) of incidents (2012–2021)	No. of incidents (2017–2021)
Crop raiding	190	55	144
Livestock injuries/deaths	91	26	57
Human injuries/deaths	55	16	40
Property damage	6	2	4
Other	3	1	2
Totals	345		247

N.b. It has not been easy to extract accurate figures of retaliatory killings of elephants in the Laikipia/Samburu area from the literature. However, as a rough estimate for the year 2018 (n = 169), figures can be accessed in this report: https://elephantconservation.org/wp-content/uploads/2022/10/Final-IEF-Report-Jan-December-2018-.pdf. For more information on elephant deaths which are HEC related, and not just the illegal killing for ivory, in the East African context, see: https://cites.org/sites/default/files/documents/E-CoP20-076-04.pdf

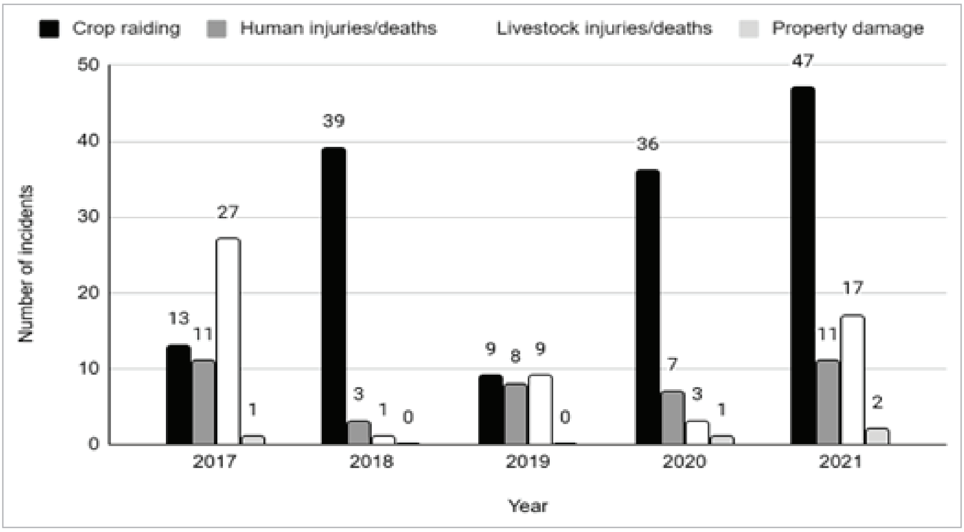

Figure 3. Annual numbers of HEC incidents by conflict type between 2017 and 2021.

represented only 7% of the non-crop-raiding incidents. Numbers of incidents by conflict type between 2017 and 2021, which were used for statistical analyses, are also reported in Table 1. We excluded property damage and "other" incidents from further analyses due to the very small sample size, but we still report descriptive statistics for both conflict types.

Unfortunately, the underreporting of HEC incidents before 2017 prevented us from identifying long-term trends in different types of conflict, since reliable data only spanned five years. During 2017–2021, numbers of human and livestock injuries and deaths were generally high in 2017 (human injuries/deaths, n = 11; livestock injuries/deaths, n = 27), lower in 2018–2019, and then high again in 2021 (human injuries/deaths, n = 11; livestock injuries/deaths, n = 17; Fig. 3). By contrast, crop-raiding incidents were markedly lower in two years, namely 2017 (n = 13) and 2019 (n = 9), and higher in the other three years, with the highest number of crop raids recorded in 2021 (n = 47; Fig. 3). No clear increase or decrease in the annual number of HEC incidents could thus be discerned. In 2018, a total of 169 elephant deaths were recorded in the Laikipia-Samburu landscape, with the proportion of illegally killed elephants (PIKE) rising from 34% in 2017 to 38% in 2018 (NRT 2018). Unpublished MIKE data indicate that conflict-related elephant killings have continued to rise in the years following 2018. Due to the small sample sizes of HEC incidents per year, data across the 2017–2021 period were pooled for further analyses.

Multivariate analysis

The multinomial logistic regression model containing the temporal predictors significantly outperformed a null model ($\chi^2 = 243.579$, df = 4, $p < 0.001$). Time of day (day or night) was the strongest predictor of conflict type ($\chi^2 = 220.852$, $p < 0.001$), with human and livestock injuries and deaths significantly more likely to occur during daytime compared with crop-raiding, which was more likely to occur at night (Table 3). Season did not have a significant effect on conflict type ($\chi^2 = 2.247$, $p = 0.266$). However, non-significant directional trends suggested that human and livestock injuries and deaths were less likely to occur during the dry season compared to crop-raiding incidents (Table 3).

HEC day/night patterns

The chi-square test confirmed a significant association between the type of conflict, and the time of day (day or night) at which incidents occurred ($\chi^2 = 195.59$, df = 2, $p < 0.001$). Crop raiding was mainly nocturnal, with 98.6% of incidents (139 out of 141 incidents for which time of day was reported) occurring at night (Fig. 4). By contrast, human injuries and deaths were mostly diurnal incidents, with 77.5% of incidents (31 out of 40) occurring during the day versus 22.5% (9 out of 40) occurring at night (Fig. 2). Livestock injuries and deaths exhibited an even stronger diurnal bias, with

Table 3. Coefficient estimates and standard errors from a multinomial logistic regression model, with type of conflict (crop raiding, human injuries and deaths, and livestock injuries and deaths) as a categorical response variable. Predictors include time of day and season. Reference levels for each categorical variable are crop raiding (conflict type), night (time of day), and wet season (season). Statistically significant effects are highlighted in bold.

Conflict type	Predictor	Coefficient	Standard Error	p
Logit 1 (Human Injury/Death versus Crop Raiding)				
Human Injury/Death	Daytime	5.316	0.811	<0.001
Human Injury/Death	Season: Dry	-1.052	0.721	0.145
Logit 2 (Livestock Injury/Death versus Crop Raiding)				
Livestock Injury/Death	Daytime	8.184	1.236	<0.001
Livestock Injury/Death	Season: Dry	-0.599	0.808	0.458

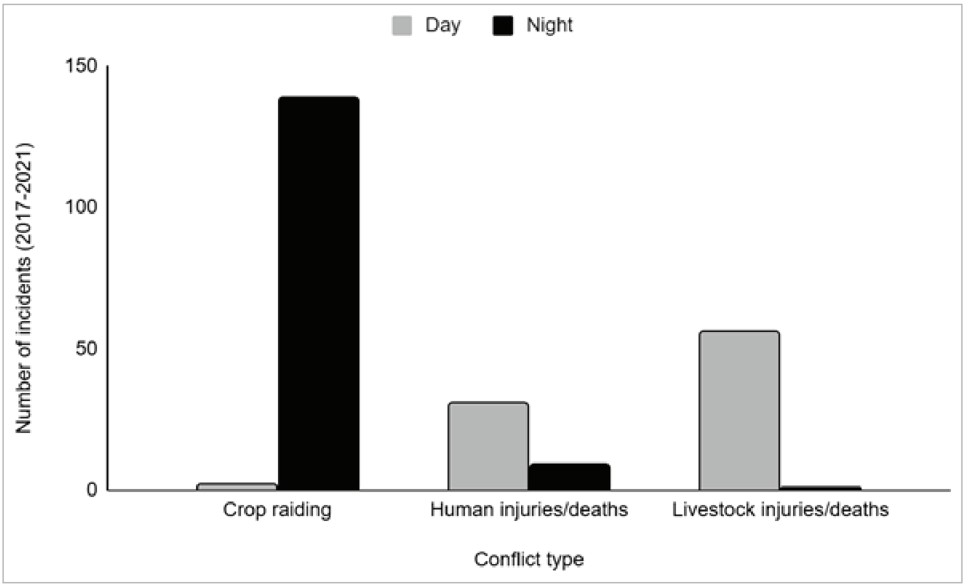

Figure 4. Day and night occurrences of HEC incidents by conflict type, 2017 to 2021.

98.2% (56 out of 57) of incidents happening in daytime hours, likely due to the night penning of livestock (Fig. 4). Property damage incidents (n = 3) were exclusively nocturnal (Fig. 4).

HEC seasonal patterns

We found that 79% of conflict incidents occurred in the dry season; specifically, 89% of crop raiding incidents (n = 128), 60% of human injuries and deaths (n = 24), and 67% of livestock injuries and deaths (n = 38; Fig. 3). Property damage was recorded too sporadically to identify seasonal trends. There was a statistically significant association between conflict type and the season in which incidents happened ($\chi^2 = 22.289$, df = 2, p<0.001). However, this pattern was no longer significant after excluding crop-raiding incidents ($\chi^2 = 0.210$, df = 1, p = 0.647). This could be due to the relatively small sample size of incidents associated with human and livestock injuries and deaths.

HEC monthly patterns

We found a significant association between conflict type and month ($\chi^2 = 115.13$, df = 22, p < 0.001). Crop raiding followed a clear monthly pattern, with most of the incidents occurring in August (42%, n = 60) and July (26%, n = 37; Fig. 4). The months with the lowest number of crop-raiding incidents were February (n =

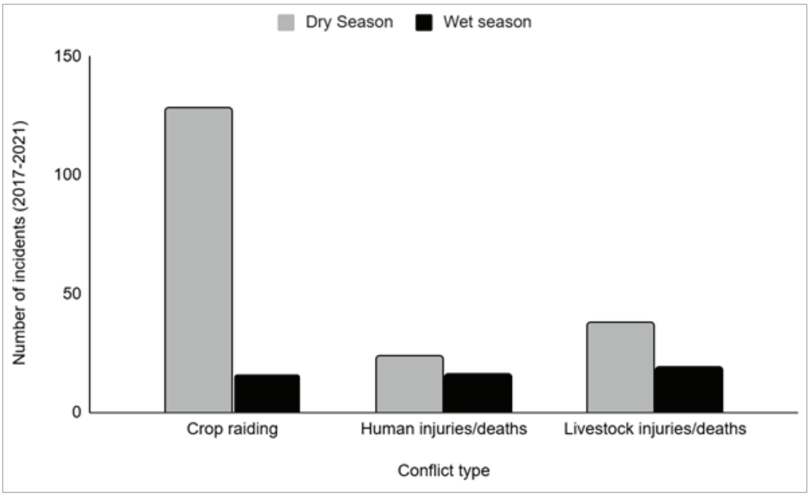

Figure 5. Seasonal distribution of HEC incidents by conflict type, between 2017 and 2021.

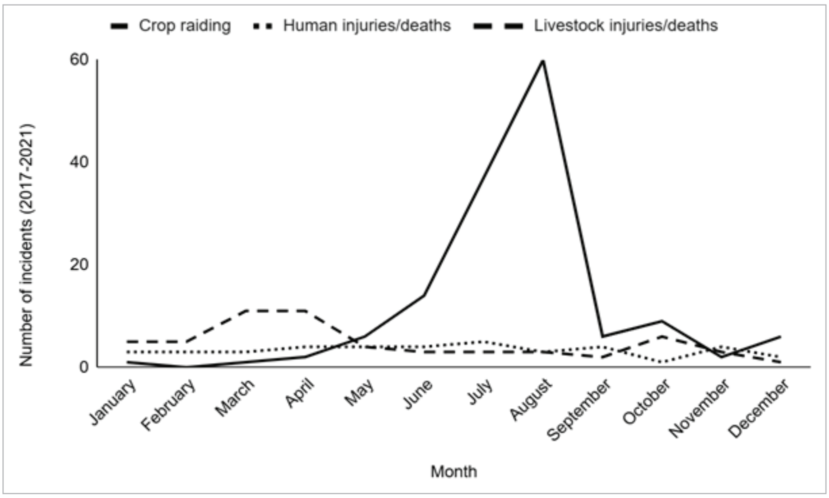

Figure 6. Monthly distribution of HEC incidents by conflict type, between 2017 and 2021.

0), January (n = 1), and March (n = 1; Fig. 4). The highest number of livestock injuries and deaths occurred in March (19%, n = 11) and April (19%, n = 11; Fig. 4), while human injuries and deaths were most common in July (15%, n = 5; Fig. 4). However, after excluding crop-raiding incidents, the association between conflict type and month was no longer significant ($\chi^2 = 11.571$, df = 11, p = 0.397). Again, this was likely due to the small sample sizes.

Spatial distribution of HEC incidents

Crop-raiding was mostly limited to the western sector of the ecosystem, concentrated in and around Ltungai conservancy (Fig. 1). This is an area of recent agricultural development, where existing communal grazing land has been subdivided into individually owned plots and converted to crop farming. Ltungai accounted for 89% of all crop-raiding incidents in the 2017–2021 study period. The remaining crop-raiding incidents were concentrated in smaller areas of crop farming at the southern and eastern edge of the ecosystem (Fig. 1). After excluding crop-raiding incidents from analyses, a heatmap revealed that the main hotspot for human and livestock injuries and deaths (i.e. the area with the highest density of incidents) was the Kalepo area of the Greater Namunyak conservancy (Fig. 5).

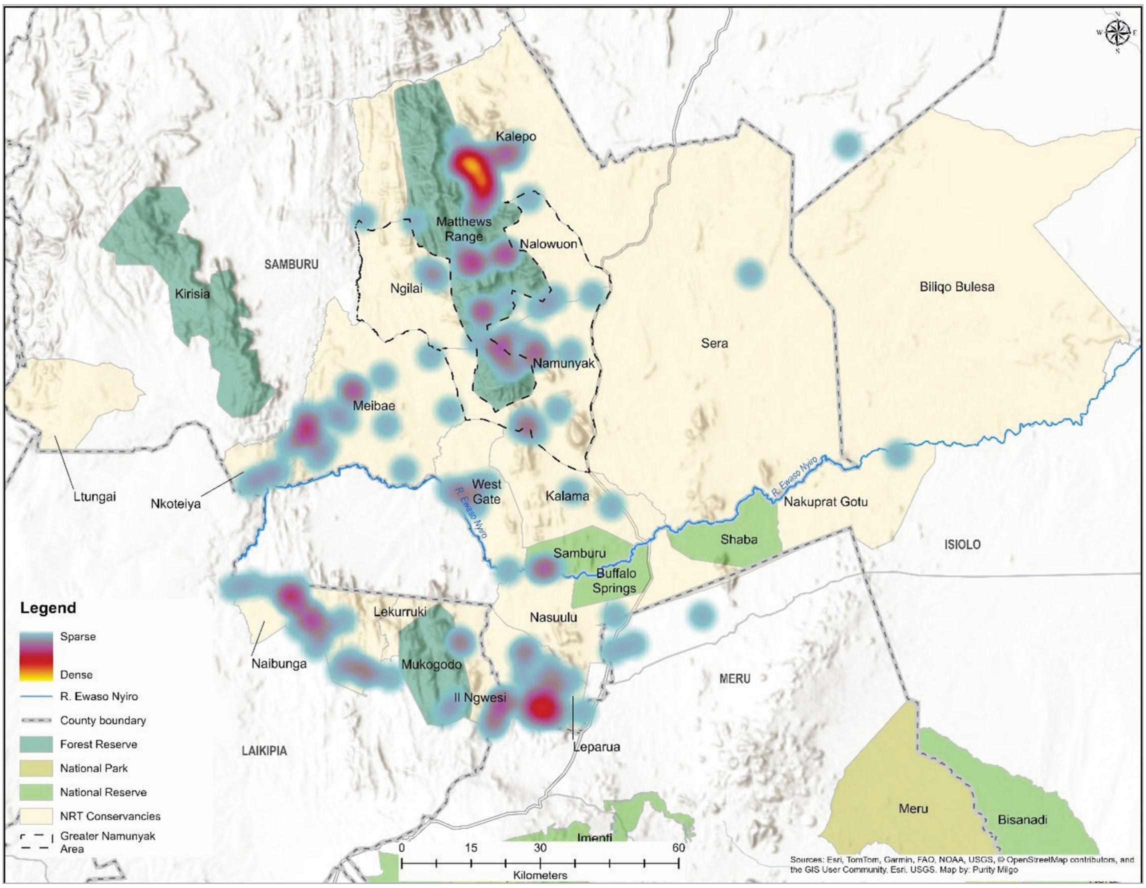

Figure 7. Distribution of human and livestock injuries and deaths as a heatmap, highlighting conflict hotspots across different conservancies (2012–2021).

Other hotspots of human and livestock injuries and deaths could be observed in the Leparua, Naibunga, and Meibae conservancies (Fig. 5). This was confirmed by calculating the proportion of incidents by conservancy: Greater Namunyak accounted for 36% of human/livestock injuries and deaths (n = 35), followed by Leparua (18%, n = 17), Naibunga (14%, n = 14), and Meibae (13%, n = 13). Nonetheless, differences in the proportion of incidents across multiple conservancies need to be interpreted with caution, as conservancies differ by size, human and elephant population densities, and ranger patrol efforts (for example, Greater Namunyak is also the largest of the study conservancies).

Interview results

The interviewees generally felt that HEC is increasing in the region, and with it, conflict-related mortalities, with conflict particularly likely during failed rainy seasons. Several social and ecological factors emerged as potential drivers of HEC and the conflict killing of elephants during the interviews. These included socio-cultural breakdown, consumerism and an increasing focus on economic rather than cultural valuation of elephants, invasive species, feelings of marginalization, and discontent with the lack of response to HEC incidents, among others (Fig. 8).

According to the interviewees, increasing occurrences of HEC and elephant killing in areas like Greater Namunyak could be attributed to the influx of herders from surrounding areas during drought periods. These herders are unfamiliar with the location and afraid of elephants, partly because of a lack of knowledge about elephant behaviour. This leads to more encounters when livestock herding and a high likelihood of herders shooting elephants out of fear.

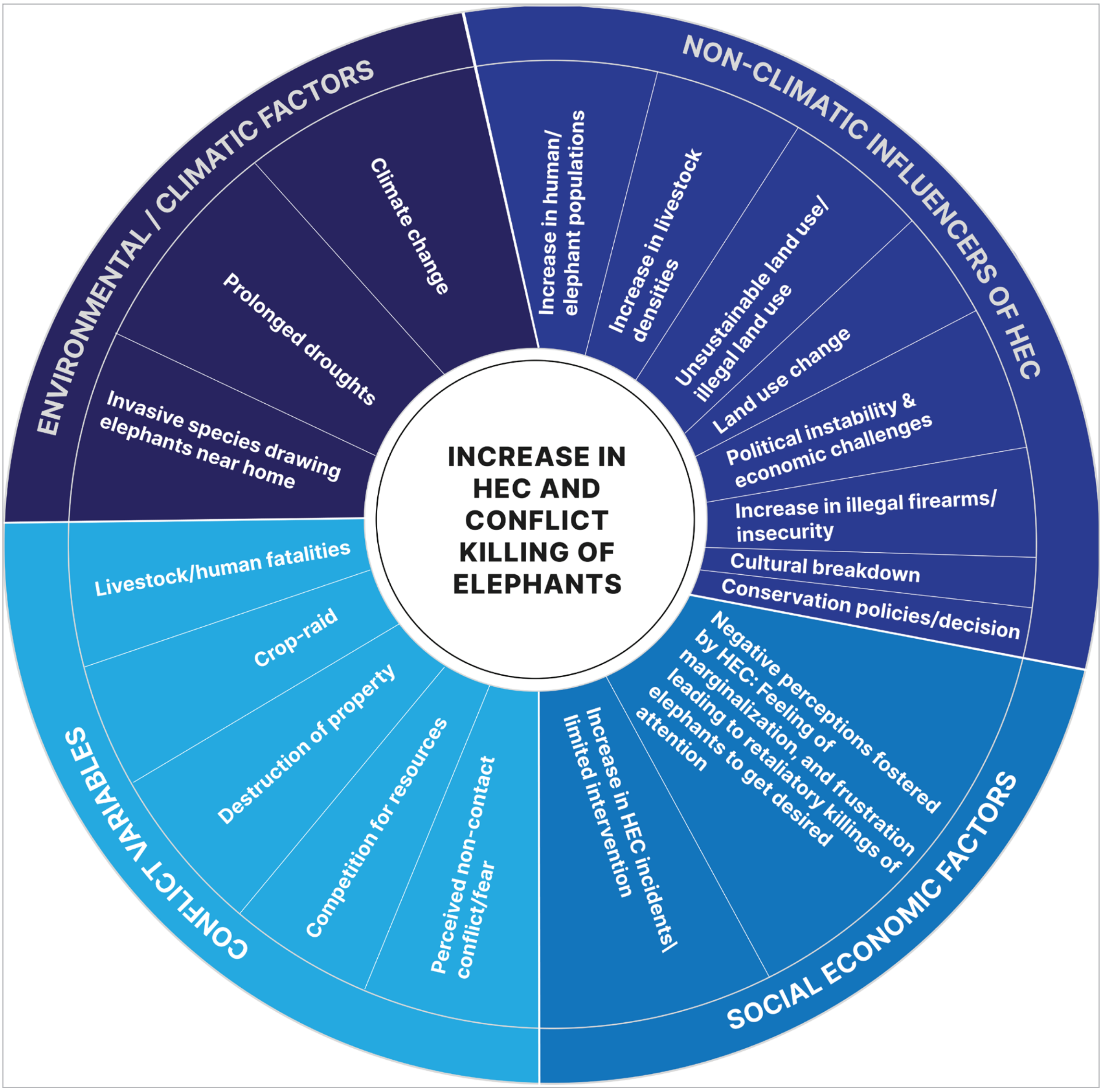

Figure 8. Diagrammatic representation of the factors that contribute to the increase in HEC and conflict-related elephant mortalities identified from interviews with conservation practitioners and researchers[1].

Although HEC was perceived as increasing, one interviewee (W4) noted that with conservancies having a history of recruiting reformed poachers, "*people are shooting elephants to see if they will be hired like poachers were hired ...*"; although, the shooting might also be "*to retaliate against HEC.*" These violent reactions stem from accumulated frustration and neglect that have remained unresolved over time. Another interviewee (W5) emphasized that "*...one of the reasons that conflict cases are underreported is because the communities are tired of reporting cases which are unaddressed... the collection of these records is [perceived as] an extra attack on people, by raising their hopes but not addressing the problem. The collection of the records is like stepping on a fresh wound*".

[1]It is worth noting the difficulty of obtaining elephant mortality data, particularly retaliatory killings due to data access and release policies stipulated in CITES Resolution Conf. 10.10. We include this here to guide future research.

Discussions

In this study, we aimed to elucidate the spatiotemporal trends and potential drivers of HEC in a landscape formerly dominated by pastoralism, but increasingly comprising a mosaic of pastoral and agricultural land uses. While traditional pastoralists historically coexisted with elephants (Galvin 2009), recent research reveals escalating HEC in Kenya. Between 1992 and 2017, 19.9% of 9,182 elephant deaths in Kenya were HEC-related. Laikipia recorded the highest national elephant mortality due to HEC incidents (22.1% of total HEC-related mortality), with Samburu ranking fourth (13.0%); thus, together the LSE accounted for 35.1% of all cases (Mukeka et al. 2022). Our findings confirmed that HEC is a serious issue in the LSE. Although we could not prove that HEC incidents have increased, based on available data, this was the perception of key informants we interviewed. The results of this study suggest that socio-economic, political, and environmental changes such as land-use changes, resource scarcity, and climate change are disrupting long-standing patterns of human–elephant coexistence. These results highlight the urgent need for conservation strategies that account for shifting socio-ecological dynamics while balancing elephant conservation with the livelihoods of affected communities to foster sustainable coexistence in rapidly changing landscapes.

Patterns of HEC

While crop-raiding incidents represented most HEC cases in the LSE, they were limited to a small part of the study area under agricultural development. These events took place at night, when humans are not in the fields and are less likely to be guarding their crops (Hichoonga et al. 2024), conforming to elephant crop-raiding patterns in other sites (Munyao et al. 2020). In contrast, elephant-induced human and livestock injuries and deaths were spread much more widely across the ecosystem and occurred primarily during the day. This is likely because humans and livestock shelter in pastoral settlements (bomas) after dark. This pattern reflects the temporal overlap within shared landscapes between human routines such as herding, and other outdoor activities such as water and firewood collection, and wildlife movements. Thus, HEC in pastoral landscapes requires alternative mitigation strategies that favour co-existence during daily routines, different from the strategies used to mitigate crop-raiding incidents that involve creating barriers to prevent human–elephant interactions.

Our interview respondents reported that conflict intensity increased during the peak of the dry season, or during years characterized by failed rainy seasons or sporadic rain events. They linked this to livestock and elephants converging in areas that receive rain and those that tend to remain green during drought, where they compete for the available pasture and water resources. This aligns with the HEC incident data, which show that the majority of human and livestock fatalities occurred during the dry season. Previous studies highlight the competitive relationship between livestock and elephants for vital resources (Gadd 2005; Young et al. 2005) and the association between low or failed rainfall and HEC (Montero-Botey et al. 2024). Future mitigation strategies should thus take seasonal variation into account when considering conflict risk.

The observed spatial distribution of human and livestock injuries and deaths could also indicate competition over scarce resources in areas that both elephants and pastoralists use as dry-season refuges. For example, the Greater Namunyak conservancy is likely a HEC hotspot due to the presence of permanent water in mountain streams and green forage in evergreen montane forests, as during dry periods these features attract herders and livestock from the entire LSE and even beyond. The accounts of interviewees support this interpretation, as they attributed the high number of HEC incidents in this area to the influx of herders, particularly herders from areas where elephants are absent, and who are thus unfamiliar with the risks associated with elephant encounters. While NRT supports community-led grassland restoration and other measures to revitalize pastoral systems (NRT 2022) these efforts continue to face persistent HEC-related challenges. This suggests that ecological interventions in pastoral landscapes require complementary strategies specifically aimed a mitigating HEC.

Drivers of HEC and conflict-related elephant mortality

Anecdotal evidence from most of the interviews states that numbers of HEC incidents are positively associated with numbers of conflict-related elephant mortalities, a pattern consistent with unpublished MIKE data indicating a recent upward trend. This suggests that retaliation for conflicts plays a major role in HEC in not only in agricultural landscapes, but agro-pastoral landscapes (Mariki et al. 2015). These retaliatory killings are exacerbated by ongoing transitions in pastoralist societies where shifts from nomadic traditions to agro-pastoralism (land-use change), sedentarization (socio-cultural change), privatization of communal lands, and livelihood diversification are creating new frontiers of conflict. The interview transcripts also documented a variety of other perceived drivers of the conflict killing of elephants. Pastoralists rely on livestock as their source of livelihood and cultural identity (Spencer 2013). Human and livestock fatalities contribute to negative attitudes toward elephants (Gadd 2005). According to the interviewees, delayed or lack of compensation for property and livestock loss from HEC fosters sentiments of marginalization, alienation and frustration. These sentiments might produce a sense of distrust toward the authorities, creating a “broken promises effect” (Anthony 2021). This can then lead to communities distrusting government and non-governmental conservation agencies, and to the killing of elephants both as “revenge” against authorities and as a cry for help, to attract their attention to the conflict situation. These social issues should thus be accounted for when planning mitigation strategies in pastoral landscapes, with compensation schemes extended to people and communities in marginalized areas for the loss of human life and livestock.

The interviews identified socio-cultural breakdown, marked by a shift from traditional values to capitalism, consumerism and individual private ownership of land, as another driver of HEC. Kuriyan (2002) notes that the tolerance of the Samburu towards elephants is rooted in their traditions and cultural values. In our study, interviewees commented on the decline in traditional reverence for elephants, linked to the disappearance of the cultural norms that once protected the species. For example, the Samburu viewed elephants as tribemates; when they encountered a carcass they showed their reverence by adorning it with green twigs, signifying deep respect and honour (Kuriyan, 2002). Elephants also played crucial roles in cultural customs; for instance, elephant dung was burned to ward off malevolent spirits, and during marriage rites, newlyweds would light their first fire using dung from a young elephant, symbolizing a fresh start and a prosperous union blessed with the strength and longevity of an elephant (Kahindi 2001). Interviewees highlighted an increasing focus on the economic benefits of elephants, suggesting a shift in societal valuation of elephants (Gadd 2005). Valuing wildlife purely for economic gains might heighten elephants’ vulnerability, casting them in an unfavourable light if income from conservation is lost and/or does not meet expectations and/or fails to compensate for the perceived burdens of coexistence. Thus, it is important to strike a balance between the tangible benefits of wildlife resources and the preservation of cultural values. As the situation evolves, the fusion of both dimensions should be seen as essential to safeguard not only wildlife but also the rich tapestry of human cultural heritage.

According to one interviewee, the spread of *Opuntia* cactus species is also exacerbating HEC. Conflict is thought to occur because this invasive, non-native species draws elephants closer to settlements as they feed on its fruits, where people are using the species as a fence. Additionally, elephants might contribute to spreading the seeds of the invasive species. For example, in Kruger National Park, elephants contribute to the local spread of *Opuntia* through endozoochoric dispersal, while baboons facilitate long-distance dispersal, significantly enhancing the species' invasive potential (Foxcroft and Rejmánek, 2007). Additional research is needed to understand how to deal with this additional challenge, combining mitigation of HEC with invasive species management.

Conclusions and implications for management

The increase in HEC across Samburu and Laikipia reflects profound transitions reshaping this landscape. As pastoral communities navigate the complex shift from nomadic traditions to agro-pastoral livelihoods, driven by climate pressures, economic change, and cultural evolution, new dynamics of conflict are emerging. Our findings demonstrate that these intersecting transitions (land-use change, livelihood transformation, and socio-cultural shifts) amplify the risks of HEC. This new reality demands conservation strategies that bridge ecological and social systems. While organizations like NRT have made important advances in grassland restoration, job creation, and environmental education, persistent gaps remain, including inadequate responses to HEC, uneven community engagement, and limited integration of local knowledge into conflict mitigation. Successful solutions will require pairing institutional strengths, with deeper integration of indigenous knowledge systems (Kuriyan 2002; Williams et al. 2022), particularly those that embody cultural values fostering tolerance towards elephants. Moving forward, effective management requires a threefold approach: 1) adapting conservation planning to irreversible transitions towards agro-pastoralism via corridor designation and seasonal zoning (e.g. crop protection in July–August); 2) strengthening institutional responsiveness through expanded ranger patrols and alerts for herder communities; and 3) embedding local knowledge in coexistence strategies via stakeholder forums that balance biodiversity and livelihood priorities. By systematizing these spatial, temporal, and social interventions, governance challenges become opportunities for scaling solutions. Coexistence in a transitioning landscape requires policies that address both the ecological drivers of HEC and its human dimensions, to align conservation with contemporary realities while preparing for future challenges.

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MANAGEMENT

Advancing black rhino conservation in Kenya: milestones and the strategic outlook for sustaining population recovery

Cedric Khayale[1], Erustus Kanga[2], Patrick Omondi[1], Linus Kariuki[2], Rob Brett[3], Timothy Oloo[4], Martin Mulama[5], Benson Okita-Ouma[6], Jamie Gaymer[7], Rajan Amin[8]**

[1]Wildlife Research and Training Institute, PO Box 842, Naivasha 20117, Kenya
[2]Kenya Wildlife Service, PO Box 40241, Nairobi 00100, Kenya
[3]Fauna & Flora, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK[1]
[4]Independent Wildlife Consultant, PO Box 185, Nairobi 00517, Kenya[2]
[5]World Wide Fund for Nature – Kenya, PO Box 62440, Nairobi 00200, Kenya[3]
[6]Wyss Academy for Nature, East Africa Hub, PO Box 18, Nanyuki 10400, Kenya[4]
[7]Association of Private and Community Rhino Sanctuaries (APLRS), PO Box 259, Nanyuki 10400, Kenya
[8]Zoological Society of London, Regent's Park, London, NW1 4RY, UK

*corresponding authors: ckhayale@wrti.go.ke; raj.amin@zsl.org

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Abstract

The black rhinoceros (*Diceros bicornis*) experienced precipitous declines across Africa during the 1970s and 1980s, primarily driven by poaching. The decline was particularly severe for the eastern subspecies (*D. b. michaeli*). Kenya's population, which once supported a significant proportion of the species, declined from approximately 20,000 to 370 individuals by 1989, at the time that the Kenya Wildlife Service (KWS) was established. Over the last three decades, considerable effort and resources have been deployed, and an enabling policy and legislative framework have been enacted to recover rhino populations. As a result, the declining trend has been reversed, and the number of indigenous black rhinos is increasing. Remarkable progress has been achieved through strategic interventions and population recovery initiatives, with Kenya's black rhinos reaching a confirmed total of 1,059 individuals in 2024—marking a historic milestone. We document Kenya's rhino conservation progression, including current population status, challenges and future strategies aimed at supporting the long-term vision of achieving 2,000 individuals, thereby securing the future of *D. b. michaeli*.

[1]Kenya Rhino Programme Coordinator (1989–1995)
[2]Kenya Rhino Programme Coordinator (1995–2000)
[3]Kenya Rhino Programme Coordinator (2000–2006)
[4]Kenya Rhino Programme Coordinator (2006–2016)

Résumé

Le rhinocéros noir (*Diceros bicornis*) a connu un brusque déclin en Afrique au cours des années 1970 et 1980, principalement du fait du braconnage. Les sous-espèces de l'Est (*D. b. michaeli*) ont été particulièrement touchées. La population établie au Kenya, qui représentait une part significative de l'espèce avec près de 20 000 rhinocéros, a décliné jusqu'à atteindre 370 individus en 1989, période à laquelle le bureau kenyan en charge des espèces sauvages (Kenya Wildlife Service) a été créé. Des efforts et des ressources considérables ont été déployés ces trente dernières années, et un cadre politique et législatif favorable a été mis en place afin de permettre le rétablissement des populations de rhinocéros. Dès lors, la tendance s'est inversée et le nombre de rhinocéros noirs indigènes est actuellement en hausse. Des progrès remarquables ont été réalisés par le biais d'interventions stratégiques et d'initiatives de rétablissement des populations, et, en 2024, le nombre total de rhinocéros noirs au Kenya a été confirmé à 1 059 individus – une étape majeure dans l'histoire de cette espèce. Nous documentons ici l'évolution de la conservation du rhinocéros au Kenya, l'état actuel de la population ainsi que les défis et les futures stratégies visant à soutenir une vision à plus long terme, dans l'objectif d'atteindre les 2 000 individus et d'assurer l'avenir de *D. b. michaeli*'.

Introduction

The five extant rhinoceros' species (hereafter referred to as rhinos) are the only relics of a once diverse family of odd-toed ungulates known as Rhinocerotidae. They are not only a continuation of a major evolutionary heritage but also symbols for the protection of African savannahs and Asian grasslands and forests (Somerville 2025). All five species are now threatened with extinction (Emslie 2020a; b; c; Ellis and Talukdar 2019; Ellis and Talukdar 2020a; b).

The black rhino's status as a conservation concern cannot be overstated. Kenya's black rhino (*Diceros bicornis michaeli*) is considered a local icon, and the future of the species is crucial both nationally and globally for several reasons. Rhinos were on the brink of extinction following a dramatic decline in their population. As a flagship species, they are a highly charismatic animal and capture the attention of people worldwide with a direct economic impact for Kenya through wildlife-based tourism. In addition to its role in conservation and tourism, the black rhino is considered an umbrella and keystone species, serving the objective of broader biodiversity priorities, as their conservation depends on extensive and intact ecosystems being conserved and protected, and they play a significant role in ecological dynamics.

Black rhino declines

Pre 1970s

Black rhinos once numbered several hundred thousand and were widespread across sub-Saharan Africa, where herb and woody browse occurred in sufficient amounts to support a population. In Kenya, they occurred in nearly all except for the very arid areas in the north and the humid lowland forest belt in the west (Kingdon 1982; Stewart and Stewart 1963). During British colonisation from 1890, large tracts of land were cleared for agriculture and settlement schemes. Because the favoured habitats of rhinos generally had available water and were reasonably fertile, a high number of rhinos were killed, being deemed incompatible with development. For example, approximately 1,000 animals were shot during the Makueni settlement scheme in 1946–1948 by the game control officer JA Hunter and his colleagues (Hunter 1952). They were precipitously eliminated from more than 75% of their range by early 1970s (Fig. 1).

1970s–1980s decline

The period between 1970 and 1989 saw intense poaching of rhinos in Kenya (and across its range in Africa) due to the demand for rhino horn. Kenya's black rhinos were poached nationwide, whether inside or outside Protected Areas (PA), due to inadequate controls and reactionary law enforcement. In addition to the killing of most of the animals from lowland areas (e.g. Tsavo National Park (NP), Meru NP) by well-organised poachers and criminal gangs

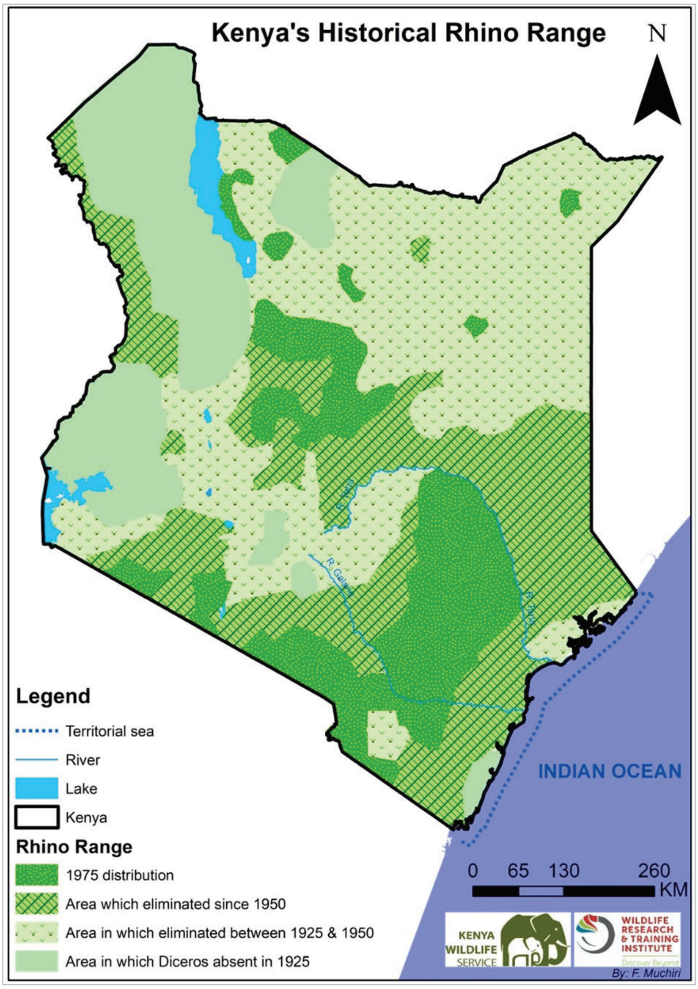

Figure 1. The distribution of black rhino in Kenya (1925–1975), Source: Kingdon 1982.

(including Shifta[5] from the east of Kenya), many of the black rhinos from the highlands were slaughtered by poachers from local areas. This was often in collusion with officers within the government game department. By 1989, the Kenyan population had declined to 370 from an estimated 20,000 in 1970 (Hillman and Martin 1979; Brett 1993); (Fig. 2). The population of the Greater Tsavo ecosystem (6,150–9,220 animals) comprising over a third of Kenya's rhinos, was reduced to less than 50 individuals by 1984 (Goddard 1969; Brett 1993).

[5]"Shifta" is a term, primarily used in the Horn of Africa, associated with armed groups, sometimes operating in remote areas, who challenge authority or engage in acts of banditry.

Black rhino population recovery

It was eventually recognised that the only hope of protecting the remaining black rhinos in Kenya was to concentrate security within smaller areas by establishing Intensive Protection Zones (IPZs) for the species. Previously, resources, such as manpower and equipment had been spread too thinly over large areas to yield any meaningful benefit (Leader-Williams 1997). Since 1984, an active conservation programme devoted to the recovery of Kenya's black rhino populations has been pursued; and conservation policy has been centred on developing dedicated IPZs or Rhino Sanctuaries (RS) (Gakahu 1989; Brett 1990;1993; Okita-Ouma et al. 2007). Within these IPZs, many of which are entirely enclosed by specially designed and monitored electric fences, a

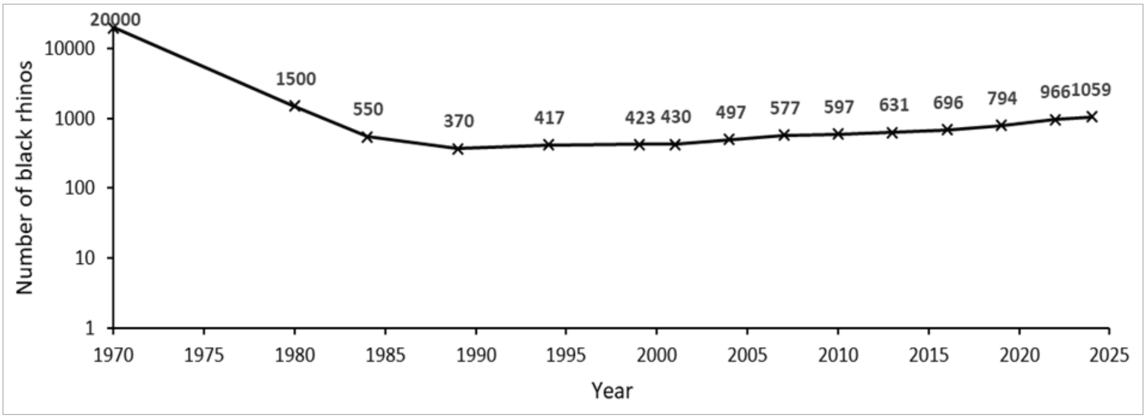

Figure 2. Black rhino numbers in Kenya from 1970 to 2024 on a logarithmic scale show a sharp decline in the 1970s and their recovery from 1990.

large proportion of the country's black rhinos have been protected from poaching. Initially, rhino sanctuaries were stocked primarily with unprotected rhinos, typically isolated and vulnerable animals living in areas outside national parks or protected areas. As numbers increased, surplus rhinos from overstocked sanctuaries have been used to supplement populations in understocked sanctuaries and to establish new rhino conservation areas.

Six ring-fenced rhino sanctuaries were established in the initial phase under the Kenya Rhino Project. These included Lake Nakuru NP, Ngulia RS in Tsavo West NP, Ngare Sergoi RS in Lewa Ranch (now Lewa-Borana Conservancy with the original fenced sanctuary removed), Sweetwaters Game Reserve (GR), (now Ol Pejeta Conservancy), Solio GR and Ol Jogi Pyramid. The latter four sanctuaries were developed through effective cooperation between the national wildlife agency, private landowners and conservation NGOs.

In addition, other areas were upgraded to rhino sanctuary status with the construction of fencing and improved anti-poaching and surveillance (e.g. Nairobi NP, the Salient section of Aberdare NP). The sanctuary policy was successful as an emergency measure, firstly to protect black rhinos, and secondly to allow successful breeding, guided by the initial national rhino conservation plans (Jenkins 1983; Brett 1993; Okita-Ouma et al. 2007).

In recognition of the importance of rapid growth after the intensive poaching period, Kenya's wildlife authorities placed a greater emphasis on biological management from the early 2000s. A national target of 5% growth per annum was set in the Strategic Plans (Okita-Ouma et al. 2007; KWS 2012; Amin et al. 2017; 2022), with the vision of at least 2,000 eastern black rhinos occurring in their natural habitat. To achieve this, specific capacity and systems were put in place for: 1) rhino capture and translocation; 2) monitoring and standardised field data collection; 3) data analysis and status reporting; 4) assessing ecological carrying capacity of rhino areas; and 5) population expansion (Amin et al. 2006).

Between 2000 and 2025, nine populations have been established, bringing the total to 18 rhino popuations (Fig. 3). The Borana Conservancy was the first to be established in 2013 and later merged with the adjacent population in Lewa Wildlife Conservancy, creating a continental Key 1 population (numbering more than 100 rhinos). Similarly, the former Sweetwaters GR was expanded in 2007 to establish the Ol Pejeta Conservancy, where additional rhinos from Solio GR were introduced, creating another continental Key 1 population. Black rhinos were also introduced into community lands, starting with Il Ngwesi Community Conservancy in early 2000 with one rhino, followed by Sera Wildlife Conservancy in 2015 with a founder population of 13 rhinos, (the first community conservancy in East Africa to operate a sanctuary for the critically endangered species), and most recently Loisaba and Segera Conservancies, which hold 26 and 19 rhinos respectively.

A 3,000 km^2 IPZ, which can support hundreds of

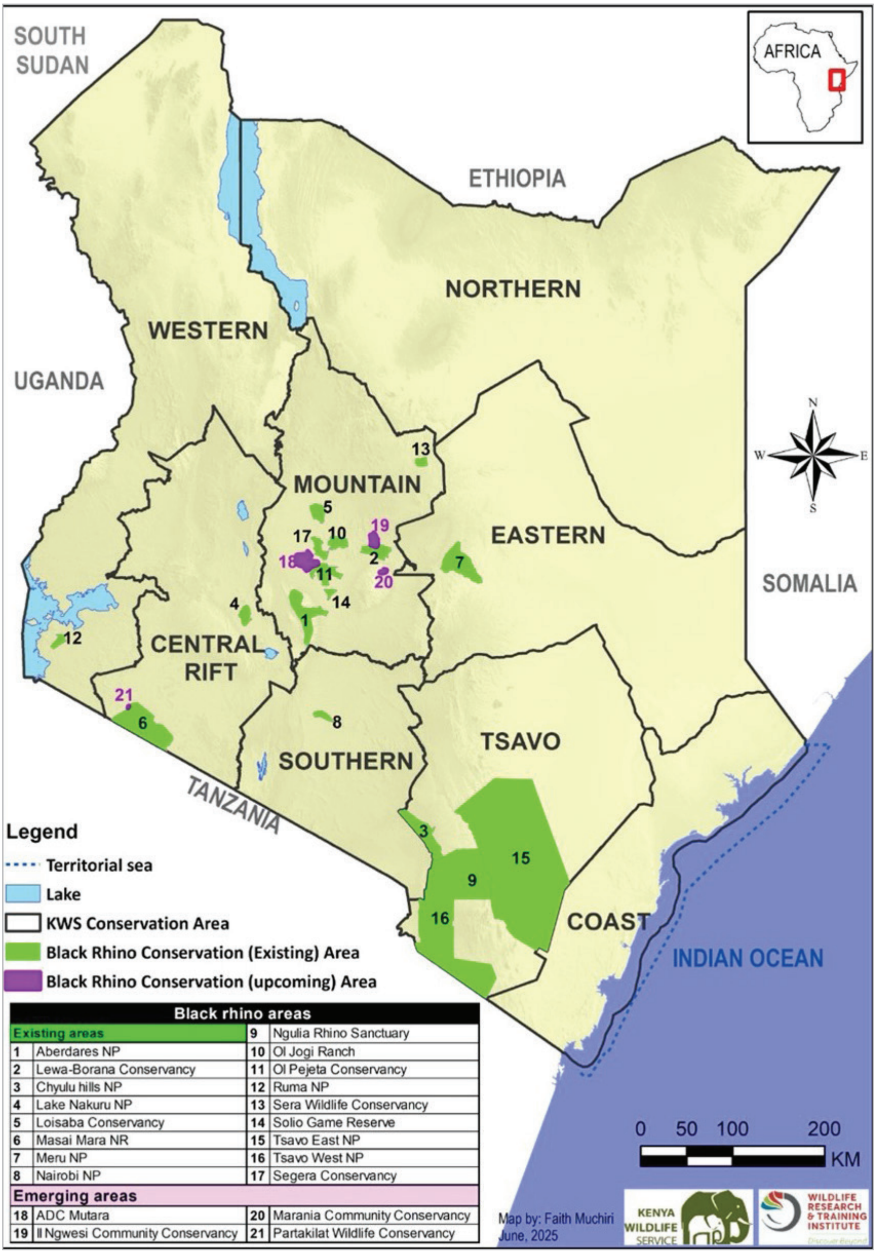

Figure 3. Kenya's black rhino conservation areas, March 2025. Note: Ol Jogi Ranch consists of two separate populations, Ol Jogi Pyramid and Ol Jogi Ranch.

Table 1. Milestones in black rhino recovery efforts.

Year	Milestones
Before 1960's	Controlled protection in parks and reserves, and legal hunting.
1977	Hunting ban came into effect for all wildlife, including the indigenous Eastern black rhino.
1979	Presidential Decree on special protection for rhino; conservation strategy developed; consolidation of non-viable fragmented populations into sanctuaries; and enhanced anti-poaching efforts.
1980–1981	Sanctuary development concept refined.
1983	First edition of the Black Rhino Management Plan officially ratified.
1985	Presidential Decree on rhino as a unique species requiring special protection. Further refinement of the 1983 Black Rhino Management Plan. Fund raising document produced, donor support invited.
1989	KWS established.
1990	APLRS established.
1993	The second edition of the Black Rhino Conservation Policy and Management Plan ratified.
2000	Third edition of the Black Rhino Conservation and Management Strategy (2001–2005) ratified.
2007	Fourth edition of the Conservation and Management Strategy for the Black Rhino and Management Guidelines for White Rhino (2007–2011) ratified.
2009	East African Community Rhino Management Group inaugurated and ratified by directors of wildlife authorities of Burundi, Ethiopia, Kenya, Rwanda, Tanzania and Uganda.
2012	The fifth edition of the Black Rhino Conservation and Management Strategy (2012–2016) ratified.
2014	Wildlife Conservation and Management Act, 2013, with enhanced penalties, enacted.
2014	The development of recovery and action plans for endangered species became a legal requirement as provided for in Section 49 of the Wildlife Conservation and Management Act, Cap 376.
2015	The first community black rhino sanctuary established in Sera Conservancy.
2017	The sixth edition of the Black Rhino Action Plan (2017–2021) ratified.
2018	National Wildlife Strategy 2030 launched.
2019	New rhino immobilization and translocation protocols for black and white rhinos developed.
2019	Amendment to the Wildlife Conservation and Management Act, Cap 376 (Amendment 2019) providing clarity on penalties related to endangered species.
2020	Zero poaching for black rhino achieved for the first time in over twenty years.
2020	Sessional paper number 01 of 2020 on National Wildlife Policy ratified.
2022	Donation of three black rhinos to the United Republic of Tanzania (Ngorongoro Conservation Area).
2022	The seventh edition of the Recovery and Action Plan for the Black Rhino in Kenya (2022–2026) ratified.
2023	The concept of Kenya Rhino Range Expansion initiated.
2024	Kenya for the first time in over three decades surpasses 1,000 indigenous black rhinos.

black rhinos, was created in 2008 in Tsavo West NP for destocking fenced sanctuaries (Okita-Ouma et al. 2006). Black rhinos were reintroduced to Meru (in 2006, 21 animals) and Ruma NP (in 2012, 22 animals) following the effective control of tsetse flies at these sites (KWS 2012). Ngulia RS was expanded from 62 km^2 to 92 km^2, and competing browsers were significantly reduced in 2007 (Brett and Adcock 2002; Okita-Ouma et al. 2008). Ol Jogi Ranch expanded its rhino habitat in 2005 from the 50 km^2 Ol Jogi Pyramid into the 235 km^2 ranch where 34 rhinos were also introduced from Solio GR, Nairobi NP, Nakuru NP and Mugie RS. The establishment of a fenced rhino sanctuary in the Aberdare Salient is expected to be completed later in 2025, supplementing and re-establishing a viable population in a montane forest ecosystem.

Establishing, protecting, and maintaining rhino sanctuaries requires significant resources. Although the population in Mugie's private rhino sanctuary had settled with 19 births, a decision was made to translocate the remaining 24 black rhinos to safer areas following an escalation of poaching in 2011–2012. Similarly, the last two remaining rhinos from the Laikipia Nature Conservancy—where eight rhinos had been relocated in 2005 to boost the population—were translocated to Meru NP (Amin et al. 2017).

Kenya's black rhino programme has grown from strength to strength, and by December 2024, the population had surpassed the major milestone of a thousand rhinos (1,059 rhinos: 31 Dec 2024). This success has been driven by an enabling environment that includes firm policy and a legislative framework, as well as sustained government support providing a solid foundation for rhino conservation efforts (Table 1). The adoption of IUCN–SSC African Rhino Specialist Group's standardised monitoring protocols, ensuring high-quality data for an informed decision-making process, was critical to the success. The partnership between the Kenyan Government (GoK), non-governmental conservation agencies, private landowners and local communities continues to support rhino conservation efforts. The Association of Private and Community Land Rhino Sanctuaries (APLRS), formed in 1990 has also provided an interface between government and the private and community rhino sanctuaries. This association persists and is entrenched in the KWS decision-making framework through the National Rhino Action Plans. This "partnership approach" to rhino conservation has been a significant contributing factor to Kenya's success.

In addition, to field rangers, who continue to be recruited, equipped and deployed, the adoption of technologies for enhanced monitoring and surveillance has been critical. Veterinary capture and translocation capacity is also continually being tailored and refined to support a healthy growing population of rhinos guided by the national immobilization and translocation protocol. As can be expected, there have been some challenges along the way with valuable lessons learned, in particular the need for effective monitoring, the dangers of not managing the numbers of rhinos and other competing browsers in fenced sanctuaries, and the necessity of using recommended translocation and veterinary procedures. Kenya's Black Rhino Action Plan is on track to achieve its long-term vision of having 2,000 black rhinos in the wild (Fig. 4).

Future for rhinos in Kenya

Poaching

Poaching was the primary cause of the population decline in the 1970s and 1980s, and its resurgence in 2009 has been largely managed over the last five years. Within this period, eight black rhino mortalities attributed to poaching accounted for less than 1% mortality over the five years, and there were zero poaching incidents in 2020. This is primarily attributed to the efforts by the GoK in collaboration with conservation stakeholders and a rallying call by the international community to stop poaching and trafficking of the rhino horn. Among the key interventions implemented were rigorous vetting systems for rhino monitoring and security teams, enhanced cross-border collaboration through joint anti-poaching patrols and strengthened multi-agency cooperation at strategic entry and exit points. To address unpredictable threats, comprehensive security contingency plans were implemented to rapidly respond to emerging rhino security challenges across all rhino sites. Central to these efforts was the adoption of a zero-poaching framework, which provided structured tools for monitoring poaching activities, tactical planning and implementation of

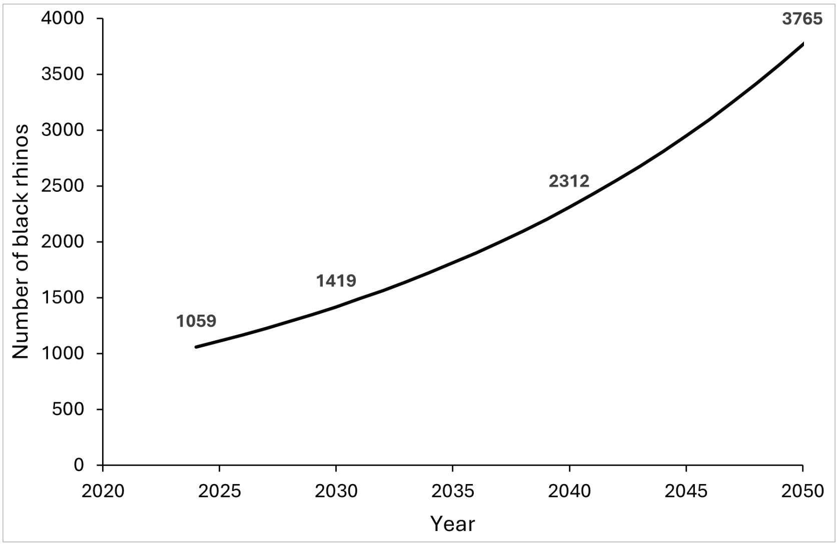

Figure 4. With a projected 5% annual increase in black rhino numbers (from 1,059 in December 2024) continuing, the estimated numbers of rhinos would be 1,419 by 2030, 2,312 by 2040, and 3,765 by 2050.

countermeasures, and systematic evaluation of anti-poaching performance.

This framework was built upon six fundamental pillars 1) conducting regular threat assessments; 2) deploying cutting-edge technology; 3) building adequate field staff capacity; 4) embracing meaningful community engagement; 5) improving prosecution methodologies and facilitating regional and national information exchange. Lastly, 6) operational capabilities were further reinforced through the standardization of field equipment across sites and professional training for field personnel. While these pillars are essential and each plays a role in reducing poaching, the key enabling factor is the political will to combat rhino poaching. The GoK has drawn a firm line and is committed to taking the necessary actions to stop the poaching of rhinos.

A wider impactful measure has been the coordinated management and analysis of rhino horn and tissue samples across the continent through the Rhino DNA Indexing System (RhODIS), which has played a pivotal role in identifying the geographic origins of confiscated rhino products and generating forensic evidence to strengthen legal prosecution cases. Security threat to rhinos continues to remain high and is cyclical, therefore these efforts will need to be sustained.

Rhino landscapes

Recent calculations show Kenya has a space capacity deficit of approximately 500 rhinos (Amin et al. 2022). Over 80% of Kenya's rhinos reside in sanctuaries that have exceeded their ecological carrying capacity, requiring relocation of over 300 rhinos. The Kenya Rhino Action Plan along with the Kenya Rhino Range Expansion initiative (KRRE) aims to address this. Kenya still has large tracts of suitable black rhino habitat, such as the Tsavo landscape and Meru conservation area. Notably, the Tsavo West IPZ (a partially fenced, intensively protected landscape of 3,000 km^2 home to 42 rhinos as of December 2024) has the ecological conditions to accommodate high stocking densities. Similarly, Tsavo East NP is vast, but security remains challenging with remote open areas to the north, and with perennial water sources only in specific locations.

There are considerable opportunities to establish new private and community sanctuaries in the Laikipia region, some of which are at an advanced stage of planning, with Loisaba Conservancy commissioned in 2024 and Segera Conservancy scheduled for 2025. There is also a longer-term aim of merging the private, community and government sanctuaries to form a contiguous rhino landscape with the support of the KRRE initiative in partnership with the KWS, Wildlife Research Training Institute (WRTI) and other stakeholders. The forested areas of Chyulu Hills and Aberdare NPs contain habitats suitable for rhinos, although their populations are currently non-viable.

