RESEARCH

A culture of aggression: the Gorongosa elephants' enduring legacy of war

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Abstract

Humans have hunted elephants since the Palaeolithic era and, as cunning predators, have likely helped shape the animals' sophisticated defensive behaviour. In recent centuries, the use of modern weapons in targeted mass killings has resulted in signs of post-traumatic stress disorder (PTSD) in elephants, including heightened aggression and impaired decision-making. During Mozambique's long civil war (1977–1992), 90% of the elephants of Gorongosa National Park were killed. More than a quarter of a century after the end of hostilities aggression towards vehicles by elephant families is an enduring legacy. This study found that females and entire families were more likely to charge when vehicles were in close proximity (<~80 m) and on, rather than off, the roads. Although aggression was primarily initiated and led by older adult females, most charges involved mobbing by entire families, including calves. Some individuals engaged in idiosyncratic defensive behaviours, while some families exhibited distinctive group manoeuvres that appeared to form traditions, indicating that young elephants were acquiring their defensive responses within this social context. We argue that the aggressive behaviour of the Gorongosa elephants is a response to the traumatic events of the civil war and that the observed patterns of behaviour are transmitted within and across groups, giving rise to a culturally learned behavioural variant that has persisted over time and generations. Given rapid environmental change, increasing contact between elephants and people, and the extreme losses caused by poaching and armed conflict, a better understanding of the role that culture plays in the response of elephants to people is urgently needed. Conservation and management strategies may have to be adapted to meet the changing cultures of specific elephant populations.

Résumé

Nous, humains, chassons l'éléphant depuis le Paléolithique et en tant que prédateurs astucieux, nous avons probablement contribué à façonner le comportement défensif sophistiqué dont ils font preuve. Depuis quelques centaines d'années, le recours aux armes modernes pour procéder à des tueries de masse ciblées a provoqué chez les éléphants des manifestations de stress post-traumatique, notamment une augmentation

du taux d'agression envers les humains et une altération des prises de décision. Pendant les longues années de guerre civile au Mozambique (1977 à 1992), 90 % des éléphants du parc national de Gorongosa ont été abattus. Les attaques de véhicules par des familles entières d'éléphants sont des marqueurs hérités de ces années de conflit. La présente étude a permis d'identifier que, non seulement les femelles, mais également des familles entières d'éléphants, sont plus susceptibles de charger des véhicules se trouvant à proximité (moins de 80 mètres). En outre, ces altercations ont lieu sur les routes plutôt qu'en dehors de celles-ci. Bien que les femelles plus âgées amorcent et mènent ces agressions, la plupart des heurts impliquent des familles entières, dont des juvéniles. Certains individus montrent des comportements de protection caractéristiques et connus, tandis que plusieurs clans identifiés présentent des manœuvres spécifiques effectuées en groupe et qui semblent former un ensemble de « traditions ». Cela donne à penser que les éléphants juvéniles acquièrent leurs réactions défensives dans ce contexte social. Nous attribuons l'attitude agressive des éléphants de Gorongosa aux événements traumatiques de la guerre civile, et nous avançons l'hypothèse selon laquelle les schémas comportementaux observés se transmettent au sein des groupes et entre eux, créant au fil du temps des variantes culturelles intégrées par les nouvelles générations. Du fait des rapides changements environnementaux, de l'augmentation des contacts entre éléphants et humains et des pertes extrêmes causées par le braconnage et les conflits armés, une meilleure compréhension de l'aspect culturel dans la réponse des éléphants en présence d'humains est vitale. Il sera peut-être nécessaire d'ajuster les stratégies de conservation et de gestion face à certaines populations spécifiques d'éléphants montrant des transformations culturelles.

Introduction

In 1915 WB Canon used the phrase "fight or flight" to describe the immediate, transitory response of animals to threat. We now know that life-threatening events can have enduring consequences for the brain and behaviour, this being most clearly demonstrated by post-traumatic stress disorder (PTSD). Zanette et al. (2019) argue that predator-induced fear can have lasting effects on the brain and behaviour of wild animals and maintain that these meet the criteria to be a non-human form of PTSD. They contend that PTSD is neither unnatural nor maladaptive; rather, the lasting effects of predator-induced fear are a natural phenomenon serving an adaptive, evolutionarily purpose, even though it may be associated with costs such as hypervigilance. But what if such trauma is caused by human predators engaged in targeted, often prolonged mass killing events that cause dramatic declines in populations and are associated with enduring changes to the behaviour of individuals, the traditions of particular groups or, indeed, the culture of an entire population?

Culture in animals has been defined by Brakes et al. (2021) as information or behaviours shared within a group and acquired from conspecifics through some form of social learning. Individual responses to anthropogenic threats combined with social learning can lead to distinct cultures, which can be important conservation indicators, as well as a resource for resilience in the face of rapid anthropogenic change (Brakes et al. 2021). In this study we distinguish between the terms *tradition* and *culture*. Following Fragaszy and Perry (2003) and Whiten (2005, 2017) we define a *tradition* as a "distinctive behaviour pattern shared by two or more individuals in a social unit [in this case within an elephant family unit], which persists over time and that new practitioners acquire in part through socially aided learning" (Whiten 2017). We define *culture* as the distinctive patterning at population level or the array of traditions across families, which are also presumably acquired from conspecifics through some form of social learning.