Conclusion

The eastern black rhino is the least numerous subspecies of Rhinocerotidae, with ~1,474 individuals in three range states within its natural distribution (Kenya, Tanzania and Rwanda). Kenya remains the stronghold of *D. b. michaeli*, with a population slightly over 70% as of the end of 2024. Having surpassed the milestone of 1,000 individuals by the end of 2024, Kenya has learned lessons and gained the required momentum to achieve its vision of 2,000 black rhinos by 2037, with a sustained average annual net growth of at least 5% (Fig. 4), thus ensuring as much genetic diversity is preserved as possible. High rhino numbers combined with growth will also minimize the impact of poaching on Kenya's populations.

A high metapopulation growth rate will be sustained through maintaining sanctuary rhino densities at productive levels, thereby leading to population expansion. Established populations will continue to serve as a 'breeding bank' providing a continuous supply of rhinos to expand into new secure and large areas with a carrying capacity of hundreds of rhinos. The KRRE, launched in 2024, aims to continue the incredible revival of the eastern black rhino in Kenya. Starting with Tsavo and Central Kenya, the initiative aims to expand Kenya's rhino habitats to become one of the largest in the world. Additionally, it will bring improved management and long-term stewardship to approximately 6% of Kenya's land and contribute to Kenya's 30 by 30 commitment (Kunming-Montreal Global Biodiversity Framework 2022).

Acknowledgements

Foremost, we recognise the Government of Kenya's unwavering commitment to rhino conservation through progressive policies, legislative frameworks and sustained support. We extend our sincere gratitude to KWS and WRTI for their leadership in rhino security, management, research and monitoring efforts. The County Government of Narok and the private and community rhino sanctuaries are much appreciated for their critical role in providing space for rhino expansion and safeguarding rhino populations beyond national parks. The milestone of 1000 rhinos would not have been possible without the significant efforts of rhino sanctuary managers, rangers and scouts whose selflessness and sacrifice in the field have been instrumental in securing Kenya's black rhinos for future generations. We, finally, express our gratitude to local and international rhino conservation partners for their support throughout this journey.

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Balancing boundaries: elephant movements in the changing landscape around Murchison Falls National Park, Uganda

Joanna F Hill[1], Charles Ochanda[2], Dipto Sarker[3], Colin A Chapman[4,5,6]*

[1]The Department of Criminology, University of Manchester, UK
[2]Uganda Conservation Foundation, Kampala, Uganda
[3]Geography and Environmental Studies, Carleton University, Ontario, Canada
[4]Biology Department, Vancouver Island University, Nanaimo, British Columbia, Canada
[5]School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa
[6]Shaanxi Key Laboratory for Animal Conservation, Northwest University, Xi'an, China

*corresponding author: joannahill@proton.mail.com

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Abstract
We examine elephant movement and human–elephant conflict around Murchison Falls National Park (MFNP) in northern Uganda, a landscape shaped by rapid agricultural expansion, displacement, and ongoing land conflict. Elephant movements beyond the Park's boundaries are still poorly understood. Between 2019 and 2022, we collected data through GPS collaring (n = 5), ground observations, and crop-raiding surveys. Collared elephants favoured areas near water, tree cover and lower elevations, with use of human-occupied areas ranging from 0–24%. Outside MFNP, they sheltered near refuge sites during the day and raided farms at night. Raiding typically targeted mid-growth crops with a median of 30% damage per affected farm. Calves were present in approximately 20% of raids, and some groups exceeded 30 individuals. Only 9% of farmers used deterrents beyond reactive chasing. Snaring injuries were recorded in 32% of the observed elephants, indicating persistent poaching pressure. Unresolved land tenure, community distrust, and evictions further complicate elephant management outside the Park. We recommend prioritizing elephant protection inside MFNP by strengthening anti-snaring operations. Outside the Park, boundary communities require training for coordinated night-guarding and locally suitable low-cost deterrents. A feasibility study, in consultation with affected farmers, should assess limited fencing on community lands while retaining a central corridor linking MFNP to areas further north.

Résumé
Nous étudions dans cet article les mouvements des éléphants ainsi que les conflits humains-éléphants se produisant autour de la zone de conservation de Murchison Falls, dans le nord de l'Ouganda – un paysage façonné par l'expansion de l'agriculture, les déplacements de populations et les conflits liés au foncier. Les mouvements des éléphants au-delà des limites du parc national de Murchison Falls sont encore mal compris. Entre 2019 et 2022, nous avons recueilli des données grâce à des colliers GPS installés sur les animaux (n = 5), des observations de terrain et des enquêtes relatives aux dégâts infligés aux cultures. Les éléphants équipés privilégiaient les espaces proches de l'eau, sous un couvert forestier et situés à basse altitude, avec une utilisation des zones occupées par l'homme allant de 0 à 24 %. En dehors du parc, ils s'abritaient près des habitats refuges pendant la journée et pillaient les fermes la nuit. Ces pillages ciblaient généralement des cultures en cours de croissance, avec un taux moyen de 30 % de dommages répertoriés par ferme. Les éléphanteaux étaient présents dans environ 20 % des pillages et certains groupes dépassaient les 30 individus. Seuls 9 % des agriculteurs utilisaient des moyens de dissuasion autres que la poursuite en réaction

au pillage. Des blessures causées par des pièges ont été relevées sur 32 % des éléphants observés, ce qui indique que la pression du braconnage est toujours très présente. Les conflits relatifs au foncier, la méfiance des communautés et les expulsions forcées des habitants compliquent d'autant plus la gestion des éléphants en dehors des limites du parc. Compte tenu de ces dynamiques et de l'accélération de la conversion des terres, il paraît peu envisageable d'entreprendre une restauration des corridors. Nous identifions ici les obstacles majeurs qui entravent la gestion des éléphants hors du parc de Murchison Falls, et nous fournissons des données de référence pour soutenir les futures interventions. En outre, nous recommandons de prioriser la protection dans l'enceinte du parc et de renforcer l'engagement communautaire par des initiatives axées sur la transparence et l'établissement de relations de confiance. S'appuyer sur le suivi des éléphants et sur l'usage, par les populations locales situées en première ligne, de moyens de dissuasion adaptés au contexte et peu onéreux, peut contribuer à réduire les conflits et à encourager l'implication des communautés.

Introduction

Mapping elephant movements is a key tool for mitigating human–wildlife conflict, identifying crop-raiding hotspots and guiding interventions such as fences or corridors (Douglas-Hamilton et al. 2005; Tiller et al. 2021). Yet implementing such measures is severely constrained in contexts of contested land tenure, where ongoing disputes and evictions can undermine conservation planning, limit community participation and exacerbate marginalization (Kobusingye et al. 2017).

We examine the intersecting challenges of elephant conservation and land conflict around Murchison Falls National Park (MFNP) in northwest Uganda. MFNP, Uganda's largest protected area, is a key biodiversity stronghold supporting over 76 mammal species and 450 bird species (Plumptre et al. 2015a). It also plays a central role in Uganda's tourism sector, which generated USD 1.28 billion in 2025 (MTWA 2025). Park entry fees support wildlife conservation and fund sustainable development initiatives in surrounding communities. These contributions are crucial in a country recovering from decades of civil conflict during the 20th century (Parker 2019), during which elephants and local communities were displaced, and habitats and settlements damaged or destroyed. As human and elephant populations recover and reoccupy areas around the Park, their interactions are increasingly marked by conflict. Crop raiding has become a major concern for communities, driven by population growth and agricultural expansion along the Park's unfenced boundary (Oniba and Robertson 2019). Open boundaries allow elephants easy access to farmland, and in areas with limited economic alternatives, even partial crop losses can be devastating (Alfred 2004; Mackenzie et al. 2012;). These pressures occur amid unresolved land tenure, conflict over land titles, and forced evictions (Mabikke 2011; Kobusingye 2017). For some, the daily threat of crop loss and displacement echoes the trauma of wartime displacement (van der Zeijden 2024). The management of biodiversity, and especially of elephants, around MFNP must account for this history while balancing conservation and community needs.

In this context, acquiring elephant movement data to guide management is urgent. Yet few studies have examined elephant movements across MFNP and surrounding areas. To address this gap, we conducted a field study (2019–2022) in regions of intense human–elephant conflict (HEC) to the northwest of the Park. Our objectives were to document 1) elephant movements within and beyond the Park; and 2) crop-raiding incidents in affected farming communities. The following section describes the socio-ecological context that shaped our study design, followed by the methods, results and discussion The conclusion reflects on the challenges of balancing elephant conservation with the needs of neighbouring communities.

Socio-ecological context of the Murchison Falls landscape

In 1894, when Uganda became a British Protectorate, elephants ranged across 70% of the country. When a trypanosomiasis (sleeping sickness) outbreak along the Victoria Nile forced the evacuation of local communities, the depopulated land was designated a game reserve, and subsequently, in 1952, gazetted as Murchison Falls National Park (Parker 2019). To the north, Aswa-Lolim (70 km²) and Kilak (1,800 km²) were established as game reserves for colonial trophy hunters. These areas supported dense wildlife populations and linked the Murchison ecosystem to East Madi Wildlife Reserve and South Sudan, forming part of a broader elephant migration network (Andama et al. 2024). As human populations and agriculture expanded, elephants were compressed into national parks and, by 1959, the elephant range had contracted to 17% of Uganda's land area (Brooks and Buss 1962). Confined to shrinking habitats, MFNP's elephant population grew rapidly, leading to exhaustion of food supplies and widespread woodland degradation (Buechner and Dawkins 1961). Between 1965 and 1967, some 3,000 elephants were culled to halt further ecological damage (Laws et al. 1970).

In the following decades, political instability, armed insurgencies and weak enforcement caused the collapse of protected area management, while poaching decimated wildlife populations, especially of elephants (Parker 2019) and rhinos (Wheater and Parker 2019). Elephant numbers fell from 14,000 in the 1960s to fewer than 300 by the 1990s (Rwetsiba and Nuwamanya 2010). In the 1970s, President Idi Amin degazetted controlled hunting areas north of the Park to promote private ranching and agriculture, but the ensuing conflict prevented these developments (Olanya et al. 2022). From 1986 onwards, fighting by the Lord's Resistance Army further destabilised northern Uganda, including areas north of Murchison. Nearly two million people were forcibly relocated to camps for internally displaced persons (IDPs), suffering violence and the loss of land and livelihoods (Mabikke 2011). During this prolonged human displacement, elephants and other wildlife progressively recolonized abandoned lands surrounding the Park. Conservation efforts by the Uganda Wildlife Authority (UWA) and partners have since supported elephant recovery, with recent estimates ranging between 1,150 and 2,700 individuals (Grogan et al. 2019; R. Lamprey, pers. comm., 1 May 2025). Building on these gains, studies have explored re-establishing historical migration corridors between MFNP and East Madi Wildlife Reserve (Fig. 1b) (Lamprey et al. 2003; Andama et al. 2024). However, the feasibility of corridor restoration remains uncertain given rapid resettlement, population growth and overlapping land claims around the Park. Elephants also face renewed threats from poaching, habitat loss caused by agricultural expansion, and oil extraction activities within MFNP (Plumptre et al. 2015b; Grogan et al. 2019).

Recognising these pressures, UWA continues to prioritize elephant conservation by combating poaching, maintaining habitat connectivity and reducing crop raiding. These efforts aim to ensure that elephant populations support socio-economic development through tourism at both national and local levels (UWA 2016). At the same time, these conservation priorities pose challenges for post-conflict recovery of local communities. After hostilities ceased in 2006, IDPs began returning to their former lands, only to encounter widespread land disputes and evictions (Mabikke 2011; Kobusingye et al. 2017). The liberalization of Uganda's land market and the discovery of oil in MFNP have intensified competition for titled land (Dowhaniuk et al. 2018). With formal titling processes remaining inaccessible to rural households, land insecurity has become ubiquitous. Tensions between UWA and communities have deepened following evictions to establish private hunting concessions (Kobusingye et al. 2017).

The absence of coordinated land-use planning has also enabled agricultural expansion up to the unfenced park boundary, creating a stark transition between farmland and protected habitat that is visible in satellite imagery (approx. 2°12'38" N, 31° 32' 13" E)[1]. This proximity enables elephants to raid crops, sometimes destroying entire harvests of smallholder farmers (MacKenzie and Ahabyona 2012; Alfred 2014). Additional impacts include property damage, human injury and fatalities, and occasional traffic collisions involving elephants. Some communities believe oil infrastructure within MFNP has disrupted migration routes, contributing to increased incursions (Dowhaniuk et al. 2018; Grogan et al. 2019). In response, local leaders have at times called for retaliatory killings of elephants (Monitor 2016).

These pressures are likely to intensify as Uganda's population is projected to increase from 48.7 million in 2023 to 85.4 million by 2050 (WHO 2025), placing greater pressure on land in and around the Park and increasing competition with wildlife. Addressing this complex landscape will require management

[1]https://www.protectedplanet.net/956?utm

approaches that carefully balance ecological and socio-economic priorities, enabling both elephants and local communities to recover and thrive without undermining each other's long-term prospects.

Methodology

Study Area

Murchison Falls National Park (3,898 km²) is located in northwest Uganda. It forms a part of the wider Murchison Falls Conservation Area (MFCA) including Karuma Wildlife Reserve (678 km²), Bugungu Wildlife Reserve (474 km²) and Budongo Forest Reserve (817 km²) (Plumptre et al. 2015b). The MFCA is bisected by the Victoria Nile that flows east to west through the MFNP from Karuma Falls to its confluence with Lake Albert (Fig. 1a). The area features expansive grasslands, acacia woodlands, and dense stands of *Borassus aethiopum* palms, whose seasonal fruits are consumed and dispersed by elephants. Elevation rises from approximately 650 m a.s.l. along the Albert Nile in the west to 1290 m on the eastern boundary. Rainfall is bimodal, with peaks from mid-March to May and mid-August to November (Grogan et al. 2019), and mean annual temperatures average 31°C, with peaks exceeding 40°C in February.

The landscape has changed substantially in recent years following the discovery of oil within and around the Park. There are now over 400 oil wells within MFNP and surrounding areas (Climate Rights International 2024), alongside new infrastructure including a bridge across the Victoria Nile and an upgraded 12 m-wide tarmac road running 85 km from Kichumbanyobo Gate in the south to Tangi Gate in the north. Speed bumps and cameras have been installed to reduce wildlife–vehicle collisions (S. Goss, pers. comm., 12 August 2025).

The study area comprised community lands along MFNP's north-western boundary (2.4512°–2.6331°N; 31.4469°–31.7709°E), bounded by the Park to the south and the Aswa River to the north, an area that was formerly part of the Aswa-Lolim Game Reserve linking MFNP to East Madi Wildlife Reserve (Fig. 1b), and now forms part of Got Apwoyo Subcounty, Nwoya District, with a population of approximately 10,000 (https://statistics.ubos.org). Kita and Latoro are small towns near the Park boundary that experience crop raiding (Oniba and Robertson 2019). Most households rely on cultivation as their primary livelihood, typically farming plots of 0.5–1.5 ha that produce cassava, *simsim* (sesame), beans, groundnuts, and maize (Alfred 2024). In the east, commercial farms grow rice and soybeans. The bimodal rainfall pattern supports two agricultural growing seasons, in March–July and August–December. However, the widespread cultivation of long-maturing crops such as cassava and sweet potato prolongs productivity beyond these periods, so fields remain under cultivation for most of the year. Most fields are bare only in February–March, after dry-season burning and before planting.

To supplement farming income, some households engage in illegal activities including poaching, charcoal production, timber harvesting, and firewood collection. Charcoal production drives extensive deforestation around MFNP, particularly in private and community forests, reducing woodland forage and cover for elephants (Forest Trends 2024; S. Goss, pers. comm., 4 July 2025). Forest clearance is linked to increased elephant crop raiding in farms near forest edges, creating a feedback loop that intensifies HEC (Puyravaud et al. 2019).

To address crop raiding, community wildlife scouts monitor elephant movements, respond to incursions, and report illegal activity. Deterrents such as "smelly repellents" have been successfully piloted (Oniba and Robertson 2019), but beehive fences installed near the Latoro ranger post were later abandoned due to lack of maintenance. Four ranger posts were operational until 2022, when one was dismantled in 2022 following community evictions in Kita village (Fig. 3). Since then, a 44 km electric fence has been built along the Park's northern boundary (Fig. 1a), with 101 km planned in total (UWA 2023). The area is an increasingly popular tourism destination, supporting about 20 lodges, mainly in the southwest, and offers trophy hunting safaris run by a private concession.

Data collection

GPS collaring was conducted between 2020–2022 in the northern section of MFNP, above the Victoria Nile. Ground-based elephant observations (2019–

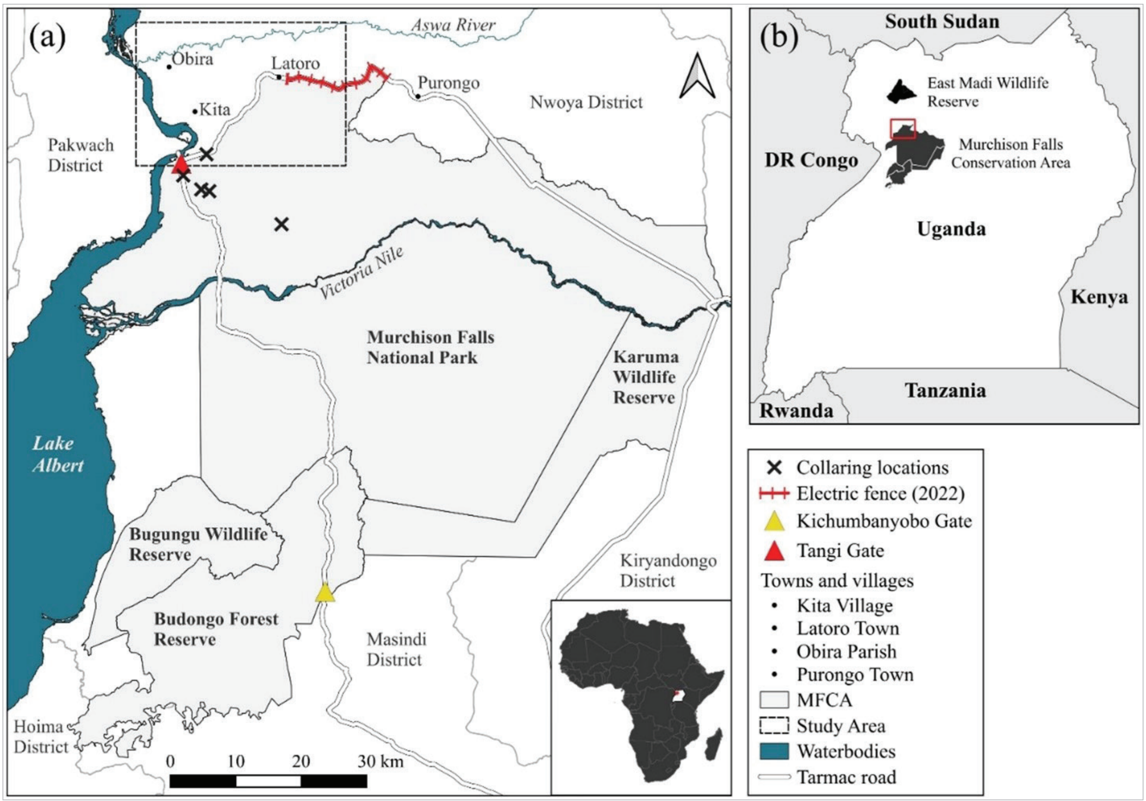

Figure 1. Murchison Falls Conservation Area. The rectangles (left panel: dashed line; right panel: red line) indicate the location of the study area to the northwest of Murchison Falls National Park.

2020) and crop-raiding surveys (2020–2021) were conducted in community areas along the Park's northwestern boundary (Fig 1b). We combined data from these sources to investigate elephant movement patterns. The study area was remote, with limited road access and several safety concerns, including dangerous wildlife in tall grass, poaching activity, active evictions (notably in Obira Parish), and proximity to military and private installations. Due to these constraints, we adopted a convenience sampling strategy that prioritized safe and accessible areas, resulting in under-sampling in the north-west. To expand coverage, we established a community volunteer network in 2019 around Kita Village (west) and Latoro Town (east), identified during early meetings with local leaders and farmers as sites of frequent elephant activity. Some residents expressed concerns that the study was related to land acquisition, and field teams were occasionally stopped for clarification. In response, we distributed informational booklets in the local languages (Alur and Acoli) explaining the project's aims and encouraging residents to report elephant sightings and crop-raiding incidents.

We conducted ground-based observations three to five times per week using a 4 × 4 vehicle or motorcycle, primarily along the Gulu–Arua highway and other accessible public roads. Each session lasted approximately three hours and occurred at various times of day. When elephants were observed, we recorded group size, number of individuals, sex, behaviour (feeding, walking, resting), and GPS location. Where possible, we took high-resolution photographs and documented indirect signs of elephant presence such as dung and footprints. As the study progressed, we noticed visible snare injuries to some elephants' trunks and legs (Fig. 2). Although snares are typically set for smaller game, elephants can become entangled while foraging, indicating ongoing poaching-related harm. As these injuries were not always easily detected in the field, we used high-resolution photographs to create an individual identification database and improve snare injury detection. Identification followed Elephant

Table 1. Summary of five collared elephants inside Murchison Falls Protected Area on 2–3 December 2020. Ages were estimated from photographs for four individuals: the age of one elephant was unknown.

Elephant ID	Group composition at collaring	Approx. age	Snare injuries
Male-3477	Adult male	35–49	Left front leg minor snare scar
Male-3478	Adult male	35–49	None
Female-3479	3 female adults, 1 juvenile	–	Trunk tip missing
Female-3480	3 female adults, 1 juvenile, 1 calf	20–25	Trunk tip missing
Male-3481	Adult male	Late 20s	Trunk tip missing

Voices protocols[2] using features such as ear notches, body markings, tusk shape and length, and tail morphology. The database continues to expand as part of ongoing monitoring.

To document crop raiding, we trained two local field assistants to conduct regular bicycle patrols in and around the same two focal areas—Kita and Latoro—between January 2020 and November 2021. Patrols occurred three to five days per week, depending on the assistants' household and farming commitments. Given the large area and variable community engagement, we adopted an opportunistic sampling approach: when assistants encountered farmers during patrols, they conducted brief interviews about recent elephant sightings or crop damage. Farmers also contacted the assistants directly to report incidents, and the team responded when possible. Where fields were accessible, we obtained permission to collect data. We used standardized forms to record crop type, estimated damage by percentage (visual), crop stage (seedling, intermediate, mature), crop quality (poor, medium, good), and protective measures (Hoare 1999). Reports also included date, time, location, estimated number of elephants, and presence of calves (as a proxy for family groups). Farmers could add other relevant observations under "other comments". Separate forms were used for fields with different crops; raids on intercropped plots were recorded as single incidents due to the overlap in damage. GPS-tagged photographs were taken during visits, and assistants recorded sightings and indirect signs such as dung and footprints.

In December 2020, we fitted five elephants with Savannah Tracking GPS collars. Collaring was conducted by UWA veterinary teams over two days using four vehicles, prioritizing individuals near the northern boundary of MFNP where elephants regularly approach farmland (inside the Park 0.15–15.24 km from the main road; Fig. 1). Three adult males and two adult females from small family groups were collared (Table 1). Four of the elephants showed signs of snare injuries. Collars were programmed to transmit hourly locations from December 2020 to November 2022, balancing spatial resolution with battery life.

Data analysis

We undertook a preliminary descriptive analysis to identify spatial and temporal patterns in elephant movements and crop-raiding incidents. The aim was to provide a foundation for future work that will undertake a more detailed examination. All summary statistics were generated in RStudio (version 2024.04.2). From the ground observation data, we calculated the proportions of male and female elephants recorded outside MFNP, the median group size and the proportion of sightings with visible snare injuries. Estimates of snare injuries were also derived from the photographic identification database.

GPS collar data were mapped and visually examined in QGIS (version 3.34.15–Prizren) to provide an overview of movement patterns. Elephant movement is shaped by environmental features such as water availability, vegetation, topography and tree cover (Mlambo et al. 2024). To investigate these relationships, we compiled relevant environmental

[2]https://www.elephantvoices.org/

Figure 2. Common snare injuries observed during ground surveys. Left: foreleg wounds (treated by UWA veterinarians, November 2020). Right: partial trunk loss (June 2019). Similar injuries were seen on four of the collared elephants.

shapefiles from open-access sources, including protected areas (National Forest Authority 2007; via DataBasin.org), roads (datashare.ed.ac.uk), 30 m SRTM elevation data, tree cover (via Digital Earth Africa), and waterbodies (global-surface-water.appspot.com). Further details are available from the authors on request.

Minimum convex polygons (MCPs) were generated to delineate the outer boundaries of individual elephant ranges, and kernel density estimation (KDE) was applied to identify core activity areas. For each collared elephant, we calculated the distance from every GPS location to the nearest tree cover, water source, Park boundary (the Gulu–Arua highway), crop-raiding GPS point (used as a proxy for farmland), and the MFNP boundary (with locations inside communities coded as 0) using the Distance to Nearest Hub tool. Elevation values were extracted directly from the elevation raster. To examine seasonal differences, we compared median distances between wet (April–May; August–November) and dry (December–March; June–July) seasons in 2021, the only year with complete data for four elephants. We also compared elephant movements and the frequency of crop raiding with rainfall patterns and local farming calendars. Seasonal MCPs were also generated to assess variation in overall range use.

Outside MFNP, we analysed distances of collar locations to trees, water, and crops. Crop distance calculations were based on recorded raiding sites collected during field surveys, rather than a comprehensive farmland layer, and therefore underrepresent the true extent of cultivated land. Therefore, we restricted the analysis to GPS points located within identified crop-raiding zones, where farmland presence was confirmed. For this component, we used the full collaring dataset (n = 1,608) rather than 2021 alone (n = 507) to increase sample size. We further limited the analysis to the two elephants (Female-3480 and Male-3481) that contributed most GPS locations outside the Park.

To examine crop-raiding patterns, we calculated monthly incidents in the Kita and Latoro zones, the proportions of incidents by crop type, crop stage, and crop quality, and the median number of elephants (including calves) involved. The total area of crops damaged was derived from reported land size and percentage damage. We also estimated the proportion of farmers who reported using protective measures such as lighting fires and constructing fences).

Results

Crop raiding

We collected 733 crop-raiding forms between January 2020 and November 2021 (Fig. 3) These reported 885 instances of crop raiding including 117 cases involving multiple crops, with damage to 988 ha (23% of the cultivated area). The number of incidents declined from 507 in 2021 to 207 in 2020. Thirty types of crops were raided, with most incidents affecting intermediate-stage crops and some regional variation in damage extent (Table 2; Fig. 3). Damage ranged from <1% to total crop loss, with a median of 30%. The distribution was right-skewed: 42% of farms lost <21%, while 25% lost >50%. Farmers reported a median of four elephants per raiding group, with the largest group comprising up to 30 individuals, and calves were present in approximately 20% of events. Most crop-raiding incidents (98%) occurred at night with a pronounced peak (n = 353; 48%) between 21:00 and 23:00. Raiding events peaked in June–July and October–November in both 2020 and 2021 and were rare during the planting season (March–April) (Fig. 4). Although most crops are dormant during the January–February dry season, long-maturing crops remain vulnerable, with 51 raids on cassava and sweet potatoes recorded during this period in 2021. Correspondingly, 19% of collaring points in January–February 2021 fell within community areas (mostly for Male-3481) (Fig. 6 below). Only 68 informants (9%) reported taking preventive measures to deter elephants before an incursion occurred. These included lighting fires (30 records), using dogs to raise the alarm (13), constructing

Table 2. Summary information from the crop raiding forms.

Summary information		**Western region**		**Eastern region**		**Total**	
		No.	**%**	**No.**	**%**	**No.**	**%**
Crop raiding forms submitted	Forms submitted	332	45	401	55%	733	100
	Records[a]	414	47	471	53	885	100
	Intercropping records[a]	83	20	57	12%	140	100
Top crops damaged[b]	Maize	129	**26**	82	**15**	211	**20**
	Cassava	170	**34**	19	3	189	**18**
	Rice	7	1	135	**25**	142	**14**
	Groundnuts	33	**7**	71	**13**	104	**10**
	Sweet potato	27	5	69	**13**	96	**9**
	Simsim	43	**9**	21	**4**	64	6
	Cotton	39	**8**	-	-	39	4
Crop age[c]	Mature	135	41	167	41	302	41
	Intermediate	175	53	218	53	393	53
	Seedling	20	6	24	6	44	6
Crop quality[c]	Good	187	57	148	36	335	46
	Medium	119	36	251	62	370	50
	Poor	23	7	9	2	32	4
Land size (ha)	Median	2.5	-	2.5	-	2.5	-
	Maximum	14.8	-	247.1	-	247.1	-
Area damaged (ha)	Total	356.7	-	641.1	-	997.8	-
	Median	0.74	-	0.49	-	0.61	-
No. of elephants per raid	Median	5	-	4	-	4	-
	Maximum	30	-	20	-	30	-
Forms reporting calves present	Total	21	6	127	32	148	20

[a]When raids on multiple crops were reported on a single form these were recorded as separate instances if they occurred in distinct plots. Otherwise, they were recorded as a single “intercropping” raid.
[b]Counts of the number of crops were drawn from all records, since a single form could include more than one crop type.
[c]Data on crop age and quality calculations exclude intercropping records, as well as records with missing or unknown responses.

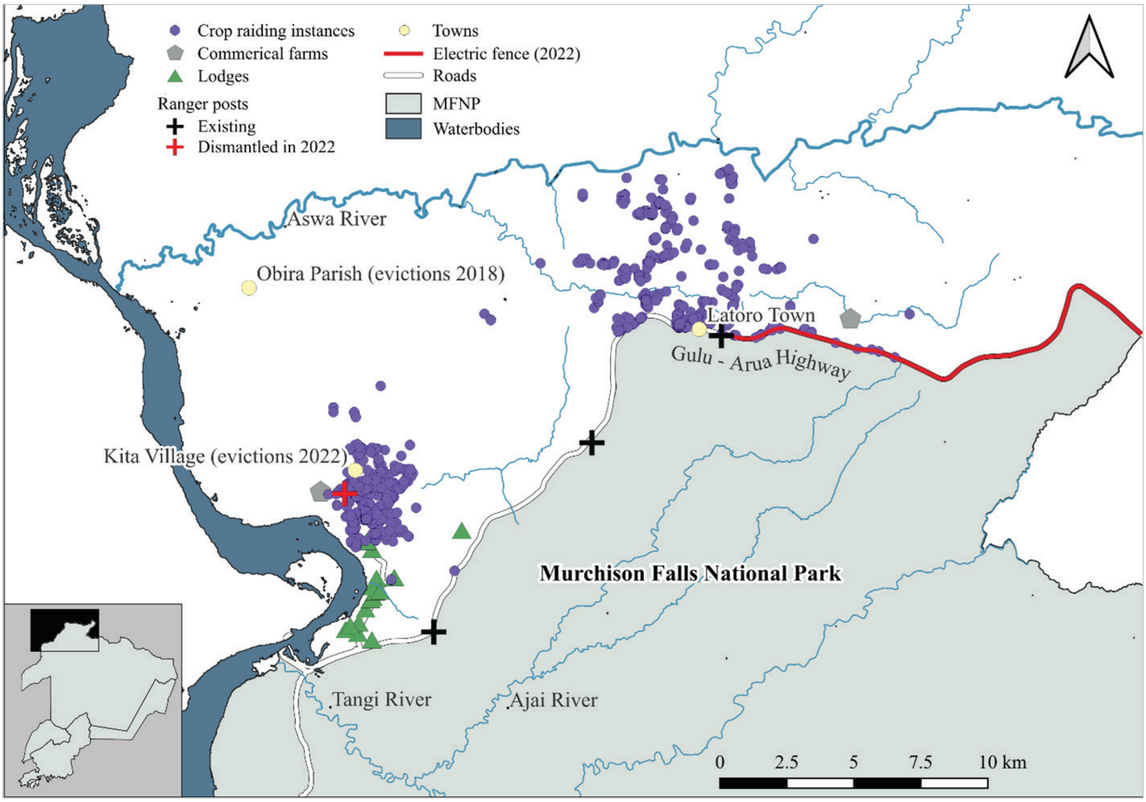

Figure 3. Instances of crop-raiding within reported in the study area between January 2020 and November 2021.

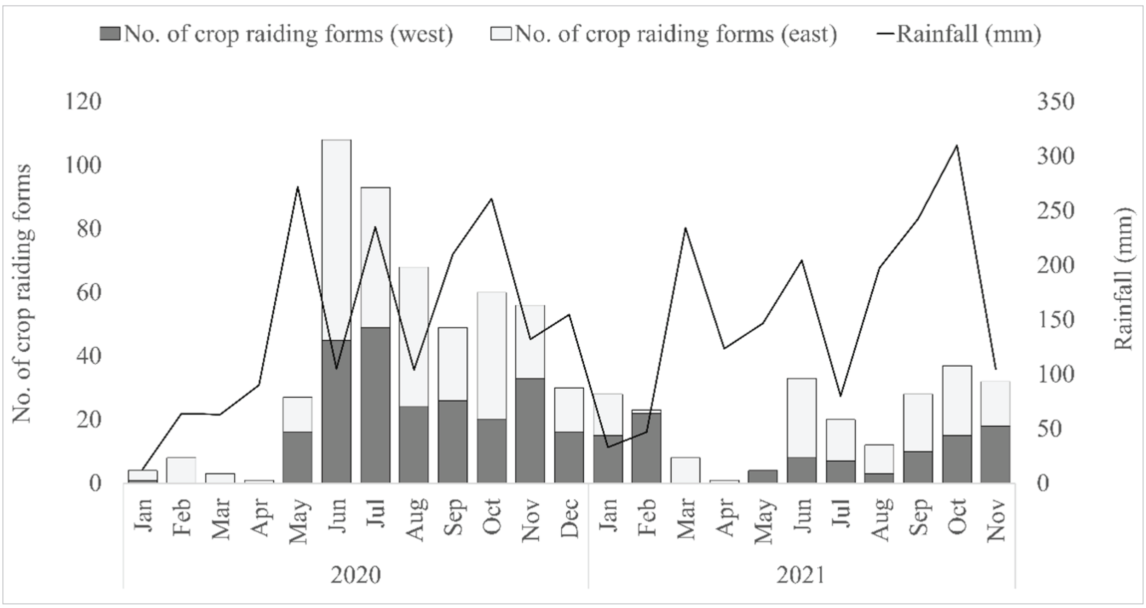

Figure 4. Monthly numbers of crop-raiding reports from communities adjacent to MFNP in the western (Kita Village) and eastern (Latoro Town) regions, 2020 to 2021. Rainfall data were obtained from Agriserve Ltd.

fences (8), burning dung or tyres (7), sleeping or guarding in fields (5), using smelly repellents (3), torches (1), and scarecrows (1). However, most households, (96%), households relied on reactive responses once elephants were already present, typically chasing them away, flashing torches, throwing stones, or, occasionally, scare shooting by UWA rangers. During the peak raiding periods, vuvuzelas were frequently heard throughout the night around Kita Village. Farmers who did not chase elephants cited reasons such as being unaware of their presence (asleep, not heard due to rain, or away from home), fear, or "lack of effort".

Elephant ground surveys and collaring

Of the 1,131 ground-based elephant observations recorded either within community areas (50%) or just inside the Park near the Gulu–Arua highway boundary (median distance 100 m, maximum 1 km), 90% involved males. The number of elephants sighted ranged from 1–24 (mean = 5) individuals. Snare-related injuries were observed in 132 cases (12%), and photographic identification of 38 elephants showed that 12 (32%) had visible trunk injuries, likely caused by wire snares.

Transmission durations of collared elephants varied among individuals, with the shortest lasting 129 days (Male-3477, ending April 2021) and the longest continuing until November 2022 (Male-3477 and Female-3480; Table 3). The home ranges of the five collared elephants (Fig. 5a) ranged from 309–883.5 km², with total movement distances of 2,165–3,528 km and 0–24% of GPS points outside the Park (Table 3). Collar tracks from five elephants revealed concentrated activity around the Tangi River in the northwest, the Nile Delta in the southwest, and along the shorelines of the Nile (Fig. 5a; 5b). Field and satellite observations confirmed that the Tangi hotspot is characterized by availability of water sources, wetlands, low terrain, and extensive *Borassus* and acacia woodland (Fig. 5b). Evidence of elephants' seasonal use of *Borassus* palm fruits (January–April) was provided by photos from the field showing dung containing palm seeds, supporting the hypothesis that the presence of these palms attracts elephants to the Tangi River area. Multiple movement paths linked the Delta to the Tangi River, suggesting goal-directed movement and possible corridor use, although Male 3481 and Female 3480 stayed mainly within the Tangi area. Elephants generally remained within the north-western section of the Park, with few excursions into the central sector, which may be linked to the rise in elevation from the west near Lake Albert toward the Park interior (600–1,000 m).

Elephants displayed different median distances to water, tree cover and the MFNP boundary, as well as elevation. Distances to trees and water were strongly right-skewed, with annual median and maximum distances, respectively, of 91.2 and 2,729.5 m to trees, and 184.0 m and 952.1 m to water, but seasonal variation was minimal, with median values differing by less than 45 m between wet and dry seasons. Elevations ranged from 619–891 m (median 648 m), with no difference between wet and dry seasons (Table 4).

For elephant movements outside the Park, most data were derived from two individuals—Male-3481 and Female-3480—who together accounted for 92% of all GPS locations recorded beyond MFNP. Their movement patterns contrasted sharply in both seasonality and extent (Fig. 6). Female-3480 had the largest home range (884 km²; Table 4) and travelled furthest from MFNP (21.1 km straight-line distance), crossing the Aswa River twice in 2021 (26 May–1 June; 17 November–1 December), with a third attempted

Table 3. Home ranges and movements of collared elephants

Elephant ID	Days collared	Points outside MFNP	Home range in 2021 (km²)	Distance travelled in 2021 (km)
Male-3477	129	228 (8%)	-	-
Male-3478	725	150 (1%)	673	2,938
Female-3479	674	16 (0%)	309	2,165
Female-3480	725	3,393 (24%)	884	3,528
Male-3481	637	1,248 (9%)	388	2,883

crossing in August 2022 (Fig, 5a). She spent more time outside the Park during the wet season (26.1%) than the dry season (2.2%), and during peak crop-raiding months (19.2%) compared to non-raiding months (9.1%). In contrast, Male-3481 had a smaller home range (388 km²) and spent more time outside the Park in the dry season (15.6%) than in the wet season (2.7%). He also used farmland differently, with slightly more time outside in non-raiding months (10.1%) than in crop-raiding months (8.2%). At the diel scale, collared elephants spent similar times in community areas during the day (48%) and night (52%). However, for the two elephants that ranged furthest into community land, distances to environmental features showed a clear day–night shift (Fig. 7). Male-3481 remained close to trees (57 m) and water (75 m) while avoiding crops (505 m) during the day, but after 19:00 moved sharply towards cropland, with distances to crops dropping to ~61 m around midnight as distances to trees and water rose to >250 m. Female-3480 showed the same pattern but less markedly: daytime distances to crops averaged 408 m but declined steadily after dusk to 144–178 m between 22:00 and 04:00, while distances to trees and water increased during the night.

Discussion

Key findings on elephant movements

Movements recorded from GPS-collared elephants varied considerably among individuals, as is typical in studies with small sample sizes. Nevertheless,

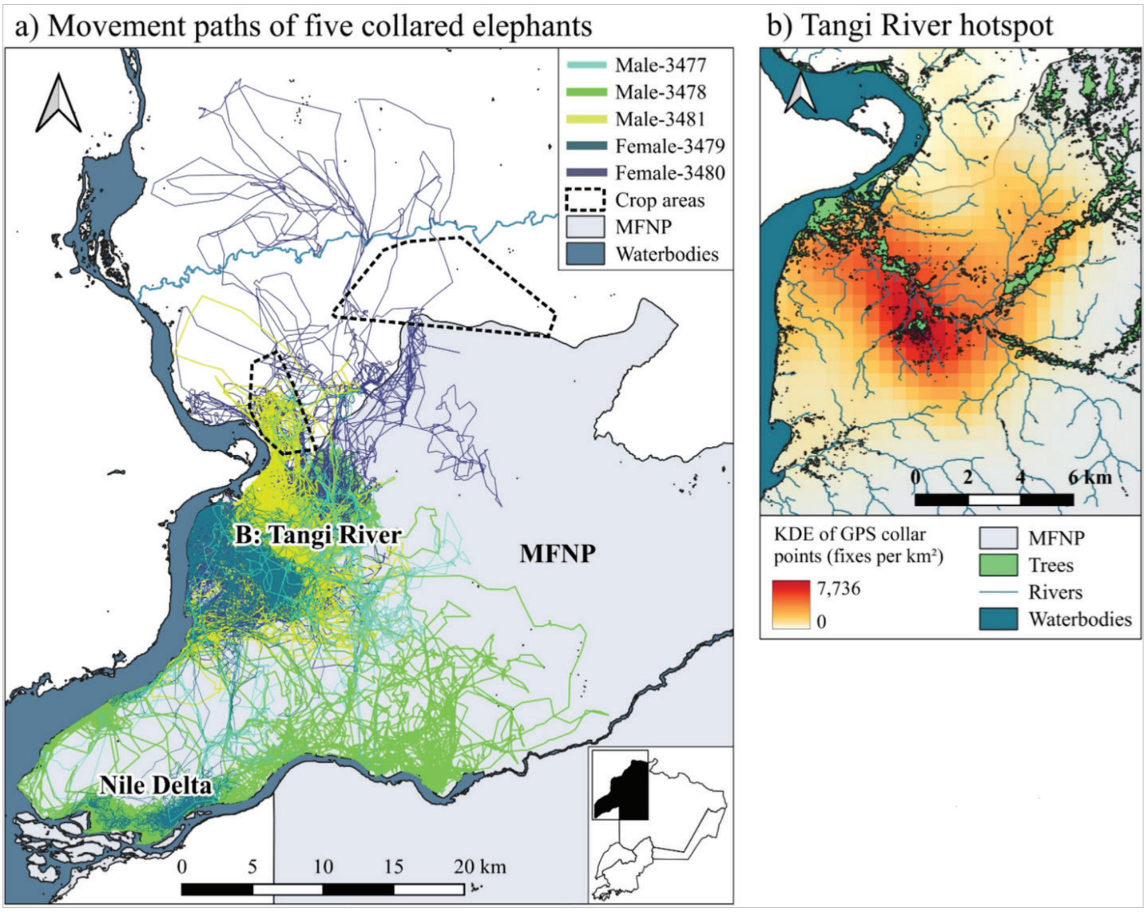

Figure 5. GPS location data for five elephants collared in December 2020. (a) Movement paths in and around MFNP and crop-raiding areas. (b) Kernel density estimation (KDE) analysis –(0.5-pixel, 2-kernel radius) of a hotspot of elephant activity near the Tangi River.

Table 4. Summary of elephant GPS data comparing wet and dry season movements within and around MFNP in 2021.

Elephant ID	Median distances			Movement range (km²)	Median elevation (m)	Points outside MFPA	
	Trees (m)	Water (m)	MFNP boundary (km)			No.	%
Wet season							
Male-3478	48	173	20	567	636	31	0.7
Male-3481	112	200	4	209	650	119	2.7
Female-3479	118	192	20	298	638	6	0.1
Female-3480	101	203	3	842	666	1,132	26.1
Total	**94**	**191**	**7**	**1,375**	**647**	**1,288**	**7.3**
Dry season							
Male-3478	41	173	19	667	654	0	0.0
Male-3481	75	156	3	247	647	673	15.6
Female-3479	140	200	5	217	646	0	0.0
Female-3480	105	177	5	620	649	93	2.2
Total	**88**	**176**	**5**	**1,391**	**648**	**766**	**4.4**

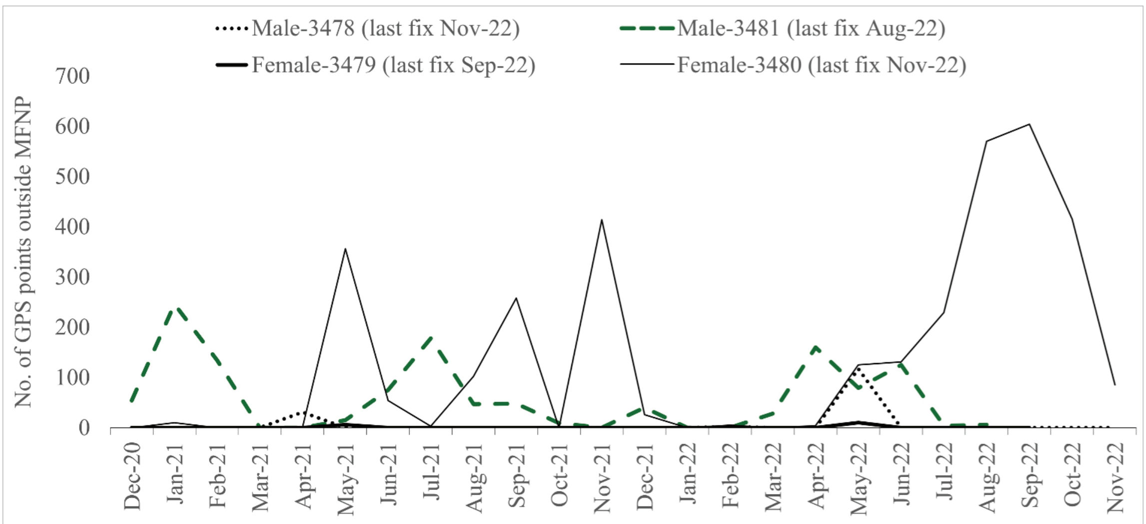

Figure 6. Monthly GPS-collared elephant locations within the community areas.

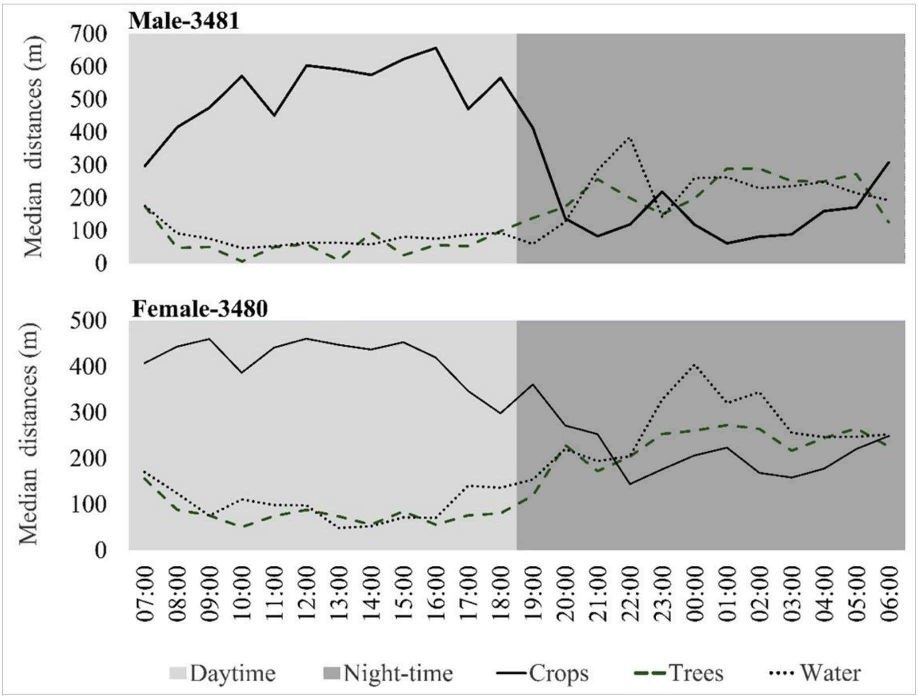

Figure 7. Median hourly distances to trees, water, and crops for two collared elephants within crop-raiding zones outside MFNP (n = 1,608).

movement patterns broadly matched earlier findings for MFNP and other studies of crop-raiding elephants (Graham et al. 2010; Wilkie and Douglas-Hamilton 2018; Grogan et al. 2019). Elephants remained closer to water and tree cover by day and shifted towards croplands at night, with minimal seasonal change, which is consistent with year-round water availability. Limited use of the central and eastern sectors of MFNP likely reflects rising elevation and topographic constraints on movement (Wall et al. 2006). Female-3480 had the largest home range, contrary to expectations of wider male ranging (Duffy et al. 2011). This may reflect the small sample size, but is compatible with mixed evidence reporting either larger male ranges or no sex-based difference (Grogan et al. 2019; Shannon et al. 2006). At the diel scale, collar data indicated that elephants spent comparable time outside the Park by day and night, and ground observations confirmed frequent daytime incursions by males. These results suggest that use of community lands is not solely driven by raiding but also by foraging on non-crop resources (such as the *Borassus* palms and other riverine woodland outside the Park). Future work will develop more detailed spatial models of elephant movements, incorporating additional covariates such as *Borassus* palms, whose fruits are dispersed by elephants. We noted many mature and newly established palms but few mid-aged trees, perhaps reflecting reduced seed dispersal during the elephant population collapse of the 1970s–1990s. *Borassus* also appears to be expanding in parts of the Park, which may be linked to elephants now being more spatially constrained compared to the past. A more detailed ecological study is needed to confirm these patterns.

Key findings on crop raiding

Crop raiding in our study was predominantly nocturnal and peaked in June–July and October–November, aligning with the main farming seasons and interview-based accounts (Alfred 2014). These months coincide with peak crop value, both nutritionally and economically. The two growing seasons and presence of long-maturing staples such as cassava and sweet potatoes expose communities to sustained pressure from raiding across much of the year. Although other studies report a preference for mature crops (Adjewodah et al. 2005; Chiyo et al. 2005), elephants in our study also targeted crops at intermediate growth stages. One explanation is that guarding effort by farmers may be lower at these stages (Tiller et al. 2021). Another is that elephants, which we observed outside the Park during the day, may monitor crop availability and raid as soon as crops become edible. Our surveys also showed that raids involved both males and family groups. This contrasts with expectations that males raid more as part of risk-taking behaviour to maximize reproductive success (Chiyo and Cochrane 2005), whereas females avoid community areas because of risks to themselves and their calves (Sukumar and Gadgil 1988). Crop raiding by mixed groups has, however, been reported elsewhere (Tiller et al. 2021). Further collars and camera traps are needed to clarify group composition in this landscape.

Farmer responses were largely reactive, involving noise, lights, and chasing, consistent with other studies (Mackenzie and Ahabyona 2012). Preventative deterrents were rarely used (e.g. fences, smelly repellents), likely due to cost or lack of knowledge. Reactive tactics rarely stopped damage; instead, they often pushed elephants back and forth between farms, creating a kind of 'elephant pinball' that increased stress for both farmers and elephants. Consequently, most farms still suffered losses, with the majority experiencing less than 20% damage, consistent with similar studies (Adjewodah et al. 2005). However, the impacts of even such modest losses can be severe for small farmers relying on cash crops to earn a living. Finally, the lower number of reports in 2021 most likely reflects research fatigue rather than reduced raiding. Several respondents stated that people would cease volunteering without tangible support, citing previous NGO activities that provided little benefit to communities. This underscores the need to pair monitoring with practical support, which we now discuss.

Implications for management in a changing landscape

Two cropping seasons expose communities near MFNP to crop raiding for much of the year. Mitigation must therefore deliver year-round deterrence while remaining financially viable and preserving habitat connectivity. Preliminary evaluation of the 44 km Latoro Town fence indicates a reduction in crop raiding (Luwaga 2025). However, extending fencing along the entire boundary would be costly, restrict wildlife movements, and risk both stranding elephants outside the Park and increasing densities inside to unsustainable levels, requiring renewed culling (Laws et al. 1970). Alternatively, UWA could deploy targeted electric fencing and trenches in community lands in the western and eastern farming zones, while maintaining a central corridor to retain historic movements from the Park northwards. Re-establishing a corridor to East Madi Wildlife Reserve (c. 70 km) is unlikely in the near term, but a shorter corridor to the Aswa River (c. 12 km) offers a pragmatic starting point.

Funding could draw on corporate social responsibility partnerships with oil companies (notably Total Energies and the China National Offshore Oil Corporation), tourism revenues, and NGO support, with resources ring-fenced for maintenance, monitoring, and community engagement. Community-led arrangements could further strengthen implementation. UMOJA is a grassroots initiative that works with private landowners to integrate conservation and livelihoods[3]. In a facilitation role, UMOJA could support inclusive consultations, design benefit-sharing frameworks, and develop lodge partnerships for tourism, while building local support for conservation through education (Gessa et al. 2024). However, re-establishing a corridor raises ethical concerns, as restricting land access in a region marked by displacement risks reinforcing past injustices. A detailed feasibility and ethical assessment would therefore be essential before implementation. The assessment should be undertaken swiftly before further land conversion forecloses the corridor option.

While broader debates over fencing and corridors continue, immediate support for communities adjacent to MFNP is essential. Our data show that most households lacked preventive measures and relied on reactive tactics such as chasing or shouting, which were ineffective and dangerous. Farmers often acted individually rather than collectively, driving elephants between fields and increasing risks at night. We recommend providing training and equipment for collective guarding, alongside expanded community scout programmes under UWA's leadership. Options include lookout towers, alarms, and low-cost tools such

[3]https://umojaconservancies.com/

as vuvuzelas and bangers, which can be effective when used cooperatively (Guerbois et al. 2012). Existing tools, such as the *Human–Elephant Coexistence Toolbox*[4] could be presented directly to communities, enabling them to select measures they are willing and able to adopt (Montgomery et al. 2022). This is crucial in a region marked by long years of exclusion from participation in management and the legacy of displacement. In March 2022, for example, all residents of Kita Village were evicted for a foreign-owned soybean plantation, and the dismantling of the ranger post has left neighbouring communities even more exposed to crop raiding. With partial protection now provided by electric fencing in Latoro Town, attention should shift to remaining communities in the Kita area and further north, focusing on the adoption of preventive strategies before elephants expand further.

Conclusion

This study examined elephant movements in and around northern MFNP and assessed the extent of crop raiding in neighbouring communities. The findings align with patterns reported elsewhere: elephants concentrated near water and tree cover, and at low elevations, shifting towards farms at night. Raiding began as soon as crops became edible, facilitated by the regular presence of elephants in community lands, which allowed them to monitor availability. Movements outside the Park were not confined to crop raiding; elephants also entered farmland during non-peak seasons and in daylight, suggesting they were seeking non-crop resources such as trees and browse. These resources are being increasingly reduced by deforestation, which may further intensify crop raiding. With crops maturing across much of the year, households are under sustained risk from crop raiding with limited deterrents. Such pressures may drive households toward coping strategies such as charcoal production or poaching, reinforcing cycles of poverty, deforestation, and conflict.

Balancing elephant conservation with community needs and an increasing population remains a central challenge. We make three recommendations. First, reduce wire-snare poaching, which causes serious injuries to elephants and other wildlife. Detection could be improved by using machine learning to map high-risk areas, guiding patrols more effectively, and deploying practical aids like snare-detecting dogs. Ground-penetrating radar may help, though cost and field conditions are major constraints (Feldmeier et al. 2025).

Secondly, investment is needed to support frontline communities in the west, especially near Kita Village, where recent evictions leave both the remaining residents and neighbouring communities to the north more exposed to elephants. Training in elephant deterrence and crop protection, together with scout programmes and equipment, could strengthen collective capacity to reduce damage and risks. Thirdly, a feasibility study should evaluate whether land between the western and eastern raiding zones could be retained as a managed corridor or wildlife tourism area. This assessment should focus initially on maintaining connectivity up to the Aswa River. It would need to address resident populations, land tenure, and the practicality of fencing or trenches, alongside financial, ethical, and ecological considerations. Adopting electric fencing as the sole strategy could cause permanent loss of elephant habitat outside the Park. The resulting concentration of elephants within MFNP could accelerate woodland degradation compel UWA to reconsider measures such as culling.

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[4] https://ste-coexistence-toolbox.info/en/

former Chief Warden of MFNP and Kibale NP; Dr Ronald Clarke, Rutgers University; and Tito Dal Lago, Doctors with Africa CUAMM. Their support and insights are still deeply valued.

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Assessing crop palatability as a tool to mitigate elephant crop raiding: trade-offs and strategies for subsistence farmers in Lower Sagalla, Kenya

Sophia L Weinmann[1,2], Kennedy L Leneuiyia[1,3], Lucy E King[1,4], Jill M Belsky[2]*

[1]Save the Elephants, PO Box 54667, Nairobi 00200, Kenya
[2]College of Forestry and Conservation, University of Montana, Missoula, MT, USA
[3]Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK
[4]Department of Biology, University of Oxford, Oxford, UK

*corresponding author: slweinmann@gmail.com (orcid: 0009-0009-9905-6701)

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Abstract

Enabling the coexistence of elephants and humans is challenging, especially in areas where elephants venture outside protected areas to raid crops. This creates human-elephant conflict (HEC), jeopardizing farmers' food production and economic security, impeding elephant conservation efforts and threatening the safety of both humans and elephants. Understanding the palatability of different crops to elephants is fundamental for mitigating raiding behaviour, however, species-specific crop palatability remains poorly understood. In this study, we conducted on-site farm experiments and semi-structured interviews to evaluate the suitability and palatability of moringa (*Moringa oleifera*) and sunflowers (*Helianthus sp.*) to African savannah elephants (*Loxodonta africana*) in comparison to the highly palatable and locally valued maize (*Zea mays*). We established 30 experimental plots of the three crops across ten farms in Lower Sagalla, a community adjacent to Tsavo East National Park, that frequently experiences elephant crop raiding. We assessed elephant crop palatability through foraging observations and evaluated agronomic suitability using germination and survival rates. Our findings revealed that farmers were divided in their opinions regarding the palatability of moringa to elephants; however, there was a consensus that sunflowers were non-palatable to them. Our experiments confirmed that both crops were significantly less palatable to elephants than maize. We conclude that cultivating non-palatable crops represents a promising strategy for reducing elephant crop raiding and diversifying livelihoods in Lower Sagalla. Nevertheless, the success of this approach as conservation and livelihood tools depends on favourable climatic conditions, and agricultural, economic, and cultural contexts, which are highly integrated and dynamic. Additional institutional support through agricultural extension services and market development is also necessary for effective implementation.

Résumé

Rendre possible la coexistence des humains et des éléphants représente un défi, en particulier dans les régions où les éléphants s'aventurent hors des zones protégées pour piller les cultures. Ces incidents, qui entraînent des conflits humains-éléphants (CHE) et mettent en péril la production alimentaire des agriculteurs et leur sécurité économique, entravent les efforts de conservation et menacent la sécurité des humains comme des éléphants. Si la compréhension de l'appétence des éléphants à l'égard de différentes cultures est fondamentale pour atténuer les comportements de pillage, l'appétence propre aux espèces envers certains végétaux reste toutefois mal comprise. Dans le cadre de cette étude, nous avons conduit des expériences sur le terrain ainsi que des entretiens semi-structurés afin d'évaluer l'adéquation et l'appétence du moringa (*Moringa* *oleifera*) et du tournesol (*Helianthus sp.*) pour les éléphants de savane d'Afrique (*Loxodonta africana*) par rapport au maïs (*Zea mays*), hautement appétant et localement valorisé. Nous avons installé trente parcelles expérimentales de ces trois cultures sur dix fermes du Lower Sagalla au Kenya, une communauté contigüe au parc national de Tsavo East qui subit de fréquents pillages de la part des éléphants. Nous avons examiné l'appétence de ces cultures par le biais d'observations du comportement alimentaire des éléphants, et évalué l'adéquation agronomique de ces végétaux selon leur taux de germination et de survie. Nos résultats révèlent que les agriculteurs avaient des opinions divergentes quant à l'appétence du moringa pour les éléphants, mais il y existait toutefois un consensus autour de la non-appétence des tournesols. Notre expérience a confirmé que les deux cultures étaient nettement moins appétentes que le maïs. Nous en concluons que la culture de végétaux non appétants représente une stratégie prometteuse afin de réduire les pillages de cultures et de diversifier les sources de revenus dans la région du Lower Sagalla. Néanmoins, la réussite de cette approche en tant qu'outil de conservation et de renforcement des moyens de subsistance dépend de conditions climatiques favorables, et de contextes agricoles, économiques et culturels dynamiques et hautement intégrés. Un soutien institutionnel supplémentaire, sous la forme de services de vulgarisation agricole et de développement de marchés de distribution, est nécessaire pour une mise en œuvre efficace.

Introduction

Kenya's elephant (*Loxodonta africana*) population is approximately 36,280, with the Tsavo ecosystem hosting the country's largest population, approximately 14,964 elephants (Waweru et al. 2021). In 2017, aerial surveys by the Kenya Wildlife Service and the Tanzania Wildlife Research Institute revealed a 15.1% increase in the Tsavo ecosystem elephant population since 2014 (Ngene et al. 2017). While growing elephant populations are a conservation victory, the simultaneous fragmentation of habitat by human development has made human-elephant conflict (HEC) increasingly common (Thouless 1994). For farmers adjacent to protected areas, elephants can represent important challenges. For instance, elephants can cause extensive crop loss through trampling or directly feeding on crops (Vogel et al. 2020). These incursions also cause property damage, pose risks to human safety, and demand considerable time for guarding, often diverting labour from other livelihood activities. In some cases, students miss school to guard family farms or avoid elephant-prone routes, with measurable impacts on academic performance such as lower mean grades in schools located within elephant ranges (Mackenzie and Ahabyona 2012). The cumulative economic losses, persistent fear, and insecurity reinforce negative perceptions of elephants and exacerbate HEC (Nyumba et al. 2020).

The foraging ecology of elephants, characterized by high nutritional demands and selective feeding, often brings them into direct conflict with farmers, especially subsistence farmers living on the boundaries of protected areas (PAs). Historically, elephants met their nutritional needs within extensive habitats, but habitat loss and compression now limit access to natural forage, leading them to rely more on crops, which offer concentrated nutrients (Chama et al. 2025). Due to their large food requirements, a small herd of elephants can deplete the crops of a small-scale farm in one night. This is especially critical when it impacts subsistence farmers whose production matches their consumption with minimal surplus as it severely threatens their food security and income generation capacity (Sitati et al. 2005; Mackenzie and Ahabyona 2012). Such vulnerability to crop depletion has compelled subsistence farmers to devise and adopt a range of defensive measures to deter elephants from their fields. For instance, subsistence farmers have historically relied on basic, traditional elephant deterrent techniques such as shouting, banging objects, lighting fires, throwing stones, and using guard dogs to protect their farms (Graham and Ochieng 2008). However, these methods demand substantial labour and time investments from farmers and may lose their effectiveness over time as elephants habituate to them (Sitati et al. 2005).

The limitations of these traditional methods have spurred the development of a wider suite of advanced mitigation strategies. Among these are physical barriers, such as trenches, stone walls, and electric fences. Although farmers often identify electric fences as a highly effective elephant deterrent, their high cost makes them inaccessible for most subsistence farmers

(Thouless 1994). As a result, significant focus has shifted toward more affordable behavioural deterrents, such as the development of beehive fences that exploit elephants' natural avoidance of bees (King 2010), as well as chilli-based (Osborn and Parker 2002) and olfactory repellents (Tiller et al. 2022). Development has also progressed on broader management strategies, including coordinated community guarding (Osborn and Parker 2002), problem-animal translocation (Tiller et al. 2022), and land-use planning for wildlife corridors (Vasudev et al. 2023). These approaches are increasingly complemented by emerging technologies like GPS-based early-warning systems. Furthermore, proactive strategies such as the cultivation of less palatable and or non-palatable crops have gained traction, with evidence supporting their use to reduce crop raiding (Gross et al. 2015).

Elephant crop foraging behaviour is highly selective, driven by a preference for high-calorie crops and a consistent avoidance of those with lower nutritional returns or strong chemical defences. For instance, African elephants have consistently demonstrated a preference for energy-dense crops like maize, bananas, and beans, which offer high nutritional returns (Matsika et al. 2020). Conversely, they actively avoid plants with innate chemical defences, such as chillies, garlic, ginger, and onions (Gross et al. 2015). The empirical consequence of this selectivity is clearly demonstrated, for instance, in the Tsavo ecosystem, where maize accounted for 61% of all crop raiding incidents (Smith and Kasiki 1999). This foraging strategy has profound implications for HEC. For example, research on chillies demonstrated that growing non-palatable cash crops instead of maize can reduce crop loss and increase income per hectare (Parker and Osborn 2006).

Therefore, to mitigate crop raiding and foster human-elephant coexistence (HECx) among subsistence farmers, cultivating less palatable crops offers a targeted strategy to reduce field attractiveness and minimize conflict. This approach aligns with optimal foraging theory by lowering the nutritional incentive for elephants to raid farms, thereby directly supporting farmer livelihoods while advancing elephant conservation efforts. Although growing non-palatable crops depends on the soil, climate, economic factors, and people's traditions (Montero-Botey et al. 2021). There is still a knowledge gap concerning the evidence of palatability of many crops, including sunflowers (*Helianthus sp.*) and moringa (*Moringa oleifera*) to elephants, and how both elephant preference and crop utility jointly influence farmers' decisions. To address this, we employed a mixed-methods approach integrating on-farm experiments with farmer interviews to: i) compare elephant preference for maize, moringa, and sunflowers; ii) evaluate their agronomic suitability via germination and survival rates; and iii) understand factors influencing their adoption by farmers.

Study area

This study took place in two villages at the base of Sagalla Hill that are home to approximately 340 households and 1,300 residents and is referred to as Lower Sagalla (King et al. 2024) (Fig. 1). Lower Sagalla is within the Tsavo Conservation Area, approximately 3 km from Tsavo East National Park (NP) and has an elevation of ~600 m (King 2010). It borders the Park along the Nairobi–Mombasa Standard-Gauge Railway (SGR), which is fenced but includes two designated wildlife underpasses. Farms in Lower Sagalla have become a hotspot for HEC; elephants regularly access croplands via these underpasses and through adjoining communal and private lands to the west. Studies have found that, some underpasses can funnel elephants into community areas, increasing the likelihood of crop raids and HEC, highlighting the need for infrastructure designs that consider both wildlife movement and the protection of local communities (Okita-Ouma et al. 2021).

Subsistence farming is the primary or only income source for many in Lower Sagalla (Smith and Kasiki 1999). Farmers predominantly grow maize, cassava, watermelons, cowpeas, and mung beans as well as farm livestock (MoALF 2016). According to the Kenya Ministry of Agriculture, Livestock, and Fisheries (MoALF 2016), "between 61 and 80% of the population of Taita-Taveta County is engaged in maize production, mostly at a small scale". Despite high levels of agricultural activity, the region has low soil fertility, which limits crop production potential; the mean annual rainfall for the Tsavo Ecosystem is 550 mm (Smith and Kasiki 1999). The Tsavo Ecosystem has two rainy seasons: a long rainy season from March to May and a short rainy season from

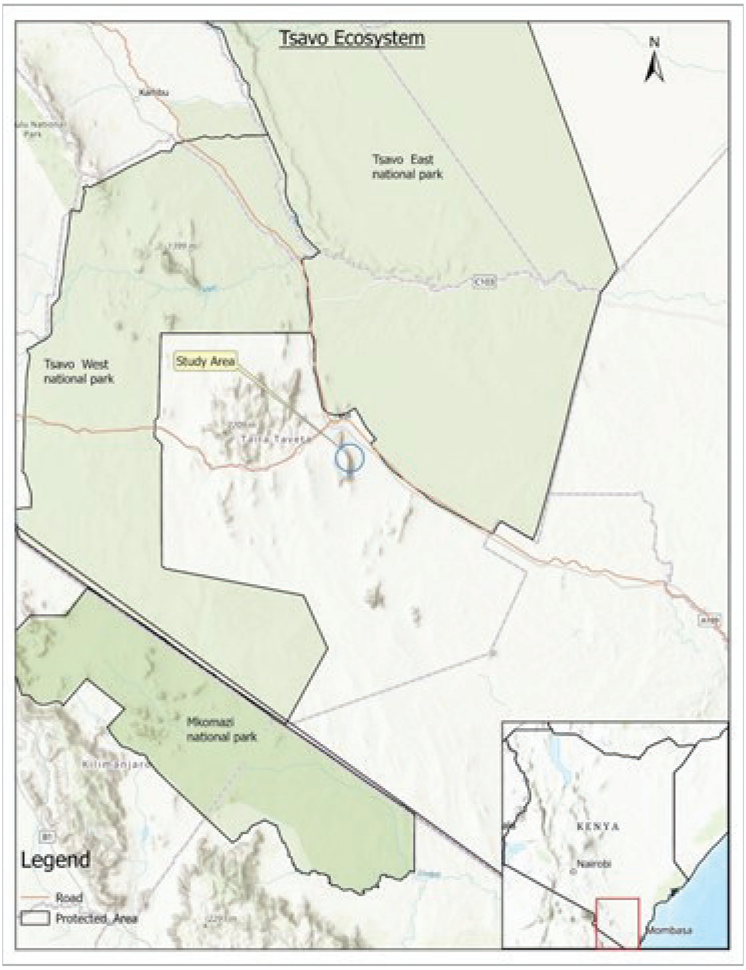


Figure 1. Study area in Lower Sagalla, Taita Taveta County, Kenya, which lies within the 42,000 km^2 Tsavo Conservation Area, 3 km from Tsavo East NP.

October to December (Smith and Kasiki 1999). This research was conducted during a peak period of elephant activity in Lower Sagalla, between August 2016 and July 2017.

Methodology

Crop experiments

We conducted on-farm experiments to assess whether two crops, sunflowers and moringa, are less palatable to elephants than maize, a local food staple, and if planting them can decrease elephant crop foraging. These crops were selected after informal conversations with 10 Lower Sagalla farmers about their farming experiences, which suggested that both crops may not be attractive to elephants but were of interest to farmers.

Experimental sites were selected at 10 farms based on the farm's history of frequent elephant activity. Plots were placed where elephants had previously crop raided and far from homes to minimize deterrent effects from human presence. At each farm, three 5 m x 5 m plots (one per crop) were prepared and arranged linearly (Fig. 2). An 8.5 m buffer zone was established between the plots with a 1 m buffer around each experimental site. Treatment of the plot was assigned using a complete randomized block.

The plot size, plant spacing, seed number and depth, and planting date were determined in consultation with farmers. On each plot 50 moringa, 100 maize, or 100 sunflower seeds were planted; less moringa were planted due to moringa's larger size,

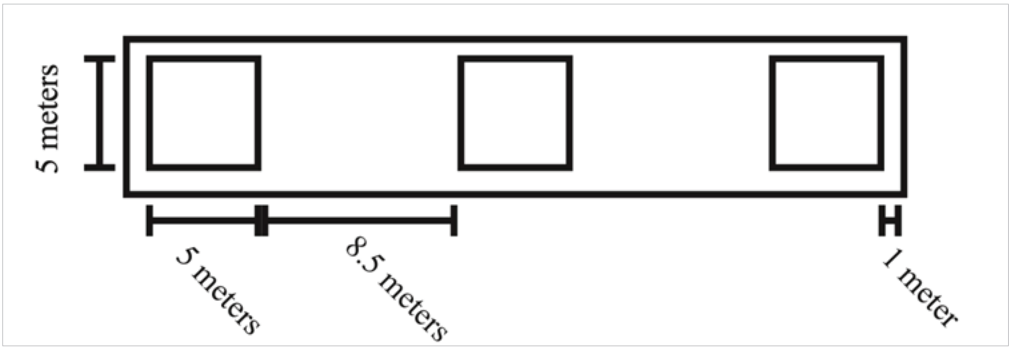


Figure 2. On-farm experimental plot arrangement. At each experimental farm, three 5 m x 5 m plots (one for each crop) were prepared and arranged linearly. An 8.5 m buffer was established between plots and a 1 m buffer around each farm's experimental area.

per farmers' recommendations. The maize and sunflower plots had 10 rows of 10 plants with a 0.5 m spacing between the plants and rows. Sunflower and maize seeds were planted 5–10 cm deep (4–5 maize seeds or 7–10 sunflower seeds) and covered with 2.5–5 cm of soil. Fifty moringa were cultivated per plot in five rows of 10 plants with a 1 m spacing between rows and a 0.5 m spacing between plants. Each plant was assigned a unique identifier.

Moringa seedlings (n = 420; 42 per plot) were sourced from a single nursery, with germination initiated in mid-September 2016. An additional eight seeds were directly sown per plot. The seed and sapling locations were determined by using a random number table. Moringa were planted in the experimental plots in the last two weeks of November, after the rainy season had begun. The maize and sunflower seeds were planted between mid-October and mid-November. None of the sunflowers germinated, and new seeds were planted in mid-December in the same plots.

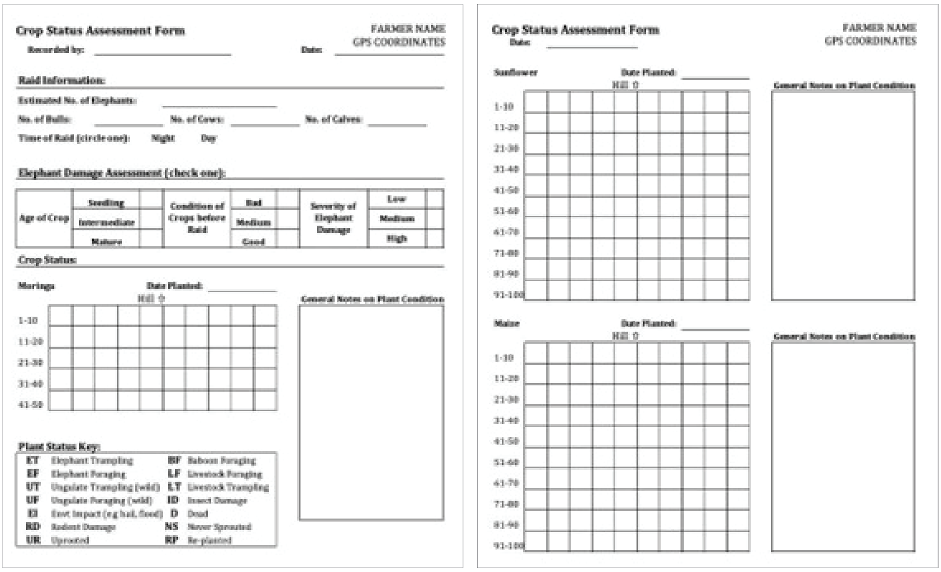
Data collection

Throughout the experiment, we visited the experimental plots weekly and within 24 hours after farmers reported elephant activity. During visits, farmers described any crop raiding incident, including the number of elephants, where they entered and exited the farm, and any behavioural observations. The damage to the experimental plot was recorded using a standardised form (Fig. 3). The plants were classified as seedling (< 25 cm), intermediate (> 25 cm, but not flowering), or mature (exhibiting flowers or fruit). Plant health was classified into six statuses: good, alive (accidental elephant damage), alive (intentional elephant damage), dead (accidental elephant damage), dead (intentional elephant damage), and dead (other). Foraging and uprooting were considered intentional elephant damage; trampling was considered accidental elephant damage (Fig. 4). Other causes of damage included insects, environmental stress, trampling by livestock, and foraging by baboons and birds. Trail cameras were installed at each plot to support field observations and confirm the cause of damage.

Semi-structured interviews

To understand local perceptions of and experiences with sunflowers and moringa we conducted semi-structured interviews in June and July 2017. An interview guide was developed with a combination of closed-ended and open-ended questions. Thematic areas included: i) historical experiences with elephant crop raiding; ii) perceptions of crop palatability to elephants; and iii) primary factors influencing crop selection (e.g. market access, agronomic challenges). A university-educated interpreter fluent in English and Swahili translated the interview guide into Swahili and interpreted during interviews because English is the third language for many in Lower Sagalla. The guide was pre-tested through three practice interviews to refine questions for clarity, comprehension, and appropriate interview length.

Participants were initially selected purposefully based on their farming experience in Lower Sagalla and knowledge of HECx). Snowball sampling was then employed, whereby interviewees were asked to recommend other knowledgeable community members. This method ensured a representative



Crop Status Assessment Form

FARMER NAME
GPS COORDINATES

Recorded by: ____________ Date: ____________

Raid Information:

Estimated No. of Elephants: ____________

No. of Bulls: ______ No. of Cows: ______ No. of Calves: ______

Time of Raid (circle one): Night Day

Elephant Damage Assessment (check one):

Age of Crop			Condition of Crops before Raid			Severity of Elephant Damage		
	Seedling			Bad			Low	
	Intermediate			Medium			Medium	
	Mature			Good			High	

Crop Status:

Moringa Date Planted: ______

Hill ⇧

General Notes on Plant Condition

1-10										
11-20										
21-30										
31-40										
41-50										

Plant Status Key:

ET	Elephant Trampling	BF	Baboon Foraging
EF	Elephant Foraging	LF	Livestock Foraging
UT	Ungulate Trampling (wild)	LT	Livestock Trampling
UF	Ungulate Foraging (wild)	ID	Insect Damage
EI	Envt Impact (e.g hail, flood)	D	Dead
RD	Rodent Damage	NS	Never Sprouted
UR	Uprooted	RP	Re-planted

Crop Status Assessment Form

Date: ____________

FARMER NAME
GPS COORDINATES

Sunflower Date Planted: ______

Hill ⇧

General Notes on Plant Condition

1-10										
11-20										
21-30										
31-40										
41-50										
51-60										
61-70										
71-80										
81-90										
91-100										

Maize Date Planted: ______

Hill ⇧

General Notes on Plant Condition

1-10										
11-20										
21-30										
31-40										
41-50										
51-60										
61-70										
71-80										
81-90										
91-100										

Figure 3. Crop status assessment form utilized to record individual plant health status following crop raiding events.

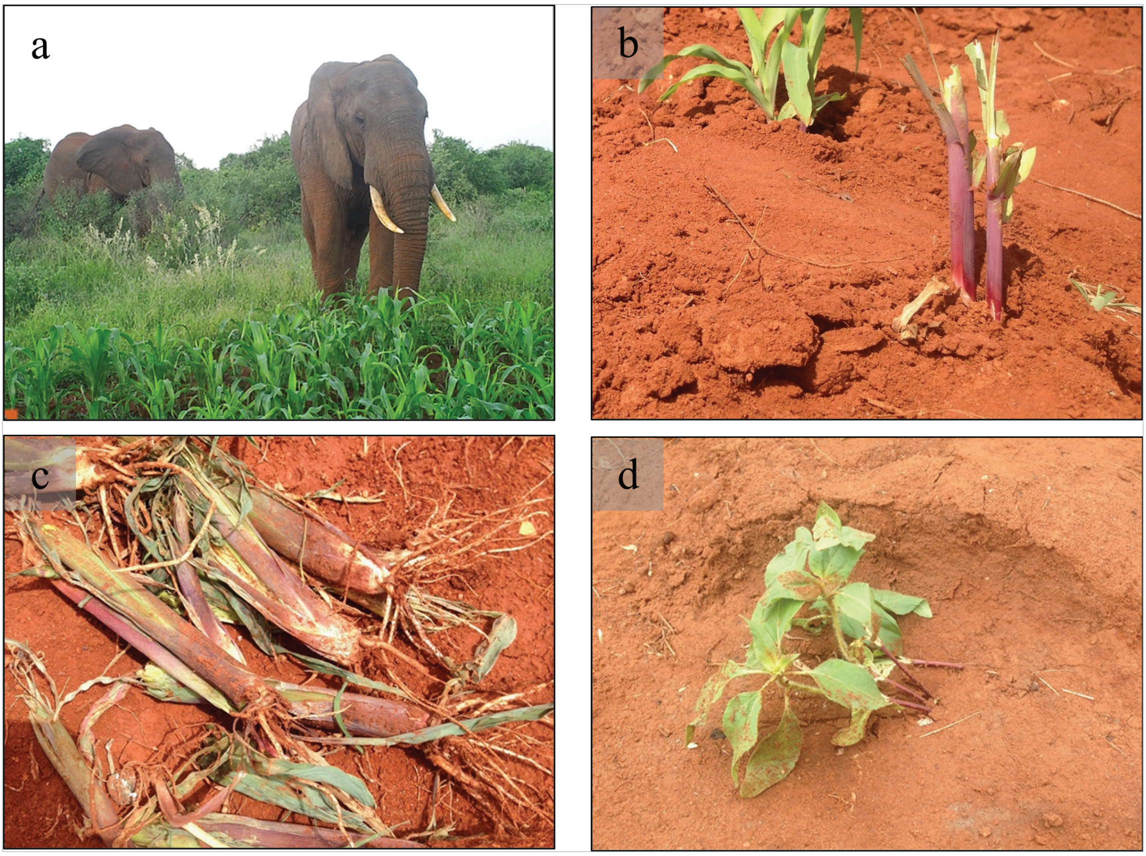


Figure 4. a) Elephants foraging at experimental farm plot. b) Intentional elephant damage (foraging) of maize. c) Intentional elephant damage (uprooting) of maize. d) Unintentional elephant damage (trampling) of a sunflower.

pool of participants, including farmers (n = 26), community leaders (n = 5), and local non-profit staff (n = 5). The total number of interviews conducted was 31; all community leaders were also farmers. Eighteen farmer interviews were with men, six were with women, and two involved couples. Farming experience was 10 to 56 years. Twelve farmers farmed 5–10 acres, seven farmed 10–20 acres, and one farmed 30 acres. Three people were not currently farming, and three did not know their farm size. Each interview lasted between 45 minutes and 3.5 hours. Verbal consent was obtained at the outset, with a clear outline of the interview topics and an emphasis on voluntary participation and confidentiality. Responses were audio-recorded and translated into English for analysis.

Crop experiment data analysis

Plant health was analysed twice during the study period, mid-January and late March 2017. Mid-January was selected because a large period of elephant crop raiding occurred between December 17 and January 20. Late March was the end of the growing season and showed what proportion of plants remained. These two timeframes answered four questions: 1) was there a difference in germination rates? (January); 2) was there a difference in the number of plants alive and healthy at the end of the growing season? (March); 3) was there a difference in intentional elephant damage mid-growing season? (January); and 4) was there a difference in intentional elephant-caused mortality at the end of the growing season? (March).

Data were analysed using SPSS and coded by crop type and farm. To account for variable germination rates among plots, the proportion of plants that germinated at a plot within each plant status was calculated instead of using the number of plants. Proportions were compared using Kruskal-Wallis and post-hoc pairwise comparisons.

Throughout the experiment, there was below-average rainfall. In 2017 only 2.2 mm of rain fell (King et al. *in prep*). To compensate for the lack of rainfall, we purchased water, and two farmers were hired to water each plot with 20 L of water three times a week. All crops were watered the same way. However, as the drought worsened, it was difficult to obtain sufficient water, which impacted plant growth.

Interview coding and analysis

All interviews were audio-recorded and supplemented with extensive field notes taken during and immediately after each session to capture contextual details and initial observations. Participants were assigned codes to maintain anonymity. For example, P1 indicates participant number 1. We reviewed and manually coded notes for overarching themes and created spreadsheets to organize interview topics: Sagalla history, land use, HEC, social and emotional impacts, economic impacts, elephant deterrents, beehive fences, and non-palatable crops. When an interviewee's response coincided with a topic, the participant code and the reference line number were recorded. In the interview notes, we highlighted references for each topic in a different colour. The topics most frequently discussed were identified and divided into themes, subthemes, and quantified. Responses to each closed-ended question were recorded and tables detailing the responses were created.

Results

Crop experiment

During the study period (December 2016 to March 2017), we documented 37 distinct crop raiding events; elephants raided in 9 out of 10 farms, and the frequency of raids per farm ranged from 2 to 8. The ecological suitability of the crops was compared using the germination rate and the percentage alive in March as proxies. The percentage of plants that germinated in mid-January 2017 (Kruskal-Wallis n = 30, df=2, p=0.41) and the post hoc pairwise analysis did not show statistically significant differences in the germination rates between the crop types. However, by the end of the season, significantly more sunflowers and moringa were alive than maize; this included plants that were damaged but still in good health (Kruskal-Wallis (n = 30, df=2, p=0.000). The pairwise analysis showed significant differences between maize and sunflowers (p=0.044) and maize and moringa (p=0.000).

To assess the relative palatability of each crop, the rates of intentional damage by elephants in January and March 2017 were compared. The January 2017 findings strongly suggest that sunflowers are less palatable to elephants than maize. Kruskal-Wallis (n=30, df=2) yielded a p-value of 0.002; pairwise comparison showed significant differences in intentional elephant damage between sunflowers and

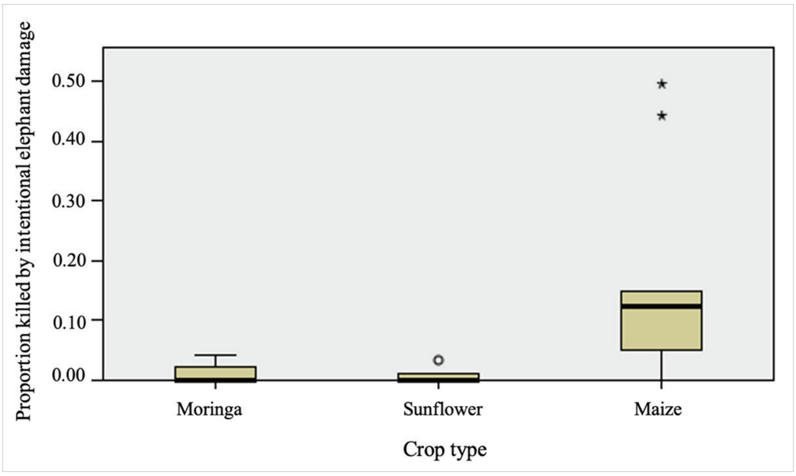


Figure 5. Proportion of plants intentionally damaged by elephants by crop type (March 2017) Kruskal-Wallis analysis of the proportion of each crop intentionally damaged by elephants (foraging and uprooting). Statistically significant differences were evident between sunflowers and maize (p=0.002) and moringa and maize (p=0.004).

maize (p=0.001) but not between moringa and maize (p=0.23). Similarly, the analysis in March 2017 showed that elephants intentionally foraged upon and/or damaged maize significantly more than sunflowers or moringa. Kruskal-Wallis (n=30, df=2, p=0.001), and pairwise comparisons showed significant forage damage differences between sunflowers and maize (p=0.002) and moringa and maize (p=0.004) (Fig. 5).

Interview results

Our interview results revealed three primary themes concerning the cultivation of alternative crops: 1) the critical trade-off between agronomic viability and economic security; 2) the perceived efficacy of crop palatability as an elephant deterrent; and 3) the significant structural barriers to adoption, namely market access and initial investment costs.

Farmers (n = 26) had strong crop preferences, with clear seasonal variation. For example, maize was favoured by 81% of farmers during the short rains (October–December 2015) but was only grown by 54% (of farmers) during the long rains (March–May 2016). In the latter period, legume cultivation became predominant, with 86% of farmers growing mung beans and 81% growing cowpeas.

Farmers considered many factors when selecting crops. For instance, 69% considered rainfall and relied on the annual rains, growing different crops during the two rainy seasons. Other top factors considered were market value (27%) and food security (19%). Thirty-one per cent of farmers prioritized maize's cultural importance and role as a staple food; however growing maize is a challenge for coexistence with wildlife. Fifteen per cent considered crop attractiveness to elephants. A farmer noted, "I tried growing pigeon peas, but didn't harvest anything . . . Elephants raided. Elephants came when they were ready" (P2).

Farmer experiences with sunflowers

Fifty per cent of the 26 farmers interviewed had previously grown sunflowers. Regardless of cultivation experience, the majority (69%) believed that sunflowers were non-palatable to elephants.

Farmers reported numerous benefits of growing sunflowers: oil production (58%), bee fodder (46%), market value (38%), livestock fodder (15%), and food (15%). A farmer explained their versatility, "when it is used to make oil then the outer part you can give to livestock" (P2). Another farmer remarked, "sunflowers are food. Money when you sell it" (P16). However, there are significant agronomic and socio-economic challenges when cultivating sunflowers that may limit farmer adoption. For example, 38% mentioned drought and unreliable rainfall. A farmer noted, "I tried to plant sunflowers, but they did not do well because of drought" (P22). Fifteen per cent of farmers were

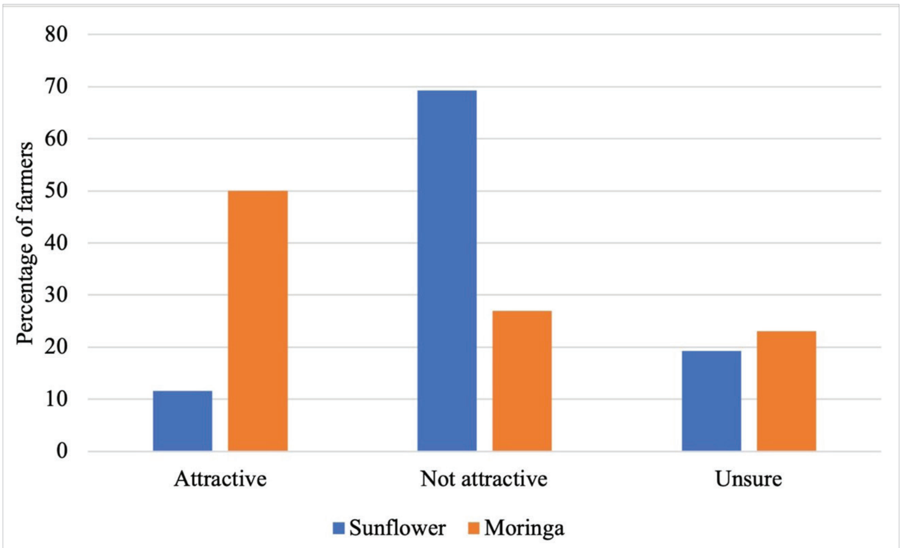


Figure 6. Farmers' perceptions of crop attraction to elephants (%) (n=26) as reported during interviews.

concerned about the impacts of wildlife, including rodent seed predation and damage by elephants and baboons. Twelve per cent of farmers cited lack of seeds as a challenge to growing sunflowers.

Fifty-four percent of farmers thought there was a local market for sunflowers. A farmer attested, "there is a market for sunflowers. You can sell it" (P20). During interviews, farmers cited local market prices of 50–140 KSH/kg (USD 40 cents to 1.20) for sunflower seeds. However, some mentioned they did not profit from growing sunflowers. A farmer explained, "there is an industry in Voi. But you see, when people grow sunflowers, they grow it in too small quantities, and the industry needs large quantities" (P21). Fifteen per cent of farmers thought there was no local market. The remaining 31% were unsure.

Farmer experiences with moringa

Of the 26 farmers interviewed, 42% had experience cultivating moringa. However, they expressed divergent views on its palatability, with 50% believing it to be attractive to elephants (Fig. 6). A farmer explained: "elephants love moringa. A close neighbour... is raided every time that her moringa plants are ready. Elephants trample and consume (the plants)" (P15). However, 27% of farmers believed that moringa is not attractive to elephants. A farmer remarked: "moringa? I think it is not attractive because there are some lands [do these people farm areas where they don't have title deeds?] where they have grown moringa, but I have never seen elephants destroy them or eat them" (P19). However, as pointed out by one farmer and clear from other farmers' responses, moringa is a relatively new crop; therefore 23% of farmers were unsure about elephants' attraction to moringa.

The most reported benefits of moringa were its medical uses (73%) and role as a food source (46%). A farmer noted, "seed pods are a good vegetable . . . The leaves, when dried and taken with porridge, are good for my health" (P14). Other commonly reported benefits of moringa were market value (42%) and pressing for oil (12%). Two farmers noted its drought tolerance. Despite its benefits, 35% of farmers noted that drought and lack of rainfall were impediments to its adoption. Damage by elephants (27%) and pests (12%) were also reported as cultivation challenges. Fifteen per cent noted that a lack of awareness limits moringa cultivation. A farmer remarked, "moringa is, to us, a very new plant . . . We are being told it is a medicine, which cures a lot of sickness, but I don't know myself because I haven't used it. But now I'm planting this crop, maybe I'll learn more" (P18). Despite a lack of knowledge, they were eager to learn more about moringa.

Sixty-nine percent of farmers believed there is a local market for moringa. One farmer remarked, "everything about moringa means money. You sell the flower for money. You sell the seeds for money"

(P22). Several cited local moringa market prices of 200-300 KSH/ kg of seeds, 800 KSH/ kg of leaves, and 1,000 KSH/kg (USD 7) of flowers. Two farmers thought there was no local moringa market; the remaining 23% were unsure.

Discussion

In this interdisciplinary study, combining elephant crop-palatability trials, agronomic assessments, and qualitative socio-economic analysis, we aimed to assess the role of non-palatable crops in mitigating HEC. In Lower Sagalla, an area affected by recurrent HEC, while maize, the staple food and a culturally important crop is widely cultivated (MoALF 2016), elephant foraging heavily impacts its cultivation; farmers invest their money and time in growing maize but often reap minimal harvest (Smith and Kasiki 1999). A local farmer summarized, “if I continue fighting with the animals, trying to grow the maize and fighting with them, I won’t end up anywhere” (P21). Non-palatable crops like sunflowers and moringa hold potential to support agricultural diversification and, consequently, household livelihood resiliency, in the face of increasing climatic uncertainty and elephant crop raiding pressure. Understanding the palatability and adoption potential of these crops, particularly among subsistence farmers living at the edge of PAs is important to develop locally grounded strategies for coexistence.

Crop palatability to elephants

We found that sunflowers are a climatically viable, non-palatable crop that suits the sandy, iron-rich soil conditions of the community lands and that could provide multiple benefits for Lower Sagalla farmers. At both the mid-growing season (January 2017) and end of the growing season (March 2017), elephants had intentionally foraged upon or damaged significantly more maize than sunflowers (Fig. 5). This suggests that sunflowers are much less palatable to elephants than maize and that incorporating sunflowers into farms may decrease intentional elephant damage and increase the harvest income for these at-risk farmers.

The evidence for moringa's non-palatability compared to maize was less definitive in the initial stages of the study. Specifically, at the mid-growing season (January 2017), the incidence of intentional elephant damage did not differ significantly between the two crops. At the end of the growing season (March 2017), significantly less crop death was attributed to intentional elephant activity in moringa than in maize. However, this may be due to differences in life stage; maize grows faster and fruits within one growing season while moringa reaches maturity in two years. This may have led elephants to preferentially forage maize instead of early stage moringa and suggests that a longer time window is needed to fully assess the palatability of moringa to elephants across all life stages before conclusions are drawn.

Based on our findings, we propose that dedicating a portion of farmland to cultivating sunflowers and moringa instead of known elephant preferred crops like maize may reduce the attraction for elephants to enter farms. Previous research by Matsika et al. (2023) showed that greater crop diversity reduced crop raiding vulnerability. Furthermore, non-palatable crops could be coupled with effective elephant deterrent methods to increase farm profitability. For example, farmers could strategically plant high-value elephant favourites inside beehive or electric fences while planting less palatable crops outside, reducing the time and money needed to protect crops. Additionally, effective land-use planning can promote human-elephant coexistence (Buchholtz et al. 2019). For example, “frontline” farms could grow non-palatable crops, thus creating buffer zones in front of individual farms or farm clusters for farmers growing maize “behind’ in the rest of the community (Matsika et al. 2020). This benefit of effectively protecting second or third layer farmers by mitigating the indirect consequences of elephant movement and foraging could be an attractive strategy for village land use plans.

Climatic suitability

Most Kenyan farmers, including those in Lower Sagalla, rely on rainfall for their agriculture, so considering crop resiliency is essential as climate change makes rainfall less predictable and drought more common in eastern Kenya (Marigi 2017). Two ways farmers across sub-Saharan Africa are adapting to climate change are crop diversification and adopting drought-tolerant crops (Magesa et al. 2023). In Taita Taveta County, MoALF (2016) reported that climate change has diminished maize yields and recommended cultivating drought-tolerant crops. We found that both sunflowers and moringa grew better than maize in Lower Sagalla despite low rainfall. In mid-January 2017 there were no significant differences in germination rates among crops; all germinated equally well. However, at the end of the growing season (March 2017), significantly more sunflowers and moringa remained than maize. Both crops better withstood the cultivation challenges in Lower Sagalla including soil conditions, slope, elephant crop raiding, drought, and insect damage; they germinated well and persisted throughout the growing season. An agriculture expert highlighted moringa's climate resiliency: "[moringa] are drought tolerant . . . it is also good for agroforestry if someone is rotating crops and growing other plants. It is also a nitrogen fixer" (P27). Growing both rapidly maturing non-palatable crops like sunflowers and chillies as well as slow-maturing non-palatable trees, including moringa could provide farmers with both short-term harvests and long-term agroecological benefits that withstand the challenges of elephant foraging and climate change.

Challenges to crop diversification and household livelihood resiliency

While elephant crop raiding has undermined the economic viability of small-scale agriculture in Lower Sagalla, crop diversification, a potential strategy for reducing losses, is itself hindered by challenges, including the superior market value and cultural significance of staple crops, alongside the perceived risk and agronomic uncertainty of cultivating alternatives. As one farmer (P5), in our study explained, that they would be in a better position economically if the elephants in the area did not crop raid. The threat of crop damage necessitates vigilant field guarding to deter marauding elephants, which reduces farmers' abilities to pursue off-farm income-generating activities. Farmers become exhausted and hopeless as they lose crops to elephant foraging and struggle to transition to alternative livelihoods, which often fosters animosity towards elephants and protected areas and creates resistance to elephant conservation initiatives (Sitati et al. 2005).

Despite the cultivation challenges of growing and protecting maize from elephants, it is still widely grown and highly valued. A farmer explained the local importance of maize, "farmers plant maize because they say that you cannot prepare porridge from green grams or cowpeas. Even when you tell that person to change, it will take a lot of time to change" (P15). Therefore, increasing non-palatable crop cultivation to replace maize needs to be better understood before being promoted as a simplistic solution to HEC especially understanding the trade-offs that farmers would make based on their historic diets, farming, and broader livelihood strategies. Although planting non-palatable crops may be a useful strategy to reduce elephant foraging, our findings demonstrate that it must be understood within farmers' broader agricultural, socio-economic, and cultural contexts. Furthermore, our findings underscore the necessity of evaluating the opportunity and labour costs of reducing, let alone replacing, known crops such as maize or legumes with less known crops such as sunflowers or moringa (Lukanu et al. 2024).

Although sunflower seeds can be eaten directly, they are not a staple food and are commonly consumed (or sold) as oil. This requires the cost of a grinding machine to convert the seeds into sunflower oil (a staple need for households as well as a valuable commodity). Grinding can be done at a village level through a shared grinder, potentially providing frontline farmers needing to plant non-palatable crops with a highly valued oil product that can be sold in local markets. Similarly, moringa can benefit farmers as both a food source and a marketable crop. Moringa leaves can be eaten fresh as a vegetable or dried and crushed by farmers into a nutritious powder that can be consumed by the household or sold at market. Importantly, dual-purpose crops may hold greater potential for adoption than "purely cash crops" (Lukanu et al. 2004).

While Lower Sagalla farmers already grow and sell sunflowers and moringa, it is predominantly on a small-scale. The agriculture expert noted, "people have not gone full out to exploit the potential of moringa here, which is huge" (P27). This highlights key adoption barriers, including the relative newness of the crop in the region, a consequent lack of technical knowledge and processing capacity, and a strong cultural preference for established staples like maize. Therefore, overcoming these barriers will likely require targeted support from government extension services or non-profit organizations to provide training, market linkages, and initial resources (Lukanu et al. 2004; Ogunjinmi et al. 2024). An agriculture expert recommended, "there is a market for sunflowers, but the problem is when the community sells it raw. There is exploitation. So, we would have to find a market and try to negotiate prices for the community or encourage people to invest in factories" (P27). There is also concern if too much supply comes on the market simultaneously. Issues of future supply, demand, and price are critical components of whether or not new cropping systems serve their initial objectives (Lukanu et al. 2004).

Although farmers would want to diversify their incomes and grow non-palatable crops, challenging farming conditions, including saving the necessary capital, have made it difficult for them to do so. For example, one farmer explained, "I'm not planting [sunflowers] because of lack of finance, though I am hoping to plant" (P11). Similarly, Mackenzie and Ahabyona (2012) found that small-scale farmers who take out loans to pay for farming supplies at the beginning of the season and suffer crop raiding often find themselves in further debt. Therefore, without reliable harvests or outside assistance, farmers cannot accumulate enough surplus to invest in alternative livelihood activities.

An important factor regarding challenges to raising financial capital is that Lower Sagalla farmers cannot leverage their land to gain capital to invest in other economic activities because it is titled at the community level. Instead of purchasing individual land parcels, community members pay a one-time fee authorizing them to use community land. Thus, they can claim land for farming or grazing but cannot sell claims or use it as loan collateral. In Taita Taveta County, only 40% of farmers have title deeds (MoALF 2016); so many have few options except to engage in low productivity farming where the land is free, but production unreliable, risky and invariably limited.

Despite the challenges of adopting moringa and sunflowers, these crops hold potential for households to diversify from sole reliance on maize cultivation and to increase resilience in the Lower Sagalla conflict zone. In sub-Saharan Africa, greater household livelihood diversity is associated with higher total household income, increased food security, and improved future economic opportunities (Alobo Loison 2015) and is a principal strategy to adapt to a changing climate (Magesa et al. 2023). Thus, growing sunflowers, moringa, or other non-palatable crops has the potential to improve resiliency of farmer livelihoods. It can help by reducing the amount of time farm household members spend guarding fields, producing both unprocessed and value-added products for market sale, and diversifying livelihood sources. Since the conclusion of our study in 2017, sunflowers continue to demonstrate non-palatability to elephants, and their adoption is increasing (LE King, pers comm., 2025).

While this study offers valuable insights from interviews and experimental plots into HECx challenges in Lower Sagalla, we acknowledge the small sample size, short temporal scale, and impacts of drought limit its generalizability to other communities. Therefore, additional research on sunflowers and moringa in additional sites, focusing on palatability to elephants, socio-economic implications of changing a livelihood resource, planting strategies, climatic vulnerabilities, and opportunities, is necessary to assess our findings' significance. To increase the robustness of future studies, we recommend including greater replication over multiple growing seasons, especially for moringa to fully assess its palatability to elephants at all life stages.

Conclusions

The unfenced boundary of Tsavo East NP is essential for ecological connectivity and genetic flow for elephants, yet it consistently generates HEC, resulting in food insecurity and economic hardship for adjacent communities. Our study demonstrates that cultivating non-palatable, drought-resistant crops such as sunflowers can reduce the attractiveness of farmlands to elephants, offering an ecologically grounded foraging deterrent. However, the integrated approach employed here, combining palatability trials, agronomic evaluation, and socio-economic analysis, shows that crop adoption is constrained less by agronomic potential than by profound socio-economic and cultural factors, most, notably, the irreplaceable role of maize as both a dietary staple and a culturally significant crop.

Based on these findings, we propose the following recommendations:

For policy: Conservation and agricultural policies should integrate market-based interventions, such as developing stable value chains and providing economic incentives for alternative crops, to enhance their financial viability and reduce smallholder reliance on high-risk staples. 2) For extension services: Training programs should address knowledge gaps related to the cultivation, processing, and commercial use of non-palatable crops while acknowledging and working within cultural preferences for maize. This should include an assessment of the differences in labour demands between maize and non-palatable crops. Finally, for future research, studies should prioritize the evaluation of landscape-level planting schemes such as sunflowers as perimeter buffers and longitudinal assessments of how alternative crops affect both elephant movement and household income resilience.

Sustainable HECx will require strategies that are not only ecologically functional but also economically compelling and culturally sensitive. Interventions must be co-developed with local communities to ensure they support both conservation goals and livelihood security, thereby bridging the gap between ecological theory and on-the-ground applicability.

Acknowledgements

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Depictions of relationships between elephants and San people in the rock art of the Cederberg mountains, Western Cape

Andrew Paterson

African Centre for Coastal Palaeoscience, PO Box 77000, Nelson Mandela University, Gqeberha 6031, South Africa

Email: andypat@iafrica.com

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Abstract

The rock art of the San people in the Cederberg mountains of the Western Cape has the highest concentration of elephant paintings anywhere in the world, providing a unique insight into the historical relationship between the San people and elephants. This relationship was one of symbiotic commensalism, whereby the San benefited from the relationship, which neither helped nor harmed the elephants. These paintings provide evidence of the reverence felt by the San towards elephants. The San regarded the elephants as beings to whom they were connected by *n|om*, a vibratory life force which comes directly from God the Creator and animates all living beings. The San encountered elephants not only in their daily lives but also in their imaginary mythological world, suggesting that elephants were deeply embedded in their psyche. The artwork, storytelling and mythology of the San were thoroughly practical in effect and depicted a harmonious relationship between elephants and the San. To understand this relationship, this paper compares and analyses various behavioural contexts linking the San to elephants, as depicted in 17 Cederberg rock art sites. Most researchers believe that the paintings, still visible on the rocks of the Cederberg, were created in the last 7,000 years and the bulk of the paintings of elephants, eland and lines of dancing people are at least 1,500 years old.

Résumé

L'art rupestre du peuple San dans les montagnes du Cederberg (province du Cap-Occidental) présente la concentration la plus élevée de représentations d'éléphants au monde et offre un aperçu unique des relations historiques que ce peuple entretenait avec ces animaux. Ce sont des liens de commensalisme symbiotique, desquels les San bénéficiaient et qui ne visaient ni à aider les éléphants, ni à leur nuire. Ces peintures témoignent de la vénération portée par les San à leur égard, qu'ils considéraient comme des figures auxquelles ils étaient connectés par le *n|om*, une force vitale vibratoire directement issue du Créateur et qui anime tous les êtres vivants. Les San côtoyaient les éléphants, non seulement dans leur vie quotidienne, mais également dans leur monde mythologique imaginaire, laissant suggérer que ces animaux étaient profondément ancrés dans leur psyché. L'art, les récits et les mythes de ce peuple étaient essentiellement

pragmatiques et dépeignaient une relation harmonieuse avec eux. Afin de comprendre les liens qui les unissaient, cet article s'attache à comparer et à analyser les différents contextes comportementaux reliant les San aux éléphants, tels qu'ils sont restitués dans les 17 sites d'arts rupestres du Cederberg. La plupart des chercheurs estiment que ces peintures, toujours visibles dans cette région, ont été réalisées au cours des 7 000 dernières années et que l'essentiel des représentations d'éléphants, d'oryx et de rangées de danseurs datent d'au moins 1 500 ans.

Introduction

The Cederberg Mountains (henceforth Cederberg) in the Western Cape Province, South Africa, are located at the southernmost tip of Africa (Fig. 1). They are part of the Cape Fold Mountains and form a series of parallel mountain ranges that follow the south-western coastline of South Africa, producing a rugged mountainous terrain, characterized by a sequence of elevated ridges and peaks separated by broad, linear valleys. These tributary valleys form convenient routes through these fold mountains, and many of them are known to have been used by precolonial hunter-gatherers and elephants. Most of the San rock art sites today are located along these drainage systems, which provided permanent or seasonal water sources (Parkington 2003).

The Cape Floral Kingdom is the smallest of the six floral kingdoms in the world and is divided into five different types of vegetation or biomes. Two of these are found in the Cederberg, namely the Fynbos and the Succulent Karoo biomes. The Cape climate is Mediterranean, characterized by warm, dry summers and mild, moist winters.

The San hunter-gatherer peoples in southern Africa have the most genetically diverse DNA in the world, establishing them as being directly descended from the earliest human ancestors (Tishkoff 2009). The San languages are noted for their distinctive click sounds and are regarded as the earliest form of language. These languages comprise around 30 dialects and constitute a rich linguistic heritage; however, the number of fluent speakers has dwindled to approximately 16,000 since the start of the 20th century (Ungarsky 2022). The San culture is a living record of the earliest ways

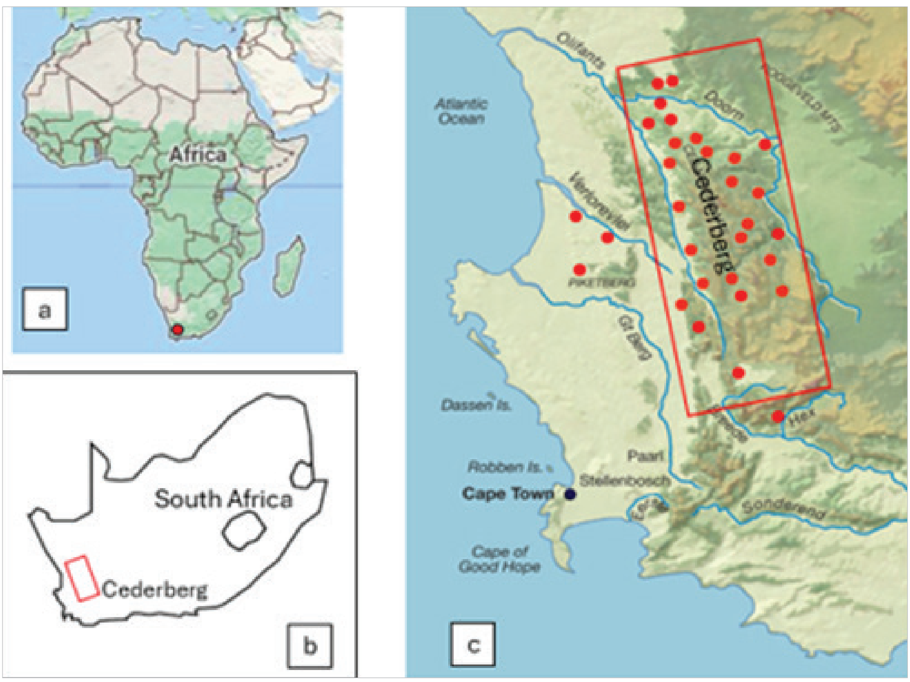

Figure 1. The location of the Cederberg mountain range in (a) Africa and (b) South Africa. (c) The distribution of rock art sites in the Cederberg mountains.

and means of human expression, ranging from art to dance, music, and religion.

Archaeological sites in the southern Cape suggest that people of the same physical type as the San were living in this part of the continent as long as 120,000 years ago. (Deacon 1994). Today, there are approximately 160,000 San people in southern Africa with around 7,000 residing in South Africa. However, there have been no San hunter-gatherers in the Cederberg since the mid-1800s. This paper therefore draws on the culture, ways of life, social interactions and beliefs of the southern */Xam* San people who lived in the Northern Cape during the 1880s, and the northern *!Kung* and *Ju|`hoansi* San people who currently reside along the Namibian/Botswana border. The San do not paint rock art today, and their hunter-gatherer traditions have all but died out, as they are irrevocably drawn into the vortex of modern civilisation (Johnson 1979).

The San and elephants in the Cederberg

San hunter-gatherers and elephants, as evidenced in the San rock art paintings, coexisted in the Cederberg for thousands of years. Southern African rock art dates back 27,500 years, with the age of the Cederberg elephant paintings ranging from 500 to 7,000 years (Parkington 2003).

The presence of elephants and San in the Cederberg was confirmed by the earliest colonial expedition into the area. In 1660 Jan Danckaert led a group of European explorers into the fertile valley of a large river, about a three-week journey from the fort in Cape Town. Danckaert noted: "We caught the most beautiful fish in the world. West of us, on the slopes of the mountains, we saw 200 to 300 elephants together" (Fig. 2a) (Thom 1952; Parkington 1977). This river, now known as the Olifants River, was referred to by the San as the *Tarakamma*. The mountains referred to by Danckaert, where elephants were seen, surround the present-day town of Citrusdal and are well known for their many San rock art sites with painted elephants. After the arrival of colonialists in the Cape of Good Hope in 1652, the San hunter-gatherers and elephants began to vacate the area. It appears that within 200 years of the arrival of colonialists in 1652, the San and elephants had all but disappeared from the Cederberg.

San beliefs, mythology and art

To understand the relationship of the San and elephants over time, one needs to understand the San culture.

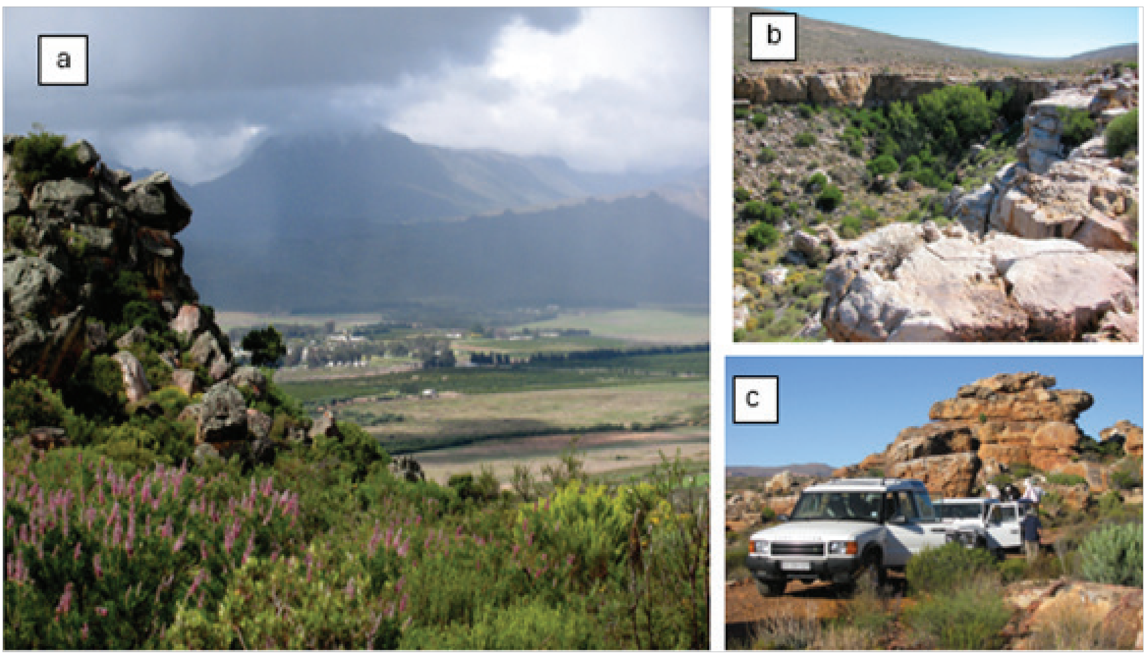

Figure 2. (a) Citrusdal in the Olifants River valley with the backdrop of Cederberg mountains, where colonial explorers counted 200–300 elephants in 1660. (b) Hidden rock art shelters in the Cederberg. (c) Large free-standing outcrops with rock art paintings.

The first written record of South African San folklore, beliefs and life stories was compiled by Dr Wilhelm Bleek and his sister-in-law, Dr Lucy Lloyd, in Cape Town in the 1870s and 1880s (Deacon 1994). Three southern San men spent several years at the Bleek family home in Mowbray, Cape Town. Bleek and Lloyd learnt the language of the southern San, developed a method for recording the clicks and other sounds that had no equivalent in English, and began transcribing verbatim what they were told. They then translated the southern San language into English and ultimately built up a testimony of more than 11,000 pages in 130 notebooks. (Deacon 1994). Their records reveal a way of seeing the world that underpins our understanding of the San rock art of the Cederberg today (Parkington 2003).

In the early mythological accounts recorded by Bleek and Lloyd in 1878, a San informant named *han ≠kass`o* described a period that the San called the First Creation, a period of time when elephants were people. This mythology offers a glimpse into the deep cultural and spiritual significance that elephants had in the San culture. Bleek and Lloyd were convinced, from their interviews, that the paintings of the San were not merely daubing of figures of idle pastime but were a truly artistic conception of the ideas which most deeply moved the Bushman mind and filled them with religious feelings (Deacon and Dawson 1997). Years later, Megan Biesele (1978), who worked with the northern San people in Botswana and Namibia, confirmed the Bleek and Lloyd findings and, moreover, that southern and northern San story traditions were homogeneous in one important respect: "All the animals in their mythology and stories were originally people and only later became animals" (Biesele 1978).