Like humans, elephants are known for their close, complex, and enduring social relationships (Moss and Poole 1983; Archie et al. 2006) that develop over long lifespans and are assumed to involve social transmission of knowledge between generations (McComb et al. 2001, 2011; Shannon et al. 2013). Elephant society is highly adaptable and flexible (Moss and Lee 2011), and elephants' behaviour and communication are malleable; with many social, behavioural and communication traits presumed to be acquired through social learning (Poole et al. 2005; Bates et al. 2010; Chiyo et al. 2012). Elephants also adopt novel and idiosyncratic behaviour that may

Table 1. Examples of some elephant culling programmes in Africa

Country	Location	Years	Number killed	Source
Kenya	Tsavo NP	1966	300	Parker and McCullagh 2021
Namibia	Etosha NP	1983–85	570	reported in Slotow et al. 2008
South Africa	Kruger NP	1967–97	14,629	Slotow et al 2008, Whyte 2007
Tanzania	Mkomazi NR	1968–69	600	Parker and McCullagh 2021
Uganda	Murchison Falls (Kabalega) NP	1965–67	2,000	Parker and McCullagh 2021
Uganda	Budongo Forest	1965–67	269	Parker and McCullagh 2021
Zambia	Luangwa Valley NP	1965–69	1,453	Astle 1971
Zimbabwe	Hwange NP (mostly)	1960–91	~50,000	Martin et al. 1996 cited in Slotow et al. 2008

be learned or imitated by others (Poole et al. 2005; Poole and Granli 2021), making them ideal candidates for examining whether and how the culture of populations might be shaped by anthropogenic threats.

Humans have likely been hunting elephants for meat since the Palaeolithic era (Agam and Barkai 2018). Hunting expeditions for ivory have been documented as far back as 1500 BC (Wilson and Ayerst 1976; Meredith 2001). Demand for ivory caused the extinction of elephants in the Middle East by 500 BC, and by the end of the 4th century AD, there were no elephants remaining in North Africa. Europeans began collecting ivory south of the Sahara in the mid-1400s, and in and around what is now Gorongosa National Park (NP), Mozambique, in the late 1500s, though considerable amounts of ivory were already being exported there to the Arabian Peninsula and India (Meredith 2001). Since the 1600s demand for ivory has been responsible for catastrophic declines in populations across Africa (Meredith 2001). During the last half century sophisticated weapons and other resources (e.g. automatic rifles, machine guns, vehicles, and helicopters) have been used to hunt elephants on a massive scale.

It is impossible to give an accurate figure of the number of elephants killed for ivory, which varies enormously among time periods, regions and populations. For example, Thouless et al. (2016) estimate that between 2007 and 2015 illegal hunting (poaching) was the primary cause for the loss of some 114,000 elephants continent-wide (~21% of the total population). During the same period, East Africa's elephants as a whole declined by 50%, while Tanzania's population declined by 60% (Thouless et al. 2016) and the Selous population, specifically, fell by 74% from 50,000 to 13,000 individuals (Kyando 2014). Between 1946 and 2010, armed conflicts occurred in 71% of Africa's protected areas (PA) (Daskin and Pringle 2018); and many were associated with catastrophic local declines in elephant populations of up to 90% (Beyers et al. 2011; Bouché et al. 2010, 2011, 2012). The appalling loss of elephants during the Mozambican civil war is well documented (Campbell-Staton et al. 2021; Poole and Granli 2022) and is the subject of this paper.

While demand for ivory has by far caused the largest number of elephant deaths, the impact of targeted mass killings on the behaviour of elephants is best documented by studies of the survivors of culling operations (systematic killing to control elephant numbers). From 1960–1997, at least nine populations across Africa experienced large-scale culls during which more than 66,000 elephants were killed (Table 1). Such operations involved rounding up groups of elephants, sometimes immobilising adults from helicopters, before shooting them at close range and, in some cases, capturing calves for sale or reintroductions.

Such killings have both short- and longer-term effects on elephant behaviour (Slotow et al. 2008). As Martin et al. (1996) observed, "it is naïve to believe that, if an entire herd is killed, the remainder of the population knows nothing about the event." In the shorter term, elephants may spend less time in places where they feel vulnerable, such as waterholes (Martin et al. 1996), or may disappear from the area where the killing occurred (Whyte 1993). Anecdotal reports suggested that in the long term, in areas of Kruger

NP where culling occurred, elephants were more aggressive (Whyte 2001), acted in a "secretive and skittish manner" (Slotow et al. 2008), and were easily disturbed by vehicles (Slotow et al. 2007).

Anthropogenic disturbances that cause significant deaths or separation of bonded individuals, such as culling programmes, legal and illegal hunting, translocation, and capture for captivity, can fragment patterns of social attachment by eliminating the supportive stratum offered by family members. Severely disturbed populations may experience both initial trauma associated with the disruptive event and loss of opportunities for interacting and learning from older group members who could act as role models or repositories of knowledge (Slotow et al. 2000; McComb et al. 2001, 2011; Shannon et al. 2013).

Studies also indicate that such disruption appears capable of driving aberrant behaviours (e.g. impaired decision making and hyper-aggression) in elephants that are akin to PTSD experienced by humans following traumatic events (Bradshaw et al. 2005). Examples include the killing of rhinoceroses by male elephants (Slotow et al. 2000) and reduced ability of family groups to respond appropriately to social threats (Shannon et al. 2013) in populations that were established from translocated survivors of culls.

Psychological trauma in humans is often encountered as a legacy of war and/or disruptions of a socio-ecological nature (Bradshaw et al. 2005). Long-term studies have found that survivors of severely traumatic events may face a lifelong struggle with sometimes debilitating behavioural dysfunctions (i.e. PTSD). Furthermore, their children and families can exhibit similar symptoms, such that an entire society can be affected: directly through an individual's experience and indirectly, through social transmission and the breakdown of conventional social structures (Leiner 2009). Indeed, trauma can define a culture (Bradshaw et al. 2005). Since neuroscience has demonstrated that all mammals share common stress-regulating neurophysiology and developmental attachment mechanisms, we should not be surprised to find that elephant survivors of war, poaching and culling have been observed displaying symptoms similar to those of human PTSD (Bradshaw et al. 2005). Might such traumas experienced by elephants have also shaped their cultures?