The first recorded discovery of a San painting of an elephant mother and baby appears to have been by Thomas Bain when he was building a road through the Cederberg Pakhuis pass between 1875 and 1877. Over the past 150 years, more than 200 art sites depicting elephants have been found in the Cederberg, scattered over an area of approximately 10,000 km2, containing a total of around 600 painted elephants.

One of the earliest tracings made of a San painting with elephants in the Cederberg was by Ginger Townley Johnson in 1961 at a site called Monte Cristo. This tracing was featured on the front cover of the South African Archaeological Bulletin published in September 1962 (Fig. 3a). The site was close to where the Danckaert expedition had crossed into the Cederberg in 1660. The tracing of paintings at this site, illustrating elephant-headed people dancing with the San (Fig. 3), confirmed the findings of Bleek and Lloyd (1880) and Biesele (1978). Townley Johnson's insightful personal comment on his tracing was that

> "elephants are more numerous among the paintings of the region than elsewhere, which may mean that they were of special symbolic importance. At first sight, this painting could be interpreted as a series of natural or artificial barriers, perhaps pitfalls. However, many of the lines, such as the zigzag sections, do not seem to represent any physical barrier or other object. Furthermore, the human figures with trunks suggest a symbolic association between elephant and man." (Townley Johnson 1979).

The study of San rock art paintings featuring elephants in the Cederberg was initiated by Townley Johnson in 1961 and continues to this day (Woodhouse 1985; Deacon 1994; Slingsby 1998; Paterson 2007; 2019; 2020; Paterson and Parkington 2016; Parkington and Paterson 2017; Paterson et al. 2025).

San culture and elephant behaviour

Anthropologists have researched present-day San culture since the early 1950s, when Lorna Marshall and her family began working with the northern San in the *Tsumkwe* area in northern Namibia, near the Botswana border. Since then, numerous anthropologists have studied the northern San people, the *!Kung* or *Ju'hoansi* (Biesele 1978, 1993, 2009; Liebenberg 1990; Marshall 1999; Keeney and Keeney 2015). These studies provide insights in San culture, social behaviour, religious beliefs, teachings, healing practices, childbirth procedures, ritual dances, hunting and rain rites, male and female initiation ceremonies, mythology, storytelling, language, hunting, tracking, and food gathering. All of these aspects of northern San culture and behaviour, as described by anthropologists, correspond to depictions of daily life in the Cederberg rock paintings.

Comprehensive studies of elephant behaviour

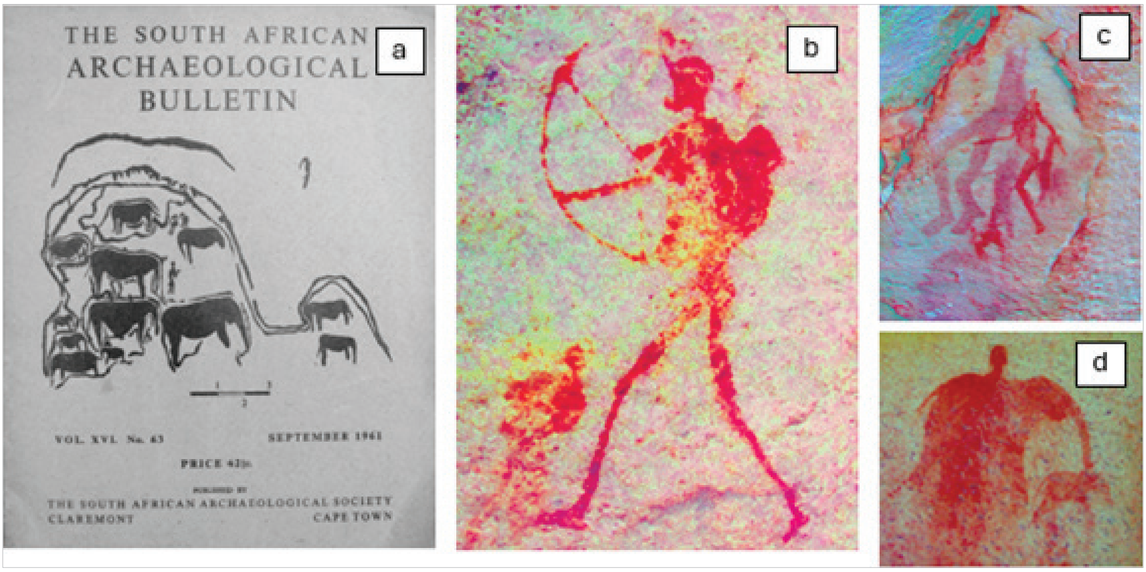

Figure 3. (a) Tracing of elephants by Townley Johnson, 1961. (b) A San hunter stalking an animal. (c) San figures running. (d) A San person and two elephants walking together.

(Douglas-Hamilton 1975; Moss 1988; Poole 1997; Payne 1999; Mortimer et al. 2018) underpin knowledge of the social structure of elephant society, female family units, male bond groups, communication methods, musth, mating and birthing behaviour, rearing and protection of young, and many other aspects of elephant behaviour. Again, all these can be found accurately depicted in the Cederberg rock art.

San rock paintings of elephants

The San painted elephants in a detailed and natural way, which confirms that they had an intimate understanding of elephant behaviour. The San artists' understanding of elephant social structure, physical characteristics and proportions, sounds, movement, feeding and breeding habits came from their direct observations of elephants in their natural environment. Early anthropologists have described the extent of northern San knowledge regarding animal behaviour as remarkable (Blurton Jones and Konner 1998).

The ability of San artists to draw elephants with such accuracy is believed to be directly linked to their extraordinary tracking skills. San trackers were able to hold visual images in their short-term memories that were almost photographic in clarity. The success of the San's hunting strategies, and thus their survival, was dependent upon this highly refined eidetic memory, which enabled them to visualize animal behaviour and movements from their tracks (Liebenberg 1990). All of these features, drawn by the San from memory, were painted directly onto the walls of rock shelters (Fig. 4).

Fieldwork and database

This paper represents the culmination of 20 years of research on elephant paintings found in the rock art of the Cederberg. It includes visits to San rock art sites alongside Professor John Parkington from the Department of Archaeology at the University of Cape Town, as well as field trips with the Eastern Cederberg Rock Art Group (eCRAG), which was established by Dr Janette Deacon of Stellenbosch University.

The Parkington and eCRAG field work for this paper involved finding and visiting rock art sites containing paintings of San and elephants together. The GPS coordinates of each site location were recorded, and the dimensions of the shelter site were measured. The painted sections on the walls of the shelter were divided into two-meter panels, observed, described and recorded. The painted images were then photographed and enhanced using DStretch Rock Art Digital Enhancement, a programme developed by Dr

Figure 4. (a) Measuring the dimensions of a San rock art shelter with the Eastern Cederberg Rock Art Group (eCRAG). (b) DStretch lre.jpg enhanced image of a San painting of elephants. (c) Tracing of the elephants from the above DStretch image used to inform the research.

J. Harman that analyses photographs of rock art sites and then shifts the image colour to highlight designs and patterns that are faded or invisible to the naked eye. The result is a false colour image that often appears much more detailed than the original (Fig. 3). All the digital data was uploaded onto the South African Heritage Information System (SAHRIS) database for further research and comparison with incoming data from other sites and researchers.

A total of 17 elephant sites, from my research database of 60 elephant sites in the Cederberg, were selected for analysis in this study of the relationship that existed between elephants and San thousands of years ago. These 17 sites contain 122 elephant paintings, 201 San figures, and a special group of 25 elephant-headed people (elephanthropes) that are unique to San rock art.

Methodology

The study adopted a multidisciplinary approach, combining insights from anthropological, archaeological, ecological, biological, behavioural and artistic studies. The interpretations of paintings in this paper are based on empirical in situ field evidence, verifiable by observation, experience and research.

In the field of anthropology, this study draws in particular on Geertz's (1973) work on symbolic and interpretive anthropology. He suggests that human beings as individuals are bound up in a series of symbolic or mythic representations, and that "man is an animal suspended in webs of significance that he himself has spun". These webs of symbols and myths serve to generate and maintain meaning and provide the structure for humankind's worldviews. This conceptualisation informs our interpretation of the rock art in the Cederberg.

Geertz's work resonates with the cultural concept of San called *n/om*, which they regard as a life force that comes directly from God the Creator, which animates all living beings and is the source of all "inspired energy" (Keeney and Keeney 2015, p.213). *N/om* is at the heart of San spirituality and healing. To the San, nature is seen as a web of interconnected ropes, strings and threads. The San perceive themselves as being directly connected to animals and plants in their ecosystem and especially to elephants. For the San, this web of nature is literal and, in an awakened state, a healer, or *n/om-kxao*, may see the world as a giant spider web. Song and dance can send *n/om* throughout the entire weave and thereby contribute to the wellbeing of the whole of nature (Keeney and Keeney 2015). The analysis of the paintings draws on Panofsky's (1972) iconographic approach to interpreting the content of artworks across three stages of analysis: description, understanding, and interpretation.

The first stage, description, focuses on the natural subject matter depicted in the painting. This is the most basic understanding of an artwork, which is perceived in its purest form, devoid of any added cultural knowledge. We relate San depictions of elephants to the detailed catalogue of the behaviour and communication of African savannah elephants (*Loxodonta africana*) in the Elephant Ethogram, an online resource[1] compiled by Joyce Poole and Petter Granli of ElephantVoices and launched in May 2021. The Ethogram describes and illustrates 322 behaviours, 103 behavioural constellations and 23 behavioural contexts. A behaviour is a unique movement or action in response to a particular situation or stimulus, while a constellation is a suite of behaviours that typically occur together, and a behavioural context refers to the circumstances or setting in which a behaviour takes place. We drew on the Ethogram to classify the behaviour of elephants and the behavioural contexts depicted in the 17 painting sites selected for analysis. (Table 1). This classification was made possible because the San artists painted elephants in natural behavioural contexts that can still be observed in the wild today.

Another important aspect of interpreting the paintings is the ability to distinguish between genders. This distinction was possible because the San paintings illustrate the unique behaviours of female and male elephants. Adult females and their dependent offspring live in tight-knit family groups, while adult males live in small bond groups and have more solitary, independent lives (Poole 1997). This informed our interpretations of different groupings of elephants in the paintings. For example, a large elephant with a small elephant directly in front of, behind or underneath are a mother and her calf. A large group of elephants consisting of four different relative sizes and a single large elephant is a female family unit led by a matriarch (Fig.10). A group of elephants of similar size and without small elephants present is interpreted as a male bond group. A very large elephant standing close to, walking towards, or running next to another elephant is a male and female elephant in consort during the mating season. A single large elephant is a solitary bull elephant. Similarly, in the paintings of people, the San artists broadly depict San males with a penis and usually carrying a bow, quiver and hunting bag (Fig. 3b) or wearing a kaross. Females are broadly identified by breasts, digging sticks, and skirts or aprons.

The second stage of analysis, understanding, goes a step further to consider cultural, behavioural and iconographic knowledge contained in the painting. This requires input from anthropological and elephant behavioural knowledge to decipher what the San artists intended to portray in each painting. Here, the spatial relationships and interactions between the elephants and the San figures are most important. At this level, the relative movements of the San and elephants become very important; for example, whether the elephants and San in the painting were moving in the same direction or different directions. Were the San figures superimposed on top of the elephants or walking beside them? Equally important are painted sounds, a notable feature of San depictions of social events and of elephants themselves (Figs. 8 and 10). The Cederberg San paintings frequently depict scenes of reverence and celebration, with people singing and dancing, clapping hands and making handprints, activities associated with significant San life-cycle celebrations such as birth, mating and initiation ceremonies. The behaviours of the elephants and San figures in the paintings provide the key to understanding the relationship between the San and elephants millennia ago.

The third stage, interpretation, is the most sensitive and critical part of Panofsky's analysis. This level considers personal, technical, and cultural history, looking at art not as an isolated incident, but as the product of its historical context. The historical context of the paintings analysed in this article covers a period of 7,000 years (Deacon 1994). Thus, each painting embeds a store of cultural knowledge that was meaningful and significant to the San people (Biesele 1993). The San did not have a written language. They relied solely on storytelling and painting of the celebration of life cycle events to preserve their mythology and culture.

Results

The objective of this study was to describe, understand and interpret the San paintings as accurately as possible. Specifically, we aimed to identify the behaviours of both the San and elephants, and their contexts, depicted in the paintings. We chose 17 painted Cederberg rock art sites out of a total of 60 sites to highlight specific aspects of the relationship between the San and elephants.

[1] https://www.elephantvoices.org/elephant-ethogram.html

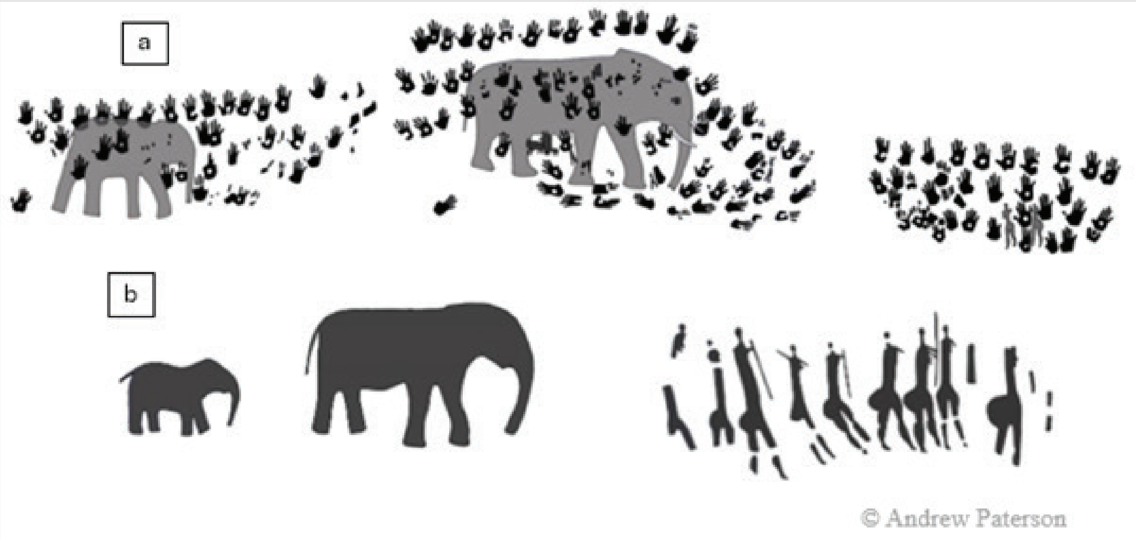

Figure 5. (a) **Steenkampskloof**. Elephant mother's pregnancy and pending birth are celebrated with handprints and San women singing and dancing. (b) **Brakfontein** Female elephant and her previous offspring with San women singing and dancing and holding digging sticks out in front of them.

Steenkampskloof and Brakfontein: pregnancy and weaning

The Steenkampskloof painting (Fig. 5a) consists of two yellow elephants walking in the same direction, one behind the other, and with a large gap between them, and with two dancing San women facing them. More than 135 red handprints are deliberately superimposed on top of and the figures. The larger elephant in front (78 cm) is the mother and the smaller elephant (34 cm) from its proportions, her juvenile calf. The Brakfontein painting (Fig. 5b) has the same arrangement of two elephants (15 and 7 cm) but with nine San female figures singing and dancing in front of them, holding digging sticks, and no superimposed handprints.

Females give birth to their first calf between 10 and 20 years of age. Thereafter, depending on food availability, females can produce a calf every four to six years (Poole 1997). At birth, newborn elephants are welcomed into the tightly knit female elephant society by loud roaring and rumbling from the older relatives. Young calves continue to suckle until they are between four and six years old. Typically, these older "calves are then weaned amidst loud protests, when their mother is in late-stage pregnancy preparing for her next calf" (Poole 1997).

We interpret these paintings to be illustrations of a female elephant in the late stage of pregnancy, is in the process of weaning her current juvenile calf. The San women, with their intimate knowledge of elephant behaviour and childbirth, would have known that birth was imminent by observing the distance of the calf behind its mother. The handprints (Fig. 5a) and digging sticks (Fig. 5b) are the artist's rendition of women celebrating this significant upcoming female event and their own fertility and the role of motherhood—elements crucial to the survival of the San people. This painting honours pregnancy and signals the beginning of a new life cycle. The artists who created these works were likely women, given the focus on female-oriented themes.

Zuurvlakte: birth

This painting is located on an outcrop of sandstone adjacent to a large salt pan. It shows two elephants rendered in yellow ochre, one large (105 cm) and the other tiny (9 cm) by comparison, suggesting a mother and her newborn calf. Both elephants are facing in the same direction (Fig. 6a). The calf has an unusually long painted line trailing behind it that is most likely an umbilical cord (Fig. 6b). This corresponds to field observations that a newborn calf can stand within an hour of birth (Poole 1977); while the dragging of an umbilical cord may continue for up to two days after an elephant has given birth. (Moss 1988).

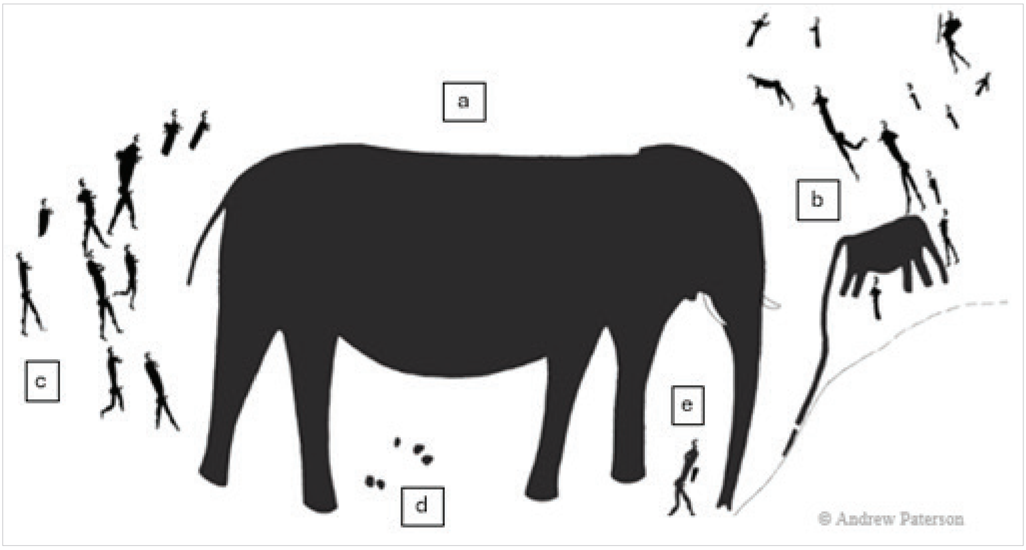

Figure 6. **Zuurvlakte** (a) A very large female elephant. (b) A newly born baby with an umbilical cord still attached. (c) San males, unarmed, celebrating the birth of the baby elephant. (d) Yellow paint marks where the baby would have first touched the ground at birth. (e) A single San male, very close to the elephant`s trunk.

The umbilical cord was an important aspect of birth for the San. According to Marshall (1997), after giving birth, a female relative/woman cut the umbilical cord with a small stick leaving about seven inches of the cord protruding from the baby's navel. The cord dried and shrivelled over a period of three days before it naturally fell off. The mother kept the baby's umbilical cord in a small, decorated leather pouch, specifically made for this purpose, and it was hung from thongs around the mother's neck. The umbilical cord was kept to safeguard the baby's health. When the child reached about four years old, the San mother then ritually disposed of the umbilical cord.

The San figures in this painting are all men, encircling the two elephants and facing inwards toward them (Fig. 6c). The figures have been drawn with their arms in the air. None of the men have bows or arrows in their hands. Neither of the elephants exhibits signs of stress or being hunted. The attitude of these men is one of excitement and celebration. One reason for the absence of female figures in San art may be that young San girls were prevented from witnessing any form of childbirth, as it was believed that observing a birth could instil fear and dread of childbirth in them (Marshall 1997). Similarly, San men are also prohibited from witnessing a San woman giving birth. However, they would likely have encountered elephants giving birth, which might explain their presence in the artwork. A similar painting of San males witnessing an elephant female giving birth exists at a site called Springbokoog, some 500 km away.

We suggest that this painting represents San men witnessing and celebrating the birth of an elephant calf (Figs. 6a, b). The San men were probably present during the actual birth to learn about the birthing sequence of labour contractions, breaking of the water, and the importance and function of the amniotic sac and umbilical cord. The San believe that at the instant the uterine fluid touches the ground (Fig. 6d), the vital force called *n!ao* is produced inside the baby. This, they believe, is the same force that determines the weather, including rainfall and seasonal dryness or cold (Marshall 1997). Adjacent to this painting, on the same outcrop, is a painting of two large eland with rain symbols superimposed on top of them. Finally, a single San male is walking very close to and in the same direction as the mother elephant (Fig. 6e), suggesting a close personal relationship between certain elephants and the San. This interpretation would support the idea that the San paintings themselves were a vital means of preserving and passing on fundamental birthing knowledge to San males and celebrating a new cycle of life.

Tandfontein, Bo Tuin and Voëlvlei: movement, space and leadership in female family units

In the Tandfontein painting (Fig. 7a), the lead elephant (10 cm) in a female family unit is depicted with her head and trunk raised, scenting a set of rain and cloud symbols, and is leading the group towards the rain. Over 65 rain images have been observed at 30 rock art sites throughout the Cederberg (Paterson 2018). Field observations of elephant behaviour reveal that the position of the elephant's trunk, and particularly the trunk tip, is highly informative, providing subtle clues to behaviour that is occurring or an interaction that is about to take place (Poole 1997).

The Bo Tuin painting (Fig. 7b). illustrates 16 elephants with a matriarch (13 cm) and family unit comprising three generations. The elephants are standing close together and facing in both directions. They appear to be alert and forming a protective circle, which is an accurate representation of how a family unit stands at night.

The Voëlvlei painting (Fig. 7c) illustrates a small female family unit of six elephants walking from left to right. The matriarch (15 cm) appears to be at the rear and an assertive female is leading the group. This straight-line formation is normally adopted by elephants as a means of protection and managing their young when walking from one place to another. This same formation is used by the San themselves when walking from place to place, and for the same reason, namely protection (Johnson 1979).

These three paintings, over 40 km apart, clearly show elephant female family units. Such paintings of elephants, measuring between two and ten centimetres, are found across the Cederberg area. As female family units dominate elephant social structure, they were likely to be encountered regularly by the San. The accuracy and rendition of the natural behaviour of the elephants in these three paintings confirms the San's intimate understanding of elephant behaviour. The San perceived that the elephants had their own characteristic behaviour which was governed by their customs *kxodi* (customs), and each had its particular *kxwisa* (speech, language). Elephants are believed by the San to have acquired special capabilities by means of rational thought (Liebenberg 1990).

Salmanslaagte: courtship and celebration

This painting is within one of the largest single shelters depicting San and elephant paintings in the Cederberg, stretching over 30 m across.

There are seven elephants in this painting composition. We interpret the four elephants on the left (Fig. 8a) as females, and the three elephants on the right

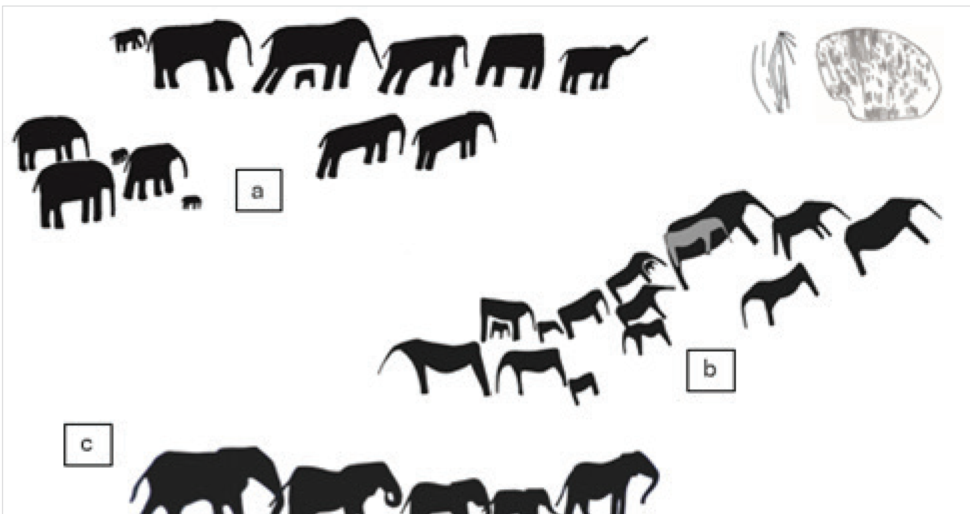

Figure 7. **Tandfontein** (a) Elephant female family unit being led toward a set of rain symbols with the foremost elephant scenting. **Bo Tuin** (b) Elephant female family unit with young standing and facing both directions. **Voëlvlei** (c) Family unit walking in single file with the matriarch in the rear.

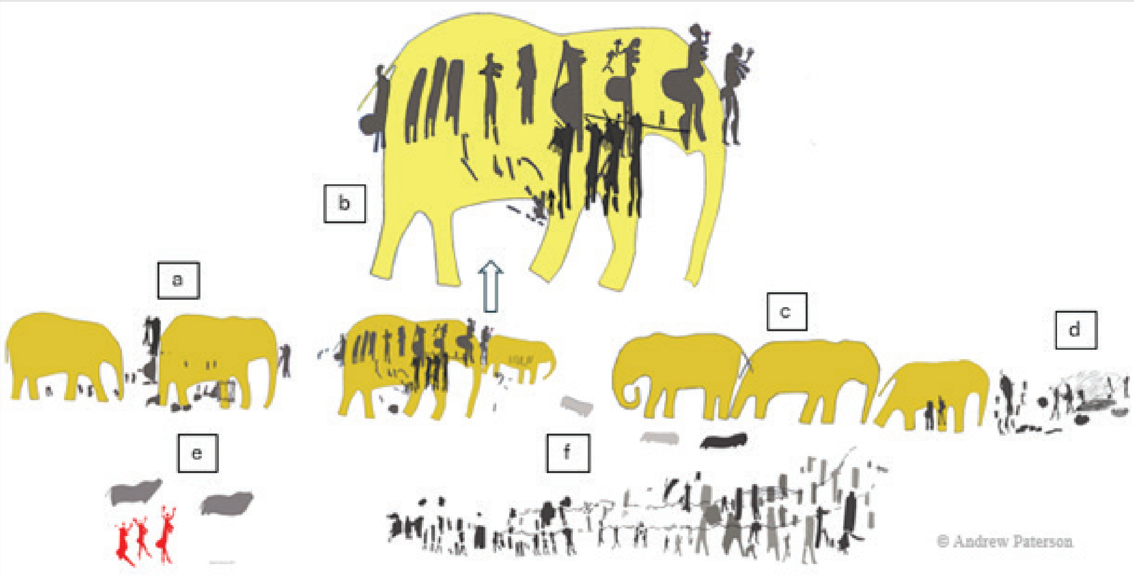

Figure 8. **Salmanslaagte** (a) Three large female elephants guiding a younger female towards a bull. (b) Enlargement of the central female matriarch with dancing female figures superimposed. (c) Bull elephant facing the female elephants, with trunk lifted to his mouth and two other bull elephants behind it. (d) Dancing San men with rain and cloud symbols. (e) San women singing and dancing with eland torsos. (f) Parallel lines of San people dancing on sound lines with eland torsos between them and the elephants.

(Fig.8c) as males. The male elephant closest to the female elephants has its trunk curled up toward its mouth. The left-hand group of female elephants has been painted as converging on the three standing male elephants, and this convergence takes place at the centre of the composition in the shelter. The focal point of the painting is a large female elephant (14.5 cm) (Fig. 8b), who is guiding a much smaller and younger female elephant (7.8 cm) in front of her.

We interpret this painting as depicting a matriarch guiding a younger female member of her family unit, who is in oestrus for the first time, towards a bull of her choice (Moss 1988). She is guiding the younger female through the steps that precede the act of mating (Poole 1997). This is a risky time for an inexperienced young female, who often finds herself chased by several younger bulls, all attempting to mount her. The bull elephant (Fig. 8c) facing this youngest female elephant in the painting appears set to roll the tip of his trunk to the back of his mouth to reach the duct leading to the vomeronasal organ, to assess the female's reproductive status (O'Connell 2007).

A group of 10 San females, led by two older females, are vigorously clapping their hands, singing and dancing, superimposed on top of the leading matriarch (Fig. 8b) at the centre of the composition. Four San men with bows slung over their shoulders are walking in full hunting regalia directly below these dancing women (Fig. 8b). A rain symbol and two cloud symbols (Paterson 2018) and dancing San males appear on the far right of the composition (Fig. 8d), while three dancing women and two eland torsos are to be found on the far left of the shelter (Fig. 8e). More than 60 San men and women with children are singing and dancing in two lines (each about 180 cm in length) below the elephants (Fig. 8f). Three eland torsos have been painted above this long line of dancing figures. The San people are clearly focused on the behaviour of the elephants, and the mood is one of excited celebration.

Eland and rain paintings are of great symbolic importance to the San. Elands symbolise abundance and well-being. As mentioned above, the vital force *n!ao* plays a key role in San mythology, connecting men's and women's procreative powers of hunting and childbirth to the polarities of weather, which are vital importance to hunter-gatherers. Indeed, life and death are closely bound up with the vagaries of the weather (Biesele 1993). Animals are used as metaphorical operators to steer humans away from undesirable states and towards desired ones of maturity, individual and social well-being, and safety (Biesele 1993). The painting appears to depict the natural mating behaviour of elephants and the weather, to symbolize and celebrate the San's own important life cycle events, such as procreation.

Stadsaal: elephant and human male bond groups

This painting depicts a group of six elephants (Fig. 9a), standing in three rows and facing in both directions, which is a natural position for elephants called an alert circle.

Except for one slightly smaller calf, there are no calves or juvenile elephants among the group, which could be a subadult. We take this to be a male bond group (Fig. 9a). The uppermost elephant is an incomplete line drawing (15 cm). It is larger than the others, with small tusks just visible, and appears to be the dominant elephant in this bull group (Paterson and Parkington 2016). Tusks on elephants are rare in the Cederberg, which could be due to white pigment weathering faster than the regular red or yellow ochred pigments. To date, no panels of elephants with clearly large or long tusks have been discovered. The white paint was made from substances like gypsum, kaolin clay, bird droppings, or powdered ostrich eggshells. This was then mixed with binders like blood, egg white, or animal fat to create the white colour, which, over time, has proved less robust than darker colours. (Mullen 2020)

The painting also depicts a group of 18 San males arranged in three rows, facing the three rows of elephants. The group of young San men in the top row standing opposite the largest elephant (Fig. 9b) are naked, while the other San males are dressed in karosses (Fig. 9c). This is suggestive of the San initiation ceremony known as *Tshoma* (see next panel). The elephants in the painting are depicted as being aware of the San; at the centre of the composition the youngest elephant is scenting a San male (dressed in a white cloak) with its extended trunk. This suggests a connection and mutual respect between San men and male elephants. The San were cognizant of the importance of the elephant's trunk |(*ai jako*) for multiple forms of communication. For example, San informants described to Bleek and Lloyd (1880) how the elephant "uses its trunk like a hand". The painting projects the image of a natural and harmonious relationship between the two groups. It is quite probable that the San knew all the various male elephant bond groups within their hunting area (Fig. 9c).

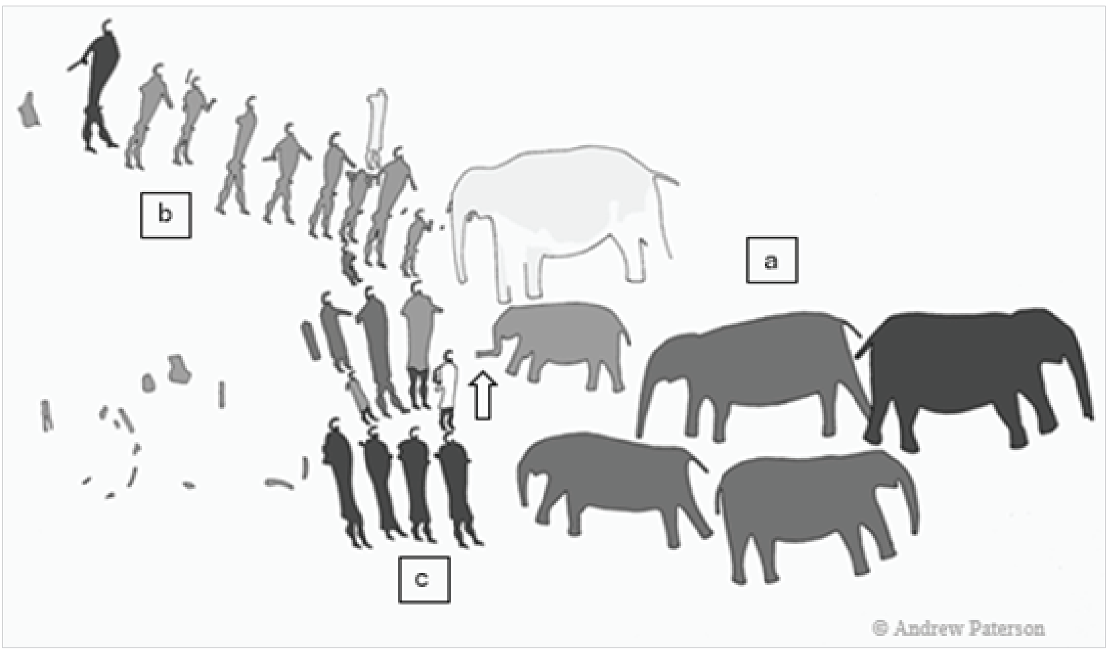

Figure 9. **Stadsaal** (a) An elephant male bull group standing in an alert circle. (b) A line of naked San males facing the dominant bull. (c) Two rows of adult San males wearing kaross cloaks.

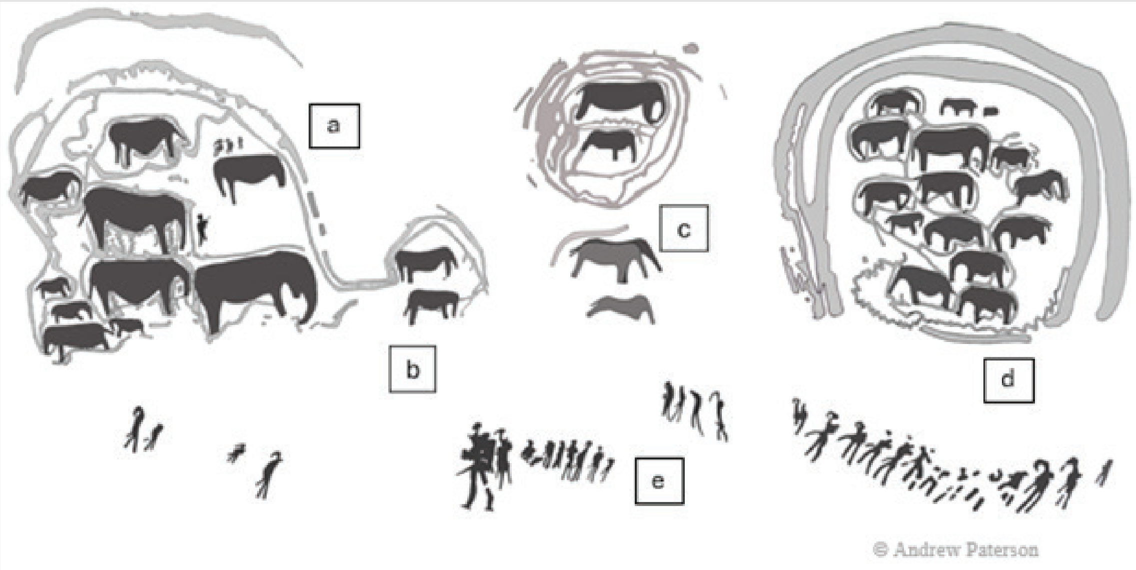

Figure 10. **Monte Cristo** (a) Female family unit. (b) Two young bulls who have been ejected from the family unit. (c) Male and female elephants consorting. (d) Female family unit. (e) San men participating in a male initiation ceremony, singing and dancing with elephanthropes, the ancestors of the elephants, with both elephants and people in musth.

Monte Cristo: male initiation and affiliation

This is a large painting of two female elephant family units (Fig. 10a–d) with lines of San male figures dancing in close formation below them (Fig. 10e). These lines of figures are made up of both San men and male 'elephanthropes', regarded by the San as mythical people with elephant heads and human bodies (Paterson 2019). Elephanthropes are a form of therianthrope, a term derived from the Greek words *Therion*, meaning beast, and *Anthropos*, meaning man. Their appearance in this painting suggests that the San are dancing with their ancestors in the 1st Creation, and with the ancestors of the elephants, shown as elephant-headed people.

The painting depicts the two female family units (Figs. 10a, 10d) to the left and right and, between these, a pair of subadult bull elephants (Fig. 10b), ready to leave their family units and join a male bond group when they arrive during the breeding season, and two pairs of male and female elephants in consort during the breeding season (Fig. 10c). The entire painting is only 107 cm wide with elephants ranging in size from 1 to 7 cm.

This would be a typical scene at the end of the rainy season when the male elephants go into musth and move down to the female areas to seek out females in oestrus. It is common for male elephants in musth to consort with females from one to four days, during which period they mate regularly (Moss 1988).

The dancing San males and elephanthropes (Fig.10e) have distinctive long and enlarged penises, similar to those of a bull elephant in musth. The San male Tshoma initiation rite is marked by the rising of the Pleiades in mid-June, which is the coldest time of the year (Marshall 1999). Most of the rainfall in the Cederberg region occurs during the winter months, from June to August. All these features combined in the painting (Fig.10) suggest that the artist is illustrating a San male initiation ceremony that symbolises the transition from the 2nd creation into the 1st creation, and back to the 2nd creation again. The initiation represents the San male's movement from boyhood to manhood.

The ceremonial male dance depicted here is the *Tshxai !Go*, or Men's Dance (Marshall 1999). By depicting both San men and elephanthropes in musth, this painting affirms the close symbolic connection between San and elephants, first proposed by Townley Johnson in his commentary on the tracing of painting from this site in 1962 (Fig. 3a) (Townley Johnson 1979).

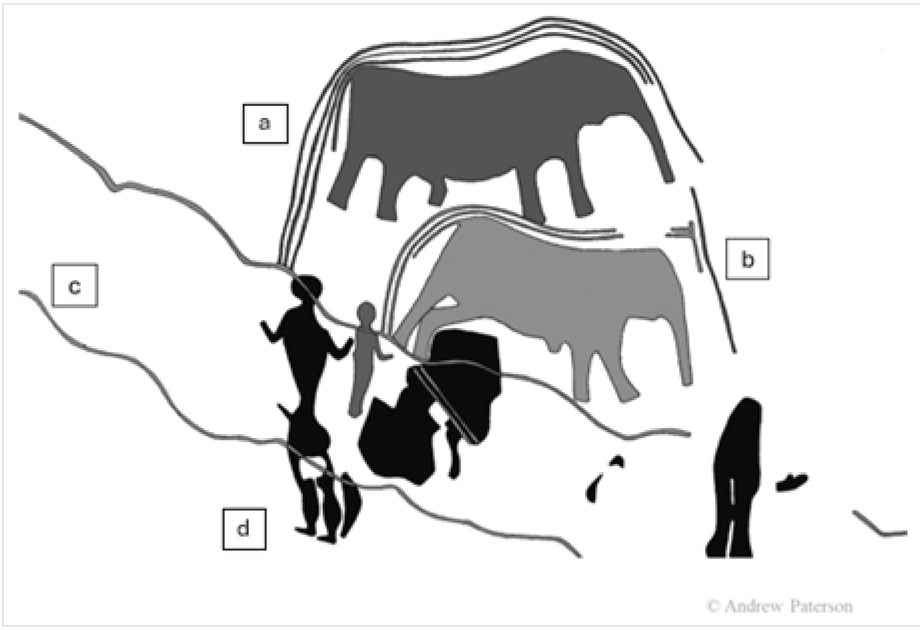

Figure 11. **Klipfonteinrand** (a) Bull elephant in musth with triple sound lines. (b) female elephant in oestrus with double sound lines. (c) Large pulsating female chorus sound lines. (d) San male and female observing the elephants mating.

Klipfonteinrand: mating and courtship

This painting is located at the entrance to a deep well-defined cave filled with numerous paintings of San males, eland torsos and fingerprints. There are two elephants on the left side of the cave entrance. The larger elephant is above and directly behind the smaller elephant with both elephants running in the same direction. The rear elephant (14 cm) has an extended penis (Fig. 11a), and the front elephant (11 cm) appears to have breasts (Fig. 11b).

There are different sets of fine parallel red lines surrounding each elephant and connecting them both to a large set of wide, pulsating parallel lines below (Fig.11c). This large set of lines, about two meters in length, runs into the cave along the left wall. Superimposed on them are two San figures, one male and the other female, standing facing the elephants. These parallel pulsating lines, that run into the cave, connect to another group of San males and eland torsos.

We interpret the lines surrounding the two elephants as sound lines (Paterson 2020). In this interpretation, the three fine parallel lines surrounding the male (Fig. 11a), represent the sounds made by a male in musth (Moss 1988), while the two parallel lines surrounding the female (Fig. 11c) represent the sounds of a female in oestrus, when pursued by the male (Moss 1988). These two sets of lines are connected to the widely spaced set of parallel pulsating lines (Fig. 11c), which represent the female elephant chorus typically heard from other females in the family unit during mating (Moss 1988; Poole 1997). The presence of San figures in the painting is significant in that it illustrates that the San were acutely aware of the specific sounds associated with elephant mating behaviour. Again, the San are showing respect for this significant life cycle event.

Sevilla Trail: non-confrontational encounter

This painting is of a single elephant (17 cm), possibly a young bull elephant (Fig. 12a), facing right with its head lowered and three San men directly in front of it (Fig. 12b). Two of the men have hunting bows that are not drawn. The front San figure without a bow is crouching down and facing the elephant directly. The second figure is beckoning to a third figure behind him to come towards them. The third figure in the rear is walking cautiously, with bow down, and towards the elephant.

There is no sense of hunting, stress or antagonism in this painting. The elephant is interacting with the three

Figure 12. **Sevilla Trail** (a) Single elephant aware of the San figures in front of it. (b) Three San men cautiously approached the elephant, gesturing to one another and with their bows lowered.

San males in a non-threatening way. There are specific San individuals in the San communities who lead the elephant storytelling occasions, and songs and dances at the San healing ceremonies. They have been called "owners of the feeling for elephants" (Keeney and Keeney 2015). This painting may illustrate such an individual, with an affinity for elephants, interacting with an elephant.

Bushmanskloof: confrontation

This dramatic painting (Fig. 13) suggests a dangerous confrontational situation between a mother elephant, her baby and two San males. The two elephants, one large (9 cm) with its tail erect and the other small (3 cm) with its trunk raised, are very close to, and appear to be challenging two San males, who are facing the elephants with drawn bows.

This painting was called 'The Elephant Hunt' by earlier researchers. The San appear to have fired as many as seven arrows into the head of the larger mother elephant. However, this does not appear to be a hunting scene; rather it suggests a mother elephant's instinct to defend and protect her offspring when endangered. Hunting an elephant head-on would be a very dangerous and unusual thing for an experienced San hunter to do. The numerous arrows fired directly into the elephant's head suggest that they are ineffectual and that the shooting is probably the San's defensive action. Many San people avoid consuming elephant meat today, as it is believed to resemble human flesh (Biesele 1993).

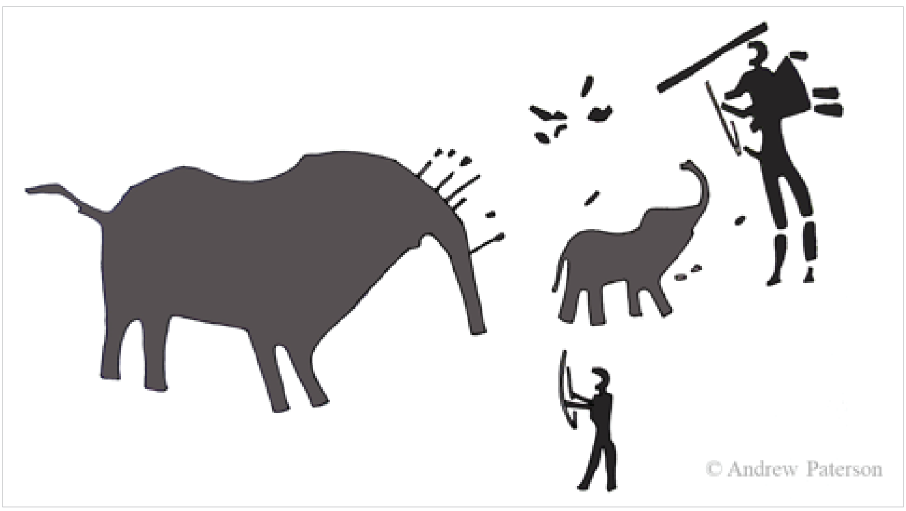

Figure 13. **Bushmanskloof** Two San men defending themselves in a confrontational situation with elephants.

Olifants River: Elephanthropes and water

This painting shows six elephanthropes (6–12 cm) walking in a single file from left to right, carrying elongated objects on their backs, tied on with thongs (Fig 14a). The elephanthropes are painted as described in San mythology: as early beings, with elephant heads, hands and feet, and human bodies, who lived in the primal time of 1st creation when elephants were people, as told by the San to Bleek and Lloyd 1880. (Paterson 2018), (Fig. 14b). The lower panels show 23 San males who appear to be participating in a San male *Tshoma* initiation ceremony in the present time of the 2nd creation (Paterson 2018; 2019). On the left, 11 adult males are standing in a line (Fig. 14c); while the right-hand panel shows two standing adults and 10 smaller figures, presumably young boys, lying scattered randomly on the ground (Fig. 14d) (Paterson 2020; 2022; 2023). Below the men and boys, torsos of eland are shown, symbolizing hunting and meat (Fig. 14e).

Townley Johnson, who traced this painting in 1962, describes this panel as a row of human figures with elephant-like heads and trunks, each carrying an unidentified object on its back. They resembled the elephant-headed humans from Monte Cristo which again suggests that the elephant was of symbolic importance to the people of this region (Townley Johnson 1979). Townley Johnson (1979), suggests that the elephanthropes in this painting are carrying woven baskets of vertically oriented ostrich eggshells filled with water. Accepting this suggestion, we interpret this painting in the light of San mythology, which recounts that it was elephanthropes "who first found water so that the San people could drink" (Biesele 2009).

The availability of and access to water is critical for the survival of both elephants and the San. Elephants can pick up the vibrations of thunder more than 100 km away (O'Connell 2007) and start moving towards it before other animals. Elephants are also able to locate running water below dry riverbeds using their ultra-sensitive feet. The San were well aware of these elephant characteristics and relied on elephants finding water in drought conditions.

Figure 14. **Olifants River** (a) Elephanthropes carrying baskets of ostrich eggshells filled with water. (b) "When the elephants were people" (Bleek and Lloyd 1880). (c) San men participating in an initiation ceremony connected by lines of *n|om*. (d) Following an initiation ceremony young San boys lie on the ground recovering from the experience. (e) Eland torsos, symbolic of hunting and meat.

Other features of the painting support this interpretation. The cross-hatched marks above the head of the largest elephanthrope, at the rear of the group (Fig.16a), appear to be a rain symbol, similar to others encountered throughout rock art panels in the Cederberg (Paterson 2018). The location of the painting site may also be site-specific, as it is only about 50 m from the Olifants River, where the river's banks narrow significantly with cliffs on either side, in which the site is situated.

Finally, we interpret the thin red parallel lines connecting each of the standing San men in the painting to each of the young initiates lying on the ground (Fig. 14d) as lines of *n|om*. This vibratory life force animates all living beings. The same lines connect the San to the eland torsos below.

The whole composition can be seen as a depiction of the San celebrating the significant life cycle event of boys becoming men at an initiation ceremony, and highlighting the importance of water for the survival of the San, and elephants.

Rietvlei: rain symbols

The focal point of the painting is two adult elephants (14 cm) facing one another head-to-head (Fig. 15a) with a smaller elephant above them with an extended trunk. The two large elephants appear to be drinking from a water hole that they have dug in a dry riverbed. Superimposed on the central elephants is a single, large vertical male rain symbol (Fig. 15b) (Paterson 2018). The San distinguish between male and female rain, which are shown differently in the paintings. Male rain symbols converge at the top and spread out towards the base. This large male rain symbol appears to be associated with a near-vertical lightning symbol (Fig. 15b). Female rain symbols consist of a series of short parallel lines that emerge from and connect to a single horizontal line above them (Fig. 15c) (Paterson 2018), or sometimes to a line of finger dots (Fig 15d). Finger dots and handprints are associated with the sound of women clapping their hands.

In each of the three lower panels, San figures, male and female, are shown dancing and singing in the midst of rain, among the elephants and eland symbols. We interpret this as a celebration of life, survival and protection from starvation, to which all the most

Figure 15. **Rietvlei** (a) Two elephants standing head-to-head and drinking at a waterhole with eland and dancing figures superimposed. (b) Male rain symbol with a lightning bolt. (c) Four elands with female rain symbol and dancing figures. (d) Four elands with a female rain symbol and 13 male and female figures. (e) San word for female rain. (f) San word for male rain.

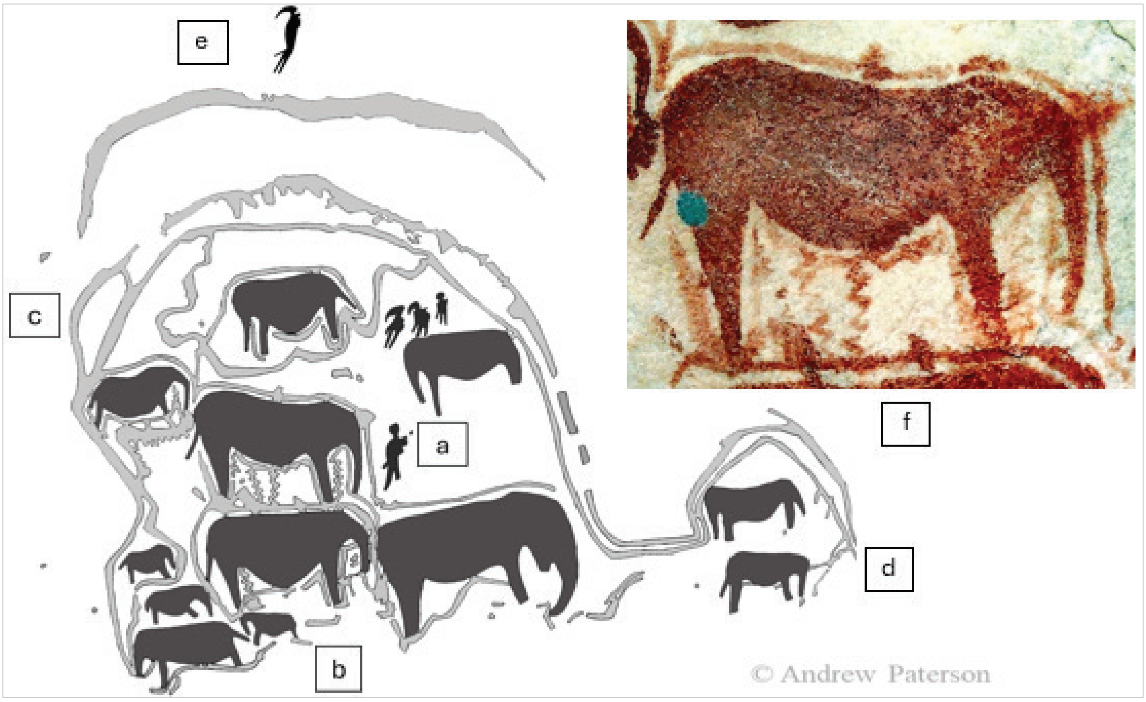

Figure 16. **Monte Cristo** (a) San figure and elephanthropes among the elephants. (b) Elephant female family unit enclosed by sound lines. The lines touch all their body parts that send and receive sound. (c) Set of parallel lines surrounding the entire family unit and two young bull elephants. (e) Sound wave moving up and away towards other family units in the area. (f) D-Stretch image of sound lines surrounding the elephant at the centre of the family unit.

frequently performed San rites and informal ritualistic practices are directed (Marshall 1999).

Monte Cristo: female sounds and communication

This enlarged portion of the painting at Monte Cristo (see Fig. 10) ranks as one of the most important elephant paintings in the Cederberg. It is believed to illustrate elephant sound and communication and, dating from between 1500 and 3500 years ago, is possibly the first painted rendition of sound in African rock art (Paterson 2007; Paterson and Parkington 2016). There are 12 elephants (1–7 cm) in this painting, comprising a single female family unit (Fig. 16a). As stated earlier, the fundamental component of elephant social structure is that of a female family unit and its dependent offspring living in a tight-knit stable family group. Each elephant begins its life within a family unit (Poole 1997), which consists of a matriarch and up to four generations of offspring.

There are thin, wavy/zigzag lines surrounding each elephant in this family unit and connecting all the elephants in the family to one another. We interpret these as sound lines, since they are shown contouring and connecting the various elephant body parts (Fig.16a; 16b;16f) associated with elephant sound and communication, namely the head, throat, trunk, stomach and feet (Paterson 2007; Parkington and Paterson 2017; Paterson 2025).

A second set of larger parallel lines, connected to these internal lines between the elephants, surround the whole family unit (Fig. 16c). There are also two smaller elephants connected by this set of parallel sound lines (Fig. 16d) We propose that these two young bull elephants have reached sexual maturity and, as a result, have been pushed to the periphery of their family unit. Although they are distanced from the main group, they still maintain communication with their family. They appear poised to leave once the next male bond group arrives during the breeding season. Finally, a third broad single sound line (Fig. 16e) appears to be radiating up and away from the family unit towards other possible elephants in the area. Elephants emit a broad range of sounds from low-frequency vibrations to high-frequency trumpets.

Figure 17. **Floreat** (a) A male elephant bond group, surrounded by sinusoidal waves, communicating with one another and with (b) a second male bond group. (c) "And the elephant again said rrrr" (Bleek and Lloyd 1880)

In all, some 60 different elephant calls are known, with rumbles being the most numerous and complex class of at least 30 elephant calls, which are used for long-distance communication, and can be sensed by other groups of elephants a long distance away. All of the rumbles contain components below the level of human hearing, with some being totally infrasonic (Poole 1997; Mortimer 2018: Helm et al. 2024).

This painting suggests that the San had an in-depth understanding and appreciation of the communication system and social structure of elephants, which they associated with their own social structure and communication system, vital to their survival.

Floreat: male communication

This site is located on a large, isolated rock outcrop, in the open valley of the Olifants River, near Citrusdal. There are two groups of elephants (4–6 cm) in the painting, one of three (Fig. 17a) and the other of four elephants (Fig.17b). The elephants are all similar in size, which suggests they are a male bond group, and are standing head-to-head, which is a typical stance when communicating. Surrounding each group of elephants is a set of precisely drawn sinusoidal waves connecting all of the elephants. We interpret these sinusoidal waves as vibrating sound lines. They, in turn, connect to sets of zigzag lines radiating up and away from the two groups of elephants, similar to in the previous painting of a female family unit.

This painting illustrates that the San clearly understood and appreciated the structure of elephant male bond groups. They also understood that good communication and group coordination among bull elephants is vital to their survival. When not in breeding season, elephant bulls prefer to stay in their own territory separate from the females. Although San men do not have a seasonal separation from women, as do elephants, San men do form powerful bonds in male-only hunting groups.

The most striking aspect of these Floreat elephant sound lines is that they have been drawn as near-perfect sinusoidal waves. According to Bleek and Lloyd (1880), their San informant described elephant sound in general when he referred to: "elephant again said *rrrr*" (Fig. 17c). They also recorded the word *!nhuru*, meaning to make a trilling noise. The San would have understood that elephants produced regular vibrating sounds and painted these *rrrr* sounds as sinusoidal waves. It is also quite possible that the San felt the same "pulsating vibrations and throbbing in the air" made by elephants that were described by the elephant behaviouralist and acoustic biologist Katy Payne, in the account of her pioneering studies of elephant communication in 1984 (Payne 1998).

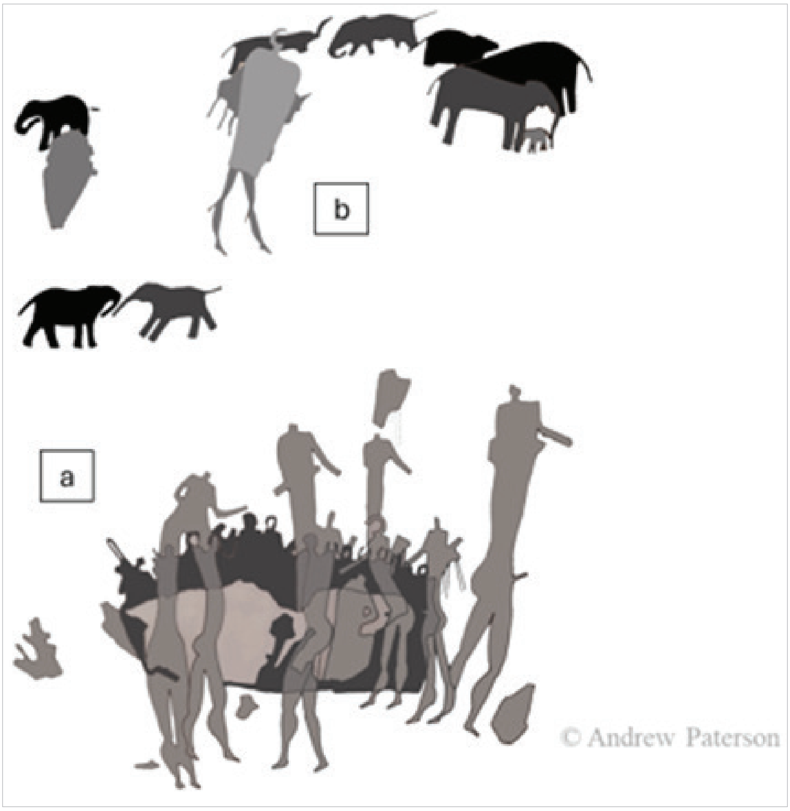

Figure 18. **Sevilla Trail** (a) Singing women seated next to a fire with men dancing in a circle around them. (b) A female family unit of nine elephants surrounding a single San male wearing a kaross.