Patterns of fear and aggression in response to human-induced trauma can vary significantly among elephant populations, suggesting cultural variants. As described above, a behavioural variant of aggression towards rhinos was observed in several disturbed populations in South Africa, with the majority of events perpetrated by young males in musth (Slotow et al. 2000). Furthermore, provisional analysis from an ongoing study of videos posted online showing aggressive acts by elephants towards vehicles found that the vast majority were of males, often in musth, filmed in South African PAs (Sidhu et al. in prep.). While it is tempting to blame aggression on musth, or poorly behaved drivers, these traits also exist elsewhere. However, reports of musth males attacking vehicles in Kenya, for example, are extremely rare. In 50 years of study in Amboseli there has only been one instance of a musth male tusking a tourist vehicle. We suggest that the elevated frequency of aggressive behaviour in South Africa may indicate a cultural variant.

In Tsavo East and Tsavo West NPs, Kenya, where ivory poaching caused an 85% decline in elephant numbers between 1976 and 1989, a study carried out towards the end of this period found that elephants often fled from vehicles several hundred metres away, once human presence was noticed (Poole 1989b).

In Queen Elizabeth NP, Uganda, the elephant population declined by almost 95% between 1973 and 1980 (Douglas-Hamilton et al. 1980). Here, the remaining elephants permitted vehicles to approach in open habitat but moved together in one tight-knit semi-permanent aggregation of 170 elephants (Poole 1989b). In Mikumi NP, Tanzania (part of the Selous ecosystem), where the population declined by an estimated 75% during the same period (Balozi 1989), many of the survivors sought safety in small, fragmented and, often, orphan groups, near the lodge and park headquarters (Poole 1989b).

In the Maasai Mara ecosystem, Kenya, between 2011–2016, we experienced neither aggressive nor fearful behaviour during vehicle encounters with 286 groups in the Maasai Mara National Reserve (NR) and neighbouring conservancies (Poole et al. 2016; Poole and Granli 2022) despite very significant poaching in the ecosystem during this period. Elephants were, however, wary of Maasai and their livestock and, in neighbouring Naimina Enkiyo Forest, where poaching

was heaviest, elephants were extremely skittish.

Studies in relatively undisturbed Amboseli NP, Kenya, found that elephants were calm around vehicles, yet reacted fearfully if a Maasai man in traditional dress was, or had been, in the vehicle (Joyce Poole (JP), pers. obs., 1980s), as well as to garments worn by Maasai men (Bates et al. 2007) or to Maasai male voices (McComb et al. 2014). On occasion, Maasai warriors spear elephants, in some instances in retaliation, when some Amboseli elephants have killed livestock (Sayialel and Moss 2011). Thus, this population considers Maasai men a threat, but not women and children, nor members of other ethnic groups, nor tourists in vehicles.

Studies indicate that populations of elephants understand not only specifically *who* (which class of people) represents a threat, but also *where* and *when* they are safe, based on specific knowledge about the characteristics and behavioural patterns of their human predators. Satellite tracking in Samburu NR, Kenya, revealed that elephants "streak" through unsafe habitat at night and avoid areas where they are more likely to meet people (Douglas-Hamilton et al. 2005). Around Mikumi NP, crop raiding occurred less frequently on full moon nights, a period associated with greater visibility and greater human activity (Gunn et al. 2013), suggesting again that elephants use knowledge of human behaviour to try to minimize contact with them.

In Amboseli NP, elephants were more vigilant when they were outside the Park boundaries, when we carried strangers in our car, or when vehicles did not conform to their expectation of being on the road within the protected area boundary (JP pers. obs.). In Gorongosa NP, trail camera data revealed that there, too, elephants had expectations about the movement of vehicles, avoiding roads during hours when they were more likely to be present (Gaynor et al. 2018). Video footage of elephants charging after our vehicle (Poole and Granli 2021) also indicates that they understood that vehicles use roads, as they anticipated our movements, using short cuts in attempts to cut us off.

In the Mara ecosystem, we filmed young elephants repeatedly rumbling "Let's–Go" (based on classification in Poole 2011 and *The Elephant Ethogram*) as they waited for their matriarch to initiate movement out of the Conservancy, which she did only at dusk once she had determined that the sounds of Maasai herders (cowbells and voices) had moved back to their settlement. Through such daily demonstrations, young elephants likely learn from older family members to navigate their increasingly human-populated world, leading to behavioural variants in which some humans, are tolerated and others not.

While elephant populations may exhibit particular responses to humans, these may change over time if individuals learn that all or certain groups of humans are no longer a threat. In Amboseli NP, we were charged by immigrant families on initial encounters with them (JP, pers. obs., 1980s). Thereafter, they learned, presumably by watching resident herds, to respond to vehicles as members of their adopted population did. In Manyara, Tanzania, Douglas-Hamilton (1972) observed that many families were initially unapproachable, either charging or running away when hearing his Land Rover engine, but over time most became habituated.

The elephants of Gorongosa NP offer an opportunity to examine the embedded behavioural reactions to humans in a population that has suffered extreme disruption and trauma caused by the mass killing of elephants during a civil war. In 1972 Gorongosa NP held ~2,200 elephants ranging across 3,674 km^2 of protected habitat (Tinley 1977). In the greater Gorongosa ecosystem, including the surrounding area and the Marromeu area of Zambezi River delta, there were an estimated 6,000 elephants (Tinley 1977). In 1977 a 15-year civil war began, during which hostilities raged in and around Gorongosa NP and >90% of the elephant population was extirpated. Elephants were shot and killed for meat and ivory by both FRELIMO[1] and RENAMO[2] forces, and large quantities of ivory were exported from the area. Animals were particularly affected around areas where forces were stationed for long periods, such as the Park headquarters at Chitengo, from where the core tourist road network stems (Hatton et al. 2001). By 1994 it was estimated that <200 elephants remained (Cumming et al. 1994; Poole and Granli 2022).