Finally, the San could have associated the low-frequency rumble of thunder in the distance with the low-frequency rumble of bull elephants. Elephants were regarded by the San as "rain animals" (Woodhouse 1992), and, in San mythology, the elephant was the one who first found water, and "caused the rain to fall so that the San could drink" (Biesele 2009).

Sevilla #1 Trail site: dance and play

The focus of this painting is a group of at least 15 San figures seated in a circle on the ground (Fig. 18a). Nine male figures are dancing around these seated figures. Above these singing and dancing figures is an elephant female family unit composed of nine elephants (6–9 cm) (Fig. 18b). Two sets of elephants appear to be playing socially. Standing in the centre of this group of elephants is a single San male figure wearing a kaross and carrying a hunting bag slung over his shoulder (Fig. 18b). Again, there is no sign of tension or hunting in this painting.

We interpret this painting as a healing dance, when women typically sit on the ground around a fire, singing and clapping in harmony. The men sing and dance in a circle around the women. There are a number of San medicine songs; many of the songs are named after strong animals. (Marshall 1999). One of the most important of these is the elephant dance (Biesele 1993). Known as *!xo`djxani*, this powerful healing dance awakens the vibrating life force *n/om* of inspired energy that animates all living beings, bringing the San close to their Creator God *!Xun!a`an*. (Keeney and Keeney 2015). The elephant dance would typically be led by a San elder known as the "owner of the feeling for elephants" (Keeney and Keeney 2015).

This Sevilla painting of San people singing and dancing, with elephants surrounding an 'owner of the feeling for elephants' above them, depicts the special healing relationship between San and elephants.

Discussion

San rock art paintings reflect the San's mind, culture, and attitude towards the elephants in their environment. Their art is uniquely accurate in its rendition of the behaviour of the elephants, of the San themselves, and the natural interactions between these two perceived beings.

For ease of comprehension, our interpretations of the painting are summarized in a single table (Table 1), showing how they relate to San behavioural contexts described by anthropologists and elephant behavioural contexts described in the Elephant Ethogram (Poole 2021). Behavioural context refers to the circumstances or setting in which a behaviour takes place. We identified these contexts by examining and comparing the behaviour of the San figures and of elephants in each painting. It is assumed that the behavioural contexts painted in these 17 sites would have been witnessed by the San artists themselves. Each painting depicts elements of specific significance to the San people, which are meant to be preserved, as part of their integrated knowledge system and handed down to future generations (Kelley 2016). The importance of behavioural contexts in the rock art is that they portray the depth and variety of relationships between the San and elephants. This paper and the summary results Table 1 are intended as an entry point for future study of San's rock art paintings and mythology; they provide a heuristic framework for understanding the complex, multifaceted San traditions of relating to elephants (Biesele 1993).

The significance of these paintings lies in their ability to codify and condense meaning. This condensation is achieved in part by "eliminating the redundancy of reference" (Biesele 1993). In other words, it stems from the various interconnections suggested by the specific attributes of the elephants depicted in the paintings. When experiences from one context can be applied metaphorically to other contexts, it enhances mental efficiency. This process of condensation allows a smaller set of experiences to create a greater impact. In essence, paintings and mythology have a multiplier effect, amplifying the significance of the San people's encounters with elephants (Biesele 1993).

Together, these paintings and mythological contexts contribute toward an overarching theme of

Table 1. Our interpretation of the San and elephant behavioural contexts depicted in the figures.

	SAN AND ELEPHANT BEHAVIOURAL CONTEXTS						
Figures	SITE DESCRIPTION AND LOCATION	SAN ROCK ART SAN and ELEPHANT Behavioural Contexts	ETHOGRAM ELEPHANT Behavioural Contexts	Sites analysed 17	Elephant paintings 122	San figure paintings 201	Elephanthrope paintings 25
5	Steenkampskloof, Brakfontein	Pregnancy	Weaning	2	4	9	
6	Zuurvlakte	Birth	Birth	1	2	22	
7	Botuin, Tandfontein, Voëlvlei	Female family unit	Movement	3	36	0	
8	Salmanslaagte	Courtship	Courtship	1	7	87	
9	Stadsaal	Male bond group	Coalition	1	6	18	
10	Monte Cristo	Male initiation	Affiliation	1	31	18	15
11	Klipfonteintrand	Courtship	Courtship	1	2	2	
12	Sevilla Trail #7	Non-confrontation	Attentive	1	1	3	
13	Bushmanskloof	Confrontation	Ambivalent	1	2	2	
14	Olifants River	Elephanthropes	Maintenance	1	0	0	6
15	Rietvlei	Rain symbols	Maintenance	1	3	19	
16	Monte Cristo	Female communication	Affiliation	1	12	1	4
17	Floreat	Male communication	Affiliation	1	7	0	
18	Sevilla Trail #1	Healing dance	Affiliation	1	9	20	

mutual respect between the San and the elephant in a relationship that was not harmful to either of them or their shared environment. The paintings are a record of the major life cycle events that the San celebrated and that elephant behaviour symbolized for them.

The San chose to paint elephants because their attributes bore a special significance. As the elephant paintings, used metaphorically, gather meaning over time, they provide the setting for performances in different media and contexts, such as ritual, singing and dancing, thereby promoting cognitive processes of relatedness and overcoming cognitive dysfunction (Biesele 1993). Taken together, the paintings and the metaphors they embody are not just descriptive; they create a dynamic connection between the San, the elephants, and their environment.

Present-day San communities living in the Kalahari are aware of the mythological stories referred to in this paper. The stories collected by anthropologists Marshall, Biesele and Keeney between 1950 and 2015 were recorded directly from the learned San themselves. However, the San no longer paint on rock faces or in rock shelters. Rock art accessible to modern San communities is limited to some excellent paintings at *Tsodilo* Hills and *Savuti* Channel on either side of the Okavango Swamp in Botswana. There are paintings of eland, giraffe, rhino, elephants, featuring handprints and San figures, at both these sites. The San in Botswana today know that their ancestors painted on rock. This suggests that they could be well aware of the extent of the relationship between the San and elephants in historical times, as evidenced in the rock art of the Cederberg reviewed in this paper. This suggests that the findings of this paper are significant not only from a historical perspective but also for modern-day San communities. It has the potential to revive traditional knowledge and promote contemporary coexistence between humans and elephants.

Most people in southern Africa today, including the San, do not want to see elephants destroyed; rather, they would prefer to see effective practices and policies put in place that reduce human–elephant conflict. In Botswana, for example, elephant numbers have increased, with estimates placing elephant numbers as high as 180,000. While historically some indigenous groups may have participated in elephant hunting, few indigenous people today hunt elephants. They do, however, engage with elephants in several different ways, including community-based natural resource projects, photographic ecotourism and/or safaris.

Conclusion

The San in the Cederberg, like todays' researchers into elephant behaviour, recognized that elephants were sentient beings. We now know that elephants are highly intelligent, emotional and social animals, exhibiting complex behaviour such as empathy, grief, self-awareness and tool use. These behaviours were observed by the early San people living in the Cederberg, which led to a deep affinity for elephants that is evidenced by their paintings, which depict elephant people of the early race, depicted as beings with human bodies and elephant heads, feet and hands.

There are several realms in life in which the San believe that human beings cannot act alone. Accordingly, they seek ways of transcending human limitations and bridging human and non-human worlds. In historical times, elephants, visible, powerful and near at hand, were a good choice for this purpose (Biesele 1993). According to the San, elephants had the strength and courage to transcend the natural and supernatural worlds, of the 1st and 2nd creations (Biesele 1993; Keeney 2003 allowing the San to dance with their ancestors and the ancestors of the elephants during their healing dances and initiation ceremonies.

The core behaviour of the San, illustrated in the rock art paintings reviewed in this paper appears to be a celebration of life. The analysis presents the symbolic work of painters and storytellers as thoroughly practical in effect. The work of San artists is best understood as a form of action upon the conditions necessary for the reproduction of their societies (Biesele 1993). In conclusion, the central context defining the relationship between elephants and San over thousands of years is one of mutual respect in a celebration of life and survival.

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The missing metric: speculations on tusk curvature

Ian SC Parker

PO Box 1115, Tolga, QLD 4883, Australia

Email: ipap@activ8.net.au

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Abstract

As weight is the criterion of commercial value, elephant tusks have been weighed in their millions across the centuries. More recently, it has been shown that weight, length and circumference-at-lip of the African savannah elephant (*Loxodonta africana*) are predictive of one another and, at the population level, related to age. Missing altogether are data on the curvature created by helical tusk growth. Describing this in population terms would require large sample sizes of tusks from both sexes of all ages. While natural mortality of elephants of known ages could, in due course, provide sufficient data for such an analysis, at present none are available. To partially fill this knowledge gap, this paper considers available evidence to suggest how the shape of the male savannah elephant tusk changes with age and how its changing curvature may influence behaviour.

Résumé

Le poids étant un critère de valeur commerciale, les défenses d'éléphant ont été pesées par millions au fil des siècles. Plus récemment, il a été montré que le poids, la longueur et la circonférence (mesurée au niveau de la lèvre) des défenses de l'éléphant de savane d'Afrique (*Loxodonta africana*) sont des données prédictives les unes des autres, et, à l'échelle de la population, sont liés à l'âge. En revanche, les informations manquantes concernent la courbure créée par la croissance hélicoïdale des défenses. Pour décrire cela en termes de population, il faudrait disposer d'échantillons importants de défenses provenant des deux sexes et de tous les âges. Si la mortalité naturelle des éléphants dont l'âge est connu pourrait, à terme, fournir assez de données pour une telle analyse, elles ne sont, à l'heure actuelle, pas disponibles. Afin de combler en partie ces lacunes, le présent article examine les données probantes existantes pour suggérer de quelle façon la forme des défenses des éléphants de savane mâles change avec l'âge, et comment la modification de leur courbure peut influencer le comportement de son propriétaire.

Introduction

Einstein (1931) observes that "imagination is more important than knowledge. For knowledge is limited, whereas imagination embraces the entire world." Yet while some imagination seems mystical, most inventions and ideologies are self-evidently stimulated by knowledge. Using the data available to me, I propose a hypothesis to fill a knowledge gap about the role tusk curvature plays in the behaviour of male African savannah elephants (*Loxodonta africana*).

In what follows, the knowledge of elephants and their tusks underpinning my speculations is grounded in both objective analysis of data from 2,900 elephants culled in Uganda, Kenya, and Tanzania (Parker 2024a; Parker and McCullagh 2021), and the subjective experience of observing elephants and handling over 100,000 elephant tusks in 14 African and eight Eurasian countries between 1956 and 2014. While I never tallied the numbers examined in traders' vaults, artists' workshops, the houses of trophy hunters, government stores or the international ivory marts of

Africa and Eurasia, they must run to hundreds of thousands. I think I am familiar with tusks.

Tusks that I observed in living elephants and post-mortem displayed wide differences in shape and size, for which there was no obvious explanation. Some seemingly old elephants had only short tusks, while those of supposedly young individuals were long; similarly, some individuals of the same age had thick tusks and others thin ones. However, such perceptions were based on observations of a few individuals, whereas establishing population norms in animals that can live for more than 60 years calls for large samples from all ages. It was not until Laws (1966) established that age and sex predictably govern tusk weight that a sense of order emerged. I expanded on that order (Parker 2024a; 2024b), showing that the average length and circumference-at-lip are commensurate, and that weight, length, and circumference are mutually predictive of one another. I further explain the differences between theoretical and actual asymptotes, which arise through wear and breakage, and how average tusk lengths are related to an elephant's height (and thus the length of its bones). Yet, while age, growth, shoulder height, tusk weight, length and circumference-at-lip correlate closely, shape does not. The reason for this is that tusks are not simple arcs but grow as spirals. This breaks the symmetry between tusk pairs displayed by the other metrics. Continuously growing from its base, in the alveolus, a broken tusk will recover lost length and catch up with its partner. The break will be worn back to a point, and the lost length recovered. However, the curve of the lost piece of tusk cannot be replicated. This results in the orientation dissymmetry we commonly see in living elephants. Yet while obvious enough, hard data describing curvature are lacking to explain this phenomenon. To partly fill this gap, I exercise my imagination and focus on how curvature affects the tusk shape of male savannah elephants and how this, over time, affects their value for fighting.

Hypothesis

Parker (2023a) observes, *inter alia*, that in an animal with continuously growing structures and a longevity spanning decades, as with humans, large samples are essential to establish population metrics. Applying this maxim, the author analysed a sample of 946 male savannah elephant tusks out of the total 2,900 culled and derived asymptote values of ~250 cm length and 40 kg weight (Parker 2024a). These are far below maximum values of >335 cm length and >100 kg weight for individual tusks given by Balan (2025 *in litt.*) in his compendium of record tusk metrics. Such maxima are widely assumed to be 'normal' and attainable by elephant bulls who live beyond 50 years. Furthermore, their rarity is taken to be a consequence of selective hunting for big tusks. However, Parker (2023a) points out that male elephants over 50 years of age whose tusks attain asymptotic lengths and weights represent <1% of elephant populations, even in Murchison Falls National Park (NP), where elephants had not been hunted for more than 50 years. Whether this low survivorship of old males with large tusks applies beyond the range of 'East African type elephants' as described by Parker (1979) is moot.

Unpublished ancillary evidence supports the rarity of old male elephants with tusks weighing >40 kg. In 1965, Uganda's Murchison Falls NP held ~14,000 elephants. In the open habitat where elephants were easily and regularly observed from both ground and air, such tuskers (some individually named e.g. *Tangi Monster* and *Lord Mayor of Paraa*) were certainly fewer than 50 (0.4% of the population). Similarly, in South Africa's Kruger NP in the late 1970s, only six such exceptional tuskers were known, namely *Mafunyane, Shawu, Shingwedzi, Dzombo, Hlanglene* and *Kambaka* (Raubenheimer et al. 1989; A. Hall-Martin, pers. comm., 1985) accounting for <0.1% of the total elephant population of ~7,000 individuals. Wherever males with tusks exceeding 40 kg became known, they attracted the attention of hunters and conservationists, who commented on both the size of the tusks and their rarity. For organizers of commercial safaris at the turn of the 20th century, securing tusks over 40 kg was both a goal and ground for comment when achieved. Incomplete as such evidence may be, it nonetheless gives grounds for confidence in the findings from the 2,900 culled elephants that male tusks rarely exceed 40 kg weight. Contrary evidence is provided by photographs[1] taken across the past 150

[1]As shown in Simon Trevor's monumental documentary series Tsavo: *A Moment in Time (2024)* listed in References

Figure 1. How I imagine the tusk shape Laws (1966) describes. © Travis Tischler.

years of many male tusks of >40 kg on warehouse floors, which are presented as proof that such elephants were once common. The evidence establishes abundance, which is hardly surprising given that elephants occurred in virtually all biota of sub-Saharan Africa. Yet this abundance of large elephant tusks does not challenge the finding that old male savannah elephants form very small proportions of their populations.

Obtaining statistically robust data from reliably aged male African elephants older than 40 years is not possible. A further complication is the probability that metrics on any parameter may differ regionally (Elder 1970; Parker 1979). All the foregoing has a bearing on any analysis of the savannah elephant tusk curvature—the missing metric—and how it might influence behaviour.

Curves abound in nature and in proboscidean tusks in particular (Hayden and Fisher 2011; Evans et al. 2021). Laws (1966) said that East African savannah elephant tusks grow continuously throughout life in logarithmic or helical spirals. Figure 1 below illustrates what I imagine Laws had in mind.

My personal subjective observations confirm this view. Moreover, the spirality is usually chiral; that is, the tusks are non-superposable mirror images of one another. However, as illustrated in the photographs of 165 pairs of tusks from 15 culled herds laid out on flat ground and taken vertically, in two dimensions they appear as simple inward arcs without the third dimension of depth (Fig. 2).

All aspects of an elephant's tusks are obviously determined by an overarching genetic template. Yet within these limits, there is wide variation. Most herds composed of females and immatures are families (Moss and Lee 2011) and similarities among their tusks reflect genetic influences (Parker 2024a, Fig. 9). However, genetic differences among herds in the sample in Figure 2 are not so obvious, and the tusks in the different photographs appear more similar than dissimilar. As presented, they seem to be simple arcs,

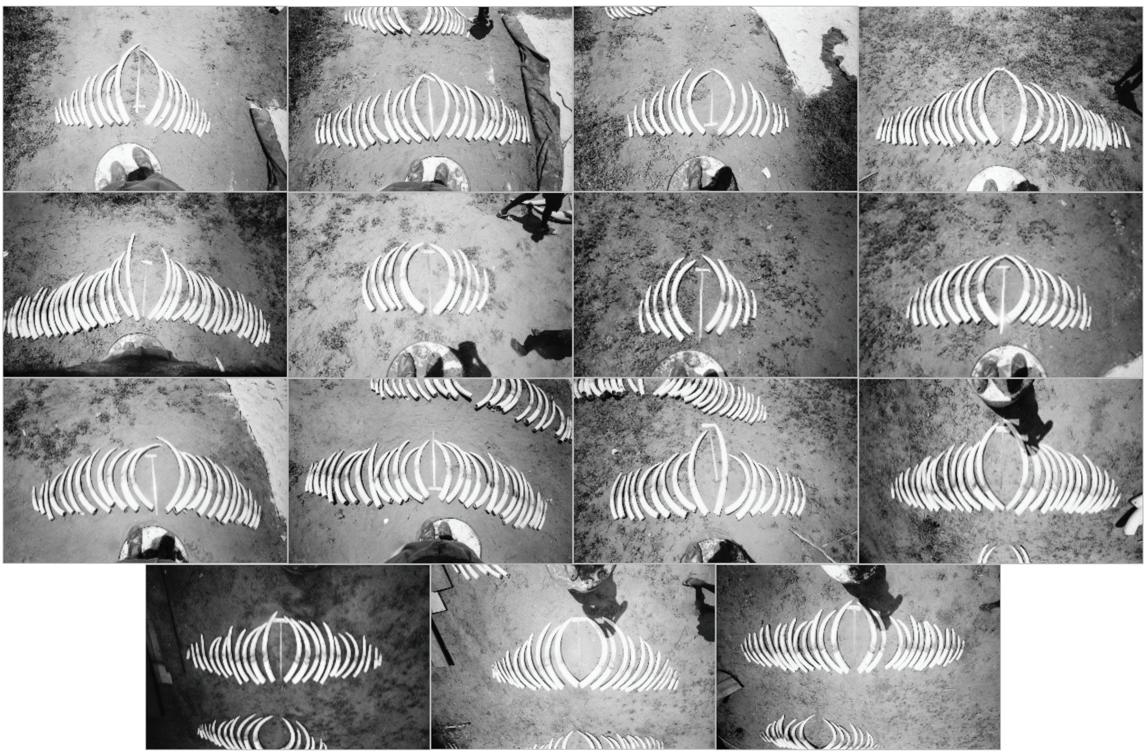

Figure 2. Tusks from 15 herds culled in Mkomazi East Tanzania laid out on flat ground and photographed vertically from above.

Figure 3. An exceptional illustration of helical tusk growth. © Suzannah Goss.

whose depth is found by drawing a line at a right angle from the centre of the chord connecting the two ends until it meets the arc. This is the arcuate tusk form of popular perception. However, the two-dimensional view conceals the third dimension of the helix. With a helix, the equivalent line connects the axis of the helix to the arc; its length is the radius of the helix, and it rotates in accordance with its direction (clockwise or anticlockwise).

Having closely inspected and handled many tusks from elephant of all ages, I believe the helical twist is intrinsic to all savannah elephant tusks in both sexes. However, the radius of the helix increases with age and is close to zero in young elephants. Thus, the helical curvature does not become apparent until it is well developed in older elephants as the tusks approach their asymptotes. Since data on three-dimensional tusk curvature are very rare, I use evidence from old elephants with tusks longer than the known population means to illustrate helical growth. Figure 3 presents an extreme case where, as the tusk grew, its tip rotated through more than 360°. Such growth in the savannah elephant tusk is anomalous, and this the only one I have seen in more than 200,000 tusks. Yet, as pointed out by Lister (*in litt.*), such curvature recalls male mammoth tusks.

Less extreme is a pair of tusks displayed in the Natural History Museum, London, shown from various angles in Figure 4 to illustrate their helical growth. It is notable that in panels (h) and (j) the tusk on the left appears as a simple arc. However, panels (a) and (e) show clearly that this is not the case. Viewing the tusk from different angles reveals the third dimension of depth.

I do not have data on helical tusk growth in African forest elephants (*Loxodonta cyclotis*)—although this does not imply its absence. As evidence from male savannah elephants aged 50 years or older is scarce, given the similarities between their tusks and those of old male Asian elephants (*Elephas maximus*), I sought proof that it occurs in Asian elephants. The instances shown in Figure 5 are from captive animals. The helical curvature is very marked, possibly because the tusks of these captive elephants have preserved more of their natural shape in captivity, where elephants are shielded from tusk loss through use and wear in the wild, and particularly from the effects of combat with rivals. Further, as captive Asian elephants are smaller than wild elephants (Sukumar et al. 1988), this may possibly be reflected in their tusk growth. Comparison of data on African and Asian elephant tusks is difficult, as the two species exhibit different population age structures and ageing processes. Nevertheless, although the male Asian elephant tusk is more slender and lighter than the male East African savannah elephant's tusk, it is basically similar, with growth following a helical path as apparent in the photographs.

Having established that helical tusk growth occurs in males of both East African savannah and Asian elephants, I now speculate on the behavioural value of curvature. Kingdon (1979), referring to the male savannah elephant, considers "the mature male skull as a structure adapted to fighting". Generalizing, combat between males for dominance and access to females occurs widely in the animal realm and, while the ability to kill an opponent may exist, the purpose is usually achieved when one combatant flees. Savannah elephant males seem unusual in going beyond chasing a competitor away and are known to actually kill their adversaries using deep, penetrating tusk thrusts into vital organs. Hall-Martin (1987) observed that in the Addo NP in South Africa, seven out of the 14 adult males in the Park were killed by other males in musth. Losing or seriously breaking one tusk would

Figure 4. A pair of mounted tusks at the Natural History Museum, London, illustrates how perspectives in two dimensions can hide the third dimension of depth and helical growth. Photos (d) and (h) show the angles of view that reveal maximum curvature. © Adrian Lister.

not necessarily be a disadvantage, but losing both would be fatal unless the adversary was physically much lighter (see below). Such an instance in the Addo NP was reported by Hall-Martin (1987) as follows: "In one case a bull broke a tusk while killing a non-musth male, broke off the remaining tusk while killing a female and, now tuskless, was itself killed by another musth bull." He recorded a case in the Kruger NP, where a male in musth pursued a larger male not in musth for four days before closing in and killing it (A Hall-Martin, pers. comm., 1990). Poole (*in litt.*) states "…having seen many fights—the victor *always* [my emphasis] chases the loser, often for kilometres". Simon Trevor's impressive film record from Tsavo NP ("Tsavo: a moment in time"[2]) records several of these chases, where the victor uses scent to track down an opponent that has fled out of sight. Trevor was never able to document the conclusion of such chases. However, such a pursuit, when the loser is out of sight, is not 'display'. Logically, it must be with the intent to inflict harm.

In the East African ivory trade, pieces of broken ivory recovered in the field (which, from size could only have been lost in male combat) were sufficiently frequent to have their own trade category: 'chinai'. (This was the term used in the Mombasa ivory auctions, whose market was China) (Parker and Graham 2020).

In Bardia NP, Nepal, Lister and Blashford-Snell (2000) recorded that one of two male Asian elephants seen regularly together suffered a fatal tusk wound into its skull, which could have been inflicted by its erstwhile constant companion. While dealing here with extant elephants, their many morphological similarities with mammoths (genus *Mammuthus*) and mastodons (genus *Mammut*) invite seeking evidence of fighting among their remains. Hormones preserved in fossils (Cherney et al. 2023) have proved that musth not only featured in male mammoth and mastodon behaviour but was also associated with evidence of wounds that reasonably could only have been inflicted in fighting. In Fisher's words, "this led me to suggest that adult male *Mammut americanum* engaged in musth battles in which a characteristic pattern of engagement involved lowering the head, followed by

[2]Trevor S. 2024. *Tsavo: A Moment in Time*, Chapter 10. https//:f.io/SpeStOaChapter

Figure 5. Examples of helical growth of tusks of captive Asian male elephants. © George Dian Balan.

swinging the head upward and forward forcefully, thrusting a tusk tip into the cheek region of an opponent" (Fisher 2008). Such a hooking upward tusk thrust was witnessed by Tom Tischler (pers. comm., February 2025) by a male Asian elephant in Perth Zoo.

Although the outcomes of combats are rarely witnessed, ancillary evidence that it occurs far more frequently than observed cannot be brushed aside. Parker (2023a) observes that in two clans that had been protected from hunting for more than 50 years, male mortality rose steeply between the ages of 30 and 40 years, when individuals should be in their prime. In the absence of other evidence relating death to that age class, he attributed this accelerated male mortality to musth-driven combat (Parker 2023a). That similar increases in male mortality are recorded in three other clans that had been hunted (for trophies) suggests an overstatement of the influence of hunting as the sole or major cause of the absence of older male elephants.

If the savannah elephant's tusks were straight lances pointing forwards, with an aggressor's weight behind both in a thrust, they would inflict double wounds. However, they are not straight but rather curved in opposing directions. Inflicting a penetrating wound with a curved tusk requires combining weight with an upward hooking thrust following the trajectory of its curve, as seen by Tischler and posited by Fisher (2008).

However, if the tips of the tusk pair are close, such a thrust would be countered by the partner tusk being curved in the opposite direction. Theoretically, consider a pair of tusks, evenly matched without breakage or wear. Like cork screws, those with a dextral spiral have to be turned clockwise to penetrate, while those with a sinistral spiral have to turn anticlockwise. Although the helixes in elephant tusks are not as severe or regular as those in corkscrews, the principle is embodied in the opposing helixes.

When the tusk tips are close together, and because their curves oppose each another, they act as safety mechanisms preventing deep wounds, as with young males sparring. Yet, with increasing age, the tips of the developing spiral grow further apart. The position that I hold, developed in the course of conversations with collaborators, and especially Tom and Travis Tischler (see Acknowledgements), is illustrated diagrammatically in Figure 7, which presents vertical and lateral views of male tusk stages in 10-year age cohorts.

The tips are at their widest apart between 30 and 40 years when the helix curve is upward and outward. It is then that a single tusk can be deployed with the least hindrance from its partner in a lethal, hooking thrust with weight behind it. It is in this cohort that male mortality accelerates steeply (Parker 2023a). Beyond this age, the helix goes 'over the top' and begins to curve downward and inward, negating the effect of the upward thrust and, with the tusk tips closing towards one another, making the tusks progressively less dangerous and more unwieldy in combat.

A combat that occurred between two male elephants at Mudanda Rock in Tsavo East NP in late 1956 illustrates how tusk pairs are most dangerous when at their widest. Two Park rangers stationed on a rock above witnessed the combat. About 12 hours later, I visited the site, listened to their account, and examined the carcass forensically. A small family unit with a large male (A) was leaving the pool below the rock, when a second large male (B) appeared at the run. Bull A wheeled and clashed with Bull B head-on without preliminaries. B's right tusk went into A's mouth, through the palate deep into its skull; and his left tusk passed along the right side of A's head. A reared backward to draw himself off B's tusk, off-balance, head up and throat exposed. As B's right tusk was freed, he lunged forward again, driving it deep into A's thorax above the sternum; his left unopposed tusk passed outside A's right shoulder. A wheeled sideways right, exposing his left flank, and B lunged again, thrusting the right tusk deep into A's thorax behind (or through) A's left scapula, and B's left tusk, again unopposed, passed under A's neck. Done for, A fell on his right side and B took off after the female/calf herd. It had not gone more than a few paces when a dikdik (*Madoqua kirkii*) burst out from under a bush near its feet, giving its 'wheeze wheezy' alarm call. B wheeled around and, in an apparent paroxysm of rage, charged back to where A, lying on its right side, still groaned. Approaching from A's back B drove its left tusk through A's skull, through the occiput, down through the brain and out through the throat just behind the lower jaw: its right tusk passed unopposed down A's upper trunk. Withdrawing, B then thrust both tusks under A's back

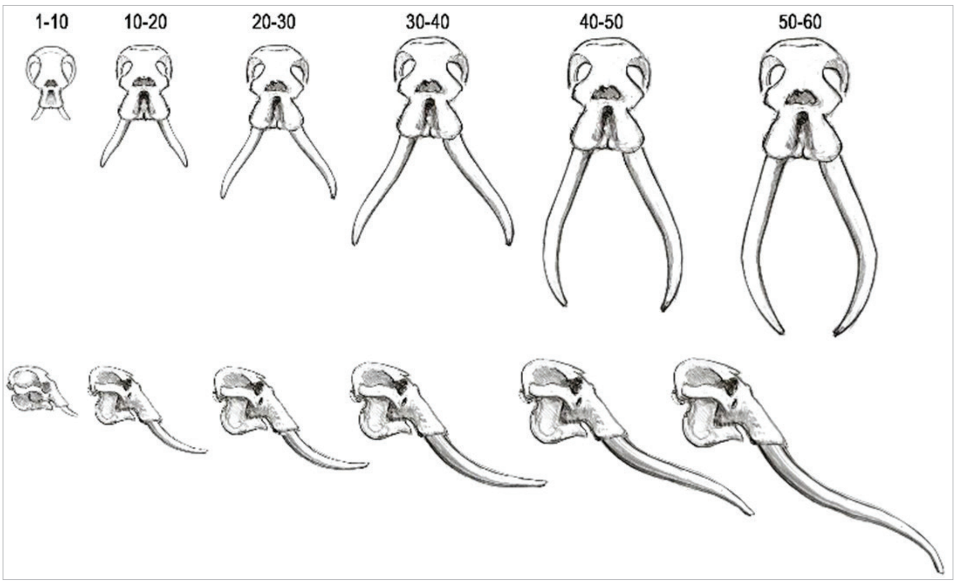

Figure 7. Hypothetical illustrating of helical tusk growth, showing how the tusk tips grow further apart until age 30/40 and then, as the tusks continue to grow, come closer together. © Travis Tischer.

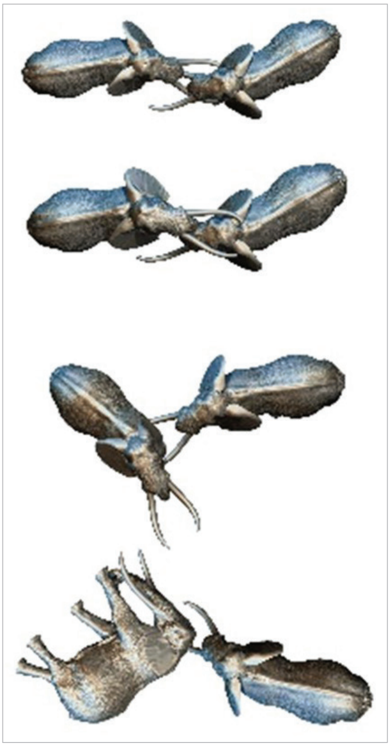

Figure 6. Illustrating the four lethal thrusts made at Mudanda Rock. © Travis Tischler.

and flipped A's body over on to its left side. The whole episode was over quickly and is illustrated in Figure 6. The combatants were both large bulls and likely in musth. The tusks of the vanquished bull weighed over 45 kg and the rangers recalled that the victor's tusks had been both longer and straighter. Instructive was that the four thrusts into the palate, sternum, thorax and skull were inflicted by one tusk, with its partner unopposed and, through curvature, out of the way.

Musth episodes continue into old age (Hollister-Smith et al. 2007), although declining late in life. However, quantitative data at the population level are again hard to come by, due to the rarity of old males. Accepting that musth is hormonally driven, and assuming that a general decline related to old age would be reflected throughout the endocrine system, the few data I have access to indicate that the weight of testes (n = 1,120) and seminal vesicles (n = 291), and sperm counts (n = 241) all decline in the oldest animals (Parker and McCullagh 2021). This reduced reproductive fitness, together with the declining value of the tusk as a weapon, would place the oldest bulls at an increasing disadvantage when competing with younger, fitter bulls of virtually the same size. If these males are still musth-driven to fight, this goes a long way toward explaining the rarity of old male savannah elephants.

Clearly, from the great rarity of congenital bilateral tusklessness in savannah elephants (Parker 2023b), tusks would appear essential in both ritual and combat for successful reproduction. Here, note has to be taken that congenitally bilaterally tuskless Asian elephant males (Makhanas) can both defeat tusked opponents and mate successfully (Chelliah and Sukumar 2013). However, in such contests, the tuskless winner is invariably the larger of the two (S. Pokharel, pers. comm., April 2025). This highlights the importance of weight in fighting, which can vary greatly between individuals in the same age cohort. To illustrate this point, out of the sample of 946 male savannah elephants (see above), in 11 aged between 41 and 50, the heaviest weighed 5.67 metric tonnes and the lightest 3.74 metric tonnes; that is, the heaviest weighed 52% more than the lightest. Two of the 11 aged 43 years weighed 4.79 and 3.74 metric tonnes; the heavier weighing 22% more than the lighter. When clashing head-to-head, a weight difference of such an order becomes a weapon in itself. Using it, a heavier tuskless animal could keep a lighter tusked opponent off-balance and unable to apply the momentum necessary to deliver a deep tusk thrust. This would explain how a tuskless Asian elephant male could defeat a lighter tusked opponent. In the savannah elephant, where both combatants are likely to be tusked, such weight advantage would be either enhanced or reduced by differences in tusk metrics and orientations.

Sukumar[3], suggests that the number of tuskless male Asian elephants in India may be human induced through selective removal of tusked males over millennia. If this can be verified, logically a similar evolutionary process could occur in the savannah elephant. Some support for the idea is given by Campbell-Stratton et al. (2023).

As male elephants, both African savannah and Asian elephant species grow older, their tusks continue to grow as well. In later life, the size and curvature of these tusks eventually compromise their effectiveness

[3]Sukumar R. https://www.youtube.com/watch?v=M9GYEVoTTng

as tools or weapons. In contrast, increasing age compromises their value as displays of virility. This extravagant ivory production automatically invites comparison with other proboscideans extant and extinct.

The straight, downward-pointing and seemingly less curved tusks of African forest elephants (*Loxodonta cyclotis*) would be difficult to employ in combat, (as *L. africana* does with its more forward-oriented tusks), and imply different behaviour. As the two species are known to hybridize, this apparent vulnerability of *L. cyclotis* could lead to its gradual evolutionary replacement by *L. africana*. However, the field of elephant genetics is something of a puzzle, as indicated by the title of Roca's (2019) paper "African elephant genetics: enigmas and anomalies", which convincingly argues that the genetic relationship between the two species is not yet "done and dusted". A piece in this puzzle is the presence of mitochondrial DNA of *L cyclotis* (i.e. F clade mtDNA haplotypes, where F indicates "forest derived") in many eastern and southern savannah elephants far from the forest elephant's distribution. It challenges the prevailing view that the two species hybridize only in restricted areas peripheral to Africa's equatorial forests. While this view hints at a process of gradual replacement, in these areas, of *L. cyclotis* by *L. africana*, the DNA evidence highlights the need for an understanding of the Pleistocene expansions and contractions of *L. cyclotis*' putative habitat: the Congo Basin and West African equatorial forests (Moreau 1966; Kingdon 1990). It further suggests that hybridization driven by these processes predates human influence and that, despite this influence, the current evolutionary status of African elephants may be as fluid as at any point in the past. While the straight lines in evolutionary 'trees', as drawn for elephants by Kingdon (1979) and Roca (2019), among others, unavoidably show abrupt changes between predecessors and successors, the actual process of one species evolving into another is likely to be protracted over epochs. This is what I imagine is happening between these two elephant forms.

I have been drawn into this speculative digression into the relationships between Africa's two extant elephant species by reflecting on my subjective experience. Historically, the ivory trade distinguished between two quite distinct types of African ivory. Ivory from the rain forest and surrounding areas was referred to as hard and/or yellow, and the tusks were very straight; while ivory from the rest of Africa was soft and/or white and the tusks were curved. As these different qualities affected usage and commercial values, the distinctions were not fanciful but well-established commercial fact. Yet many tusks from countries in and around the Congo basin exhibited features that were intermediate between the two ivory forms and traders had problems deciding which type they were. Parker (1979) refers to such elephants and their tusks as 'cyclotiform' and suggests that such hybrid ivory originates from a far more extensive area than the very limited hybridization zones suggested, for example, by Groves and Grubb (2000). Sources of information on forest elephants mapped by Roca et al. (2019) tend to be peripheral to the equatorial forests, and I suggest relate to cyclotiform or hybrid elephants rather than pure *L. cyclotis*.

The findings presented here raise wider questions about elephantid evolution. It appears that tusks of extant elephants with extreme helical curvature grow to lengths when they no longer function as weapons and tools, other than possibly being used as clubs, as Lister and Bahn (2007) suggested for mammoths, or for display. The extinct genus of *Mammuthus* (but not *Mammut*) shared the extravagantly curved helicoid tusk forms seen in old mature males of both *L. africana* and *E. maximus*. Yet were they also symbols of old age? If male mammoth tusks displayed the excessive curvature that compromised their effectiveness as lethal weapons earlier in life when the animals were in their primes, then this would persuasively support the argument that they evolved for display. This question will only be satisfactorily answered when the tusk shapes and lengths of extinct elephantids are classified by sex and age in suitably large samples. In male savannah elephant, tusks are at their most dangerous when the pair tips are furthest apart, when the animals are in their primes. At this state, tusk lengths are still far short of asymptotes achieved in old age, when elephants are beyond their competitive prime and display would be pointless. I thus concur with Kingdon (1979) and, modifying his words slightly, conclude that "the mature [savannah] male skull [and its curved tusks] are structures adapted to fighting."

Acknowledgements

This essay was stimulated by continuous conversations with and comments from a gifted naturalist and sculptor Tom Tischler and his equally gifted son Travis, who have researched proboscideans, both extant and extinct. To both my gratitude is great. Equally influential have been two professors, Adrian Lister and Dan Fisher, who went out of their way to help a layman bridge the realms of modern biology and palaeontology with generous comments, criticism and advice. Would that we were younger and could expand these interactions. Once again, I thank Joyce Poole for her help and, e'en tho' we may not agree on all points, I am very grateful. Sanjeeta Pokharrel helped me appreciate work on the Asian elephant of which I had been unaware. I acknowledge, with appreciation, the use of Dian Balan's images illustrating the helical growth of tusks, as well as the informative exchanges we had regarding tusk shapes and their roles in African and Asian elephants. I also appreciate my reviewers' and editors' comments.

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Pleistocene rhinoceros tracks from the Cape coast of South Africa

Charles Helm[1], Hayley Cawthra[1,2], Oma Daqm[3], Jan De Vynck[1,4], Steve Kunta[3], Uce/N‡amce[3]*

[1]African Centre for Coastal Palaeoscience, Nelson Mandela University, George, South Africa
[2]Minerals and Energy Unit, Council for Geoscience, Bellville, South Africa
[3]Nyae Nyae Conservancy, Tsumkwe, Namibia
[4]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

*corresponding author: helm.c.w@gmail.com

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Abstract

Ichnological sites have the potential to corroborate and complement the traditional body fossil record. Seven Pleistocene tracksites, attributed with varying degrees of confidence to rhinoceros trackmakers, have been identified on aeolianite surfaces on South Africa's Cape south coast. Thus far only one track has been assigned to a trackmaker species. In combination, these sites appear to provide the only reported fossil rhinoceros tracks from the middle and late Pleistocene. They thus form an important part of the global record.

Résumé

Les sites ichnologiques représentent des ressources à même de corroborer et d'enrichir les archives fossiles traditionnelles. Sept sites à empreintes datant du pléistocène, que l'on attribue, avec plus ou moins de certitude, à des rhinocéros, ont été identifiés sur des surfaces d'éolianite situées sur la côte sud du Cap, en Afrique du Sud. Jusqu'à présent, l'appartenance à une espèce n'a été confirmée que pour l'une de ces empreintes. Ces sites seraient les seules zones connues à disposer de traces de fossiles de rhinocéros datant du pléistocène moyen et supérieur. Ils constituent par conséquent une part importante des archives mondiales.

Introduction

The origins of rhinocerotoids can be traced though the body fossil record at least to the Eocene; the Family Rhinocerotidae includes five extant species and many extinct species (Prothero 1993, but see below for Oligocene records). Two species occur today in southern Africa, the black rhinoceros (*Diceros bicornis*) and the white rhinoceros (*Ceratotherium simum*). In southern Africa the rhinoceros body fossil record extends back to the Miocene (Avery 2019). The southern African Pleistocene rhinoceros body fossil record has been reviewed by Badenhorst et al. (2021).

The ichnology (trace fossil) record has the potential to complement the traditional body fossil record. There have been brief descriptions of Pleistocene rhinoceros tracks from South Africa's Cape south coast, as detailed below. At a global level, there are many such reports, and in 1965 Vyalov coined the term *Rhinoceripeda tasnadyi* for tracks from the lower Miocene (Lucas 2007). The first report of preserved rhinoceros tracks might be from southern Africa: Wilmer (1893) reported Holocene tracks of elephant and rhinoceros in the Walvis Bay area in what is now Namibia. The oldest track attributed to *Rhinoceripeda* appears to be from the Oligocene of France (Costeur et al. 2009). The record includes a Miocene example of ichnopathology (Belvedere et al.

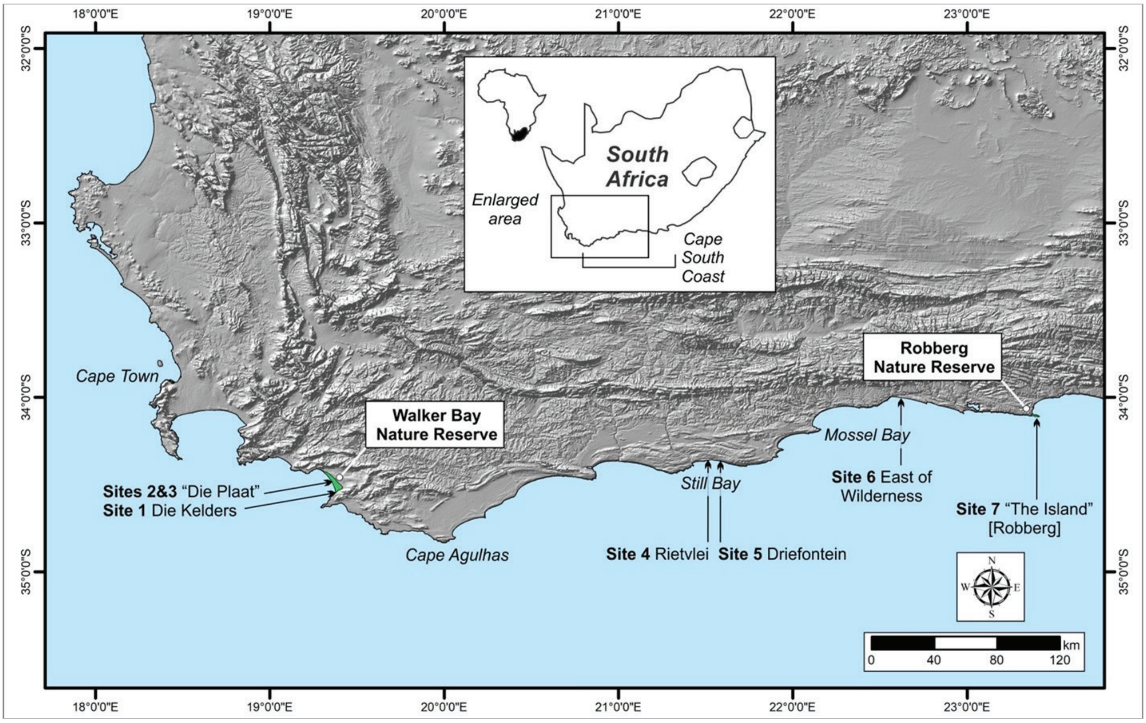

Figure 1. Map of South Africa's south Cape coast, showing the sites mentioned in the text.

2025). The African record includes the Pliocene site of Laetoli in Tanzania (Musiba et al. 2008) and the early Pleistocene site of Ileret in Kenya (Roach et al. 2016; 2018). A middle Pleistocene track assemblage at Swanscombe in the United Kingdom contains 'probable' rhinoceros tracks (Sutcliffe 1985; Davis 1996).

Through the Cape South Coast Ichnology Project, more than 350 vertebrate Pleistocene tracksites have been identified along 350 km of South African coastline (Helm 2023). The sites containing tracks attributed to rhinoceros trackmakers are described here (Fig. 1). All occur in aeolianites (cemented dunes) of the Waenhuiskrans Formation. Sites were measured and photographed, including for photogrammetric analysis where appropriate (Matthews et al. 2016). 3D models were generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 um). The final images were rendered using CloudCompare (v.2.10-beta). Locality information is reposited in the African Centre for Coastal Palaeoscience, to be made available to researchers upon request.

Rhinoceros track morphology

Well-preserved extant rhinoceros tracks, exhibiting high anatomical fidelity, are readily identifiable through a combination of track size and tridactyl form with distinctive digit impressions, and are identifiable to species level (Liebenberg 2000; Stuart and Stuart 2019; Van den Heever et al. 2024). When tracks of the black rhinoceros (*Diceros bicornis*) and the white rhinoceros (*Ceratotherium simum*) are compared, those of the black rhinoceros are slightly smaller, the medial and lateral digit impressions are relatively smaller, and the lateral digit impression has a relatively more posterior location. In addition, the indentation in the posterior margin is relatively less in black rhinoceros tracks (Liebenberg 2000; Stuart and Stuart 2019; Van den Heever et al. 2024).

A caveat exists if the tracks were registered in a soft, unconsolidated sandy substrate, as the two central digit impressions of a hippopotamus (*Hippopotamus amphibius*) track may appear to fuse, in which case a tridactyl track pattern resembling that of a rhinoceros track might result (Van den Heever et al. 2024). In addition, confusion may exist between juvenile elephant tracks and poorly-preserved rhinoceros tracks that do not display obvious digit impressions. Figure 2 illustrates

Figure 2. (a) A track of a white rhinoceros; scale bar = 18.5 cm; (b) a track of a black rhinoceros; scale bar = 18.5 cm; (c) a well-preserved hippopotamus track. (d) A hippopotamus track registered in a sandy substrate, in which the two central digit impressions are partially fused, causing it to resemble a rhinoceros track. © Alex Van den Heever.

typical tracks of black rhinoceros, white rhinoceros and hippopotamus, as well as a track in which the central digit impressions in a hippopotamus track partially fuse and thus create confusion.

Sites attributed to rhinoceros trackmakers on the Cape coast

Seven possible rhinoceros tracksites have been identified. They are described here from the perspective of traversing the coastline from west to east. In each case, our estimate of the likelihood of a rhinoceros trackmaker is expressed.

Site 1

On the coastline north of Die Kelders in the Walker Bay Nature Reserve, a single track with maximum length of 23 cm and maximum width of 19 cm exhibited tridactyl morphology (Helm et al. 2024—their Site 23, fig. 9C). It was located on a loose slab on the beach. Favouring the interpretation of a rhinoceros track were the apparently bifid heel outline and plausible impressions of the medial and lateral digits. However, the central digit impression appeared less rounded than expected, and 'off-centre' (Fig. 3). We view this as a probable, but not definite, rhinoceros track.

Figure 3. The single Site 1 probable rhinoceros track; scale bar = 10 cm.

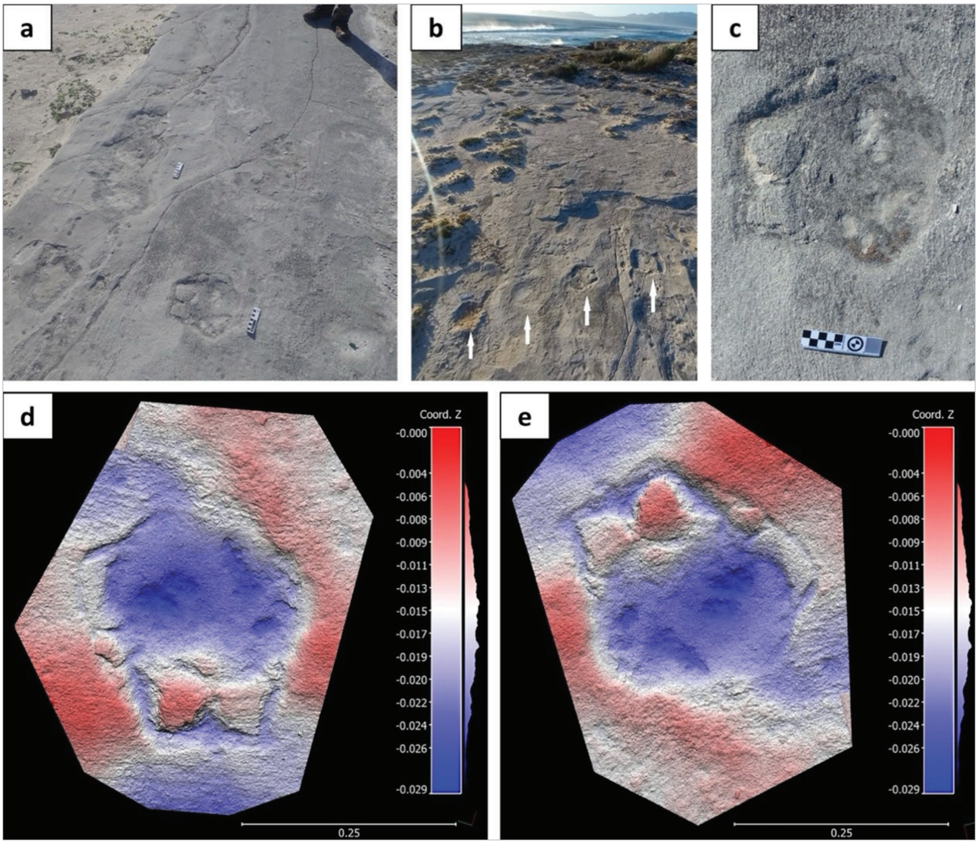

Figure 4. (a) When first examined, a trackway was not obvious; scale bars = 10 cm. (b) Late-afternoon sunlight allowed the trackway to be visualised; the tracks are indicated by arrows. (c) The best-preserved track at Site 2; scale bar = 10 cm. (d) 3D model of the best-preserved track at Site 2, with north-south orientation. (e) 3D model of the track shown in (c) and (d) Here with a south-north orientation. Horizontal and vertical scales are in metres. Both a rhinoceros and a hippopotamus could have made the tracks, making either option equally possible.

Site 2

Site 2 was reported as a possible hippopotamus tracksite (Helm et al. 2024 – their Site 17, fig. 7D). It was reanalysed by members of our research team (now including San Master Trackers) in 2025 under different lighting conditions, following removal of surrounding sand and vegetation to expose a larger track-bearing area. These efforts resulted in the identification of a trackway comprising at least four large, evenly spaced tracks (Fig. 4b). The north-south axis of the trackway could be determined, but no clues (e.g., displacement rims) were present that might indicate the direction of travel. Other tracks of similar size were present in the immediate vicinity. Maximum length of the best-preserved track was 27 cm, and maximum width was also 27 cm (Fig. 4c). Depending on the inferred direction of travel (from north to south or from south to north), it either exhibited a bifid heel impression and a typical ‘cloverleaf’ pattern suggestive of a rhinoceros trackmaker (Fig. 4d), or possible tetradactyl morphology suggestive of a hippopotamus trackmaker (Fig. 4e). A consistent pace length of 67 cm was measured. We consider the two possibilities to be equally plausible.

The Site 2 tracks were preserved in epirelief, in situ, on ‘Die Plaat’, a relatively level series of aeolianite palaeosurfaces located just inland of the coast. While Die Plaat contains genuine tracks, it presents challenges. In many areas it is encrusted with calcrete, which may be hard to distinguish from aeolianite. Furthermore, rounded or oval depressions that form in calcrete may resemble vertebrate tracks. Caution is advised, and long trackways provide one indication that pseudotracks are not being visualised, following the ‘ten paleoichnological commandments’ of Sarjeant (1989).

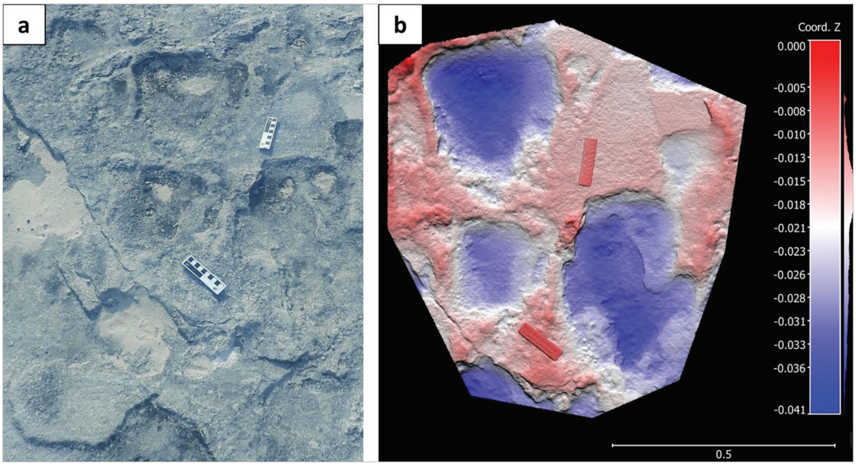

Figure 5. (a) These are purported rhinoceros tracks at Site 3; scale bars = 10 cm. (b) 3D model of the Site 3 tracks—the middle track is seen in (a) Horizontal and vertical scales are in metres.

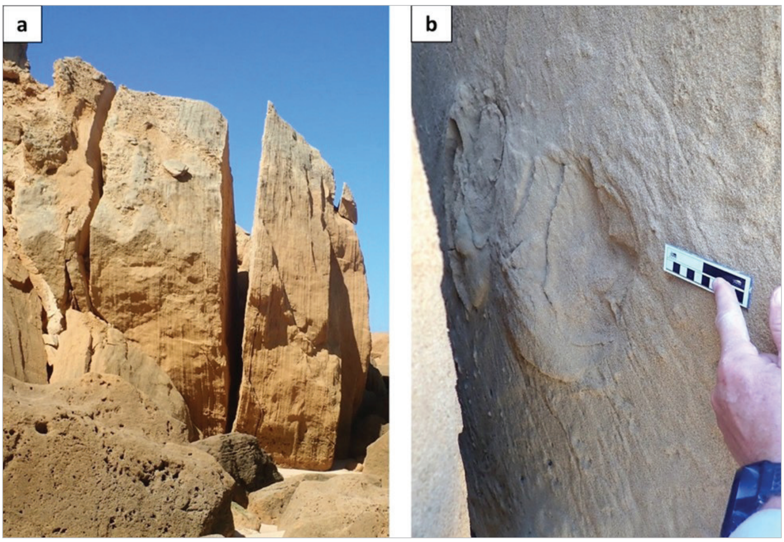

Figure 6. (a) The large, split fallen block at Site 4. (b) One of the tracks in the gap in the split rock at Site 4; scale bar = 10 cm.

Site 3

Site 3 is also situated on Die Plaat in the Walker Bay Nature Reserve, as reported in Helm et al. (2024— their Site 3, figs 2D and 2E). Several large depressions, 30–40 cm in length, occurred in a linear pattern beside and on a 4WD track (Fig. 5). While the quality of preservation was poor, irregularities in their outlines were detectable, and we consider a rhinoceros origin likely.

Site 4

In the Rietvlei area, east of Still Bay, a large block has fallen from overlying cliffs and come to rest at the upper end of the beach (Helm 2023). It has split down its centre along a bedding plane (Fig. 6a). Peering into the resulting narrow gap, six large tracks are evident, preserved in epirelief on one side and in hyporelief on the other. Because the gap is so small, the tracks cannot be viewed adequately, but measure ~20 cm x 16 cm in maximum dimensions, with digit impressions and natural casts evident (Fig. 6b). Although a rhinoceros origin is consistent with the findings, a confident identification is currently not possible.

Figure 7. The single Site 6 track; scale bars = 10 cm.

Site 5

Further east, in the Driefontein area, a single track was attributed to a possible rhinoceros trackmaker, although the 'heel' portion appeared deeper and longer than expected (Helm et al. 2020). Unless this is a composite track, the probability of a rhinoceros origin is relatively low. The track was of interest because the rock surface was thought also to contain tracks of elephant (*Loxodonta africana*), the extinct long-horned buffalo (Syncerus antiquus) and the extinct giant Cape zebra (*Equus capensis*). Maximum length of 24 cm and maximum width of 20 cm were recorded (Fig. 7).

Site 6

East of Wilderness, two trackways, containing a total of twelve tracks, were noted in situ in epirelief (Helm 2023). Maximum length of ~24 cm, maximum width of ~20 cm, and pace length of 65–70 cm were recorded (Fig. 8). The tracks would have been registered in soft sand, with a resulting lack of morphological detail. This makes it impossible to confidently attribute the tracks to family level, although the trackmaker was probably a rhinoceros or hippopotamus. Subsequent visits to the site aimed at performing photogrammetric analysis were unsuccessful, as the area was covered by metres-deep beach sand.