In 2004 a public–private partnership was established between the government (Republic of Mozambique) and the Greg Carr Foundation to restore GNP and began to provide elephants and other wildlife with protection and stability. Almost three decades after the war elephant numbers are now beginning to recover (Poole and Granli 2022), but the enduring

consequences of the violence perpetrated are still visible in the markedly changed distribution of elephants (Stalmans and Peel 2020), the prevalence of tusklessness and its' genetic markers (Campbell-Staton et al. 2021), avoidance of roads by elephants during peak game drive hours (Gaynor et al. 2018), and markedly changed behaviour toward vehicles.

Prior to the war, visitors to the Park described the elephants of Gorongosa as "wonderfully relaxed ... absolutely friendly, no fear, no aggression whatsoever" (Jens M. Lucke, pers. comm., January 2018). The Park ecologist, Dr Kenneth Tinley and Lynne Tinley, who lived in Gorongosa NP from 1967 to 1973, reported that they never encountered any untoward aggression by elephants, nor did they hear of any overt aggression (Lynne Tinley, pers. comm., October 2013). Yet, 19 years after the end of the war, when we were invited to Gorongosa NP to gather baseline data on the population, the elephants had a reputation of threatening and charging vehicles. It was generally believed that the dramatic change in behaviour was a consequence of the atrocities that the elephant survivors of the war had experienced.

In this research paper, we suggest that elephant aggression towards vehicles is another legacy of the war. We further argue that the behavioural variants observed in population responses to humans represent different elephant cultures acquired through social learning.

Between 2011 and 2019, authors JP and PG carried out nine field trips to document the status of the Gorongosa NP elephants, to better understand the lasting physical and behavioural scars inflicted by civil conflict, and to provide scientific data to ensure the strategic protection, management, and recovery of the Gorongosa NP elephant population (Poole and Granli 2022). In this study we examined the responses of the Gorongosa NP elephants toward vehicles. We wanted to understand: 1) how context (distance to the elephants, vehicle location on or off the road) influenced the reaction of elephants; 2) whether those who were aggressive were more likely to belong to a particular sex or age class, or were specific individuals; 3) whether particular patterns of aggressive behaviour were exhibited by specific individuals or families; 4) whether there was evidence of behaviour being acquired by younger elephants; 5) whether the number and intensity of aggressive events declined over time; and 6) if the behavioural response of GNP elephants to vehicles was distinct from those of other heavily poached populations. All named behaviours are capitalised and are described in *The Elephant Ethogram* (https://www.elephantvoices.org/elephant-ethogram.html).

Methodology

Study site

Gorongosa NP covers 3,674 km^2 of Sofala Province, Mozambique. Elephants historically ranged throughout Gorongosa NP and the Marromeu area of the Zambezi River delta to the east. After the civil war, the range of the surviving elephants in GNP contracted to the area south of Lake Urema (Fig. 1) in the vicinity of the Urema River and Pungue River, with some venturing into human settlements south of the Pungue.

Within Gorongosa NP, 15 landscape types are recognized, with floodplain grasslands and Acacia–Combretum savannah predominating in the Rift Valley and miombo woodlands occurring at higher elevations to the east and west (Stalmans and Beilfuss 2008). The mean annual rainfall is 700–900 mm, with peak rain falling in December–February, when the floodplains around Lake Urema are inundated (Stalmans et al. 2019). As the dry season progresses, elephants begin to concentrate near two primary permanent water sources: (a) around Lake Urema and along the upper Urema River; and (b) along the lower Urema River and the Pungue River (Fig. 1).

Number of visitors and vehicles in Gorongosa NP

Due to seasonal flooding, Gorongosa NP is typically closed to tourists between December and late March. The road network around the floodplains, the core elephant habitat, usually does not open again for vehicle access until April.

Vasco Galante, the Communications Director of Gorongosa NP, provided us with visitor records from 2006 to 2017. Data for earlier years are estimates as precise figures were not available. Since 2012 tourists have only been allowed to enter the Park in Land Cruisers driven by guides. Test Malunga, the Tourism Manager provided records of the number of tourist vehicles entering the Park for game drives in 2018 and 2019.