Site 7

Trackways preserved in hyporelief on the ceiling of a tunnel on The Island in the Robberg Nature Reserve provide the best example of rhinoceros tracks reported until now from the Cape coast (Helm et al. 2019). The tracks occur in hyporelief on a truncation surface and are only accessible during very low tides. The tracks are being eroded by wave action. Two rhinoceros trackways are present, with a total of at least six tracks (Fig. 9). Mean track length of 23.4 cm and mean track width of 23.2 cm were recorded. One track in particular (the middle track in Figure 9b) exhibited the track morphology of a rhinoceros, probably a black rhinoceros: the lateral digit impression was relatively small and was located relatively far from the central digit impression (Liebenberg 2000; Stuart and Stuart 2019; Van den Heever et al. 2024). In one case, a track pointed in the opposite direction, indicating a trail that had been used in two directions.

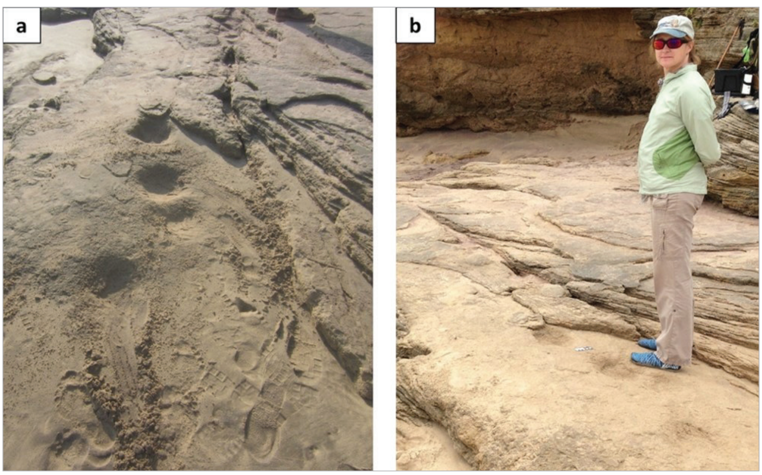

Figure 8. One of the Site 6 trackways; a person is included, for scale.

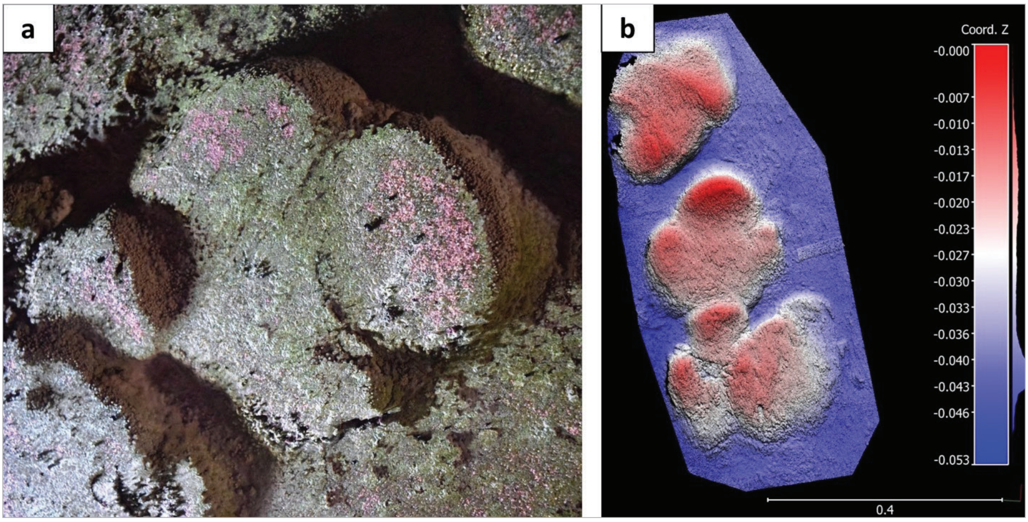

Figure 9. (a): The best-preserved track at Site 7—direction of travel is from left to right. (b) 3D model of one of the Site 7 trackways—the middle track is seen in; (a) and is attributed to a rhinoceros trackmaker, probably a black rhinoceros; horizontal and vertical scales are in metres.

Discussion and Conclusions

In the abovementioned examples, the trackways at Site 7 are confidently attributed to a rhinoceros trackmaker. Tracks at the other sites are interpreted as possible or probable rhinoceros tracks with varying levels of confidence or illustrate the confusion that can arise between rhinoceros- and hippopotamus tracks. We suggest that all reported rhinoceros tracks from Africa Musiba et al. 2008; Roach et al. 2016; 2018) be subjected to scrutiny to ensure that the possibility of a hippopotamus trackmaker has been excluded.

Site 1 and Site 5 only contain single tracks, whereas a trackway clearly provides more morphological clues. Time will tell whether the tracks at Site 4 were registered by a rhinoceros when the split in the large block opens up. The tracks would all have been registered in unconsolidated dune sand, a substrate that may contribute to less-than-optimal morphological preservation. The relatively coarse-grained size of dune sand may be another contributing factor, as fine-grained substrates typically allow for the preservation of finer track detail.

Distinguishing between the tracks of the two rhinoceros species presents more of a challenge. Enough evidence is present at Site 7 to suggest a black rhinoceros trackmaker, but identification to species level is not possible at the other sites.

The black rhinoceros was historically more common than the white rhinoceros in the south-western Cape and has been recorded more often in the Pleistocene body fossil record (Avery 2019; Badenhorst et al. 2021). Distinguishing between tracks of these two species has paleoecological implications, given their different feeding niches (Skinner and Chimimba 2005).

Sites 1, 2 and 3 all occur within the Walker Bay Nature Reserve. These three sites lie close to the archaeological site of Die Kelders 1 Cave (Klipgat Cave). Klein and Cruz-Uribe (2000) recorded the remains of black rhinoceros in the cave, as well as many rhinoceros bones that could not be identified to species level. This site has yielded the majority of Pleistocene rhinoceros remains from the coastal Western Cape and Eastern Cape (Badenhorst et al. 2021). As the database of rhinoceros tracksites from the Cape south coast expands, it may be possible to identify the trackmaker to species level in more cases, and thus corroborate or complement the body fossil record.

Dating through optically stimulated luminescence (OSL) suggests that the Walker Bay Nature Reserve sites are close to 76 ± 5 ka in age (Helm et al. 2024). Sites 4 and 5 lie within kilometres of a section dated through OSL to an age range of 140 ± 8 ka and 91 ± 4.6 ka (Roberts et al. 2008). Deposits in the general region of Site 6 have been dated to 131 ± 7 ka and 133 ka ± 7 ka (Bateman et al. 2011). Dating samples obtained adjacent to Site 7 yielded an age range of 56 ± 5 ka to 43 ± 4 ka (Helm et al. 2019).

The tracksites thus appear to date to a range between marine isotope stage (MIS) 6 and MIS 3. They appear to be the only rhinoceros tracksites thus far reported from the late Pleistocene. As such, they form an important part of the global rhinoceros palaeontological record.

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We thank Peter Todd, Mike Fabricius, and the staff of CapeNature and Grootbos Private Nature Reserve for providing site access and facilitating our visits, and Linda Helm for invaluable assistance. We appreciate the funding and organization from the Discovery Wilderness Trust and trustees and donors Jan Glazewski and Clive Thompson, which enabled Indigenous Trackers #oma Daqm, Steve Kunta and /uce N‡amce to visit the Cape south coast and collaborate on this project. Alex Van den Heever kindly provided the images used in Figure 2. We thank Reviewer Greg Botha and rhino subeditor Keryn Emslie for their thoughtful suggestions, which led to an improved manuscript.

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FIELD NOTES

Using drones as ground-based camera systems with multiple coordinated sensors to study African elephants (*Loxodonta africana*)

Angus Carey-Douglas[1], Liam Jasperse-Sjolander[1,2], Giacomo D'Ammando[1], Frank Pope[1], Paul Kokiro[1], Gideon Galimogle Ilterewa[1], Zephyr Goriely[3], Fritz Vollrath[1,3]*

[1]Save the Elephants, PO Box 54667, Nairobi 00200, Kenya
[2]Department of Environmental Studies, University of Colorado, MacAllister Building, Boulder, Colorado, 80303-0397, USA
[3]Department of Zoology, University of Oxford, 11a Mansfield Road, Oxford OX1 3SZ, UK

*corresponding authors: angus@savetheelephants.org

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Introduction

Advances in drone technology over the last two decades have enabled the collection of a wide variety of ecological data with increased accuracy while reducing overall costs (Watts et al. 2012; Christie et al. 2016; Hodgson et al. 2016; 2018). Elephants are ideal candidates for drone-based monitoring due to their size, making them easily visible from a height (Koh and Wich 2012). However, there are concerns over the potential for drone-generated noise, which induces a fear response in elephants due to its perceived resemblance to the sound of swarming bees, ultimately altering the behaviour of elephants under observation. Furthermore, the majority of commercially available drones have relatively short flying times of around 30 minutes before battery depletion occurs, which puts limits on the length of time that elephants can be studied from drones. This concept paper discusses a novel use case for drones in which their cluster of integrated sensors is used to collect valuable data on elephant physiology and morphology without the drone being airborne—and thus without generating any propeller noise. Additionally, it provides the advantage of longer observation periods than would be possible if the drone were flying. Here, we present this technique solely in the context of data collection on elephant physiology and morphology. The potential applications of this method are manifold and could extend to other species of appropriate size (e.g. rhinos) across different landscapes.

Many commercial drones have a carrying capacity of some kind (defined as a payload), often in the form of high-performance cameras and sensors with the ability to record data in non-visible spectra (Esposito et al. 2021; Tuğrul 2023). Sensor integration is already a built-in feature in most drones, with gyroscopes, accelerometers, and magnetometers combining with GPS data to guide the drone's flight path and adjust its speed and direction (Tuğrul 2023). In addition, on-board deep learning processors can use sensors to enable object tracking, which is increasingly commonplace across drones of different makes and models (Tang et al. 2023). Consequently, the sophistication of drone cameras and sensors creates a wealth of potential applications for this integrated data, which can be even more useful when recorded at ground level.

A significant issue with flying drones over wildlife is the noise they produce, which can disturb the species they are being used to observe (Duporge et al. 2021; Hodgson and Koh 2016). Elephants are disturbed if drones are flown in close proximity to them and will flee in response (Hahn et al. 2017), but show some tolerance to a drone flown at a distance (Bennitt et al. 2019; Hartmann et al. 2021; Mesquita et al. 2022). This disturbance can be mitigated by using a drone on the ground, and disturbance levels can be further kept to a minimum if the target animals are already habituated to the method used to collect data (Blumenstein 2016).

Methods

For our study, we used a DJI Matrice M30T quadcopter drone (hereafter M30T; DJI, Shenzhen, China) because its payload contains both an optical zoom camera and a laser rangefinder, both of which are essential for accurate morphometric data collection. The zoom camera has a 1/2" CMOS sensor with 48M effective pixels, and a focal length equivalent of 113–405mm, while the laser rangefinder can detect objects from 3–1,200 m with an accuracy of $\pm$ (0.2 m + D × 0.15%), where D is the distance to a vertical surface.[1]

This study was conducted in the Samburu and Buffalo Springs National Reserves (NR), northern Kenya, which is home to a population of at least 744 individually identified elephants, that have been studied continuously since 1997 (Wittemyer 2001). We collected morphometric data from 156 elephants on 25 different occasions, resulting in a total of 220 images for analysis. Images were taken during daylight hours between 10.00 am and 5.00 pm. Given that elephants in Samburu NR and Buffalo Springs NR are already habituated to the presence of vehicles (Goldenberg et al. 2017; Wittemyer et al. 2005), we were able to position ourselves at close range to the elephants. This distance ranged between 3.5 m and 172.3 m, with a mean of 27.4 m, and was dependent on factors such as the size and dispersal of the elephant group, as well as vegetation density and terrain.

The drone was placed in different positions depending on the configuration of the vehicle used, but included: i) the roof via an open hatch; ii) a bench in the rear; or iii) held in a raised position by the observer. All positions ensured that the drone camera had an unobstructed view of the target elephant. We used the drone for two main objectives: i) measuring the shoulder height of an elephant; and ii) thermal imaging.

Shoulder height measurements

To measure the shoulder height of individual elephants we positioned the vehicle at close range to the target elephants and enabled the M30T's laser rangefinder function (Fig. 1A). The rangefinder crosshairs were visually aligned on the upper part of an elephant's front leg, approximately in the middle of the humerus, while ensuring that both the bottom of the elephant's foot and the top of the shoulder were visible in the frame. Pictures were then taken with the elephant perpendicular to the camera, with a simultaneous recording of the rangefinder reading. This coordination meant that the pictures and measurements could be cross-referenced, allowing accurate calculation of elephant shoulder heights using digital photogrammetry.

We calculated the drone image resolution at various distances by comparing the height in pixels to the actual height of a known object, resulting in an equation describing the resolution (cm/px) as a function of distance to the object (m). With repeated measurements, we found that this process had a measurement accuracy ranging from ±0.1cm at a distance of 5 m to ±1.2 cm at 120 m, while the error of the rangefinder could result in a difference in resolution of ± 0.0026 cm/px at 5m, to ± 0.0048 cm/px at 120 m.

We measured the height of the elephant's shoulder in pixels as a straight line from the top of the shoulder to the bottom of the foot (Fig. 1b), and then using the resolution equation, we could estimate the elephant's shoulder height in cm using the distance from the rangefinder. Previous morphometric studies of wildlife have encountered challenges with data accuracy when using a camera and rangefinder independently, since it can be difficult to ensure that they are both exactly the same distance from the study subject and differences in focal lengths must be accounted for (Della Rocca 2007; Shrader et al. 2006). The combination of a camera

[1](https://enterprise.dji.com/matrice-30/specs).

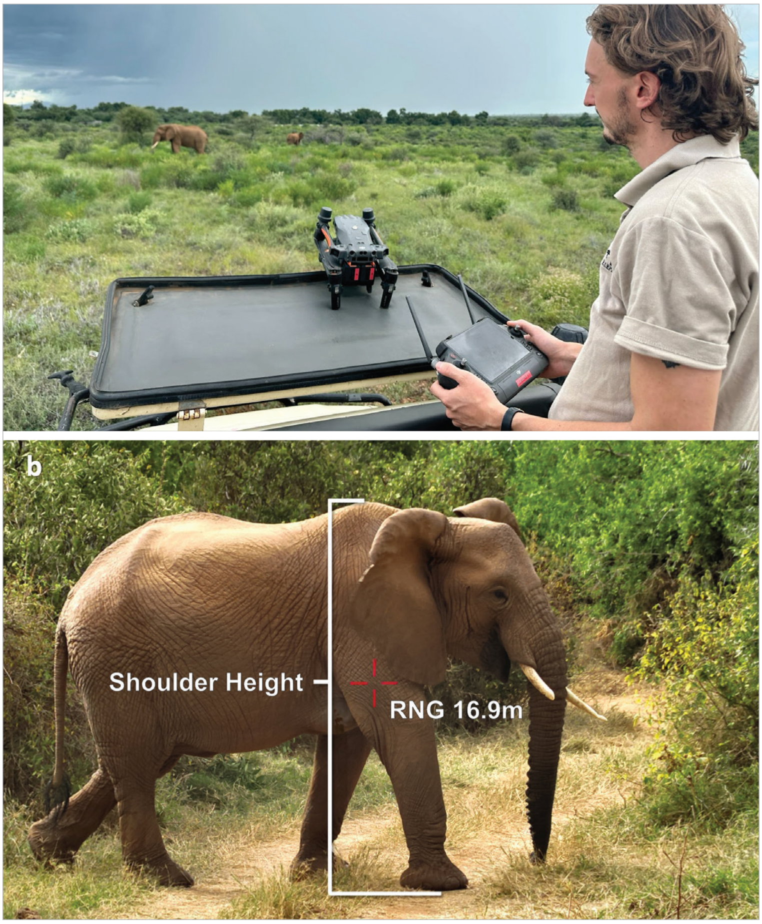

Figure 1. Using the drone from the roof of a vehicle to calculate shoulder height (a); and example shoulder height measurement (b); where shoulder height is measured as a straight line from the top of the shoulder to the bottom of the foot.

and laser rangefinder contained within the same payload made this calculation straightforward, eliminating much of the potential error if it were to be recorded with an independent camera and rangefinder. We found that height measurements made with the drone were 25.6% more accurate than measurements made with a separate rangefinder and DSLR camera. The drone was able to estimate the height of a known object with an average accuracy of ±0.76 cm, while the independent camera and rangefinder had an average accuracy of ±1.02 cm.

Elephant thermal imaging

We took high-resolution infrared footage of elephants, again without the need for an aerial drone. The M30T is equipped with a thermal camera with 640×512 resolution, which results in relatively poor image quality for detailed analysis when the drone is at altitude but offers much greater detail when used at close range (Fig. 2). For example, it could be clearly seen that the surface temperature was lower on the outer margins of the ears (where heat dissipation generally occurs). This opens the possibility of making detailed analyses of elephant surface body temperatures, heat dissipation techniques and temperature differences between individuals. Thus, by approaching elephants in a vehicle and using the drone in the same way as described above, we were able to obtain thermal footage with a level of detail which would otherwise have been impossible without disturbing the elephants, or without acquiring a highly expensive thermal camera (carrying no additional sensors, unlike the drone).

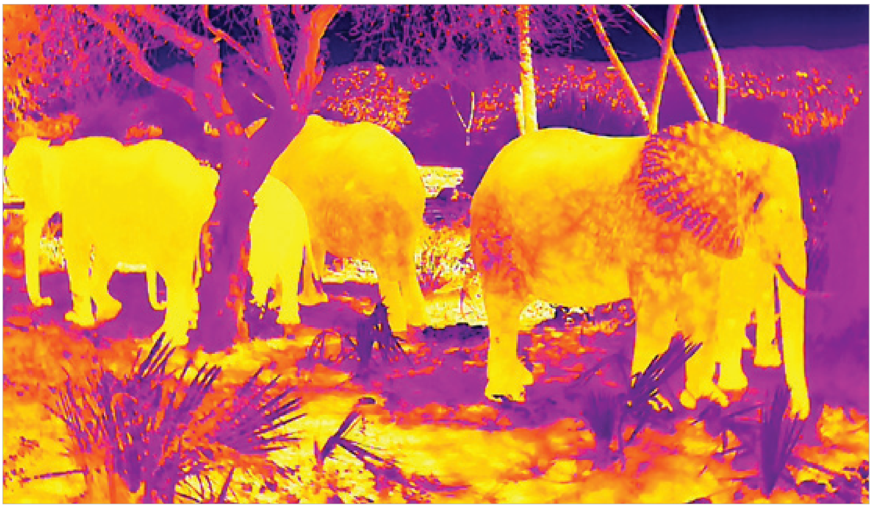

Figure 2. Thermal image of elephants when taken from the DJI M30T at close range (<10 m).

Conclusion

The specifications of each drone will ultimately dictate its suitability as a ground-mounted camera, but the majority of commercially available drones are small enough to allow for the possibility of this. Mounting options other than those described in this paper could include a fixed position on a vehicle or a telescopic boom, both of which would provide a stable and secure platform to operate the camera. Other techniques, such as placing the drone on a hard, flat surface, the use of a harness, or simply holding the drone, could offer an inexpensive, time-efficient and low-disturbance method to observe elephants. In addition, there can be a considerable cost-benefit advantage in purchasing a drone equipped with an array of built-in sensors, rather than individual pieces of equipment, which could together outweigh the cost of a drone, and without the additional versatility that the drone brings as an aerial platform.

The use of drones without being airborne under their own propulsion extends to being mounted on manned aircraft, thus significantly expanding the area over which data can be collected when compared to ground-based methods, such as those described in this paper, or if flying using the drone's own propulsion. There are a number of improvements that this technique could bring to aerial monitoring and wildlife surveys versus traditional camera options, which typically have fixed positions and settings on aircraft. These include the native integration of numerous sensors as well as the stability afforded by a drone’s gimbal and the resultant improvement in footage quality, in addition to the capacity for in-flight adaptability by using the drone’s remote controller to adjust the camera’s direction and change its settings according to the research objective.

Drones are becoming an increasingly important tool in elephant research and conservation, with their sophisticated cameras and in-built sensors enabling the collection of critical baseline data such as body condition, morphometrics and growth curves with centimetre-level precision. This accuracy can be further enhanced by using drones on the ground, informing vital metrics such as population health and stress level measurements. Crucially, our technique of using drones as a ground-based data collection tool expands the scope of data that elephant researchers can collect while minimizing disturbance to elephants or other target species.

In conclusion, the deployment of drones as ground-based cameras has several advantages which could be of use to researchers using this technology. Advances in camera and sensor capability have made drones a tool that can outperform many DSLR cameras while offering the versatility to record many different types of data at once. The method outlined in this paper demonstrates one that can be easily applied to a range of research objectives. We recommend that researchers consider the use of ground-based drones as a safe, effective and low-disturbance method to gather empirical data for a wide range of wildlife observations.

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The reaction of African elephants towards African honeybees in northern Botswana

Tempe Adams[1], Lucy E King[3], Tracey Rogers[2], Michael Chase[4], Keith Leggett[1]*

[1]Centre of Ecosystem Science, School of Biological Earth and Environmental Sciences, University of New South Wales, Australia
[2]Evolution & Ecology Research Centre, School of Biological Earth and Environmental Sciences, University of New South Wales, Australia
[3]Save the Elephants, PO Box 54667, Nairobi 00200, Kenya
[4]Elephants Without Borders, PO Box 682, Kasane, Botswana

*corresponding author: tempea@unsw.edu.au

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Introduction

There is compelling evidence to suggest that areas of outstanding conservation value, which often coincide with expanding human populations, are at risk (Balmford et al. 2001). The African elephant (*Loxodonta Africana*) is the world's largest generalist herbivore and, due to its large size, requires a substantial amount of space and resources (Dublin et al. 1990; van Aarde et al. 2006). Consequently, mitigating human-elephant conflict (HEC) has become a focal topic in elephant conservation and research (Karidozo and Osborn 2005). Many countries in southern Africa that still have substantial elephant populations face the challenge of managing these populations. At the same time, biodiversity has declined in protected areas (PAs) while reducing the impacts on humans (Balmford et al. 2001). Encounters between elephants and people (/communities) often result in negative interactions, which pose serious social, political and conservation conflicts (King et al. 2009). Botswana holds the largest elephant concentration on the African continent with approximately 130,000 individuals (Bussière and Potgieter 2023). Botswana's need for effective deterrents is vital in managing and maintaining its current elephant population. A wide range of mitigation methods have been trialled and used in high HEC areas across African elephant range States. These include the use of chillies, explosive devices, lights, organic repellent, trenches, and electric fences (Sitati et al. 2003; Osborn and Parker 2003; Graham and Ochieng 2008; Davies et al. 2011; Oniba and Robertson 2019; Adams et al. 2021; King et al. 2023). Davies et al. (2011) outlined the importance of first evaluating deterrent methods to determine their effectiveness, before wide-range deployment. Each deterrent method has varying degrees of success, which are dependent on the local elephant population, the location, deployment of the deterrent, and the community buy-in both economically and socially (Osborn and Parker 2003; Davies et al. 2011).

The use of African honeybees (*Apis mellifera scutellata*) and beehive fences is one of the most novel deterrent innovations. The development in Kenya from 2007 has been a success, as evidenced in studies there (King et al. 2009; 2017; 2024), where it was observed that elephants exhibit avoidance behaviour when exposed to acoustic playbacks of African honeybees (King et al. 2007). Beehives are interlinked and hang between posts to function as a fence-like barrier between crops and elephants (King et al. 2017). They have shown positive deterrent results during field trials elsewhere, including Mozambique (Branco et al. 2019), and Tanzania (Scheijen et al. 2019).

However, some field studies using bees have shown limited results (Kazidozo and Osborn 2005), possibly due to challenges with bee activity (Ngama et al. 2016) or occupation rates (Kiffner et al. 2021). Hence, it is essential to assess the validity of the deterrent under local conditions before implementation in the Chobe area of Botswana. Currently, it is unknown how Botswana's elephant populations respond to the sound of African honeybees.

This study aimed to assess the behavioural reactions of elephants in northern Botswana to audio recordings of disturbed African honeybees. By determining how different elephant populations will respond to the sound of bees, we can assist in determining the relative success of beehive fences in relieving and reducing HEC in the country.

Methods

Study Area

The research was conducted in Chobe district in the north-east corner of Botswana, which shares borders with Zimbabwe, Namibia, and Zambia. The area is made up of Chobe National Park (NP) (10,740 km^2), community settlements, smallholder farms and forest reserves (Adams et al. 2021). The area has a high density of elephants, with approximately 34,087 elephants in the district (Bussière and Potgieter 2023). The townships of Kasane and Kazungula are the urban administration centres of the district, with a combined human population of 17,655 (Census Office 2022).

Playback procedure

The playback experiment is based on the methodology and recordings of King et al. (2007). Two signals were used for the playback trials: 1) the test stimulus was 180 seconds of sound produced by disturbed wild African bees (*Apis mellifera scutellata*); and 2) the control stimulus, which was natural white noise recorded from a waterfall.

Playbacks were conducted on randomly selected, resting family units, preferably with small calves present, and replicating the same protocol as King et al. (2007). Playbacks were performed on families that were resting under trees (Fig.1) with no mature bulls present, as male elephants can disturb the family's resting behaviour (King et al. 2007). Upon identification of a resting family unit, the number, demography, the matriarch's distinguishing features, and whether individuals were lying down were recorded. The age and sex were based on traits defined in Moss (1996). The playbacks were conducted in the dry season (May–October in 2013), at the hottest time of day (10.00 hrs–15.00 hrs).

Before starting a playback, the resting behaviour of the focal elephants was recorded for two minutes. A wireless Bluetooth speaker (A33 TDK) was placed as close to the family as possible, and a vehicle was parked at a 90-degree angle to the speaker. After the playback finished, a further 30 seconds of the family's behavioural reaction were recorded. All images were recorded using a Nikon Camera. The stimulus output and the background noise were measured using a sound level meter.

Although a total of 95 playbacks were attempted, only 30 playbacks on 30 family units (15 in the Park and 15 in the community area) were successfully conducted, as the elephants frequently moved away when our vehicle stopped or we drove by. This could be due to high-density safari vehicle traffic in the area or the presence of other elephants or other wildlife.

Figure 1. An example of a resting family unit, in the shade of a tree (with no mature bull present with the group).

Table 1: Summary of the number of playbacks, average family unit size, number of resting calves, and the estimated distance subjects were from the playback speaker during the 30 trials.

Playback Trial	Total number of playbacks	Mean number of animals in family unit (±SE)	Number of playbacks with calves lying down	Estimated mean distance herd from speaker (m) (±SE)	Mean max./min. The sound output of the speaker (at herd distance from the speaker dB) (±SE)
Bee	15	7.3 (0.8)	7	15–18 (5)	-
Control	15	6.6 (0.6)	6	15–18 (5)	-
Combined	30	7.0 (0.5)	13	15–18 (5)	49.6(1)–46.1 (1.5)

Playback behavioural reactions

For this study, behavioural reactions were defined into four separate categories based on behavioural definitions from Poole and Granli (2021) studies, which were as follows:

1. *Non-reaction*: where no individuals show any behavioural reaction to the sound being played.
2. *Weak*: behavioural response includes not moving from the resting place and only displaying a mild behavioural reaction (smelling, raised heads, or swaying of the body).
3. *Medium*: behavioural responses include movement/shuffling within the rest area, changes in body orientation, smelling, head shaking, the family not moving off, further than 10 metres from the shade, but there is a clear response to the audio playback.
4. *Strong*: behavioural response is a marked reaction in the entire resting family unit. For example, when they move away from their resting area, out of the shade area (distance measurement >10 m). This can involve rapid, bunched movement, smelling, a change of body orientation, and/or fanning out of mature individuals. The results are that the entire family unit behaves adversely because of the playback.

Additionally, aggressive displays were recorded during playbacks; these included mock charges, or ears moving forward, and individuals leaning in on their front legs.

Statistical analysis

A Chi-squared Fisher's Exact test was used to test whether the bee stimulus altered the distribution of counts for different behaviours in the controls compared to the control (behaviour versus treatment interaction). A Mann-Whitney U test was used to test significance in specific behavioural responses between the bee and the control playback. A Pearson's correlation was performed to test whether or not there was a correlation between the number of individuals to show a reaction and the time to show the first reaction. The total percentage was calculated for behavioural response within each playback and the reaction across all playbacks. All statistics and data processing were done within IBM SPSS Statistics Version 22.0 (2010).

Results

Overall, 86.6% of the bee trials, compared to 60% of the control trials, produced a reaction from the resting family units. The number of reactions for each defined behavioural category between the bee and control playbacks (Fig.2) was not significantly different (Fisher's Exact test, $\chi^2 = 4.14$, $p>0.23$).

The data revealed that more elephants responded to bee sounds with a medium or strong reaction compared to elephants responding to white noise (Chi-squared test 3.39, $p>0.06$).

The control stimulus produced a slower reaction time (mean of 18.3 s; SE ± 4.5 s; n = 15) compared to the reaction time of the bee trial (mean reaction time = 11.1 s; SE ± 2.8 s; n = 15). The difference between the latency of response for the herds was not significantly different between the bee and control playbacks (Mann-Whitney U, U = 77.50, $p>0.145$).

Aggressive displays were recorded from 26.6% of the control trials and 33.3% of the bee trials.

Of the family units, 53.3% moved to within the resting area in response to the bee trials compared with the control trials, which was 26.6%. Four family units moved away completely (>20 m) from the resting/shaded area during the bee trial, whereas only one resting family unit moved away during a control trial.

Discussion

Family units showed a greater behavioural reaction to the bee stimulus than to the control stimulus (Fig. 2). A higher proportion of families and a higher number of individuals showed a behavioural reaction to the bee stimulus (86%; 61 individuals) compared to the control stimulus (60%; 35 individuals). Though the response latencies—the latency response between the bee and control playbacks—were not as statistically different.

When all behavioural reactions were compared to one another per playback, the bee stimuli, overall "strength of behavioural" responses, did not display a significant difference from the control. However, when specific behavioural responses were combined in the analysis, a small p-value (0.06) was obtained, testing the medium and strong reaction to the non- and weak reaction between each stimulus.

This study demonstrated that elephants in the north-east of Botswana reacted to the recorded sound of the bees; however, their reactions varied between individuals of the same family and between different family units. The inconsistent behavioural reaction of elephants in response to the playbacks could potentially be related to the current state of the African honeybee population in Botswana. If it is the case that certain elephants "know about" bees as was suggested by King et al. (2007), whereas others do not, then it can be predicted that areas with large bee populations would have an elephant population that shows a strong negative reaction to the sound of bees. Following a study conducted by Lepetu et al. (2009) investigating the potential of the beekeeping industry in Botswana it was revealed that the current beekeeping culture is not well developed and needs to be strengthened for it to be profitable (Government, 2005). The major problems outlined for Botswanan beekeeping are the lack of bee management skills (Lepetu et al. 2009). Additionally, high summer temperatures in Botswana that frequently reach 36ºC–40ºC (Nkemelang et al. 2018) could affect wax consistency and hive cooling capabilities, which might in turn impact honeybees' activity levels, as well as their ability to breed.

Acknowledging non-significant results in HEC mitigation is relevant as it helps prevent the repetition of ineffective strategies and highlights the context-specific nature of such interventions (Catalano et al. 2019). A "one size fits all" approach rarely works to mitigate HEC, as the conflict is related to both location and situational factors (Kiffner et al. 2021). Testing and assessing mitigation methods in HEC priority areas and regions ensures that interventions are both ecologically

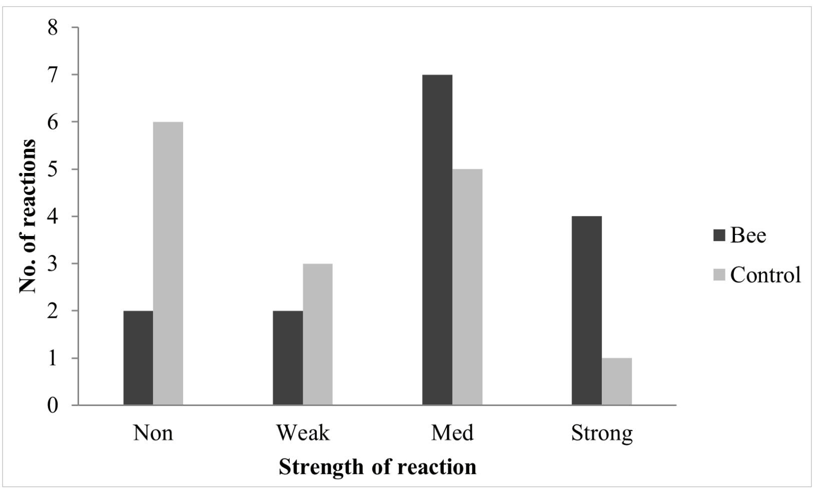

Figure 2. The number of different reactions of the behavioural family unit to both the bee (n=15) and the control playback (n=15).

and socially appropriate, increasing the likelihood of long-term success and community acceptance.

Future research is needed to unravel the relationship between honeybee density and behaviour, and elephant crop-raiding activities in Botswana. This study demonstrates the value of conducting behavioural trials on specific elephant populations under local conditions to gauge reactions to differing deterrents before investing in mitigations. It has been suggested that the function of the elephant's reaction to the sound of bees is one of fear because of the associated sting the bee can deliver, especially in sensitive areas such as the inside of the trunk, eyes and ears (King et al. 2010). However, if an individual or matriarch elephant has never had a negative association with bees, then it may not know how to react. Despite the need for further research, our preliminary results demonstrate that Botswanan elephants did display elevated reactions to the sound of bees. However, it does highlight the value and need to test and trial mitigations first before implementing these management tools more broadly.

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Morphometrics: elephant back and tail lengths

Ian SC Parker

PO Box 1115, Tolga, QLD 4883, Australia

Email: ipap@activ8.net.au

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Introduction

East African savannah elephant (*Loxodonta Africana*) back lengths are shown to be the same as their shoulder heights. As the latter are reasonable criteria for estimating ages, back lengths from aerial photographs taken vertically over individuals and herds can also be used to establish elephant population structures. The mean tail lengths are a constant proportion of shoulder heights regardless of gender or age; however, the variance of 22.8% around the mean renders them unusable as ageing criteria for individual elephants.

To record information on the morphometrics of a population of savannah elephant, Laws et al. (1975, Appendix B, 1. Body measurements) took 11 body measurements from culled carcasses. This field note compares three measurements: shoulder heights, back lengths, and tail lengths. These data have been referenced previously (Laws et al. 1975; Laws 1969), but due to being hidden amidst a wealth of other material, they warrant representation for potential use in analysing elephant populations.

Materials and Methods

Elephant culling in Uganda between 1965 and 1967 has been described in detail by Laws et al. (1975) and Parker and McCullagh (2021). The measurements (taken with a steel tape to the nearest cm) presented here were made immediately post-mortem. The height of the shoulders was a straight line from the side of the forefoot to the leg column locked straight to where it was intersected at right angles by a straight line across the two scapulae crests (n = 2,877 adopted as standard measure of elephant size). The back lengths (n = 393) and tail lengths (n = 185) were taken as subsamples of the 1,200 animals culled in Murchison Falls National Park (NP) north of the Victoria Nile. The length of the back was a straight line from where the posterior border of the ear met the head, touched the convexity of the dorsal ridge, and the point where a straight line, a right angle from the tape, touched the posterior outline of the body. (Fig. 1). Tail lengths were the straight-line distance between the end of the extended tail (excluding hairs, which can be more than 50 cm long) and the point where the underside of the tail meets the body.

Results

Shoulder heights and back lengths are presented as means in five-year-of-age cohorts (for reasons see Parker 2023) for both genders separately and combined in Table 1 and Fig. 2. Differences between the means of shoulder heights and back lengths are all <5% of shoulder height, with a single exception (males in the 20–25-year cohort 5.9%). There were no significant differences between shoulder heights and back lengths for either sex, independently or in combination (t test 0.867).

Table 2 and Fig. 3 present tail lengths as proportions (%) of shoulder heights as the means of five-year age-cohorts, showing genders separately. Across the nine (female) and eight (male) cohorts for which data were available, tail lengths, respectively, averaged 43.4% and 43.8% of the average shoulder heights. However, the raw data of the individuals from whom the cohort data are derived indicate that <5% fell within the cohort means (variance ranging between 33.8% and 56.6% of shoulder height). Consequently, as a metric to establish individual age or body size, tail length is inappropriate.

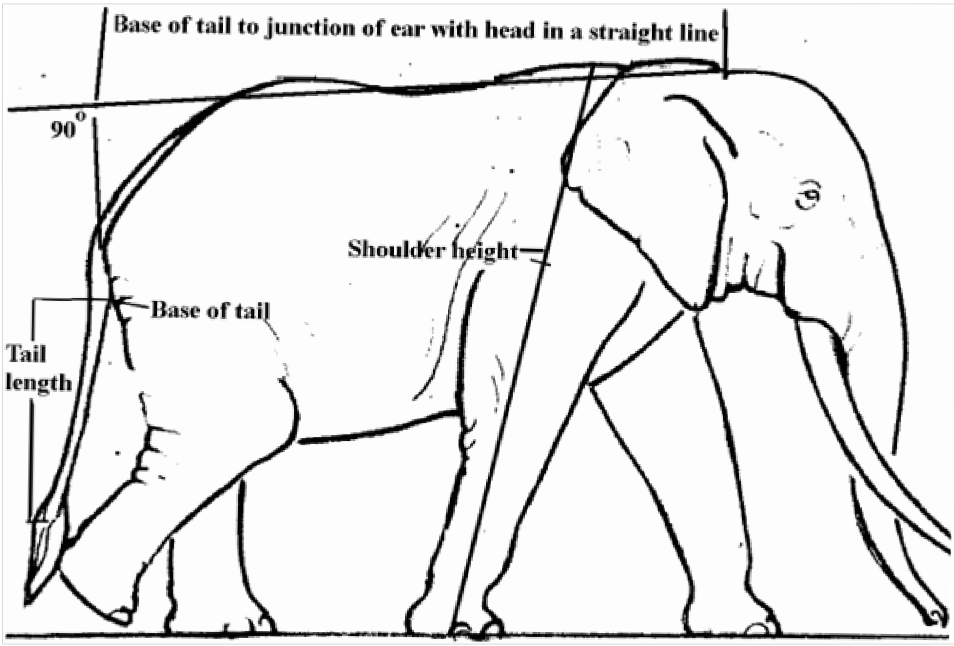

Figure 1. The measurements of shoulder, back and tail lengths are illustrated diagrammatically.

Discussion

Morphological measurements of culled elephants were made because no such data set had previously been available at the population level. At the time, there were few keys to estimating wild elephant ages: among them were dentition (Laws 1966; Sykes 1966; Buss and Smith 1966), shoulder heights (Laws and Parker 1968), and eye lens weights (Laws 1967). Dentition and shoulder heights are both obtainable from anaesthetized animals or, with the addition of eye lenses from dead specimens, but measurements are difficult to acquire quickly in the field at population levels. To do so, a method to achieve this without killing or anaesthetising subjects has always been desirable. Photographs of elephants taken vertically above and calibrated for height permit back length to be transformed into the age of the elephant. Aerial photography allows population structures to be assessed quickly and on a large, albeit coarse scale, without physical contact. This was applied by Laws (1969) in Kenya's Tsavo East and West NPs. However, as illustrated here, while back length can be taken as an ageing key as shoulder height, the 1:1 ratio between shoulder and back may not apply elsewhere. As reported by Hall-Martin in Bosman and Hall-Martin (1986), the proportions of elephants seem to differ across Africa. For example, the back lengths of elephants in Botswana and western Zimbabwe subjectively appeared to the author, to be greater than their shoulder heights. Back length as an ageing key needs recalibration regionally, raising a point: the relationship between shoulder height and age established from dentition illustrated in Laws et al. (1975), seems widely used outside East Africa (Whyte and Hall-Martin 2017). Has it been validated as a population parameter anywhere else?

Tail lengths averaging 43.3% of mean shoulder heights were constant for both genders of all ages. However, while that is a population overview created by deliberately smoothing the data into five-year cohorts, at the individual level, a variance of 22.8% about the mean renders the metric unreliable as an index of age or any other morphological parameter.

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Table 1. Compares shoulder heights to back lengths as averages of 5-year cohorts, the difference between them in cm, and as a proportion (%) of shoulder heights. Cohorts in years **I** = 0–5.5; **II** = 6.5–10.5; **III** = 11.5–15.5; **IV** = 16.5–20.5; **V** = 21.5–25.5; **VI** = 26.5–30.5; **VII** = 31.5–35.5; **VIII** = 36.5–40.5; **IX** = 41.5–45.5; **X** = 46.5–50.5, **XI** = 51.5–55.5; **XII** = 56.5–60.5.

Sex	Age in 5-year cohorts	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Females	Sample size 221→	59	31	16	23	22	23	14	7	10	5	8	3
	Shoulder cm	140.0	191.4	220.6	225.2	236.0	239.0	248.0	252.3	252.0	263.0	248.0	251.0
	Back cm	139.0	190.6	219.5	224.9	232.0	239.0	246.0	254.7	255.0	263.0	248.0	249.0
	Difference shoulder/back cm	5.5.0	5.9	6.9	9.4	9.7	9.4	8.2	3.4	9.8	11.6	9.0	3.0
	Difference as % of shoulder	3.9	3.1	3.1	4.2	4.1	3.9	3.3	1.4	3.9	4.4	3.6	1.2
	SD	2.1	2.2	2.4	2.7	2.8	2.9	3.4	4.5	2.9	3.3	2.8	1.3
Males	Sample size 172 →	69	34	16	15	20	13	3	2	0	0	0	0
	Av. Shoulder height cm	141.0	230.9	246	262.8	252.0	305.0	290.0	285.0				
	Av. Back Length cm	138.0	226.4	234.0	252.2	273.0	287.0	285.0	304.0				
	Av. Difference cm	4.7	8.6	12.1	11.5	10.5	18.0	5.5	19.0				
	Av. difference as % of shoulder height	3.2	3.7	4.9	4.4	3.7	5.9	1.9	6.7				
	SD	2.3	2.1	3.3	3.2	3.1	4.2	2.2	4.4				
All	Sample size 393	129	65	32	38	42	36	17	9	10	4	8	3
	Av. Shoulder height cm	141.0	196.2	226.0	233.5	249.0	254.0	258.0	254.3	252.0	263.0	248.0	251.0
	Av. back length cm	140.0	193.4	229.0	228.5	242.0	251.0	253.0	255.8	255.0	263.0	248.0	249.0
	Av. difference cm	5.0	6.0	7.8	10.4	10.5	9.8	9.9	3.9	9.8	11.1	9.0	3.0
	Difference as % of Shoulder height	3.7	3.1	3.4	4.5	4.3	3.9	3.9	1.5	3.9	4.4	3.6	1.2
	SD	2.0	2.3	2.5	2.9	3.0	3.0	3.0	1.7	3.0	3.3	2.8	1.3

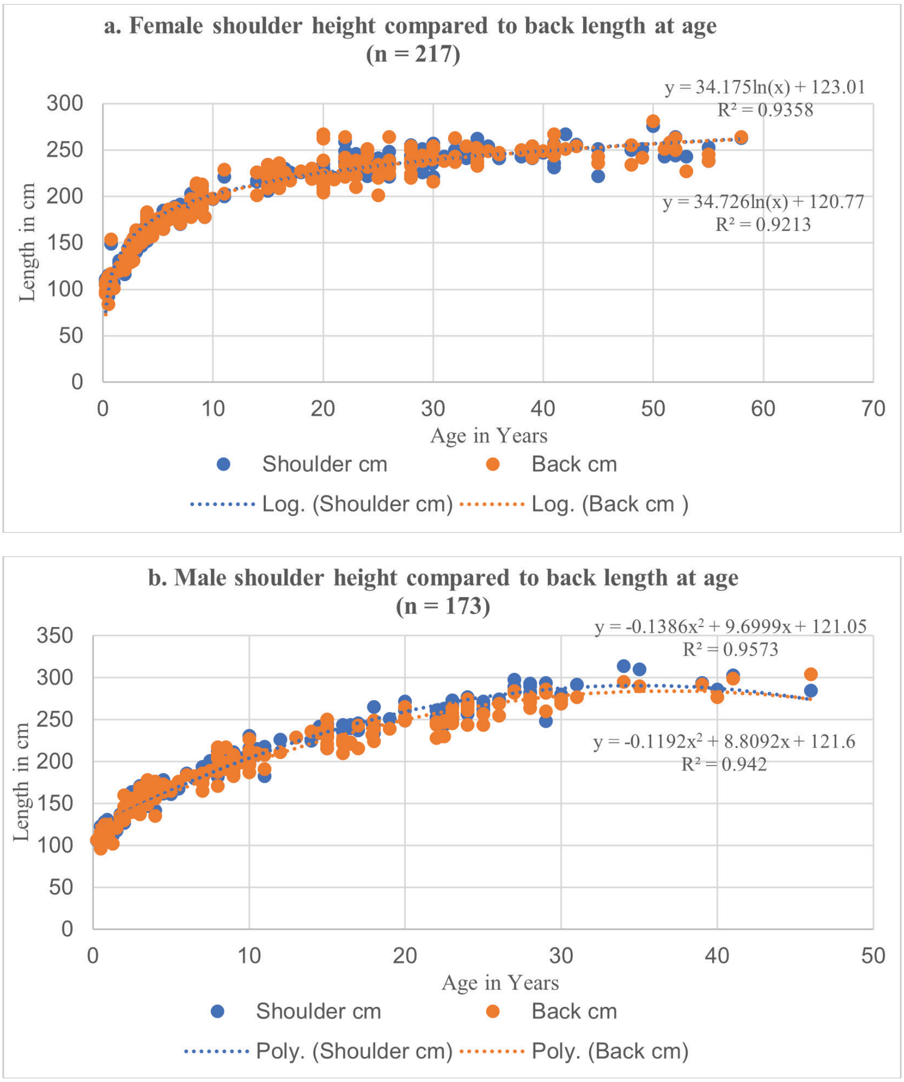

Figure 2. Panel a = females and Panel b = males comparing shoulder heights with back lengths, showing that they were almost mirror images of each other.

Table 2. Elephant tail lengths as proportions (%) of shoulder heights presented as means in 5-year cohorts. Data were not available for females >50.5 years and males > 45.5 years.

Sex	Age cohort	Sample	Mean cm of the shoulder	Tail mean cm	Tail as % of shoulder	SD
Females	0–5.5	n = 10	143.9	61	42.5	6.73
	6.5–10.5	n = 21	183.9	77.7	42.1	6.51
	11.5–15.5	n = 13	218.6	91.3	41.8	6.46
	16.5–20.5	n = 8	224.8	98.5	43.8	6.62
	21.5–25.5	n = 17	233.7	99.3	42.5	6.52
	26.5–30.5	n = 7	240.3	102.4	42.7	6.53
	31.5–35.5	n = 11	249.1	109.5	44.0	6.62
	36.5–40.5	n = 3	259.3	117.0	45.2	6.72
	41.5–45.5	n = 2	268	122.5	45.7	6.76
Males	0–5.5	n = 9	133	62	46.6	6.81
	6.5–10.5	n = 19	187.2	83	44.3	6.64
	11.5–15.5	n = 13	231.6	102.8	44.4	6.66
	16.5–20.5	n = 12	257.7	109.2	42.4	6.51
	21.5–25.5	n =11	272.7	118.7	43.5	6.59
	26.5–30.5	n = 24	287.3	125.4	43.6	6.60
	31.5–5.5	n = 4	290.8	121.3	41.9	6.47
	36.5–40.5	n = 1	319	140	43.9	

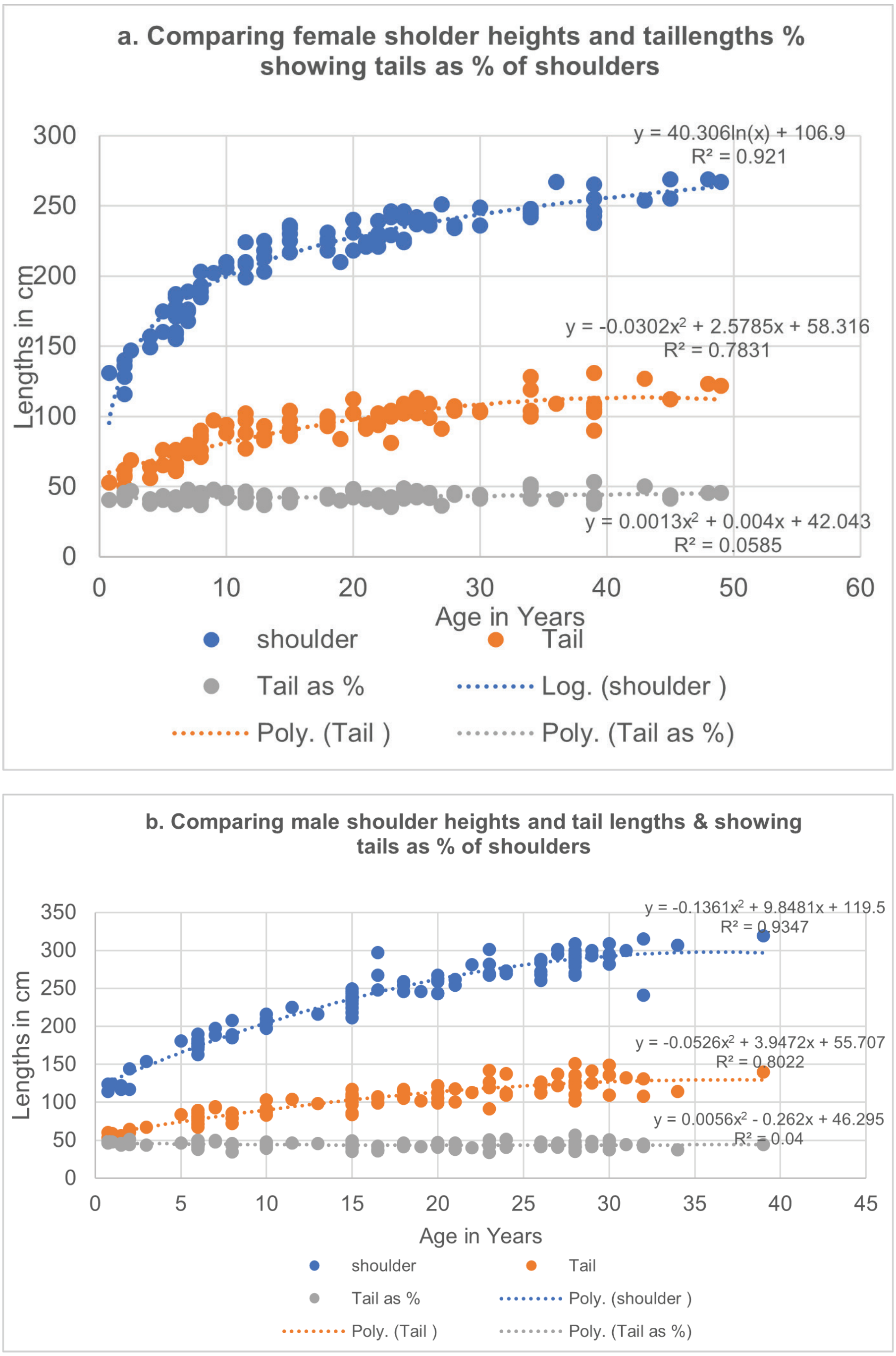

Figure 3. Panel a = female data, and Panel b = male data, which present tail lengths as constant proportions of shoulder height regardless of age or gender.

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Savannah elephant foot metrics

Ian SC Parker[1], Don Franklin[2]*

[1]PO Box 1115, Tolga, QLD 4882, Australia
[2]Research Institute for Environment & Livelihoods, Charles Darwin University, Darwin NT 0909, Australia

*corresponding author: ipap@activ8.net.au

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Introduction

The lengths and circumferences of all four feet in a sample of 162 (85 female and 77 male) elephants are presented. From these datasets, 159 had corresponding shoulder heights and 160 had estimated live weights. The results confirm constant relationships between foot metrics and shoulder height for East African elephants, and the load that elephant weight places on the ground in kg/cm^2 to be calculated.

Trophy hunters' and Asian elephant handlers' lore holds that front feet metrics are reliable indices of an elephant's height for both savannah elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*). Biologists have examined this position, and Sukumar et al. (1988) methodically tested it for Asian elephants, concluding that forefoot circumference x 2.03 gave an accurate measurement for shoulder height. Western et al. (1983) tested hind foot length as an indicator of size and age in the African elephant (*Loxodonta africana*). Chapman et al. (2016) used footprints to estimate body size in Asian elephants indirectly. Wijanto et al. (2021) correlated foot circumference with body length, shoulder height, and pelvic width in Sumatran elephants (*E. m. sumatranus*). All the foregoing research indicated a close correlation between the foot metrics and shoulder heights. We add our findings to this body of information by presenting data sets of all four feet from 77 male and 85 female / East African savannah elephants across a wide age range.

In this field note, the authors seek answers to the following questions: 1) Do the lengths and circumferences of the savannah elephant fore and hind feet differ between left and right; and is there any change with age? 2) Do these metrics differ between males and females? 3) Do these metrics show any evidence of lateralisation analogous to right/left-handedness in humans or other animals? 4) Do these metrics show sufficiently consistent relationships to shoulder heights to be reliable guides to an elephant's size and sex?

Methodology and data analysis

Data for the analyses were obtained from elephants culled to reduce numbers on the north bank of the Victoria Nile in Uganda's Murchison Falls National Park (NP) in 1965, as described by Laws and Parker (1968). All measurements were taken in cm using a steel tape immediately post-mortem. Lengths were a straight line across the sole of the foremost and hindmost point on each foot. On field data sheets, the length data were recorded as diameters. This error persists in the archived material held in the University of Florida[1]. Lateral widths were not recorded. Circumferences were the distances around the edge of the sole, including toenails. Live weights in kg were routinely calculated (Laws et al.1967) and shoulder heights in cm taken from the locked foreleg of all elephants culled. The latter was used as the standard measure of an elephant's size as described in Laws et al. (1975). Ages were estimated using the molar key provided by Laws (1966).

To compare variability in the foot length and circumference measurements, we used the left and right of each forefoot and hindfoot length and circumference as pairs of measurements. We

[1]https://ufdc.ufl.edu/IR0001446

calculated the absolute difference between each pair and the mean of the pair for each elephant, (from the left and right forefoot and hindfoot length and circumference) and then averaged these values across all elephants for each metric.

For analyses including age as an effect, we first created annual classes by standardising ages into year classes 0.5, 1.5, 2.5 ... where 0.5 = 0–0.9, 1.5 = 1.0–1.9 etc. For statistical analysis requiring age as a categorical variable, we grouped these into five categories (five age categories): ages 0–5, 5–10, 10–18, 18–28 and 28–61.

Permutational ANOVAs were performed in the Permanova add-on (Anderson et al. 2008) to Primer v6 (Clarke and Gorley 2006). We used Euclidean distance, Type III (partial) sums of squares, fixed effects summing to zero for mixed terms, and 9,999 permutations of residuals under a reduced model.

To examine the relationship between age and foot dimensions, we evaluated four PERMANOVA models, one for each of the mean within individuals of forefoot length, hindfoot length, forefoot circumference and hindfoot circumference. Fixed terms in the analyses were sex and five age categories, and we considered their interaction. We then fitted exponential rise-to-maximum equations with a y-intercept to each dimension for each sex; the y-intercept expresses size at birth.

To examine the role of sex and foot dimensions in predicting shoulder height, we used hindfoot and forefoot circumference and divided it into five approximately equal classes: 50–75, >75–90, >90–100, >100–110 and >110 cm. Shoulder height was then modelled as a PERMANOVA with sex, hindfoot circumference class and the interaction between them as factors.

We calculated the ratio of circumference to length for each foot to examine the variation in foot shape, as expressed by the relationship between foot length and circumference. This was then modelled as a PERMANOVA with fixed effects of sex, age5cat, side (left, right), and front/rear. Individuals (nested in sex and five age categories) were included as a random effect because the feet of an individual may not be regarded as independent. Second-order interactions involving sex and age were included in our calculations, but no other interaction terms were included.

To estimate weight loading, we need the cross-sectional area of each foot. Elephant's feet are elliptical in cross-section. In the following calculations:

A = area
a = length/2
b = width/2
C = circumference.

The area of an ellipse is:

$$A = \pi * a * b.$$

As we have data for length but not width, width was approximated from circumference and length as follows, using the simple first approximation:

$$C = 2 * \pi * \text{square root } ((a2 + b2)/2)$$

https://www.mathsisfun.com/geometry/ellipse-perimeter.html, viewed 27 May 2025. This approximation is accurate within 5% for the relatively rounded feet of elephants.

This was resolved for half-width as:

$$b = \text{square root } (2 * (C/(2\pi))2 - a2)$$

We calculated b and hence A for each elephant foot. We summed A across all four feet and, using weights for each individual, calculated weight loading. We then modelled weight loading in a PERMANOVA with sex and age5cat as fixed effects.

Results

The absolute difference between left and right pairs for measurements of foot length and circumference was zero for just over one-third (35.5%) of pairs. Mean absolute differences were similar but somewhat lower for hindfeet and circumference (Table 1). This is inconsistent with the notion that length is the more accurate measurement, though alternative explanations relating to foot shape are possible.

Table 1. Comparison of mean absolute difference as ratios in measurements between left-right pairs of foot measurements of African savannah elephants.