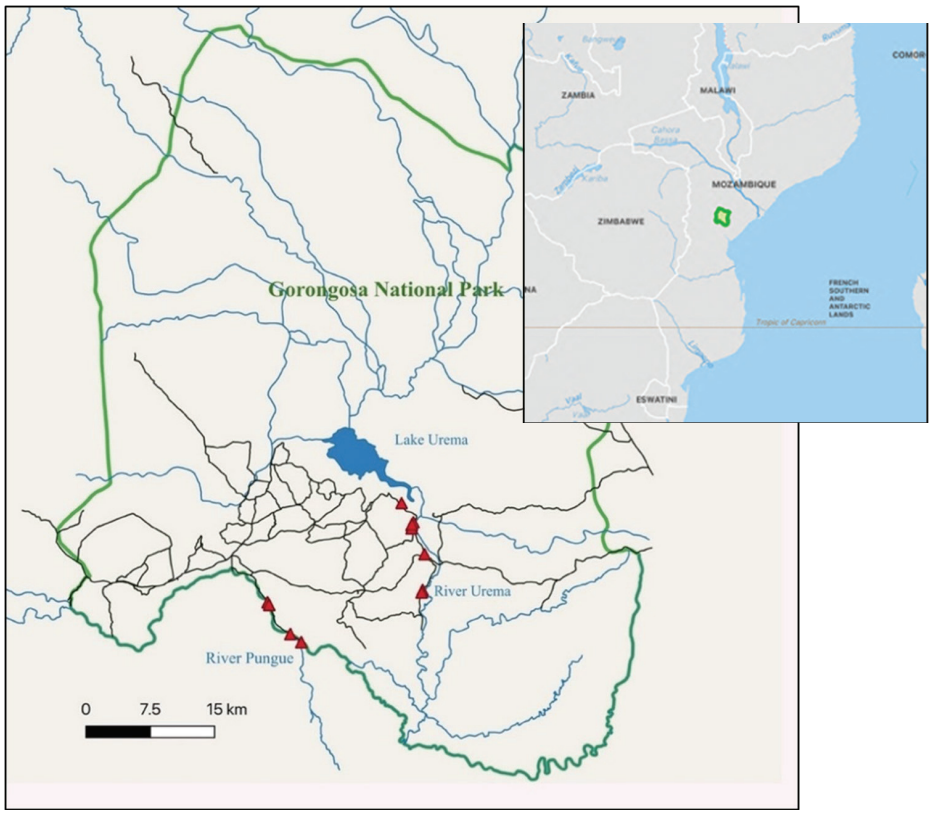

Figure 1. Gorongosa NP [Key: green-Park boundary; blue-Lake Urema, permanent rivers (Urema and Pungue) and seasonal waterways; black-murram roads; red triangles-positions of trail cameras].

While the number of vehicles given in the results do not include those used by NP rangers, management, and researchers, it offers a picture of the seasonal level of activity on the NP road network. The lower numbers in March, April, and May 2019 correspond to Cyclone Idai, which caused the closure of Gorongosa NP for longer than usual.

Sightings, registration and re-identification of elephants and assigning family membership

We searched for elephants as we drove on the network of roads in the south-central section of GNP (Fig. 1). We occasionally drove off-road to observe elephants spotted from the road. The collection of elephant sightings data, registration, re-identification of individuals, and assigning of family membership are described in detail in Poole and Granli (2022). We collected sightings data via the Gorongosa *EleApp* and uploaded the information to the *Gorongosa Elephants Who's Who & Whereabouts Database* (Granli and Poole 2022). The database contains 879 sightings records, collected by the authors (487 records), other scientists (67), park management officers (112), experienced guides (207) and tourists (6). We specify when we relied on subsets of these data. Authors JP and Peter Granli (PG) collected 392 records during nine field trips (between 2011 and 2019), while Jason Denlinger (JD) (2016–2018) and Dominique Gonçalves (DG) (2016–2021) collected data opportunistically as they carried out other duties.

Elephants were grouped according to methods developed in Amboseli (Moss 1996) into the following age classes (estimated years): 0A (0–4.9), 0B (5–9.9), 1A (10–14.9), 1B (15–19.9), 2 (20–24.9), 3 (25–34.9), 4 (35–49.9) and 5 (50+). We refer to individuals aged 0–1 year as infants; 0–4.9 years as calves; 5–9.9 years as juveniles; and 10–14.9 years (or until they gave birth if female or became independent if male) as adolescents.

Scoring vehicle distance and location and elephants' behavioural responses

For each group observed we aimed to note: 1) the group type, family name, and adult individuals identified; 2) whether our vehicle was on or off the road; 3) the estimated distance (metres) we were from the elephants when they reacted and/or we turned off the engine; 4) the behavioural response of the elephants. We used an iPhone Voice Memos app to record the behavioural response of the elephants (Table 2 below). Often the response escalated, e.g. from Vigilance to Advancing–Toward or Charging our vehicle. In these cases, the score used in analyses was the maximum level of either attack or retreat. We had a complete set of these records for 174 encounters.

Since many encounters culminated in elephants charging, the collection of data was often challenging. We have photographic records of most encounters, and many were also filmed. No method is completely accurate, however, when up to 40 elephants are mobbing the vehicle. It is simply not possible to record all behaviour, nor to film or photograph the behaviour of each individual in a big group.

We scored the responses of elephant(s) based on behaviours observed (Table 2) and noted the identity of individuals who instigated or took the lead in a charge. According to convention (Poole and Granli 2021) behaviour names are capitalized and hyphenated if they contain more than one word. Full written descriptions and video examples of all behaviours mentioned and some of the encounters described can be found in *The Elephant Ethogram* (https://www.elephantvoices.org/elephant-ethogram.html) (Poole and Granli 2021).

We stopped the vehicle and turned off the engine as soon as the elephants indicated by their behaviour that they were reacting to our presence. Our aim was to show them that we understood and respected their signals. Exceptions included instances when we were ambushed at high speed while we were driving, whereupon we continued to drive. Once we were stationary, we resolved not to respond when charged. In other words, we aimed not to drive off, start the engine, or cause any kind of disturbance in the vehicle, until the elephants departed. Exceptions occurred, for example, when an elephant head-butted our vehicles.

Analysis of charging behaviour across families and individuals

Analysis of charging behaviour across families included only records in which individuals could be positively identified. Most of these observations were made by JP and PG. Records collected by others were included if: 1) they were of a well-known individual/family; 2) identity could be verified via satellite collar; 3) we were able to obtain photographic or videographic documentation.

We made a special effort to identify the perpetrators of physical attacks on vehicles as this information was important for GNP management. In each case where photographs or videos were available (six out of nine attacks), we were able to identify the

Table 2. Behavioural response to vehicle and scores assigned. Descriptions of key behaviours can be found in *The Elephant Ethogram*

Context	Key behaviours	Score
Avoidance	Panic-Running	-2
Avoidance	Full-Retreat, Retreat-From, Walk-Away, Look-Back, Rear-Guard	-1
No response	No obvious reaction	0
Vigilance	Freezing, Listening, Periscope-Trunk, Ear-Spreading, Bunching	1
Confrontation	Standing-Tall, Head-Shaking, Ear-Folding, Throw-Debris, Kick-Dust, Stand-Guard, Head-Swinging, Chin-Up	
Advance	Perpendicular-Walk, Advance-Toward, Group-Advance	2
Charge	Charge, Group-Charge, Trunk-Bounce, Trumpet-Blast	3
Sustained Charge	Sustained Charge, sustained Group-Charge (>25m)	4
Physical Attack	Push, Tusk, Ram, Head-Butt vehicle	5

aggressor. The extra effort we made to identify elephants who attacked vehicles means that the proportion of charges that ended in attacks in our data represents an overestimate of their relative frequency of occurrence.