	Forefeet	Hindfeet
Length	0.01176	0.00698
Circumference	0.00557	0.00411

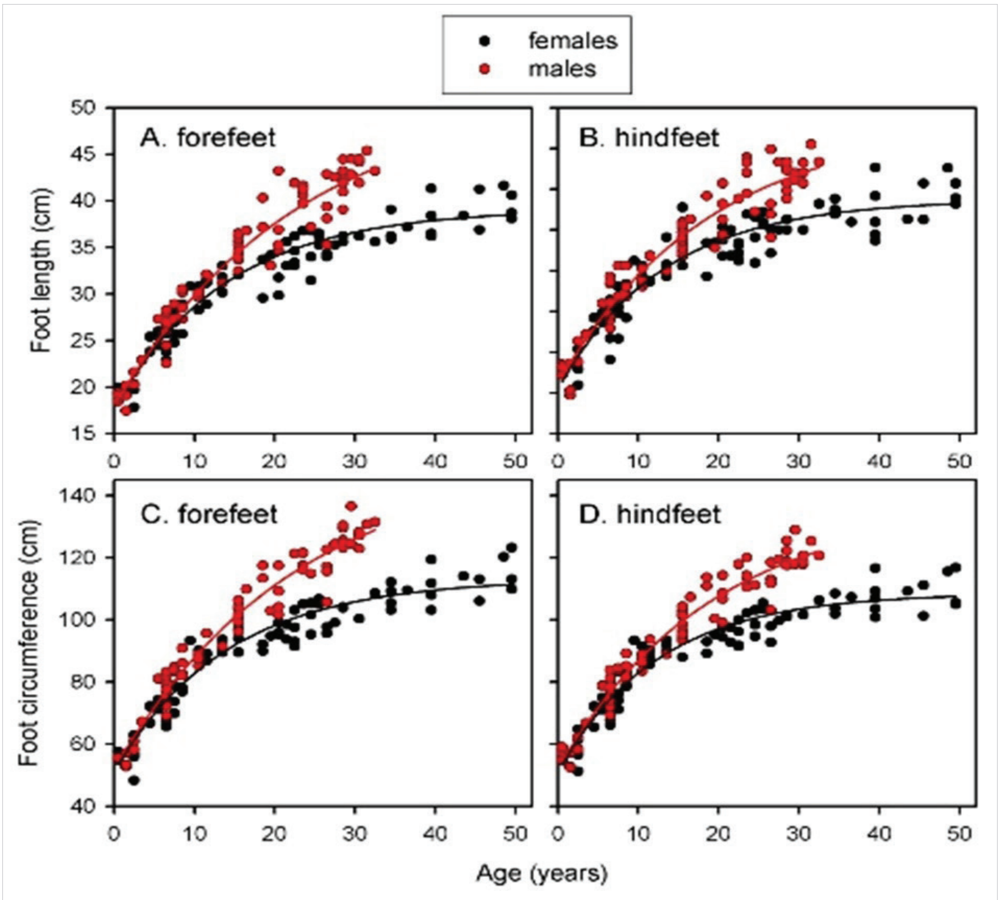

Figure 1 Growth of feet metrics with age in African savannah elephants. See Table 2 for regression equations.

Table 2. Exponential rise-to-maximum regression equations for the growth of feet in African savannah elephants (from Fig. 1).

Metric	Intercept	a constant	b exponent	Adjusted R^2 (%)	p
Female forefeet length	17.657	21.445	0.0718	90.5	< 0.0001
Female hindfeet length	20.466	23.248	0.0764	87.7	< 0.0001
Female forefeet circumference	51.091	62.087	0.0712	90.5	< 0.0001
Female hindfeet circumference	50.922	57.629	0.0808	90.8	< 0.0001
Male forefeet length	17.909	33.832	0.0434	93.4	< 0.0001
Male hindfeet length	21.149	32.262	0.0532	91.6	< 0.0001
Male forefeet circumference	51.763	101.703	0.0438	95.7	< 0.0001
Male hindfeet circumference	52.040	86.015	0.0520	95.0	< 0.0001

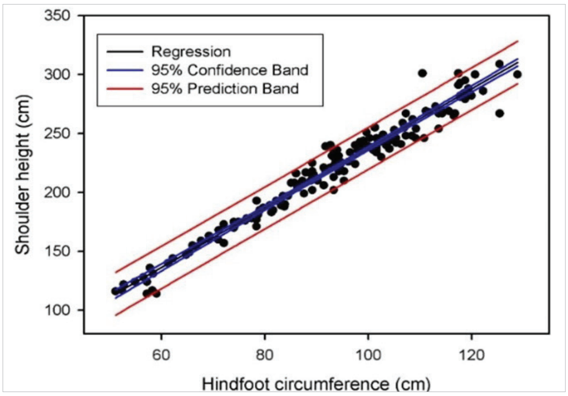

Figure 2. Hindfoot and forefoot circumferences as predictors of shoulder height in 159 African savannah elephants. The regressions are: shoulder height (in cm) = 2.524*hindfoot circumference – 15.1521 (R^2 = 96.3%; F1,155 = 4114.4, p<0001). Shoulder height (in cm) = 2.287* Forefoot circumference (in cm) + 2.6955 (R^2 = 96.4%; F 1.155 = 4182.5, p<0.0001.

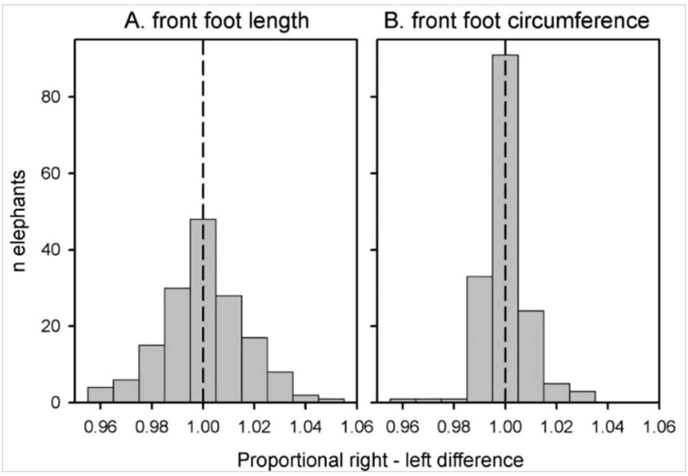

Figure 3. Proportional differences between left and right front feet dimensions in 161 African savannah elephants. The dashed lines indicate perfect symmetry.

Growth

Fore- and hind-feet lengths and circumferences varied significantly with sex and age and the interaction between the two (p = < 0.001). For all four parameters, males grew quicker and larger than females (Fig. 1).

Shoulder height differed strongly among hindfoot circumference classes (p = 0.0001), but not between the sexes (p = 0.778), though the interaction term was significant (p = 0.018). The relationship between shoulder height and hindfoot circumference was strongly linear, even when the sexes were combined (Fig. 2).

Laterality

The length of left and right forefeet of 30.2% of elephants were within 0.5% of equal, whilst the equivalent figure for circumference was 57.2%, with no indication that more had larger left than right feet or vice versa (Fig. 3).

Foot shape

In cross-section, elephant feet are elliptical and slightly to markedly elongate (indicated by circumference: length < π), rarely marginally wider than long (Fig. 4). Foot shape varied between individuals, between front and rear feet, and less strongly between the

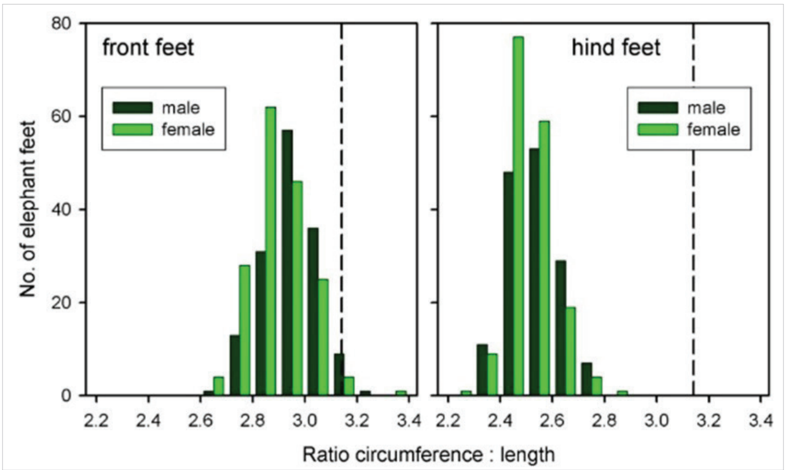

Figure 4. The shape of the front and hind feet of male and female African savannah elephants is indicated by the ratio of circumference to length. Mean ratios are: male front 2.95; female front 2.89; male hind 2.53; female hind 2.51. The dashed line is π, the value at which feet would be as wide as long.

Table 3. Significance of terms in a PERMANANOVA model of foot shape (the ratio of foot circumference to length) of African savannah elephants. Significant terms are highlighted.

Term	**Probability**
Sex	**0.003**
Age	0.252
Side of feet	0.942
Front/rear feet	**0.0001**
Individual (nested in Sex and Age)	**0.0001**
Sex x Age	0.460
Sex x Side of feet	0.775
Sex x front/rear feet	**0.007**
Age x Side of feet	0.160
Age x Front/rear feet	0.804

sexes (Table 3). Neither age nor any interactions involving it were significant, and there was no suggestion of consistent laterality—the side of the foot term. Hind feet are markedly more elongate than front feet, and females have a little more elongate feet than males, more so on the front than hind feet (the interaction term ‘Sex x front/rear feet’ in Table 3).

Weight loading

The area of all elephant feet (four feet summed for the individual) ranged from 660.6 cm^2 in a 2-yr-old female to 5,476.2 cm^2 in a 29-year-old male. Estimated weight loads of elephants ranged from 0.280 to 1.092 kg/cm^2. Loads varied between the sexes (p=0.0004) and age classes (p=0.0001), and the interaction between sex and age class was also very highly significant (p=0.0001). Weight load increased with age, with males and females having similar loadings up to approximately 10 years of age, males developing heavier loadings thereafter (Fig. 5). In the age range available for the analysis, males showed no asymptotic weight load, but females did, with those aged 50 years having an estimated weight load of 0.81 kg/cm^2.

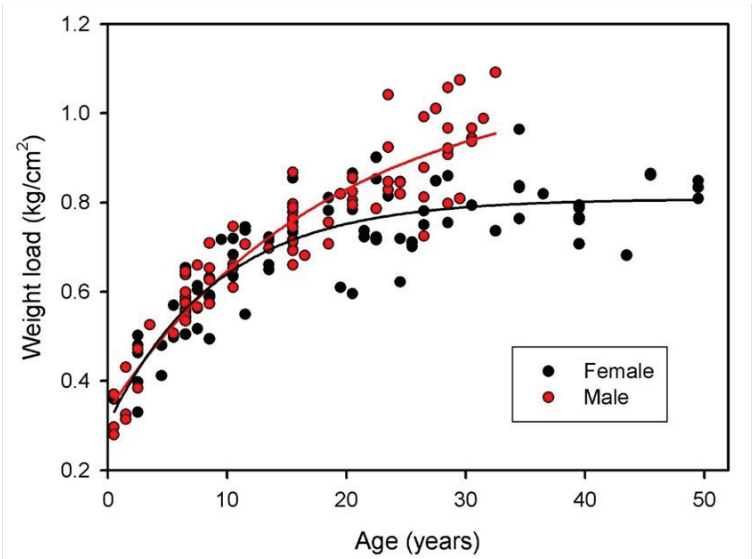

Figure 5. Weight loadings (mass/area of feet) in African savanna elephants. Model parameters are:
males: 0.7518(1–e^(-0.0542*age))+0.3321; R2 = 87.2%, p<0.0001; and
females: 0.5046(1–e^(-0.1102*age))+0.3031; R2 = 76.3%, p<0.0001.

Discussion

Answers to questions asked in the introduction follow. Do the lengths and circumferences of the savannah elephant fore and hind feet differ between right and left, and is there any change with age? They do not differ significantly between the right and left, and there is no noticeable change in the ratios of one to the other with age.

Both hindfoot and forefoot circumferences are strong predictors of shoulder height regardless of age and sex, and regression equations are provided for this. Do these metrics differ between males and females? Yes, they do, and this is in accordance with the other morphological data (e.g. shoulder heights) recorded, for example, in Laws et al. (1975).

Do these metrics show any evidence of lateralisation analogous to right/left-handedness in humans or other animals? In keeping with the similar finding on tusk use (Parker 2024), there is no obvious evidence of lateralisation. However, this does not eliminate the possibility of innate lateral bias. Proof of its existence now rests on observing behaviour rather than upon morphological features.

It is an assumption that an elephant's footprint will exactly mirror the sole that made it. Self-evidently, they must be more or less the same. Pedantic perhaps, but this assumption has not been objectively verified. From IP's experience tracking elephants, their footprints are strongly influenced by the hardness or softness of the substrate was (i.e. compacted earth, sand or mud) onto which their feet were placed, as well as the pace at which the imprinters (elephants) were travelling. If running, the central toenail at the front of an elephant's foot digs into the ground, leaving a small mound inside the anterior aspect of the imprint, and upon withdrawal forward, will extend the print length. The print of a walking or standing elephant will be close to the size of the imprinting sole, but where it is soft, as in sand or mud, this precision is less likely. Beyond giving a general idea of the imprinting elephant's size, the overlap between male and female lengths makes determining sex uncertain. Consequently, beyond providing a general idea of size, and until footprints have been objectively contrasted to foot soles, their relationship remains a subjective assumption. We conclude that while footprints are guides to an elephant's size, they are not precise indices and should be treated as such.

We have confirmed that in shape savannah elephant's forefeet are not circular, but slightly elliptical, whereas the rear feet are strongly elliptical. An elephant's gait and the broad soles of its feet spread its live weight load on the ground more widely than the gaits of equines and bovids, whose hooves concentrate their weights on more restricted areas. While self-evident and somewhat esoteric, it is an aspect to consider when comparing the influences of elephants on their environments with those of other large animals, for example, in their respective roles on soil erosion.

Acknowledgements

We thank Adrian Lister for giving references to previous publications relating to elephant feet metrics.

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The relationship between *Gyrostigma rhinocerontis* and rhinos in East and southern Africa

*Charles Dewhurst[1]** and Graham Reid[2]**

[2]4 Windsor Lodge, Strathpeffer IV14 9DX, Scotland

*corresponding author: dargreid@gmail.com
[1]**Deceased (May 2025)

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Introduction

Gyrostigma rhinocerontis, commonly known as the Rhino Bot Fly is uniquely the largest species of fly found in Africa, reaching lengths of up to 40mm, with an impressive wingspan of 70mm and a dark body, orange head and legs. It is specific to and entirely dependent upon either the black or white rhinoceros of the savannahs of East and southern Africa for the completion of its life cycle and subsequent reproduction. Sadly, it may well become extinct before the rhinos with which it has evolved and cohabited for millions of years.

The relationship between the Rhino Bot Fly and the rhinoceros

In former times, when rhino populations were healthy and large numbers would be found roaming throughout the savannah regions, one could support the view that *Gyrostigma*, along with other diseases and parasites, may have played a role in regulating the populations of these mega-herbivores, most likely when they were at high densities near ecological or social carrying capacities. (See, for instance: Shrader et al. 2025) The larval stages, attached to the rhino's stomach lining, often in huge numbers, would seem to certainly compete with the host by attaching and feeding on the gut lining, thus compromising nutrient uptake. In times of food shortage, drought, injury, or disease, one can envisage that this competition for nutrients could tip the balance, increasing the stresses and risks for weaker and older animals, thus rendering them more susceptible to starvation, disease and predation. *Gyrostigma* may contribute somewhat by helping to limit populations to numbers that can

Figure 1. *Gyrostigma rhinocerontis*, Rhino Bot Fly, This adult insect was reared by the author (CD) from larva to adult in May 1987, from host rhino Black rhinoceros "Kiserian" who was captured on the Athi Plains and translocated to Nakuru NP. The adult bears the reference number 680. © Bob Campbell.

be supported by available resources, thereby maintaining the overall health of ecosystems. This is in contrast to its historic labelling, whereby it was dismissed as an undesirable parasite with no apparent benefits. Currently, however, with rhino populations having been devastated much more directly through human impacts of poaching and habitat loss, issues related to *Gyrostigma's* potential benefits have not featured as priority areas for research.

Present and future concerns

Despite the massive funding and efforts being undertaken to conserve their black and white rhino hosts, *Gyrostigma* suffers from being little known, rarely observed and poorly understood. Now identified as a "harmful parasite", it is being forced into extinction through the precipitous population declines of its rhino hosts both in terms of range and numbers, as well as the highly effective and widespread use of antiparasitic drugs for domestic stock (e.g. *Ivermectin*) for many years. One smaller species of Rhino Bot Fly from East Africa (*Gyrostigma conjugens*) has almost certainly gone extinct already, last recorded from Tsavo East NP in the early 1960s. By the late 1980s, there were too few black rhinos in the Park left for it to parasitise.

The life cycle of *Gyrostigma* is as interesting as it is risky (Shrader et al. 2025). The adult female fly lays its eggs around the neck of the host rhino. These hatch in about six days and make their way actively towards the mouthparts to be licked and swallowed. Upon entering the digestive system of the rhino, they migrate to the gut lining, attach with their oral hooks and commence to feed and grow. As the 'youngster' develops, three larval stages may take weeks or months to complete. Once mature and with a length now of around 40mm, they will be deposited out of the anus to land unceremoniously in a heap of dung.

The timing and location of this 'landing' are crucial, as these larvae now need to quickly bury themselves into the soil where they will become pupae from which the adult flies will form within about six weeks. Emergence of the adult fly is meticulously timed, and the males emerge some 3–4 days before the females. This helps to promote outbreeding, but as neither the adult males nor females have mouthparts, there is only a finite energy source combined with a minimal lifespan of around 6–8 days and thus, a potential lottery with respect to the number of partners available to them with which to successfully perform their mating flights.

This solution to increasing the odds, no doubt pieced together over the aeons of coevolution, comes in the form of a rhino midden. Individual rhinos have overlapping territories but may not meet very often. Hence, the midden or dung heap has evolved as a communication/information centre. Individuals of all ages and both sexes intermittently deposit dung at these sites despite rarely meeting their fellow contributors. Through scenting at these dung piles, information exchange between overlapping but solitary rhinos is made possible around a variety of issues such as sex, age, dominance, territorial status and female oestrous state (Owen-Smith 1973). Additionally, the multiple individual dung contributions to these hotspots push up the number of deposited *Gyrostigma* larvae, thus ultimately ramping up the number of adult flies emerging and increasing the chances for successful mating. This is particularly important given that the adult flies are only active at dawn and dusk, providing yet another reason why sightings of these magnificent flies have been minimal.

Thankfully, it was possible for Dr Rob Brett and his KWS Capture Unit led by George Rakwan, to collect larvae from rhino faeces during translocation exercises. Charles Dewhurst, assisted by "chum" van Someren, were then able to rear these through to adult flies. These emergence studies, plus additional field studies of rhino middens by Charles Dewhurst and Graham Reid, have allowed important additions to our knowledge of the life cycle of these ephemeral creatures.

Despite being the largest known fly in the whole of Africa, albeit with a very short lifespan, and having an intimate relationship with an iconic flagship species, this may not be enough to save *Gyrostigma* from extinction. As it has only rarely been observed, it will perhaps never be fully appreciated. Now is undoubtedly a good time to celebrate this beautiful and bizarre creature both in its own right as well as for its potential contribution to rhino population dynamics and ecosystem health before it ultimately disappears, most certainly ahead of its rhino hosts.

Further research is encouraged to explore the relationships between black and white rhinos and their parasites, such as *Putative filariosis* and trypanosomosis. Potential density impacts (of rhinos) indicate that the matter is quite complex and not straightforward. These impacts may depend on the specific life history of the parasites and interactions with other parasites in the ecosystem. Density-related factors are also influenced by habitat loss and disruption, as well as food availability.

An accessible link to read the first author's obituary published May 2025 in the Times, newspaper, London has been kindly provided by the first author's son: https://drive.google.com/file/d/1C--Ny0Od5LV_QwG-YqAvxBjnjzkoHgvM/view?usp=sharing

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LETTERS TO THE EDITOR/CHAIRS

The most endangered extant rhino species is now on the verge of extinction

Dear Editor and AsRSG Chair,

Re: The most endangered extant rhino species is now on the verge of extinction

In a letter to the Editor Payne et al. (2019) stated "At some time in the very near future a point will be reached when the sheer technical and logistical inability to capture and translocate the last rhinos from remote sites, coupled with the reproductive condition of all those remaining rhinos still able to mate, and bureaucracy among the indecisive decision-makers, will together conspire to condemn the 20-million-year-old genus *Dicerorhinus sumatrensis* to inevitable extinction." The inability of humans in the last quarter of the twentieth century to critically assess field data and collaboratively determine science-based conservation strategies to avert the extinction of the Sumatran rhinoceros is the underlying cause of the dire status of the species today. The Sumatran rhino story holds lessons for many parties, not the least for the IUCN and its SSC specialist groups. This follow-up letter provides a historical overview and shows how international systems in place have failed the most endangered extant mammal genus, and that the onus now rests with Indonesia to prevent its extinction.

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Historical decline and early warnings

In prehistoric times, the Sumatran rhinoceros's range extended from north-eastern India and southern China through mainland Southeast Asia to Borneo and Sumatra. Over the past few thousand years, its range contracted markedly from north to south. A century ago, the species persisted only in low population densities, isolated, declining clusters (Payne 2022). Hubback (1939) warned that the species was "on the threshold" of extinction due to a lack of breeding.

In 1960, commissioned by the Survival Service Commission (SSC) of IUCN and based on field visits, Lee Talbot (1960) highlighted that the few remaining Sumatran rhinos had little chance of finding mates. (The SSC became the Species Survival Commission in 1980). Successful captive breeding of the Greater one-horned rhinoceros (*Rhinoceros unicornis*) in the 1950s prompted attempts to capture Sumatran rhinos. Ten Sumatran rhinos were captured in Riau in 1959, but the sole male escaped. While the Bogor, Basel and Copenhagen zoos each received a single female rhino, the rest were released back into the forest (Skafte 1964). Surveys four years later found that their habitat had disappeared (Milton 1963).

The World Wildlife Fund (WWF), in its first report, 'The Launching of a New Ark', proposed the establishment of reserves to bring together scattered animals, and a few years later, the SSC called the species a "cause for very grave anxiety" (Scott 1965). However, no actions were taken.

The first serious attempts to prevent the extinction of the Sumatran rhinoceros

Thomas Foose, the conservation coordinator of the American Association of Zoological Parks and Aquariums (AAZPA, now AZA), invoked captive breeding to prevent the extinction of the Sumatran rhinoceros, arguing that "Although a few populations of Sumatran rhino can hopefully be preserved in the wild, it may still not be possible to maintain large enough numbers to ensure long-term survival. In contrast, a captive programme could provide significant advantages against these problems" (Foose 1983).

By then, three endangered large herbivores—the European bison (Pucek et al. 2004), Przewalski's horse (King et al. 2015), and Arabian oryx (IUCN SSC Antelope Specialist Group 2017)—had been rescued from certain extinction through captive breeding and collaborative management. Most striking in those recovery efforts was the absence of bureaucracy, of rules to prevent cross-border exchange, of mainstream conservation NGOs, of stakeholder consultation, and of plans drawn up by supervisory institutions.

Following Foose's proposal, SSC convened an "Ad Hoc meeting on Sumatran rhinoceros" in Singapore in 1984 (Scott 1984), where opposing viewpoints emerged. Schenkel (the Chair of the Asian Rhino Specialist Group, AsRSG) was against any form of capture. While van Strien's (1985) study showed that there were several tens of Sumatran rhinos in Aceh, Sumatra, with a reasonable breeding rate, this finding provided false hope that similar sites might exist elsewhere, and that protection from poaching might allow a population recovery. It is now evident that this study area contained the only remaining cluster of Sumatran rhinos that was potentially viable at that time. It is the only one that still exists, although now as a much smaller cluster. All other Sumatran rhino clusters that existed in 1984 have been extirpated (Havmøller et al. 2015; Payne 2022).

The possibility of capturing Sumatran rhinos from protected areas (PAs) for captive breeding was not raised explicitly—most present knew this was not up for negotiation. In this, we can see a common human cognitive bias: for managing a critically endangered mammal, whether or not those mammals live in a PA is often irrelevant. The boundaries of those areas were based on what was possible at the time of their establishment in the context of human society, and do not necessarily bear any relevance to whether or not the habitat will be adequate to allow the recovery of a depleted population of a particular species (Kretzschmar et al. 2016; Payne 2022).

One problematic disagreement at the 1984 meeting was whether captured rhinos should stay in their country of origin. However, the fundamental disagreement was over whether or not to capture. An agreement was eventually reached to form a captive metapopulation, but through the capture only of 'doomed' individuals, those whose future long-term viability or contribution to the species' survival is determined to be unsatisfactory. This conservative position, however, left many potential breeding animals in the wild, thereby excluding them from captive breeding.

The 1984 Singapore meeting marked a distinct shift in perspective from that seen from the late 19th century until the 1960s, exposing a sharp dichotomy in the wildlife conservation world that remains even today. The dichotomy in thinking is: either create PAs, leave animals in the wild, list the species as entirely protected in legislation, establish field teams to reduce poaching, and promote 'awareness'; or, devise and implement a metapopulation programme that includes habitat management and captivity to recover numbers by maximizing reproduction.

Between 1984 and 1994, forty Sumatran rhinos were captured in Sumatra, Peninsular Malaysia and Sabah (Borneo), and sent to eight captive facilities in Indonesia, Malaysia, USA and UK (Rookmaaker 2019). Many of them were too old, injured, or infertile to contribute to breeding in the absence of assisted reproductive technology.

Reproductive problems in wild and captive populations

In 1986, one of the earliest females taken into captivity was found, shortly after capture, to have inactive ovaries and a uterine tumour, suggesting a lack of breeding in the wild (Furley 1987). Ultrasound examinations of captive rhinos subsequently revealed that most of the Peninsular Malaysian females had uterine cysts and tumours (Schaffer et al. 1994). By 1999, reproductive pathology had become prevalent in all female Sumatran rhinos in captivity (Schaffer et al. 2001); yet, this issue had never received serious attention from people designated as experts in official circles. Much later, Schaffer et al. (2020) found that among Sumatran rhinos, both captured and captive-born between 1986 and 2018, only three females were without reproductive aberrations. Despite the high occurrence of reproductive problems in rhinos from all capture locations, this issue was not discussed in the AsRSG meetings but instead dismissed as a "Malaysian problem" (JP, MA and KD, personal observations, Miller et al. 2016).

Of the Sumatran rhinos captured for the captive breeding programme (1984–1995), only one pair (Emi and Ipuh) produced offspring at the Cincinnati Zoo. Importantly, this was made possible only through human intervention and intensive management. Every Sumatran rhino female that produced offspring in captivity (Emi, Ratu, Rosa and Delilah) needed synthetic progesterone to maintain their first pregnancy and stop a cycle of abortion. For captive breeding to succeed as a means of preventing the extinction of large mammals, it is essential to capture young, fertile animals. For the Sumatran rhino, this need was undermined from the beginning, and followed thereafter by a refusal by designated experts to address the problem of reproductive pathology.

Even by the early 2000s, only a few Sumatran rhino experts understood that the Sumatran rhino's greatest issue was not poaching and habitat loss, but the failure of small residual clusters to reproduce in the wild.

Misconceived in situ protection and the lost opportunities for preventing extinction

By 1994, two main issues had become apparent for the Sumatran rhinoceros: reproductive pathology and declining wild clusters. This applied to both Indonesia and Malaysia. However, from the early 1990s onwards, the numbers of rhinos in each cluster were repeatedly overestimated by government staff and NGOs alike, being based not on verifiable data but on optimistic guesses. Efforts by a few individuals to present an accurate picture went unnoticed. For example, a 1995 survey conducted by one of the authors (ZZZ) across Peninsular Malaysia under a Global Environment Facility (GEF) funded project counted fewer than 30 individuals, which was well below official estimates (Zainuddin 1995). In addition, there was an all-too-common tendency to lump the numbers within separate clusters as if they represented a contiguous, viable population. This false confidence allowed senior decision-makers to believe that existing PAs were sufficient for preventing the Sumatran rhino's extinction.

Influential voices in wildlife conservation, notably Alan Rabinowitz, argued strongly against captive propagation and in favour of enhanced in situ protection of wild rhinos (Rabinowitz 1995). The 1995 GEF-funded project, "Indonesia and Malaysia

Conservation Strategies for Rhinos in Southeast Asia", was a significant additional push against captive breeding, emphasizing capacity building and local human benefits rather than the species' immediate reproductive needs. The project objective was "To enhance the conservation of biodiversity in Indonesia and Malaysia by providing technical training, operational support, and a long-term funding strategy to improve the effectiveness, sustainability and benefits (to local, national, and global human communities) of protection and management programmes for the Southeast Asian rhinoceros". This set the scene for many subsequent endangered species programmes, where a few necessary actions perceived as risky by decision-makers were substituted with human benefit objectives.

Both Foose and van Strien, regarded as key international experts on Sumatran rhinos, initiated the founding in the late 1990s of the Sumatran Rhino Sanctuary (SRS) in Way Kambas NP, Sumatra, a lifeline for the species. However, the broader opportunity to create a captive metapopulation was never pursued or institutionalised. International aid, although instrumental in keeping the SRS running and achieving five births from 2000 to 2025, tended to favour projects of questionable conservation value. Rhino Protection Units (RPUs), in particular, continued to consume large sums of money after 2000 with unclear results, while necessary high-priority efforts, such as capturing fertile animals for breeding, were abandoned.

'Sumatran Rhino Crisis Summit' and aftermath

In early 2013, one of the authors (KY) scoured all existing literature on wild Sumatran rhinos and collated information from experts at known Sumatran rhino sites, concluding that almost all the numbers presented in available reports were unreliable guesses. No information could be gleaned to back up any of the numbers quoted, and there were likely fewer than 100 Sumatran rhinos in existence. This was the stark conclusion of the Sumatran Rhino Crisis Summit in April 2013. Initially conceived in Sabah in 2012 as a gathering to draw the attention of advisers and decision-makers to the dire status of the Sumatran rhino and secure buy-in from international parties and the Government of Indonesia (GoI), the idea of a 'crisis summit' was lost by the time it convened. Instead, it was subsumed into an ongoing IUCN process of international meetings on Asian rhinos in general.

At the heart of the Summit were population viability assessments (PVA) prepared by the IUCN SSC Conservation Breeding Specialist Group. The analysis for wild Sumatran rhinos indicated that to have high confidence in population survival, at least 20 fertile individuals were needed in one area, with a roughly even sex ratio and one calf born to each female rhino every four years (Lees 2013). With the possible exception of one area in the Leuser Ecosystem, no such population existed after the 1950s. Modelling of a captive population provided an even bleaker picture (Putnam 2013). Putnam stated in her report, "Given the reproductive problems seen in the current captive Sumatran rhinoceros population, there is an 85%–98% probability that the captive population will go extinct in 50 years if no additional wild-caught (fertile) animals are brought into captivity. To reduce the captive population's extinction probability below 10%, approximately 16 adult wild-caught fertile rhinoceroses need to be transferred into captivity and either be managed globally or as two populations with an interbirth interval of three years." The implication of this assessment is clear and should have formed the basis for the only possible way forward to prevent the extinction of the Sumatran rhino—namely, to capture fertile wild rhinos, wherever they may be located, in the hope that at least 16 could be found. Yet, the recommendations in this assessment have never been endorsed or promoted by any major international conservation organization.

The Crisis Summit resulted in a Sumatran Rhino Emergency Plan (Anon. 2013) and a draft Emergency Plan Framework prepared by IUCN, both of which were submitted to the GoI in July 2013. Instead of highlighting a small number of clear policy decisions that were needed to address the situation, based on the PVAs (Lees 2013; Putnam 2013), and the proven success of the SRS model at Way Kambas NP, which in 2012 had resulted in the first captive birth of a Sumatran rhino in Indonesia, the Emergency Plan introduced the ideas of 'intensive protection zones' and 'intensive management zones' (Havmøller et al. 2015). In our opinion, there were numerous disjointed recommendations on information gathering and rhino detection (involving a vast and unnecessary camera-trapping effort), protection, infrastructure, monitoring and awareness-raising. The 1984 ad hoc meeting was repeated in 2013, but the direction recommended was even less clear than before.

Unfortunately, following the Crisis Summit meeting, the Sumatran rhino expert circle became even more fragmented. The most egregious split was evident at a workshop conducted in February 2015 in Indonesia, at which another PVA for the Sumatran Rhino was conducted (Miller et al. 2016). Key experts were excluded, essential PVAs of Lees (2013) and Putnam (2013) were ignored, and assumptions from unverified sources about rhino numbers, sex ratios and fertility, along with the inclusion of irrelevant factors, to reach erroneous conclusions, including: "for the foreseeable future the viability of all remaining rhino populations will depend on complete protection from poaching" and "Reproductive pathology occurred in Malaysian populations in low populations" (sic).

Subsequently, divergent conservation factions emerged, with one advocating to retain the status quo methods, albeit with rhinos captured and released into massive forest zones, with minimal management and no assisted reproductive technology. The other prioritising assisted reproductive technology. Attempts to create an international collaborative programme bore no fruit and ended in 2019, when the last two Sumatran rhinos in Malaysia died.

Were institutions, experts, and decision-making approaches fit for purpose?

In our opinion, despite decades of institutional involvement, efforts to save the Sumatran rhino have suffered from policy missteps and resistance to proven interventions. Generally, IUCN policy and positions can be susceptible to disproportionate influence by large, risk-averse institutions such as governments and NGOs, while dissenting expert voices are ignored, sending confusing signals to government officials who must make the final decisions on next steps. Additionally, different specialist groups may not always agree on vital issues. This is rooted in the fact that the far-reaching outcome of the 1984 meeting was ultimately determined by the opinions expressed in September 2014, when IUCN experts recommended against the use of assisted reproductive technology for the Sumatran rhino and instead proposed camera trapping, habitat manipulation, and enhanced anti-poaching efforts. The One Plan approach to endangered species advocated by the IUCN SSC Conservation Planning Specialist Group was undermined because the vital elements of captive breeding and assisted reproductive technology, both essential in the case of the Sumatran rhino, were either not supported or rejected by mainstream NGOs and other advisers (Havmøller et al. 2015; Payne and Yoganand 2017).

While the problem for Africa's rhinos is mainly how to reduce poaching of relatively large populations, involving species whose propagation is not a significant problem, the challenges for Sumatran rhinos are very different. It involves acting to boost the numbers of a nearly extinct species facing reproductive isolation, where captive management of the remaining rhinos is crucial. There are also numerous differences in viewpoints among stakeholders, including private individuals, scientific advisory committees and NGOs, about how to avoid extinction. Several African nations have a long history of wildlife management involving active interventions and private interests. Indonesia and Malaysia have no such background.

Although knowledge of the species surged after initial captures in the 1980s, by 2017, even well-established capture methods were made unnecessarily complicated through consultations with numerous uninformed participants.

The role of cognitive biases

Shifting baseline syndrome (Soga and Gaston 2018) was one of the contributing reasons why the need to bring Sumatran rhinos together under a single recovery programme was not sufficiently recognized from the 1984 Singapore meeting onwards. Although those involved were aware of the species' endangered status, the survival of only a few scattered individuals since the 1930s—which signals an advanced stage in the extinction trajectory—was not fully grasped.

Additionally, several cognitive biases, including the availability, avoidance, and confirmation biases, have contributed to the misconception that habitat loss and poaching are the main problems to address. Also, there was a misperception that the capture and breeding actions were risky. All forms of technical work involved in Sumatran rhino management are already well-perfected and of low risk. However, the decision-makers opted to sidestep decisive actions, possibly due to the fear of being criticised or to avoid controversy.

How would we like this to end?

Short of a radical turnaround, the genus will likely be functionally extinct (with no breeding occurring in the wild) by around 2040 and totally extinct in the wild by around 2060. However, if Indonesia brings its last remaining Sumatran rhinos under a single expert-managed programme and works to maximise birth rate, there is a last, slim chance to prevent this extinction.

Indonesia could change the extinction trajectory by, i) placing an experienced large herbivore veterinarian in charge of the SRS; ii) involving proven experts in Sumatran rhino capture, translocation and reproduction irrespective of their nationality; iii) do everything possible to reduce birth interval and increase birth rate for all captive females, at least by removing young individuals from their mother as soon as weaning is done; iv) capture some rhinos from Aceh, targeting young animals and where logistics is easiest, and managing them where it is most appropriate for optimal reproduction; and v) continue work on assisted reproductive technology and biobanking.

Acknowledgements

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Authors and addresses:
John Payne[1], Karen K Dixon[2], Sukianto Lusli[3], Zainal Zahari Zainuddin[1], Mochamad Indrawan[4], Kees Rookmaaker[5], Nan E Schaffer[2], Ahmad ZA Wahab[6], Petra Kretzschmar[7], Rasmus W Havmøller[8], Muhammad Agil[9], K Yoganand[10]*

[1]Borneo Rhino Alliance (BORA), Kota Kinabalu, Malaysia
[2]SOS Rhino, Kansas City, USA
[3]Habitat Restoration and Enhancement at PT. Kelola Habitat, Indonesia
[4]Institute for Sustainable Earth and Resources, Universitas Indonesia
[5]Rhino Resource Center, Utrecht, The Netherlands
[6]The Habitat Foundation, Penang, Malaysia
[7]Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany
[8]Natural History Museum of Denmark, Copenhagen, Denmark
[9]Bogor Agricultural University, Bogor, Indonesia
[10]Bringing Back Our Rare Animals, Kota Kinabalu, Malaysia

*corresponding author: sabahpayne@gmail.com

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BOOK REVIEWS

Rhinos of the World: Ecology, conservation and management

(Eds.). Mario Milleti, Bibhab Talukdar and David Balfour

Reviewed by Sam M Ferreira, Daniel Stiles, Hilloljyoti Singha, Jonathan Spencer, Deba K Dutta, Keryn Emslie, Inov Sectionov, Suzannah Goss

Contact emails: Ferreira: sam.ferreira@sanparks.org; Stiles: kenyandan@icloud.com; Singha: Sangha. hilloljyoti@gmail.com; Spencer: jonathan-spencer2011@live.co.uk; Dutta: debakumerdutta@gmail.com; Emslie: Sectionov: inov@rhinos.org; Goss: pachydermeditor@gmail.com

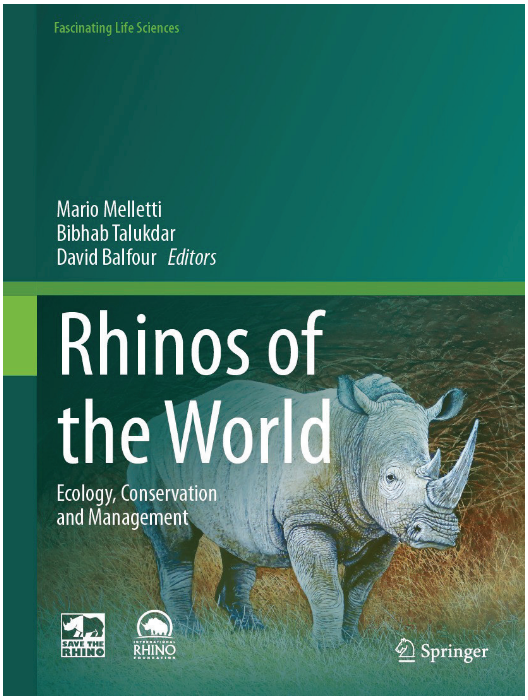

Figure 1. Front cover (https://link.springer.com/book/10.1007/978-3-031-67169-2)

Chapter 1/Phylogeny and systematics of the extant rhinoceros

Authors: Yoshan Moodley, Jan Robovský

Reviewed by Sam M Ferreira

The first chapter of the 16-chapter book on *Rhinos of the World* (under the sub-section 'Systematics and Evolution') provides a multi-scalar analysis of rhinoceros evolution, spanning extinct taxa to population-level divergence within extant species. It critically evaluates the influence of morphological traits, mtDNA (which often overestimates divergence), and nuclear DNA (with limited variability), revealing how these tools shaped competing phylogenetic hypotheses—namely, the horn, geographic, and radial models. Whole-genome sequencing emerges as a transformative approach, resolving inconsistencies, affirming a geographical model of divergence from a common ancestor ~36 million years ago, and clarifying mtDNA/nDNA discordance via secondary contact. The genomic data also inform estimates of ancient effective population sizes based on heterozygosity, of particular relevance given the fragmented and constrained population structures of modern-day rhino species.

While the chapter offers a robust synthesis of phylogenetic insights, several areas present opportunities for further development. Integrating ecological and demographic processes—such as dispersal dynamics and local adaptation—could enhance understanding of the mechanisms driving gene flow and shaping genetic structure. Additionally, many of the studies cited are based on limited sample sizes, which may not fully capture variability within populations or geographic patterns of diversity. Expanding sampling frameworks could strengthen the resolution of phylogenetic analyses. Finally, rather than emphasizing fixed, historical genetic structures, conservation strategies may benefit from a more flexible perspective that accounts for evolutionary potential and ecological responsiveness to the context of ongoing environmental change and disturbance.

The chapter concludes with a forward-looking recommendation: to move beyond rigid subspecies classifications and adopt more dynamic frameworks, such as evolutionarily significant units (ESUs) and management units, informed by historical gene flow and adaptive potential.

Chapter 2/Evolution and fossil record of Old World Rhinocerotidae

Authors: Pierre-Olivier Antoine, Damien Becker, Luca Pandolfi, Denis Geraads

Reviewed by Sam M Ferreira

The second chapter in *Rhinos of the World* offers a comprehensive synthesis of the evolutionary history of Old World Rhinocerotidae, tracing the lineage over 40 million years through dramatic climatic and biogeographical shifts. It highlights a remarkable radiation of rhinoceros species across epochs, with hundreds of genera emerging and disappearing, often in response to global environmental changes that unfolded at far slower rates than today's accelerating anthropogenic shifts. The chapter captures the Miocene as a peak of rhino diversity, followed by a stark contraction in both generic and specific richness during the Pliocene–Pleistocene. Notably, all surviving members are of the subtribe Rhinocerotina and possess nasal horns, while hornless lineages have vanished—marking a morphological legacy that survived severe attrition.

Asian fossil records provide relatively clear evolutionary trajectories, unlike the more fragmented African evidence. The chapter also candidly acknowledges the phylogenetic uncertainties that challenge fossil-based reconstructions, especially where taxa are defined from incomplete or geographically sparse materials. Despite these gaps, the review effectively outlines the deep-time patterns that shaped modern rhinoceros diversity.

The transition from the Pleistocene to the Holocene was pivotal, ushering in not only climatic instability but also the onset of direct human pressures. Anthropogenic pressures have intensified into the present, resulting in the precipitous decline of all five extant species and several subspecies. With northern white rhinos (NWR), western black, and northern Javan rhinos effectively lost, the chapter concludes with an urgent, sobering reflection: how much longer can the last wild representatives of this once-thriving 40-million-year-old lineage survive?

Chapter 3/Southern white rhino *Ceratotherium simum simum* (Burchell, 1817) Northern white rhino *Ceratotherium simum cottoni* (Lydekker, 1908)

Authors: Adrian M Shrader, Richard Emslie, Kes Hillman-Smith, Petra Kretzschmar, Courtney Marneweck, Mario Melletti, Norman Owen-Smith, Kees Rookmaaker, Kerry Slater

Reviewed by Daniel Stiles

The third chapter under the subsection 'Species Accounts' covers various aspects of the biology and natural history of the southern white rhino (*Ceratotherium simum simum*) and NWR (*Ceratotherium simum cottoni*), including names, taxonomy, subspecies and their distribution, descriptive notes, habitat, movements and home range, activity patterns, feeding ecology, reproduction and growth, behaviour, and status in the wild and in captivity. The chapter also includes a distribution map (Fig. 3.1; however the map fails to show the historical range of the NWR). There are also several photos of the species and a list of key literature.

An interesting tidbit from the taxonomic discussion was the fact that the question of whether the NWR and southern white rhinos (SWR) are separate species or

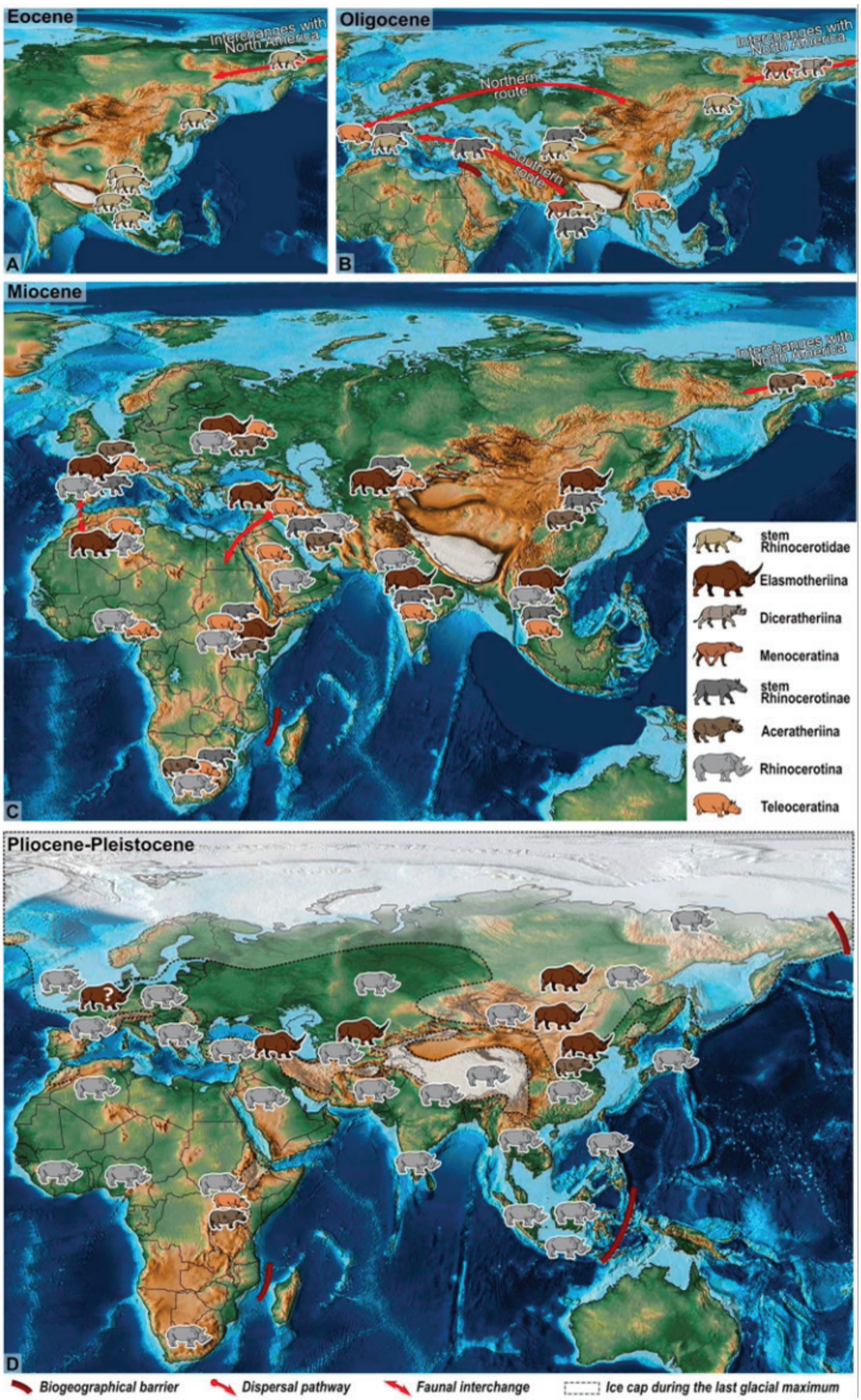

Figure 2. (Fig. 2.2) Historical paleobiogeography of rhinocerotids in the Old World, over (a) Eocene; (b) Oligocene; (c) Miocene, and (d) Pliocene-Pleistocene (c) PaleoAtlas for GPlates and the paleoData plotter programme.

Scotese CR. 2021. An Atlas of Phanerozoic Paleogeographic Maps: The Seas Come In and the Seas Go Out. *Annual Review of Earth and Planetary Sciences* 49 (1): 679–728. https://doi.org/10.1146/annurev-earth-081320-064052 subspecies, is still open. Recent genetic studies show that the differences between the NWR and SWR are greater than the differences found between any black rhino subspecies. In addition, it is not known whether the subspecies can interbreed and produce fertile offspring, which is one of the distinguishing features of the biological or taxonomic species concept. It is not difficult to tell them apart; the NWR is distinguished by the fringe of hair around the ears, which the SWR does not have.

The distribution map is quite dated, from 2012, and therefore does not include the more recent translocations of SWR from Zimbabwe to the DRC. The map also does not show the white rhinos in Angola and Rwanda as reported by the International Rhino Foundation, although these countries are listed under the 'Status in the Wild' section. The chapter would have benefitted from a table showing the population estimates by country at three or four points in time in order to clearly see the trends.

The authors categorize the last two remaining NWR as living in the wild. Having spent four years based at Ol Pejeta Conservancy in Kenya, where they are located and visited them on numerous occasions, I would consider them better viewed as living in captivity. They are under close, constant surveillance by conservancy rangers and live in a fenced enclosure within the electrically fenced conservancy.

Fig. 2 Dame Valerie Jane Morris Goodall (3 April 1934–1 October 2025) at Ol Pejeta Conservancy with Sudan, the last male NWR, before he died © Dan Stiles

Chapter 4/Black rhino *Diceros bicornis* (Linnaeus, 1758)

Authors: Adrian M Shrader, Keryn Adcock, Rob Brett, Charles Dewhurst, Vanessa Duthé, Richard Kock, Marietjie Landman, Peter R Law, Roan D Plotz, JA Shaw

Reviewed by Sam M Ferreira

Chapter 4, in this sub-section on 'Species Accounts', presents a richly detailed and scientifically grounded account of the biology, behaviour, and conservation status of the black rhinoceros, (*Diceros bicornis*). Far beyond a guidebook summary, this chapter synthesises an impressive array of literature, covering taxonomy, morphology, habitat use, dietary preferences, reproductive traits, and socio-ecological dynamics. It tracks the species' historical distribution and current range contraction, contextualising the population collapse of the 1970s–1980s and the subsequent recovery efforts. Notably, the chapter revisits subspecies designations, incorporating recent genetic and biogeographic data to support nine evolutionary lineages, seven of which persist.

The authors highlight black rhinos as ecologically generalist browsers with complex behavioural traits, such as conspecific recognition, home range fidelity, and sex-biased anti-predator responses. These observations are embedded in practical implications for translocation, habitat suitability, and ex situ conservation, offering both a retrospective and forward-looking perspective on black rhino management.

However, three caveats deserve consideration to deepen the analysis. Firstly, while the revised subspecies units are biologically defensible, they are not yet formally recognised by global conservation bodies such as the IUCN. This creates potential mismatches in policy, especially under CITES trade mechanisms. Such challenges could be overcome through emerging paradigms in dynamic ecological management, particularly those promoting dispersal and connectivity between neighbouring populations to mimic historical gene flow. Finally, insights from evolutionary theory, such as functional heterogeneity in resource use or the Trivers-Willard hypothesis on reproductive strategies, could enhance interpretations of demographic variability and life-history trade-offs.

In sum, this chapter offers a valuable scientific foundation for black rhino conservation. As pressures from poaching, habitat fragmentation, and climate change continue to mount, advancing science and adaptive management remain essential tools to safeguard this keystone browser and preserve its irreplaceable evolutionary legacy.

Chapter 5/ Greater one-horned rhino *Rhinoceros unicornis* (Linnaeus, 1758)

Authors: Bibhab K Talukdar, Deba K Dutta, Kanchan Thapa, Anwaruddin Choudhury

Reviewed by Hilloljyoti Singha

Under the series of 'Fascinating Life Sciences' by Springer Nature, this fifth of the 16 chapters, 'Greater One-Horned Rhino (*Rhinoceros unicornis* (Linnaeus, 1758) is authored by several greater one-horned rhino experts. This chapter provides an account drawing on up-to-date data covering every detail of the greater one-horned rhino (GOH) as found presently in India and Nepal.

According to the authors, due to its large body size and high mobility, the swimming prowess helped this primitive species adapt in floodplains. The historical range of the GOH rhino has been vividly depicted in historical records, from references in the *Chandogya Upanishad* of 900 BC to modern research papers. The historical documents mentioned are fascinating and important, found in various archives and sources, and have been well-researched by the authors. The authors also discuss the primary reasons for the decline of the species in its former range of distribution.

The current and recent past distribution and population trends have also been adequately described. The authors present the GOH rhino population trends of India and Nepal from 1900 to 2023 (Fig. 5.2). The latest population data (2021–2022) for the GOH rhino in the protected areas (PA) of India and Nepal are presented in Table 5.1.

Each rhino inhabiting PA has been described with its own specific history, conservation challenges and prospects with the landscape. The land cover map of each PA in India and Nepal along with the population trends of the last few decades, are consistent elements of this chapter.

The field experiences, coupled with the authors' knowledge of the GOH rhino, are evident, and the habitats, activities and behaviour of the rhinos are well described. They have reviewed works by different authors and also drawn on their own research. For example, the home range of GOH rhinos has been studied by several researchers, and the authors conclude that the expansion and contraction of home ranges depend on the unique factors of each habitat, with adult male rhinos experiencing the largest proportion. The daily activity patterns, including feeding ecology, are also found to differ in different rhino habitats, and are influenced by their surroundings and anthropogenic factors, as the authors have studied from various literature. However, it is recognized that research on the diseases affecting GOH rhinos caused by parasites has been limited.

From this chapter, readers will learn that GOH rhinos have the lowest reproductive rate among the terrestrial herbivores. Although breeding has been observed to occur 'throughout the year', it was not mentioned whether the flood season has had any impact on breeding success or not. Stated to be crepuscular, GOH rhinos are active at dawn and dusk, and the authors have described their behaviour and association with other species in the same habitat. However, defecating in a particular place and creating a dung pile (or midden), is one of the unique characteristics of the species, which should have been elaborated upon more. Similarly, the description of the animal's morphology and the status of the species should have been presented at the beginning of this chapter. Interestingly, the authors note that the body length of the GOH rhino is 160–200 cm, whereas elsewhere it has been mentioned as 310–380 cm. These differing measurements may pertain to captured GOH rhinos that have either been translocated or rescued. For clarification, the accurate range for the body length of the GOH rhino is established as 160–380 cm.

The conservation challenges, including habitat management, recurring floods, invasive plant species and negative rhino-human interactions, have been addressed through community-based anti-poaching efforts. The topics of modern technologies combating poaching, reintroduction and rhinos in captivity have also been covered. However, crime related to rhino poaching has not been given adequate mention, perhaps due to a lack of space. Indeed, this topic could be an independent chapter of the book, on its own.

The chapter is well-illustrated with excellent and rare photographs that depict both the species and its habitat. Figures, tables and an absence of scientific jargon have definitely made this readable and will be enjoyable for non-expert readers also.

Chapter 6/review: Javan rhinoceros, *Rhinoceros sondaicus* (Desmarest, 1822)

Authors: Steve Wilson, Kees Rookmaaker, Adhi Rachmat Hariyadi, Inov Sectionov, David M Leslie, Barney Long, Sunarto Sunarto, Mahmat Rahmat, Rois Mahmud

Reviewed by Jonathan Spencer MBE

Chapter 6 presents a comprehensive account of the biology, natural history, ecology, behaviour and conservation status of the Javan Rhino (*Rhinoceros sondaicus*), starting with its common name, a reflection of its relict status on the Island of Java rather than its once far wider distribution across the islands of the Sunda archipelago and of mainland Southeast Asia. The chapter does not flinch from identifying the gaps in knowledge and where these have been extrapolated by comparison with the closely related GOH Rhino (*Rhinoceros unicornis*). The chapter synthesises the available information from an array of literature on topics such as taxonomy, morphology, habitat use, dietary preferences, reproductive and population biology and behaviour. It also explores the characteristics of the vegetation of habitats found at its last remaining global location within the Ujung Kulon National Park (NP) in Indonesia. Additionally, the chapter describes how vegetation and other features—notably wallows and access to minerals from sea spray—influence rhino behaviour and distribution. Like the similar but unrelated Sumatran rhino (*Dicerorhinus sumatrensis*), the Javan rhino is clearly a creature most at home in disturbed secondary forest rich in its favoured food plants, and not at its most optimal in mature, undisturbed forest.

The chapter tracks the historical distribution and current range contraction of the species, highlighting its protracted decline in both distribution and abundance throughout the 19th and 20th centuries. However, there has been recovery in Java, attributed to successful conservation efforts that have increased the Ujung Kulon NP population from approximately 25 individuals to around 75 today (almost certainly a considerable overestimation, see review Chapter 13); it is nevertheless a precariously low number, especially given that only some 30% or so are believed to be in breeding condition. This situation is believed to have arisen from a combination of factors, including ageing, probable genetic constraints and competition for resources among potentially competing fertile females. Much of the habitat within the Park is maturing forest, not well suited to support rhinoceros, which favour early successional forest following natural disturbance, coastal forest enriched with salt spray and its associated minerals, as well as ready access to wallows for regulating their body temperature. The authors advocate both the establishment of a second population of Javan rhinos on conservation grounds and the enhancement of breeding opportunities of individuals remaining in Ujong Kulon NP. Deciding on suitable areas must therefore involve careful consideration of the extent and character of potential reintroduction sites, which could look very different from those where rhinos have persisted into the 20th and 21st centuries.

Threats to the long-term future of the Javan rhinoceros include outbreaks of disease, notably those spread by livestock from nearby villages, and potential natural disasters include volcanic eruptions and tsunamis. The Ujong Kulon NP is only 55 kilometres from the very active Anak Krakatoa. The authors advocate establishing both a captive breeding population (none are in captivity at present) and at least one (and ideally far more) captive breeding units in both this chapter and in chapter 13. Control of poaching and forest incursions has been partially achieved, allowing for the 20th century recovery of the remaining Javan rhinos in Indonesia and the time is now ripe for a further recovery phase and the consolidation of successes to date.

The authors highlight Javan rhinos as a species exhibiting resilience and potential for recovery, but with complex demands for sufficient space, appropriate vegetation and nutrition and access to key landscape features such as wallows and mineral salts. The studies collated in the chapter make clear, though, that such conditions are not necessarily confined to forests similar in character to its last surviving refuge in Ujung Kulon NP. Many other forest types and geographies might be suitable if social and other conditions are met. In summary, this chapter offers an invaluable scientific foundation for the conservation and recovery of the Javan rhino in the face of continued pressures from climate change and natural disasters, alongside the more optimistic opportunities offered by both increasing interest in nature conservation and ecosystem recovery and the recovery and "rewilding" of logged-over and secondary forests.

Chapter 7/ Sumatran Rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814)

Authors: Francesco Nardelli, Ellen Dierenfeld, Rasmus W Havmøller, Nan Schaffer, Terri Roth

Reviewed by Deba K Dutta

The Sumatran rhinoceros (*Dicerorhinus sumatrensis*), the smallest and most ancient of the five critically endangered rhino species, has long been a symbol of evolutionary resilience and conservation despair. Chapter 7 marks a comprehensive chapter in the book, and is a compelling, authoritative, and deeply reflective piece that not only explores the biology, taxonomy and ecology of the species but also critically examines the trajectory of its conservation.

The chapter begins with the Sumatran rhino's historical distribution and ecological niche, and details that the species was once widespread across Southeast Asia, from the foothills of the eastern Himalayas down to Borneo. It outlines key biological traits of the species, such as its habitat in dense tropical forests, its solitary nature, and its diet as a selective browser. The chapter also describes the elusive behaviour and rare vocalizations that make field study especially challenging. These biological insights are essential, but the true strength of this chapter lies in its systematic exploration of conservation challenges.

A central theme running through the chapter is the decline into what conservationists now describe as an "extinction vortex." The species' population has plummeted to fewer than 80 individuals scattered across a few isolated pockets in Sumatra and Borneo, and the majority of subpopulations consist of fewer than 10 individuals. The authors make clear that the causes of this crisis are multifactorial: continued habitat fragmentation, human encroachment, poaching, and, importantly, the failure of early ex situ efforts in the 1980s and 1990s.

Rather than avoiding criticism, the chapter candidly accounts for how poorly coordinated captive breeding initiatives, particularly those outside the rhino's native range, failed to produce viable offspring and contributed to the continued decline of the species. This degree of introspection is rare in conservation literature and adds substantial value to the book.

The chapter offers an insightful overview of more recent and promising conservation strategies. The Sumatran Rhino Rescue project, for example, has become a flagship effort that integrates habitat protection, targeted capture of isolated individuals, and a science-driven breeding programme. The authors emphasise the important breakthroughs in reproductive science, such as the use of assisted reproductive technologies (ART), including artificial insemination and in vitro fertilization. They also highlight the central role of institutions like the Sumatran Rhino Sanctuary in Way Kambas, which has successfully produced calves, (five have been born between 2012 and 2022), through captive breeding.

Furthermore, the chapter addresses the socio-political dynamics of conservation. It underscores the importance of involving Indonesian government institutions, conservation NGOs, and international partners in a coordinated framework. The authors emphasise that long-term funding, political will, and continued public engagement are as critical as the science itself in ensuring any chance of success.

One of the chapter's most valuable contributions is its advocacy for adaptive management and transparency. It presents a roadmap that other conservation programmes, especially those involving critically endangered megafauna, could follow. The discussion is steeped in lessons learned—not just about what to do, but also what not to repeat. The need for early collaboration between field biologists, reproductive specialists, and local stakeholders is stressed, as is the imperative to build mechanisms for honest performance evaluation.

In conclusion, this chapter is a cornerstone for anyone committed to the conservation of rhinos or endangered species in a more general sense. Its blend of ecological detail, historical reflection, and forward-looking strategy makes it informative and inspiring. It brings to light the hard truth that saving the Sumatran rhino is no longer just a matter of protecting habitat or stopping poachers—it is a multifaceted, race-against-time endeavour that must combine cutting-edge science, institutional humility, and global solidarity.

Chapter 8/ Significant developments and major trends in rhino conservation in Africa

Authors: Peter S Goodman, David Balfour, Dave Cooper, Richard H Emslie, Keryn Adcock

Reviewed by Sam M Ferreira

This chapter offers a comprehensive and insightful review of the evolution of rhino conservation efforts across Africa. It highlights the increasing importance of partnerships, particularly those involving public-private collaboration and community engagement. It aligns well with the insight from the CITES report of 2021 that populations managed through such cooperative models often showed the most positive performance trends, underscoring the value of shared stewardship in achieving conservation outcomes.

The chapter further documents technical progress in population management, including refinements in immobilisation protocols, spatial planning for range expansion, and the broader use of genetic and surveillance technologies. These innovations, supported by evolving national strategies and greater coordination among stakeholders, reflect an adaptive and maturing conservation framework.

While the chapter succeeds in capturing major advances, there are additional dimensions which could enhance future discourse. For instance, performance assessments have often emphasised maximising population growth at individual sites, frequently guided by concepts like ecological carrying capacity (ECC). Although widely used, these concepts are challenging to define consistently, especially given ecological variability across landscapes and seasons. Similarly, removal-based management models have provided operational flexibility but differ from naturally occurring regulatory processes such as delayed reproduction, age-specific mortality, and dispersal behaviour. Natural population regulatory processes, however, can result in higher rhino mortalities and lower birth rates that represent challenges when authorities seek to maximize growth, especially for populations recovering.

Another area worth exploring further is the application of spatial population ecology, particularly metapopulation theory. This approach supports the idea that not all populations will grow simultaneously, and that persistence across fragmented habitats may rely on functional connectivity, small subpopulations, and dynamic dispersal. Such perspectives could enrich current strategies, including how founder success is defined over time and how conservation value is attributed across sites.

Overall, the chapter provides a solid platform for integrating emerging ecological insights into established conservation practice, shaping a future where rhino populations are managed not only for growth, but also for their broader socio-ecological roles within resilient and interconnected landscapes.

Chapter 9/ White rhino: contrasting conservation outcomes of two subspecies

Authors: David Balfour, Kes Hillman-Smith, Herbert HT Prins, Thomas B Hildebrandt, Jan Stejskal, Susanne Holtze, Kees Rookmaaker, Sam M Ferreira

Reviewed by Keryn Emslie

Chapter 9 covers the white rhino numerical histories and the impact of humans and conservation interventions and events in the different African range States, allowing the reader to understand the contrasting fates of the NWR and SWR subspecies. It draws out key lessons for restoring and maintaining the white rhino species' demographic viability, keystone ecological role and socio-economic benefits in Africa's ecosystems and human communities.

Three of the chapter authors (Hillman: NWR, Ferriera and Balfour: SWR, mainly in South Africa) have extensive experience in rhino conservation at the field and coordination and planning level. Holtze, Hildebrand and Stejskal provide their expertise in zoo-based and assisted rhino reproduction. Prins is top researcher in wildlife ecology, and Rookmaker has highly detailed extensive knowledge of documented historical rhino reports. The listings of author affiliations and names of TB Hildebrandt, K Rookmaaker and J Stejskal are misplaced in the first page layout.

The chapter introduction summarises the evolutionary origins of the two white rhino subspecies, and their changing distributions and numbers in central and southern Africa respectively. Further details of historical records and uncertainties of their ranges and numbers are then described, up to c. 1960. At that time NWR numbered 2–3,000, but the SWR was very close to extinction.

Indiscriminate killing and expansion of European settlement are given as the main cases of the pre-'60s declines of both subspecies. There are very sparse details on these two important drivers of rhino decline, which have complex political, economic and social ramifications to this day in most African rhino range States, and human settlement/encroachment still impacts rhino conservation.

Histories after 1960 emphasize factors affecting populations in each country, and the local and international conservation actions and strategies employed. The information is interesting, building a vivid picture of just how complex white rhino conservation efforts and challenges have been.

For NWR, civil unrest, armed conflict, and widespread poaching in range States (DRC, Sudan, Uganda) caused significant declines, leading to functional extinction in the wild by 2008, despite brief periods of effective protection and population growth in Garamba NP. The last two individuals remain in Kenya. For SWR, the population in the Hluhluwe–Corridor–Umfolozi Complex expanded under secure conditions. With the entire SWR global population at this one site, major translocation efforts began in the 1960s, successfully restocking areas across southern Africa, mainly into Zimbabwe, former Swaziland (Eswatini), Namibia, and later introduced to Kenya. Global numbers grew to over 20,000 by 2015.

Widespread poaching resurged in c.2006, again causing continental declines, with a small uptick to 16,801 SWR by late 2022. Social instability and poor governance were prime factors in white rhino declines, but few details are given. (The Fig. 9.8 caption is confusing and omits the Garamba NWR population).

Translocations to private land also occurred, many with low founder numbers and potential for genetic issues. (Not mentioned: breeding females became more valuable than males leading to ongoing genetic exchange between these populations). More recently, concerns are expressed around the intensification of SWR into smaller areas in response to poaching, and a desire by some owners to engage in the rhino horn trade. (The mention of the Platinum Rhino operation doesn't do justice to the achievements of that endeavour of protecting several hundred SWR and breeding over 1,000 calves during a massive regional poaching crisis.)

In summary, these are the key strategic insights and underlying requirements for success described in chapter 9. The core insight is the vastly different outcomes: the NWR have become functionally extinct, while the SWR have recovered successfully from very low numbers to "Least Threatened" on the IUCN Red List. The ability and vision to translocate sufficient numbers of rhinos to many new areas was key to rescuing the SWR. The interdependence of rhino and human security is a key insight. Periods of decline for both subspecies are consistently linked to human–human conflict and/or high levels of corruption. Regional, country and local-level security and citizens' safety from crime and corruption are essential for successful rhino conservation. Good governance in the wider human societies provides contexts where rhinos can thrive.

Partnerships between the State, private and communities, with devolved decision-making to local participants, do better than State management alone, especially where the regional landscapes are safe and secure. The private sector typically provides critical funding, expertise and technical resources, while the State offers legitimacy, legal mandates, and streamlines administration processes like permitting. Additionally, international and national policies, laws, and conservation planning frameworks enhance legitimacy and legal authority, providing a broader perspective.

The NWR subspecies persistence is dependent on "biorescue" efforts. However, the continued ecological role of rhinos in NWR ecosystems may be achieved with the ecological equivalent SWR to replace the role of the functionally extinct taxon. (However, the NWR is a larger-bodied animal than SWR and may be better-adapted to cope nutritionally and physically with extreme long-grass, low nutrient environments of high rainfall NWR range areas. The SWR introduction to Garamba NP will be an interesting test.)

Chapter 10/ Black rhinoceros: contrasting conservation actions and outcomes across the continent

Authors: JA Shaw, K Adcock, R Amin, N Anderson, N Banasiak, P Beytell, R Brett, R du Toit, RH Emslie, J Flamand, L Kariuki, C Khayale, JR Muntifering, B Okita-Ouma

Reviewed by Sam M Ferreira

The chapter presents a thorough and balanced account of black rhinoceros (*Diceros bicornis*) conservation efforts across Africa. It highlights the diversity of strategies employed in different regions and the valuable progress made in recovering this critically endangered species. A notable theme is the increasing use of integrated approaches, especially in southern Africa, where structured coordination, translocations, and custodianship initiatives have supported population growth and range expansion.

While these different approaches have stabilised numbers, metapopulation structures are often applied without fully integrating ecological processes that influence their long-term function. For example, dynamics such as natural dispersal, asynchronous growth, and the demographic contribution of smaller populations receive limited emphasis. Including these dimensions more explicitly may help strengthen future conservation planning.

The use of growth targets, such as aiming for annual increases greater than 5% or establishing founder groups of around 20 individuals, has provided practical guidance. Sites vary in vegetation suitability for rhino and rainfall. Black rhino populations can grow at around 8% per annum, and 5% is a minimum target that is achievable, except when external events impact the rhinos or the site.

However, the ecological underpinnings of such benchmarks vary by context. More attention to species-specific life history traits, such as age-specific survival, delayed age at first reproduction, and sex-biased adolescent dispersal—could help refine population expectations and guide adaptive decision-making. In many countries, most populations are closely monitored, and most individuals are known to a sufficient degree of detail, including their life history parameters and behaviour patterns, which are used to make decisions.

The chapter closes by encouraging continued learning and collaboration across regions. By aligning emerging ecological understanding with on-the-ground practice, conservation efforts can remain responsive and resilient.

Chapter 11/The recovery of the greater one-horned rhinoceros in India and Nepal

Authors: Bibhab K Talukdar, Shant Raj Jnawali, Bishen Singh Bonal, Anindya Swargowari, Amit Sharma, Deba K Dutta, Naresh Subedi, Ganesh Pant

Reviewed by Jonathan Spencer MBE

The remarkable 20th century conservation success achieved by the nations of India and Nepal in rescuing the GOH or Indian rhinoceros from extinction is comprehensively described in chapter 11. The chapter provides a detailed account of the history of the challenges and conservation actions taken throughout the 20th century to the present day. It charts the growth in GOH rhinoceros numbers, which dropped to a low of some 200 animals in the early 1900s to the current high of over 4,000 individuals, along with a few hundred (250–300) held and managed in captivity. Past threats to the species and the actions adopted to address them are carefully and thoroughly explored, highlighting the importance of international and interstate cooperation.

Conservation measures successfully enacted in both countries have included the gazetting of land as PAs and NPs, the implementation of tough anti-poaching measures and engagement with local communities and other government agencies. In both countries, the rhinos have slowly become a source of national pride. Such actions have been extended in more recent years to reintroductions and translocations between important rhinoceros habitats within the Indian and Nepalese national park series.

The critical role of frontline staff, supported by forest officers, community engagement, fostering a sense of stewardship, innovative approaches and robust approaches to illegal poaching and habitat encroachment are presented as key components to successful rhino conservation, the basis of which was timely and effective action in the first quarter of the 20th century by committed and key individuals in India, notably in the State of Assam, and effective Royal legislation in Nepal. The critical roles of the Chitwan NP in Nepal and the Kaziranga NP in India are clearly demonstrated.

The later challenges of socio-political unrest and subsequent exposure to rampant poaching are also unflinchingly explored. Additionally, the threats from development, invasive plant species and climate change are also fully examined, as are the future potential uses of new technology, habitat expansion and population growth through translocation. Translocations are now seen as a well-established and key tool in the conservation of the GOH rhino, in mitigating genetic isolation or addressing losses due to past social upheaval. Numbers are now such that individual rhinos are occasionally found wandering into other PAs and unprotected lands. The unusual challenge of conservation success—the increase in numbers within PAs leading to intraspecies conflict and nutritional stress—is addressed and identified as offereing positive opportunities for further range expansion through the export of individuals from areas at carrying capacity for this species. An Indian government target of expanding the area occupied by the rhinos by 5% by 2030 is discussed.

Lessons for all concerned with rhinoceros conservation and translocations are presented in detail, with accounts of techniques and veterinary considerations, critical post-translocation monitoring needs and protocols, logistical needs, security and communications are covered in depth. The complex teams required to deliver successful outcomes are well described and supported in graphical form.

The chapter presents a 20th century conservation success story that addressed a dire situation and goes on to explore the challenging road ahead, with potential success rooted in further international cooperation, individual and institutional commitment and widely shared expertise. The chapter is well illustrated with maps and well-presented data and effectively captures the successful history of the conservation of this rare, iconic and enigmatic species “from the brink of extinction to a symbol of resilience and successful conservation effort”.

Chapter 12/The Sumatran rhinoceros: what went wrong and how to move forward

Authors: John Payne, Karen K Dixon, Sukianto Lusli, Zainal Zahari Zainuddin, Mochamad Indrawan, K Yoganand, Kees Rookmaaker, Nan E Schaffer, Ahmad Zafir Abdul Wahab, Petra Kretzschmar, Rasmus W Havmøller, Muhammad Agil

Reviewed by Inov Sectionov

This chapter provides a detailed history of the Sumatran rhino, tracing its evolution to the present day. Based on morphological and genetic evidence, the Sumatran rhinoceros is believed to be closely related to the extinct woolly rhinoceros *Coelodonta antiquitatis* and *Stephanorhinus*, with the split between their last common ancestors estimated to be around 9.5 million years ago. (See chapters 1 and 2).

The authors explore historical perspectives, as well as internal and external challenges to conserving the Sumatran rhino. This includes examining the political commitment of the countries that harbour the Sumatran rhino and the initiatives aimed at preventing its extinction. The chapter raises important questions, perceptions and assumptions regarding securing the Sumatran rhino into the future.

The chapter also introduces several idioms and terminologies that may interest both experts and the general public. For example, it discusses an agreement focused on preserving a reservoir of genetic diversity by using animals classified as 'doomed' in their current habitats. However, these 'doomed' rhinos (IUCN Species Survival Commission 1984) were not redefined in any subsequent discussions, which might confuse some readers regarding the rescue efforts to capture certain Sumatran rhinos from the wild and relocate them to the breeding sanctuary in Indonesia, specifically at Way Kambas NP.

The chapter highlights an important issue: "Although not all individual rhinos marked as 'doomed' are affected, the entire programme faces significant risks. Many potential breeding animals remain in the forest, while a large percentage of captured rhinos are either too old, injured, or infertile to contribute their genetic material without human assistance and the use of assisted reproductive technologies."

The section on reproductive problems in both wild and captive populations for the Sumatran rhino is clearly explained. It highlights that the reproductive potential of the Sumatran rhino differs significantly from that of other rhino species, increasing the challenges of conserving this species. The chapter discusses several examples of unsuccessful breeding programmes for the Sumatran rhino, noting that only one relatively young pair Emi and Ipuh, brought together at the Cincinnati Zoo, successfully mated and eventually produced offspring. This is from 40 Sumatran rhinos captured for the captive breeding programme between April 1984 and November 1995. This success was attributed to human intervention and intensive management.

The Government of Indonesia (GoI) protects the Sumatran rhino under Indonesian regulations, and a similar protection measure was likely in place in Malaysia when the Sumatran rhino still existed there. Most of the programmes for Sumatran rhino conservation originated from collaborations with NGOs and national and international agencies. However, the chapter does not clearly outline the government's contributions to the Sumatran rhino conservation efforts, such as the Indonesian rhino strategy and action plan (1994, 2007–2017), the emergency action plan and the small progress made in the last decade. Including the achievements, however minor, would have better highlighted the GoI's commitment to Sumatran rhino conservation.

The combination of habitat loss, poaching for horn and slow reproduction rates have severely reduced the population of this species, leaving it in great and imminent peril. Additionally, various factors affecting the Sumatran rhinos' vulnerability, such as the dire and negative impact of human activities (over three centuries), further threaten its survival. Many lowland forests on Sumatra Island, which serve as the primary habitat for this species, have been lost due to land conversion for agriculture, even in PAs such as national parks. This situation heightens the risk of declining distribution and numbers of Sumatran rhinos, and the real possibility of extinction cannot be avoided. Preserving the Sumatran rhino, one of only five surviving rhino species, will pose significant challenges for many years to come.

Chapter 13/Conservation of the Javan rhinoceros: lessons from Indonesia

Authors: Barney Long, Indra Exploitasia, Rois Mahmud, Kurnia O Khairani, Inov Sectionov, Asep Y Firdaus, Desy S Chandradewi, Drajat D Hartono, Haerudin R Sadjudin, Yusep Hardiana, Sarah M Brook, Steven G Wilson

Reviewed by Suzannah Goss

This chapter, like the other fifteen, is authored authoritatively by experts who have worked in ecology, conservation and rhino management for many years, if not decades.

The Javan (and Sumatran) rhinos have survived for 55 million years, enduring ice ages, earthquakes and meteor strikes. However, primarily due to anthropogenic impacts, *Rhinoceros sondaicus* is now listed as Critically Endangered (on the IUCN Red List). The authors paint a more optimistic picture than the situation currently warrants.

The chapter provides an overview of the last two populations of Javan rhinos, which have followed markedly different paths over the past thirty years. The Vietnamese population, decimated by poaching sometime between 2007 and 2010, is only briefly discussed. The Indonesian population had been growing modestly until a recent surge in poaching.

The last remaining population inhabits just a small area, the Ujung Kulon NP, located on the far tip of the Java peninsula.

While the authors highlight the necessary strategies to save the fourth smallest (in both size and population, estimated at 50) of the extant rhinos, newer data suggest that the situation is more precarious. (The Sumatran rhino has the smallest population at a perilously low 34–47 individuals). Due to the challenging terrain, Javan rhinos remain the least studied among all rhinoceros species; consequently, researchers rely heavily on camera traps and faecal samples to assess the health and behaviour of these animals.

> However, the chapter does not reflect recent findings: in 2023, scientists and conservation organizations expressed concerns about the accuracy of population figures for Javan rhinos following the discovery that camera traps had failed to detect numerous individuals over three years. The chapter still insists that the number is higher, 77 individuals (KLHK 2022). The sharp decline in rhino numbers stems from the poaching crisis of 2019–2023. The case came to light on 29 May 2023, when missing camera traps and a noticeable drop in rhino activity prompted an investigation. Footage from other cameras revealed armed individuals tracking rhinos inside the Park. Police traced the crime to two poaching gangs. whose testimonies confirmed that 26 rhinos had been killed over five years—a 33% loss of the global Javan rhino population. Targeting males with larger horns has also skewed the sex ratio and reduced the number of breeding males available.

The chapter examines several constraints on recovery; which help galvanise funds for strategic and urgent, tailored action. One major risks is that with only one wild population and no captive ex situ breeding programme, an eruption of nearby Anak Krakatoa occur (in an area prone to earthquakes and tsunamis), could wipe out the species overnight.

Disease transmission poses an additional threat. Water buffalo in the vicinity are carriers of anthrax/haemorrhagic septicaemia, and may have contributed to past Javan rhino mortalities. The authors explain that a well-managed domestic buffalo vaccination programme would minimise the risk. Another challenge is the ECC of the Ujung Kulon NP, which is overstretched, however, any relocation is highly risky. The chapter explains that a hypothetical newly created second population of five females and three males, (the scenario which performs the best in modelling) shows a lower extinction risk, higher population size over the longer term and lower inbreeding accumulation. (The loss of genetic diversity leads to genetic "bottlenecking" or inbreeding depression).

Other conservation interventions are less risky, such as the removal of the Arenga palm, which is not a food plant for rhinos and reduces the light due to over-shading, impeding the growth of the understory, and essential legumes that the Javan rhino feeds on.

Enhancing security is another strategy that could be strengthened. Nonetheless, rural, potentially rugged Park boundaries mean that law enforcement cannot be equally present in all places at all times. In some areas, this lack of security still places the species at risk from poachers. The communities living around the Ujung Kulon NP (and its rhinos) have benefitted from community-led environmental awareness programmes such as the Sustainable Livelihood Assessment method, and conservation is increasingly a key consideration in community discussions and decision-making. These initiatives involve residents as stakeholders, engaging them in activities related to security and monitoring.

The chapter's final section presents the continued survival of the Ujung Kulon population as a success, outlining the complex challenges ahead—especially tackling poaching and sustaining the teamwork, planning, and commitment needed to secure the Javan rhino's future. But is this outlook too optimistic? One hopes not, though the situation remains undeniably precarious.

Chapter 14/Ex Situ conservation and management of rhinoceros

Authors: Friederike von Houwald, Gina M Ferrie, Susie Ellis, Nan Schaffer, Mark Pilgrim, Lars Versteege, Adam Eyres

Reviewed by Sam M Ferreira

The chapter provides a well-structured synthesis of the role of ex situ conservation activity in supporting the long-term survival of all rhinoceros species. The chapter highlights the history and development of zoological and conservation breeding programmes across the globe, noting the increased alignment with IUCN's One Plan Approach. This integration emphasises the value of linking in situ and ex situ strategies to build resilient conservation systems. Key institutional networks, such as the European Association of Zoos and Aquaria (EAZA), the American Species Survival Plan (SSP), and partnerships with IUCN Specialist Groups, are presented as foundational pillars of this coordinated effort.

A major theme emerging from the chapter is the positioning of ex situ populations as insurance or assurance populations. These captive populations are seen as safeguards against catastrophic loss in the wild. This function is most critical for the most imperilled species—such as the northern white, Javan, and Sumatran rhinos—where wild populations are either functionally extinct or remain at critically low levels. A stronger prioritisation of ex situ resources towards these species could maximise conservation returns.

The chapter also outlines the broader value of ex situ facilities, beyond demographic support. These include educational outreach, public awareness, fundraising, and the advancement of scientific research. Zoos and breeding centres serve as platforms for engaging global audiences and building conservation literacy. In addition, controlled environments allow for behavioural and physiological research that is not easily achievable in the wild, contributing important data to species management.

One important opportunity not fully explored in the chapter is the potential for ex situ populations to serve as integral nodes within metapopulation frameworks. Expanding on the One Plan Approach, these facilities could be better incorporated into structured metapopulation strategies that span wild, semi-wild, and captive contexts. Furthermore, ex situ programmes offer unique access to develop and apply assisted reproductive technologies (ART), such as in vitro fertilisation and stem cell techniques. These tools hold particular promise for recovering functionally extinct or severely threatened species, including the northern white, Javan, and Sumatran rhinos.

Some caution should be taken seriously. Despite the improvements for white rhinos, there remain challenges linked to some husbandry practices at zoos. For instance, practices of browsing and mixed feeding in these facilities often link to reduced breeding.

In summary, the chapter effectively underscores the multifaceted role of ex situ conservation. As technologies and partnerships evolve, these efforts can make increasingly strategic contributions to species recovery within an integrated conservation framework.

Chapter 15/ The impact of poaching on rhino conservation

Authors: Michael 't Sas-Rolfes, Julian Rademeyer, Lucy Vigne, Richard Emslie, Michael Knight, Jamie Gaymer, Bibhab K Talukdar

Reviewed by Jonathan Spencer

The most significant impact on rhinoceros populations over the 20th and 21st centuries—and still the biggest threat to their conservation and recovery—is poaching for their horns. Chapter 15 reflects on the history of human exploitation of rhinos and provides a comprehensive account of the rhino poaching in Africa and Asia during these two centuries. Two distinct waves of poaching are recognized, the first began in the 1970s, and continued well into the 1990s. This was followed by a lull and then a resurgence of poaching activity in the present century, peaking in 2015. The illegal killing of rhinos continues to pose a significant threat to all rhinoceros populations. However, the Sumatran rhino has become so scarce and dispersed in Indonesia that poaching is no longer the most immediate threat it faces.

The nature of poaching is explored in depth, from the concept of poaching as a social construct, to the contested views over rights to benefit from rhinos and the various methods used in the illegal killing of rhinos and the development of increasingly sophisticated techniques. The influence of social and political conditions that drive market demand for rhino horns is examined, along with the significant risks and penalties associated with poaching rhinos, which in many African range States can be severe. The chapter goes on to explore the considerable variation in national strategies to combat poaching and the extent of corruption within both government and related organisations, with South Africa and its agencies and safari operators coming under particular scrutiny.

Strategies adopted to address poaching are reviewed, covering the importance of legal frameworks, law enforcement, policing of PAs and the crucial role of gaining local community support. It also discusses the drastic measure of dehorning rhinos. The availability of weapons and equipment varies significantly between countries, and the influence of political unrest, social upheaval and poverty play a critical role in determining the persistence of poaching across the two continents. The effectiveness and impact of these and other strategies are assessed in detail. The appalling statistics regarding the decline of rhinoceros populations in PAs across both continents highlight the grisly nature of the poaching operations.

The adverse impact of rhino poaching on surviving populations and their conservation is also covered in detail. Two species have been driven to the brink of extinction, and several subspecies have suffered actual extinction, with the ongoing impact of population fragmentation, risks of inbreeding in wild populations (and the captive populations ultimately derived from them). Additionally, the costs associated with rhino conservation have significantly increased, making it prohibitively expensive for all but the best-funded range States and conservation organisations to manage effectively.

The overall conclusion of Chapter 15 is that the future of rhino conservation must continue to address poaching for the foreseeable future. Effective conservation will rely heavily on anti-poaching measures and on sustaining funding sources that support these initiatives, especially if consumer demand for rhino horn products persists at its current high levels. The ongoing, and often selfless, dedication of wildlife department staff and enforcement agencies will remain critical, as will continued financial support from sponsors and the general public.

Chapter 16/The impact of rhino Horn trafficking on Conservation

Authors: Lucy Vigne, Michael ’t Sas-Rolfes, Tom Milliken, Julian Rademeyer, Bibhab K Talukdar

Reviewed by Daniel Stiles

This 16th and final chapter in *Rhinos of the World* presents a meticulously detailed history of the killing of rhinos and the trafficking of their horn, mainly to eastern Asia and, up until the early 1990s, Yemen. As a proportion of its total population, the five African and Asian rhino species have been poached since the 1970s and are probably the most poached animals in the world. Demand for the horn for use in traditional medicine and carved ornaments rose precipitously between 1970 and 2015, after which demand, prices and poaching rates began to fall rapidly.

The chapter delves into the highly controversial topic of conservation strategies—which approach is most effective in mitigating poaching and trafficking, legal trade or total prohibition, along with stockpile destruction? The authors recognise the complexity of economic dynamics, demand drivers, changing consumer preferences and the increase in corruption and the creation of transnational organised crime networks, all of which interact to influence poaching and trafficking rates. They discuss the effectiveness of various strategies, such as demand reduction campaigns and the use of substitutes, including growing genetically modified “rhino” horn. What is not discussed are the sources of the rhino horn entering trade, i.e. the relative proportion of wild rhinos poached for their horn versus released stockpile horn.

The chapter presents a great deal of data, including prices, numbers of rhino poached, horns entering trade, horns seized and market survey results and is generously endowed with data tables and colour photographs. A weakness, however, is that the mass of data is not analyzed to present a clear trend that rhino poaching rates and prices have fallen significantly since their peak in the years 2010–2015, and does not offer explanations of why that may be. The authors also do not discuss evidence that increasing quantities of stockpiled rhino horn entered the trade chain from at least 2019, and probably earlier, both from intended leakages and thefts, reducing the need to poach.

Despite reduced rates of poaching, the authors conclude that “Rhino horn trafficking remains the single greatest challenge to rhino conservation and a significant drain on scarce financial resources for the biodiversity conservation sector in rhino range states.” They also believe that there may be a role for “carefully imple¬mented legal use and specific trade allowances” in future rhino conservation strategies.

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IUCN African rhino conservation 2025–2035: A contemporary strategic framework

David Balfour, Sam M Ferreira, Jamie Gaymer, Claire Lewis, Humbulant Mafumo, Keitumetse Makoma, William Mgoola, Mmadi Reuben, Jo A Shaw, Simson Uri-Kbob

Reviewed by Mike Knight and Markus Hofmeyr

Corresponding authors: mknight@wwf.na; markus@wildnet.org

The rhino poaching crisis, which began in 2005, significantly challenged previous conservation strategies. The initial response often involved an isolated "fortress" approach, leading to fragmentation and a focus on simplistic, localized solutions for what is a complex, evolving international threat. The national and site-specific plans that had successfully recovered rhino populations by prioritizing breeding and security in a largely peaceful environment were no longer effective in this new era of intense poaching.

The African rhino conservation 2025–2035, a contemporary strategic framework (ACSF) aims to revitalize rhino conservation within Africa's intricate socio-economic-ecological landscape. It introduces four new themes: disrupting organized crime, understanding and influencing rhino horn markets, prioritizing the equity and rights of local stakeholders, and fostering diverse views on the value of rhinos in society. This approach seeks to break down barriers, encourage conservation managers and authorities to think beyond their borders, and recognize local communities as crucial partners. Furthermore, the CSF emphasizes maximizing ecological and social connectivity, regional and metapopulation thinking, and enhancing the broad value of rhinos, particularly to the people who coexist with these magnificent animals.

This Framework is ambitious, forward-thinking, and essential for developing future solutions for a species that has historically relied on intense law enforcement for protection. The recent surge in rhino poaching has highlighted significant socio-economic and political changes in Africa and globally. Conventional law enforcement has had major unintended consequences, often alienating local stakeholders rather than engaging them as a frontline defence. The Framework intends to address these issues with idealistic goals that may still require testing.

Delving into the details of the beautifully illustrated Framework: Table 2 outlines the “principles of environmental management and social justice, with assumptions that are embedded in this framework", indirectly referencing overlapping Sustainable Development Goals (SDGs). The IUCN supports the SDGs by advocating for the essential role that nature plays in achieving these objectives. It provides scientific and policy advice, highlighting the interdependence of environmental health and human well-being.

Exploring the illustrated Framework in detail, Table 2 outlines key principles of environmental management and social justice, along with their underlying assumptions, and implicitly links them to overlapping Sustainable Development Goals (SDGs). The IUCN advances these goals by emphasizing nature’s essential role in achieving them and by providing scientific and policy guidance that underscores the interdependence of ecosystem health and human well-being.

With estimates suggesting that Africa's population will grow by 800 million people over the next five decades, (ACSF preface), evolving conservation strategies must adapt to safeguard both wildlife and human communities. Keeping the balance between these priorities—the ideals articulated in Table 2—will be critical.

As a framework, the ACSF offers valuable direction and ideas. It is incumbent upon conservation managers and authorities to adapt it to their diverse local circumstances, which vary greatly across the rhino world and are impacted by global climate change. The ACSF encourages us to think more broadly, inclusively, fairly, and innovatively to address the continuous challenge of saving Africa's rhinos.

The ACSF serves as a guidebook for the next decade. Future iterations could include practical "on-the-ground" solutions, particularly if current strategies prove unsuccessful. In such cases, it may be necessary to implement new approaches quickly, especially in response to a potential increase in poaching.

Finally, like any forward-looking strategy, the ACSF requires clear feedback loops to track intended outcomes against real-world implementation. Ultimately, the sustained recovery of rhino species depends on the active and constructive participation of all stakeholders; without this collaboration, rhinos will remain vulnerable to criminals seeking to profit from the illegal trade in rhino horn.

Africa's Threatened Rhinos, a history of exploitation and conservation

Keith Somerville

Reviewed by Lucy Vigne

Email: lucy.vigne@gmail.com

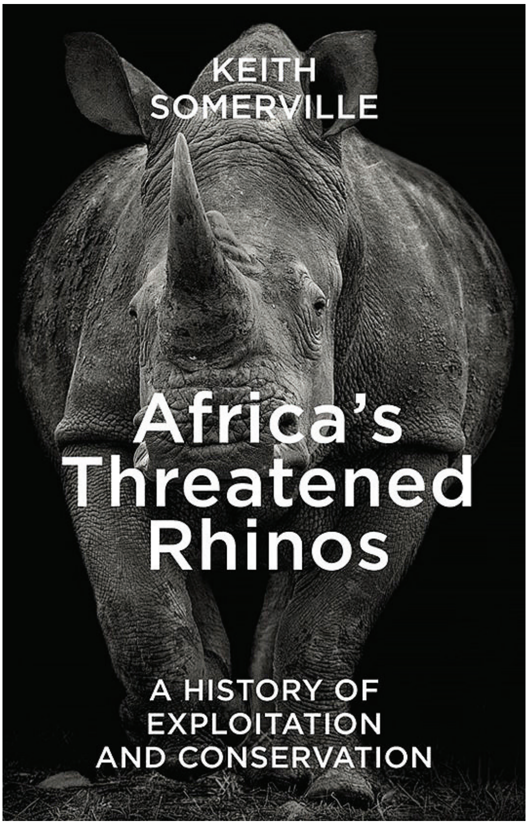

Figure 1. Front and back cover

Keith Somerville undertook a challenging task in documenting the long history of Africa's enigmatic and threatened rhino species, the black rhino (*Diceros bicornis*) and white rhino (*Ceratotherium simum*). This book provides an essential and detailed review explaining why rhino numbers have dropped and the efforts to protect them in Africa. The book documents 3,000 years of rhino exploitation, investigating the history, politics, economics and cultural aspects of human-rhino conflict and coexistence. Somerville also explores what can be done to aid the further recovery of Africa's black and white rhinos, both now and in the future.

Keith Somerville, never one to shy away from complex and contentious subjects, wrote *Ivory: Power and Poaching in Africa*, published in 2017, another fascinating book for *Pachyderm* readers and many others. Similarly, in this new book, Somerville tackles the subject head-on, without emotion, presenting the facts clearly, which are well-sourced, and distilling a mass of historical and academic literature. He has written a clear narrative that addresses the challenges involved in conserving rhinos in their natural landscapes.

Somerville dedicates the book to murdered Esmond Bradley Martin who was on the editorial board of *Pachyderm* for many years, Vice Chair of the IUCN SSC African Elephant and Rhino Specialist Group from 1982–1991, and member of both groups when they formed two, and also to murdered Anton Mzimba, who gave his life to protecting rhinos in South Africa. It is sad indeed that Keith Somerville died before seeing his book published; it is a great legacy.

Somerville's introduction explains that rhinos are not only a continuation of a major evolutionary heritage, but they are also symbols for the protection of African savannahs, as well as the more arid and forested areas that rhinos inhabit. His chronological account adeptly synthesizes historical reports and scientific knowledge using peer-reviewed papers from a range of disciplines.

In chapter 1: evolution, status and behaviour, Somerville launches us into the distant past, when more than 142 rhino species existed 55–60 million years ago. By the end of the Pleistocene 10,000 to 15,000 years ago, only five extant species remained in Africa and Eurasia. He compiles in chapter 2, information about rhinos and early *homo sapiens* from 20,000 BCE to the European penetration of Africa. Herding of cattle spread up the Nile to Sudan about 6,000 years ago, and to West and East Africa 1,000 to 2,000 years later. Human societies and their continued conversion of natural habitat for cultivation, livestock husbandry and settlements gradually pushed out wildlife from the affected areas. There were other threats. The *Periplus of the Erythraean Sea*, written by a Greek merchant in the 1st century CE, documents the export of rhino horn and ivory from Eritrea across the Indian Ocean as important merchandise. The ancient Romans captured rhinos for their entertainment. Arab merchants traded goods from East Africa, obtaining rhino horn, also from the 1st century CE onwards. Hunter-gatherers killed rhinos for their meat, hide and horns. The Portuguese and Gujarati Indians established trading posts along the East African coast from 1600 to 1800, thereby encouraging increased international commerce.

Chapter 3 examines the period of major European penetration and occupation of Africa. Improved firearms in the 19th century made hunting much more efficient and easier. Between 1849 and 1895, 11,000 kg of rhino horn annually (from about 170,000 rhinos during that time) were said to be exported from East Africa. This continued legally with licences obtained for guns as the weapon of choice, and illegally by traditional means. Many rhino and elephant poachers were apprehended in the Tsavo area in the 1950s. “African hunters were effectively criminalized, as were their hunting methods”. Rhino and elephant numbers rebounded, but by cruel irony, as Somerville says, droughts in the early 1960s and again in the early 1970s wiped out thousands from starvation.

Chapter 4 describes how rhino populations were decimated by the arrival of Europeans in southern Africa, who used firearms to clear land for livestock farming and rhino products in many areas of Angola, Botswana, Malawi, Namibia, South Africa, Zambia and Zimbabwe.

Somerville, in chapter 5, then provides details of the modern trade in rhino horn from 1960 to the present, both legal and illegal. CITES was established in 1973, and by 1977, parties had banned rhino products in international trade amongst member states from the world’s five species. Somerville relates the struggle CITES has faced ever since trying to enforce this ban globally, with valuable rhino horn still being trafficked to Asia.

Chapter 6 examines the period of post-independence in Africa to 2005. Somerville describes how wars in much of Africa, “greedy and incompetent governments intent on personal enrichment of leaders and their cronies” and “unequal international terms of trade” created conditions in which poverty remained a fact of life for tens of millions. As Somerville says, this provided a fertile breeding ground for illegal hunting and the smuggling of wildlife commodities.

The success of South African rhino conservation, in contrast, was recognized in 1994 when the 9th CITES CoP voted to transfer South African white rhinos to CITES Appendix II, allowing white rhino trophy hunting and trophy export as well as trade in live white rhinos from South Africa to CITES parties. White rhino numbers increased in South Africa, with these incentives. Many people were converting their agricultural land back to natural habitat for both rhino species and other wildlife, with ownership and sustainable utilization encouraged.

Meanwhile, in Kenya, after independence, Somerville explains that some political, public service and business elites, while publicly promoting conservation and wildlife-based tourism were covertly benefiting from poaching in the 1970s and 1980s. With rising global prices of rhino horn and ivory matching an escalating demand, rhinos were nearly wiped out of the region. He goes on to describe Kenya’s determined progress of black rhino recovery, initially translocating the country’s few surviving rhinos to well-guarded sanctuaries, consolidating their numbers to help breeding. Somerville relates similar poaching crises in much of Africa, with most rhinos gone by the early 1990s, and various rescue attempts in the region. As with all chapters, he manages to synthesize a huge amount of information, carefully and succinctly.

Chapter 7 covers the challenges in southern Africa from the 1960s to 2005, with armed conflict in Angola and Mozambique witnessing the eradication of rhinos, as well as elsewhere. Somerville describes rhino crime across the region. In contrast, the persistent dedication of those protecting rhinos, despite limited funds, is notable. In Chapter 8 the author examines rhino conservation challenges in eastern and central Africa from 2006 to 2024, and the translocation of rhinos into certain areas where they had all been rendered extinct in Malawi, Rwanda, Uganda, Chad and DRC. Chapter 9 focuses on the ‘rhino poaching storm' in southern Africa that erupted from 2009, especially threatening the large populations of white rhino in South Africa.

Throughout the book, Somerville recounts a desperately repetitive and yet brave story of efforts to weather these challenges to save Africa's rhinos, despite substantial financial constraints and the high prices paid for rhino horn on the black market. Chapter 10, 'What next?' concludes the book by presenting a toolkit of conservation measures available, according to the needs of the areas or circumstances. These range from captive breeding, establishing new populations, dehorning, and demand-reduction campaigns (he asks why campaigns had less impact than NGOs hoped). He debates the controversy of legalizing some form of international trade to provide much-needed funding, trophy hunting as a conservation strategy, and considers other financial models. He stresses that community empowerment is key to wildlife conservation.

Somerville has done an incredible job of selecting the salient points from a wide array of published sources, as well as from his own experiences in Africa, compiling a wealth of evidence-based information. The book is indeed an excellent and comprehensive compilation of many facts about the near obliteration of Africa's rhinos and their slow recovery.

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Charging at life: Peter 'Mbobo' Hitchins, a life in wildlife conservation

Peter Hitchins, Orty Bourquin, Clive Walker and Stella Hitchins

Reviewed by Lucy Vigne

Email: lucy.vigne@gmail.com

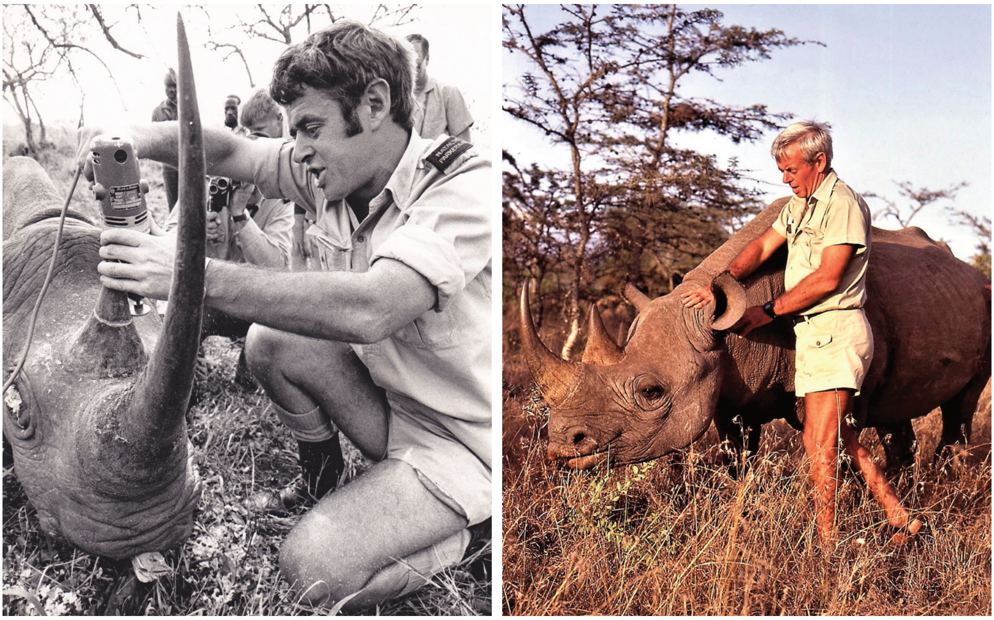

Figure 1. Front and back cover images:
(a) Peter Hitchins (c) Rodney Borland, 1968, the official photographer for the Natal Parks Board;
(b) Peter Hitchins (c) Clive Walker, 1992, either Solio or Ol Pejeta Ranch, Kenya.

Peter Hitchins (1940–2019) was remarkably engaging and deeply knowledgeable about wildlife conservation. I was privileged to meet him for the first time in 1984 in Gaborone, Botswana, at the IUCN SSC AERSG, when the two groups were combined into one. He was the first person to study the black rhinoceros in the Hluhluwe/Corridor/iMfolozi Game Reserve in detail. Here, he monitored rhinos at various intervals from 1961 to 1994. In the early years, he could recognize over 300 black rhinos in Hluhluwe, individually. With his insatiable quest to understand wildlife and habitat conservation, and his strong belief in the intrinsic value of wildlife, he believed the protection of wildlife was the government's duty.

A foreword by George Hughes, former CEO of the Natal Parks Board, provides insight into their long and valued friendship. Both were game rangers in the early 1960s. Peter's bravery and stamina in the bush enabled him to develop a profound understanding and respect for animals and conservation.

In the preface of this informative book, some of Peter's contributions and achievements are given. Peter kept innumerable diaries and data, much of which he never had time to write up; he was essentially a field practitioner. He was always adamant that his vast collection of data and slides "would be useful to someone someday"; and he left behind a wealth of information about the places he worked.

Peter had intended to write his autobiography. Sadly, in the end, he only wrote the first two chapters of this book. He vividly describes his family and upbringing south of Johannesburg, with clear memories of his school days, where his love of wildlife and the outdoors began. He was fearless, catching many snakes from a young age. Peter's second chapter describes his initial work at the Durban Aquarium. He then had a brief and less enjoyable time at Natal University. Peter was a naturalist and a lover of the bushveld, the antithesis of classrooms where he could not learn first-hand about nature.

His old friend, Orty Bourquin who had known Peter since 1959, wrote the following six chapters relying on the copious entries in Peter's diaries. He describes Peter's initial black rhino work in 1960–1961 as assistant ecologist at Hluhluwe Game Reserve; as field ranger from 1962–1964; his work on game control and black rhino monitoring and surveying from 1964–1967; as duty ranger for iMfolozi Game Reserve; section ranger for the connecting 'Corridor' area; and his black rhino work in Hluhluwe from 1968–1973. This had become the last area in South Africa where both rhino species survived up to the mid–20th century. Peter made significant contributions to rhino recovery and expansion, facilitating translocations to numerous important protected areas in Africa.

Bourquin then describes Peter's years in cane sugar farming, the family business that he ran as a young man to support and educate three young children with his first wife, Margaret.

Another close friend, Clive Walker, contributed the following two chapters, about their important work together for the Endangered Wildlife Trust, along with Anthony Hall-Martin. They were also members of the AERSG and worked closely together from 1973 to 1986. Walker describes their formation of the Rhino and Elephant Foundation from 1986 to 1992, which focused on rhino and elephant research and conservation. These chapters provide an important record of conservation work in those days.

Bourquin writes the following chapter about Peter's complex work managing Songimvelo Game Reserve from 1987–1993 (a former homeland). Peter worked incessantly, struggling against many odds. Improving the reserve and safeguarding the bush for the future was challenging work. Walker also provides a chapter about a visit to Kenya with Peter in 1992. Walker used Peter's diaries to give his impressions of the time when several people in Kenya were trying to save the last remaining black rhinos after heavy poaching.

Bourquin comments that Peter was a hands-on, pen-and-paper person, suspicious of computer modelling, believing that only in the field could a person make honest and meaningful observations. Indeed, this was Peter's forte. In 1994, he carried out another black rhino survey on foot ins the Hluhluwe Game Reserve after an absence of eight years, during which he noticed the large number of trees damaged by elephants, and commented on how few black rhinos were seen. His field assistant was lucky to survive a buffalo attack. Peter, not one for sentiment, says his assistant later came to thank him for fighting off the buffalo. Peter, too, survived a 'close shave' with a black rhino. From studying his diaries, Bourquin remarks that Peter came close to serious injury on numerous occasions but courageously made little of these often harrowing incidents, instead commenting in his diary that he enjoyed hardships in the bush as they brought him closer to nature.

Peter then entered another phase of his life, moving to Cousine Island in the Seychelles with his future wife Stella from 1995 to 2002. Stella Hitchins writes about Peter's numerous successful projects, including monitoring sea turtles and increasing bird numbers significantly, especially three endemic species. Stella Hitchins describes Peter's later years from 2001 to 2019 in the final chapter. Peter's last job was managing a wildlife ranch with black and white rhinos near Pretoria owned by Fred Keeley, who was also the owner of Cousine Island. Peter was pleased to be back in South Africa, working in ranch management from 2002 to 2005.

In 2010, he moved to England with his wife for her veterinary career. Peter was unaware that he was suffering from advanced-stage motor neurone disease. Despite his condition, he maintained a good sense of humour, and expressed a wish for some of his ashes to be scattered on a black rhino midden. This request was honoured, and his ashes were subsequently brought home to South Africa.

The book is enriched by numerous photos showing Peter with his friends, family, colleagues, dogs and various wildlife encounters. A final note expresses Peter's strong views "about the inherent importance of nature, the threat posed to it by disruptive human practices and how it must be conserved in its totality".

Appendix 1 lists Peter's 43 scientific papers and other publications. Appendix 2 describes the Game Rangers Association of Africa, which Peter helped to initiate and name. It started in 1970 with Peter as a key figure. The primary purpose was to keep game rangers informed about conservation and to maintain contact. Early members were opposed to the need for tertiary education, believing true wildlife rangership lay in understanding and managing wild areas and ensuring the biological integrity of habitat, working at the 'coal face' of conservation as the 'foot soldiers' of conservation efforts. Peter epitomized the skills needed for the job and posthumously received their Spirit of Africa award in 2020, which stated, "Peter's determination, perseverance and selfless commitment to the cause was exemplary"; indeed, they were.

This book will be enjoyed by many readers and will inspire young rangers and conservationists to follow in Peter's footsteps. He was dedicated to wild areas, and most notably, for Pachyderm readers, safeguarding healthy rhino habitat.

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Title and authors

The title should contain as many of the key words as possible, but should not be more than 25 words long. Follow with the name(s) of the author(s) with institutional affiliation, postal and email address of the corresponding author, to whom proofs and editorial comments will be sent.

Journal conventions

Nomenclature

Use common names of animals and plants, giving scientific names in italics on first mention. Generally, refer to animals in the plural form (i.e. rhinos, elephants). We do not capitalize elephant, black rhino, white rhino and greater one-horned rhino, however we capitalize Javan and Sumatran rhino.

Spelling

Use British spelling, following the latest edition of the Oxford Advanced Learners Dictionary using 'z' instead of 's' in words like 'recognize', 'organization', 'immobilized'; but 'analyse', 'paralyse', a full list can be obtained from the Managing Editor, or by referring to: https://elt.oup.com/catalogue/items/global/dictionaries/oxford-advanced-learners-dictionary/?cc=global&selLanguage=en

Numbers

Use the International System of Units for measurement (m, km, kg, ha, h) with a space between the numeral and the unit of measurement. Give measurements in figures, for example 12 mm, 1 km, 3 ha, except at the beginning of a sentence; in which case write out the full number, e.g. Forty-two black rhinos were born in 2023.

Spell out numbers under 10 if not a unit of measurement, unless the number is part of a series containing numbers 10 or over, for example: 14 adult males, 23 adult females and 3 juveniles, there were nine people watching the group of 65 elephants.

In the text, use a comma as the separator for figures four digits or more: 1,750 and 11,750. The separator will be a full stop in French papers.

Hyphen, en dash and em dash

Hyphens (narrow):

Used to separate compound words, such as long-term; seventy-two.

The en dash (wider) expresses a period of time:

The 'en' dash, so called because it is the width of a printed 'N' character, is longer than a hyphen but shorter than an 'em' dash. It should be used without spaces on either side, e.g.

A rhino census was carried out in four rhino-bearing areas during March–April, 2022.

(NB: Rhinos occurred in the area from at least 1898 until 1979;

Our field staff counted elephants born between 2009 and 2019).

The en dash is used to indicate a range of numbers, examples:

South Africa's Kruger National Park is home to 7,000–8,300 rhino as of 2016.

Overall, all of the elephants had smaller annual home ranges (~450–1,750 km^2).

The en dash is used to indicate distance, for example:

The headwaters of the Chobe River–Victoria Falls are a distance of 136.3 km.

The em dash (even wider) is used for emphasis in place of a colon, for example:

The 'em' dash, so called because it is the width of a printed 'm' character, and is used to enclose a sentence or phrase within a sentence, and it provides greater emphasis than parentheses, e.g.

Our core values—integrity, collaboration, adaptability, sound decision-making and commitment—are at the heart of everything we do.

The presence of the new species—which scientists suspected existed—was confirmed last week.

DOI

A DOI should be provided where available, especially for digital sources, in the format "doi:prefix/suffix" and hyperlinked to "https://doi.org/prefix/suffix". Whenever both a URL and a DOI are available for a source, the DOI is preferred, and the URL may be omitted. The preferred format is: doi:10.1000/182

OrcID iD

Authors are encouraged, though not required, to include their OrcID IDs at the time of submission. OrcID is an independent non-profit organization that provides a persistent identifier distinguishing you from other researchers and linking your research outputs and activities to your ID. OrcID is integrated into many systems used by publishers, funders, institutions, and other research-related services. *Pachyderm* subscribes to OrcID.

References

We use the name-year method of citing and listing references. The punctuation and typographic style are as follows:

In the text, cite a single author: '(X 2005)' or 'X (2005)'; cite two authors: '(X and Y 2005)' or 'X and Y (2005)'; cite more than two authors '(X et al. 2007)' or 'X et al. (2007)'. Note that there is no comma between the author(s) and the year. If multiple works are cited, separate them with a semicolon, and list them in chronological order: (X et al. 1998; B 2002; Z 2010). Multiple works by the same author(s) published in the same year are denoted by suffix -a or -b.

Notes: 1) that in the reference list, punctuation is minimized, and full stops are removed at the end of online cited references.

2) Journal names in full without leading article. Book titles are italicised. Journal titles are italicised.

3) For long author lists in references, only the first ten names of a citation will be included; therefore, the last two of this reference will be dropped: Talukdar BK, Burgess N:

Havmøller RG, Payne J, Ramono W, Ellis S, Yoganand K, Long B, Dinerstein E, Williams AC, Putra RH, Gawi J. 2015. Will current conservation responses save the critically endangered Sumatran rhinoceros *Dicerorhinus sumatrensis*? *Oryx* 50 (2): 355–359.

Article in a journal or periodical

Barnes RFW, Barnes KI, Alers MPT, Blom A. 1991. Man determines the distribution of elephants in the rainforests of north-eastern Gabon. *African Journal of Ecology* 29 (1): 54–63.

Foose TJ and Wiese RJ. 2006. Population management of rhinoceros in captivity. *International Zoo Yearbook* 40: 174–196.

Okita-Ouma B, Lala F, Moller R, Koskei M, Kiambi S, Dabellen D, Leadismo C, Mijele D, Poghon J, Wittemyer G. 2016. Preliminary indications of the effect of infrastructure development on ecosystem connectivity in Tsavo National Parks, Kenya. *Pachyderm* 58: 109–111.

Books

Smithers RHN. 1983. *Mammals of the southern African subregion*. First edition. Pretoria University Press, Pretoria.

Martin EB, Vigne L. 2015. *Hong Kong's ivory: more items for sale than in any other city in the world*. Save the Elephants, London.

Western D. 1997. *In the Dust of Kilimanjaro*. Island Press, Washington DC. 312 pp.

Book chapters

Dean C, Hinsley A. 2020. Campaigning to bring about change. In: Sutherland WJ. (Ed.). Conservation research, policy and practice. Cambridge University Press, London, pp. 277–292.

Lee PC, Lindsay WK, Moss CJ. 2011. Ecological patterns of variability in demographic rates. In: Moss CJ, Croze H, Lee PC. (Eds.). *The Amboseli elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago, pp. 74–88.

Masters /PhD thesis

Douglas-Hamilton I. 1972. *On the ecology and behaviour of the African elephant*. PhD thesis. University of Oxford.

Reports published online

Rookmaaker LC. 2020. Twenty years of literature on the rhinoceros 2000–2019, extracted from the Rhino Resource Center (RRC)—www.rhinoresourcecenter.com. Unpublished. Available at: http://www.rhinoresourcecenter.com/pdf_files/160/1606763476.pdf [Accessed 22 September 2021]

IUCN (International Union for the Conservation of Nature). 2009. World Biodiversity Report 2008. IUCN, Gland, Switzerland.

King L, Raja N, Kumar M, Heath N. 2023. Human–elephant coexistence toolbox. Advice, actions and tools to reduce conflict with elephants. A technical manual for trainers and community leaders (2nd ed.). Save the Elephants.

Unpublished reports

Kindly, provide a website, location, or person from whom a report can be accessed when possible:

Kuloba B, Kenana, L, Muteti D, Mwenda E. 2010. Aerial count of large herbivores in Maasai Mara National Reserve and the Surrounding Areas. Unpublished report, Kenya Wildlife Service.

Web site

Elephants of Cameroon. 2000. Saving Africa’s vanishing giants, the elephants of Cameroon http://www.nczooeletrack.org/project/index.htm. [Accessed 25 February 2000]

[AfESG] African Elephant Specialist Group. 2000. Fencing and other barriers against problem elephants. AfESG Technical Brief Series. IUCN African Elephant Specialist Group, Human–Elephant Conflict Working Group (author: Richard Hoare). Available at: http://www.african-elephant.org/hec/pdfs/hecfencen.pdf. [Accessed 15 July 2019]

Payne J and Ahmed AH. 2012. A comment on ‘sex and the single rhinoceros’ by Henry Nichols. http://www.borneorhinoalliance.org/resources/comment/a-comment-on-sex-and-the-single-rhinoceros-by-henry-nicholls [Accessed 24 August 2020]

Films and videos

We have observed that films and videos are being referenced more frequently; however, as they are not peer-reviewed, kindly add them as footnotes, and where possible, provide a link.