In some places in Africa, there is a widely held belief that tuskless females are more aggressive than tusked females. The prevalence of tuskless females in GNP gave us an opportunity to examine whether there is any credence to it. To do so we compared the frequency of charges led by tuskless, one-tusked and two-tusked females born prior to the war to the frequency of occurrence of each tusk configuration type in the same age-sex cohort.

Acquisition of behaviour

We compared Gorongosa NP videographic records held in *The Elephant Ethogram* (https://www.elephantvoices.org/elephant-ethogram; Poole and Granli 2021) of aggressive and vigilant behaviour towards vehicles, to examine acquisition of these behavioural traits by young elephants. We noted which adult female initiated and led each Advance-Toward or Charge and whether she did so alone or was joined in a Group-Advance or Group-Charge by other members of her family (including infants and calves).

We know from our behavioural studies that new-borns instinctively follow the movement of other elephants. Therefore, to better understand the age at which infants (0-<1 year) and older calves (1<5 years) become aware of older elephants' responses to perceived threats and begin to participate in learned behaviour with them, we examined videos illustrating stationary vigilant behaviour only. We examined 22 videos from Gorongosa NP which included examples of Head-Swinging, Chin-Up, Standing-Tall and Periscope-Trunk in response to vehicles. For each video we scored how many adult females, juveniles/adolescents (5<15 years), calves and infants we could see and, of those, how many exhibited vigilant behaviours. Such behaviour was taken to indicate that they had learned or were cognizant that vehicles were perceived as a threat, or that other members of their family had perceived a threat. We then summed up each behaviour over the 22 videos to arrive at a percentage response by each age/sex group.

Response to vehicles over time

We used the sightings in our database as a proxy for the relative exposure of different families to vehicles. Since we made an effort to use the entire road network, including remote tracks, and also made some off-road excursions to look for families photographed by our cameras positioned along the Pungue River (Fig. 1), it is likely that we overestimated the frequency with which some families were exposed to vehicles. Many families were only sighted a few times. To determine whether aggression declined with time, we focused on families whose range fell in the core tourist area and for whom we had >40 sightings during which data on behaviour was collected (families C, I and M). We gave consecutive sightings of each family a matching consecutive number (i.e. first sighting = 1; second = 2, third = 3, etc) and looked at the relationship between the degree of aggression and its occurrence over time.

Since not all members of a family were present on each sighting of the family, we also analysed the behaviour over time of key individuals who, based on our observations, had been among the most consistently aggressive members of the family. Focusing on the sightings of the family in which the selected individual was noted as present, we used the same method.

Comparison with other poached populations

In 1989 author JP carried out rapid assessment surveys of four heavily poached populations: Tsavo East and Tsavo West NPs in Kenya, Mikumi NP in Tanzania, and Queen Elizabeth NP in Uganda, during which JP recorded age, sex and family structure, tusk configuration (Poole 1989b) and response to vehicles. Each of these populations was experiencing, or had recently experienced, heavy poaching, as described above. The response to vehicles data, which were never published, provide a useful basis for comparison with the Gorongosa population. In the previous study, the author noted the distance to which elephants were approached and classified their responses as Retreat, Neutral or Attack.

Contribution towards management

We worked with Gorongosa NP management, guides, rangers, and scientists to promote respectful interactions with elephants to build trust. The management interventions we used have been written up separately (Poole et al. 2023). We also advised Park management that if we found particular elephants to be responsible

for serious aggression we would recommend *against* their removal, in the belief that any such violence would cause a further escalation of elephant aggression.

Results

Visitors to, and vehicular presence in Gorongosa National Park

After a public–private partnership to restore Gorongosa NP was signed in 2004 between the Government of Mozambique and the Greg Carr Foundation, the number of visitors to Gorongosa NP climbed steadily from <1,000 in 2006 to 7,000 by 2011 (Fig. 2). Subsequently, the number of international travellers declined due to a resurgence of civil conflict in central Mozambique, with only 1,312 visitors to Gorongosa NP in 2013. After 2016 visitor numbers began to recover again although in 2019 these were adversely affected by Cyclone Idai (Vasco Galante, pers. comm., September 2022).

The number of tourist vehicles on game drives varies over the course of each year. In 2018 and 2019, for example (Fig. 3), there was little if any vehicular traffic in the Park in December to February, due to seasonal flooding. For more than half the year, November to June, there were only a few vehicles on the road network each day.

Response of family and male groups to vehicles

Of the 849 group sightings in our database of known type (357 all-male groups and 492 family groups, including those with associating males), reactions to vehicles were noted from 505 groups (201 all-male groups and 304 family groups). The responses of these two types of groups were significantly different, with females showing more aggression towards vehicles than males (χ^2 = 124.95, df = 8, n = 505, $p < 0.00001$; Fig. 4). Most all-male groups showed little or no visible reaction to our approach (56% of sightings) or retreated (19%). While 22% of family groups showed no obvious reaction to the approach of vehicles, they were much more likely to engage in vigilance (18%) and to charge (Charge or Group Charge: 20%; Sustained Charge: 8%) or physically attack (Tusk, Push or Head-Butt: 3%) the vehicle. We did not experience any serious Charges by individual males. The few cases in which males Charged (1%) can better be described as Short Rushes, behaviour typical of insecure young males. All of these cases involved males less than 25 years old. A small proportion of groups exhibited Panic-Running and fled from the vehicle (all-male: 4%; family: 4%). It is likely that there were unrecorded groups of both types that retreated when they heard our vehicle approaching in the distance.

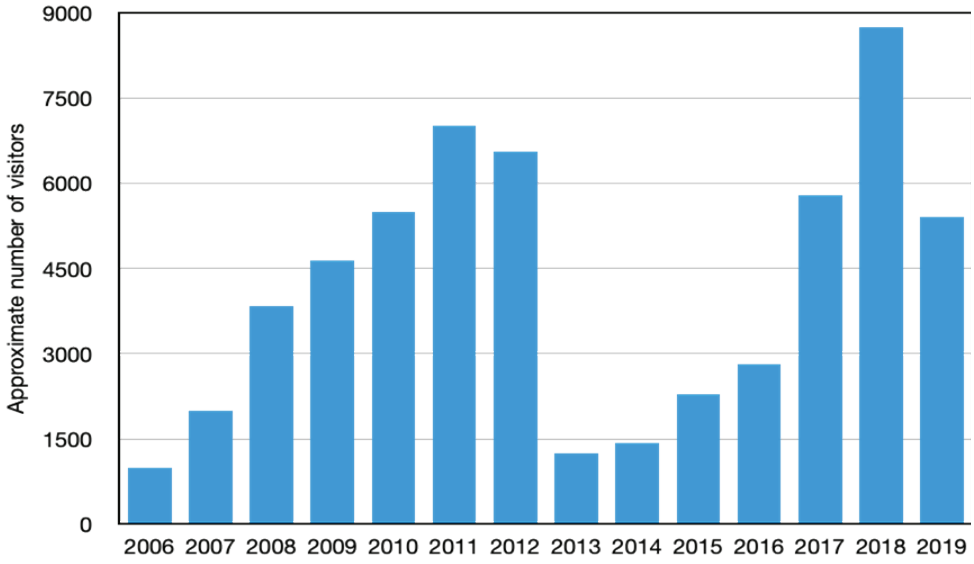

Figure 2. Number of tourists entering Gorongosa NP from 2006 to the end of 2019.

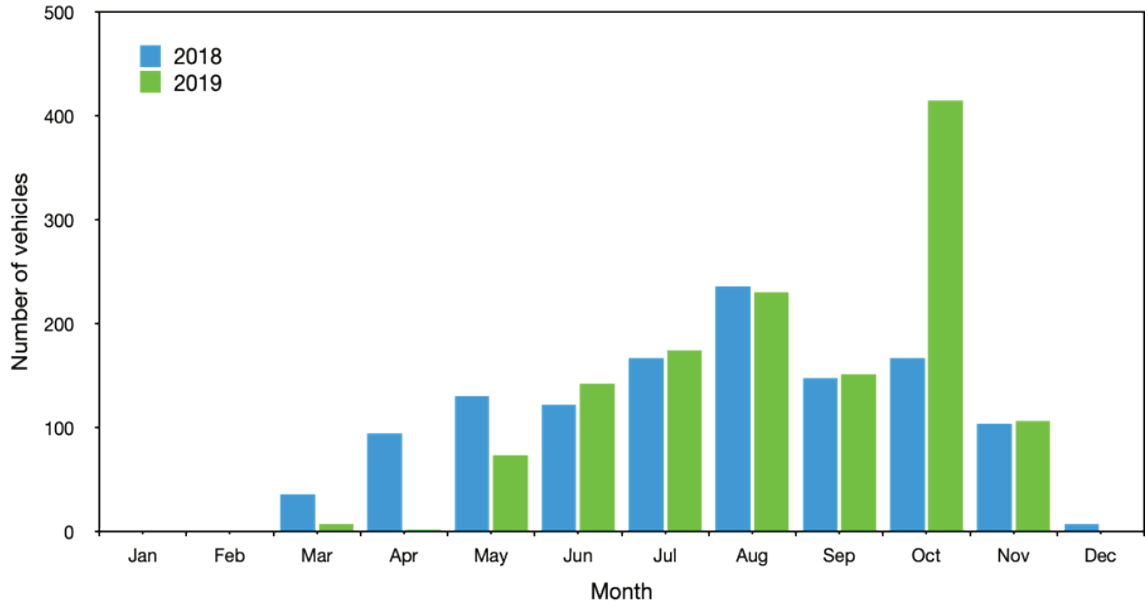

Figure 3. Number of tourist vehicles entering Gorongosa NP for game drives during 2018 and 2019.

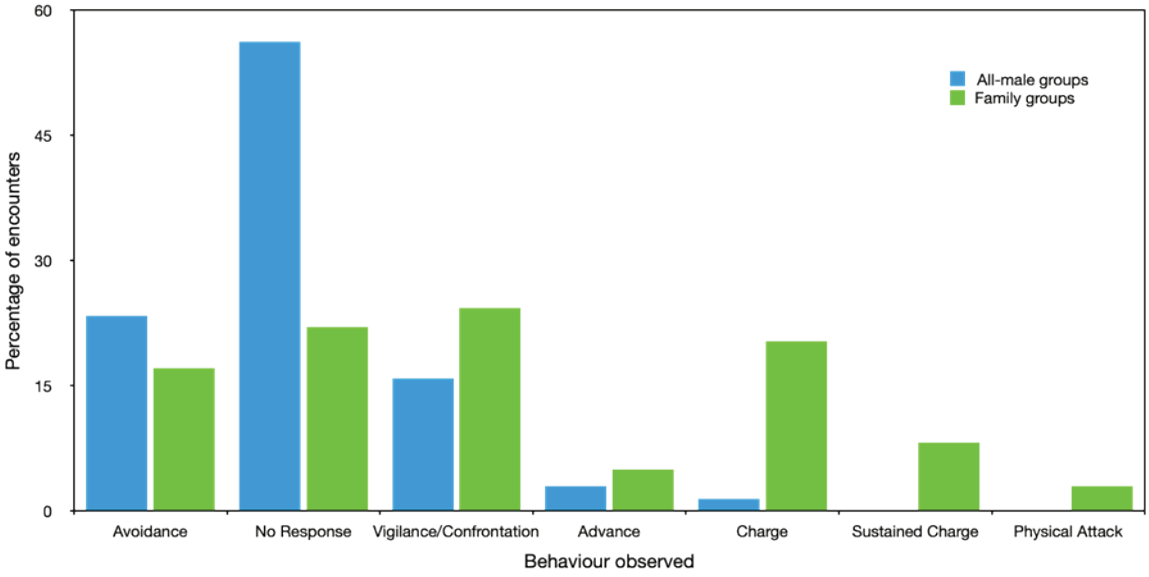

Figure 4. Behavioural responses of family groups and all-male groups to vehicles.

Behavioural response in relation to vehicle distance

Examining only those records of family groups that were characterized by avoidance (Retreat-From or Panic-Running) or aggression (Advancing-Toward or Charging), we found a significant difference in the distance at which elephants retreated from (median: 100 m; interquartile [IQ] range: 60–200 m; range: 10–400 m, n = 33) or advanced upon vehicles (median: 62.5; IQ range: 40–80; range: 20–300, n = 76) (one-tailed Mann–Whitney $U = 692.5$; $n_1 = 33$, $n_2 = 76$, $z = -3.699$, $p < 0.0001$; Fig. 5). The closer the vehicle was to the elephants, the more likely they were to respond with aggression.

Vehicles on and off the road

We found no significant difference in the distance at which family groups took evasive action based on whether the vehicle was on the road (median: 100 m, IQ range: 48–162 m, range: 10–350 m; n = 13) or off-road (median: 110 m, IQ range: 69–200 m, range: 25–400 m; n = 21) (Mann–Whitney $U = 105$; $z = 0.564$, $p = 0.287$). Nor was there a significant difference in the distance at which they advanced upon, charged or attacked based on whether the vehicle was on the road (median: 62 m, IQ range: 48–85 m, range: 20–300 m; n = 49) or off-road (median: 72.5 m; IQ range: 42–80 m; range: 25–120 m; n = 24) (Mann–Whitney $U = 704$; $z = -0.159$, $p = 0.436$; Fig. 6). However, family groups were significantly more likely to retreat if the vehicle was off-road and more likely to advance if the vehicle was on the road ($\chi^2 = 5.3$, df = 1, n = 110, $p = 0.02$; Fig. 7).

Patterns of aggression across family groups

Almost a third of all encounters with families in which behavioural responses to the vehicles were noted (n = 303) involved Charges (n = 94) at the vehicle. Aggressive behaviour was a widespread response to vehicles across most families, although some families (Fig. 8), and some individuals within families, were notorious. Of 279 encounters in our database in which families were identified, aggressive behaviour was documented in 202 cases. Of these, 74 involved Charges, of which 22 were sustained Charges and six culminated in a female Head-Butting and damaging a vehicle. Some families were well known for engaging in highly coordinated Group-Advances and Group-Charges, while in other families the matriarch or another adult female specialized in sustained lone Charges or in demonstrative Perpendicular-Walks or specific idiosyncratic defensive behaviour.

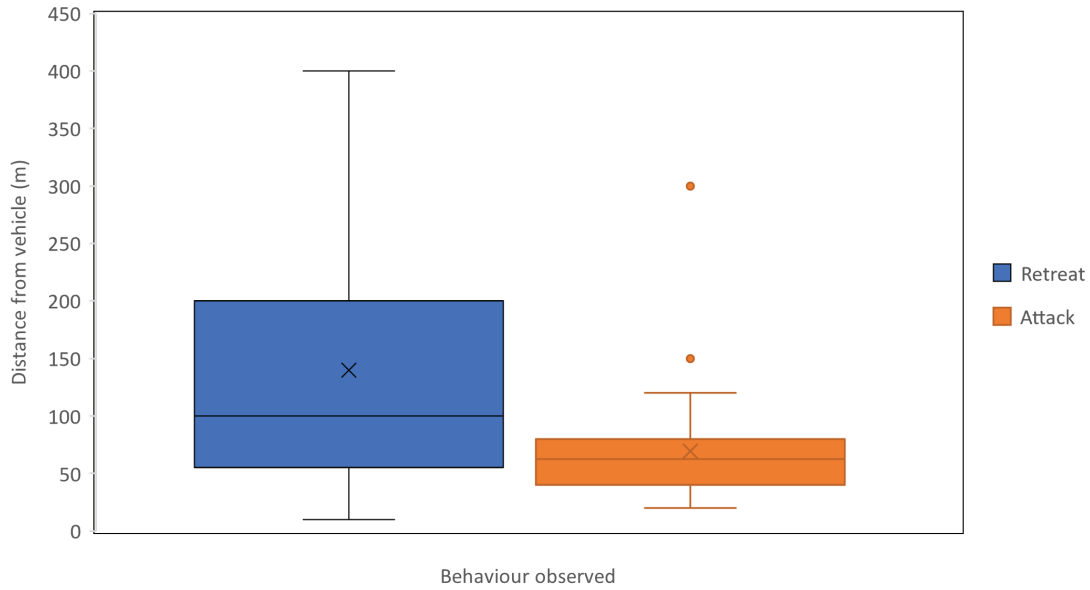

Figure 5. The median distance from the vehicle at which family groups retreated or attacked. In the box-and-whisker plot, the horizontal lines in the boxes are medians, the upper and lower edges of the boxes show the interquartile range, the whiskers indicate the range and the x mark the means.

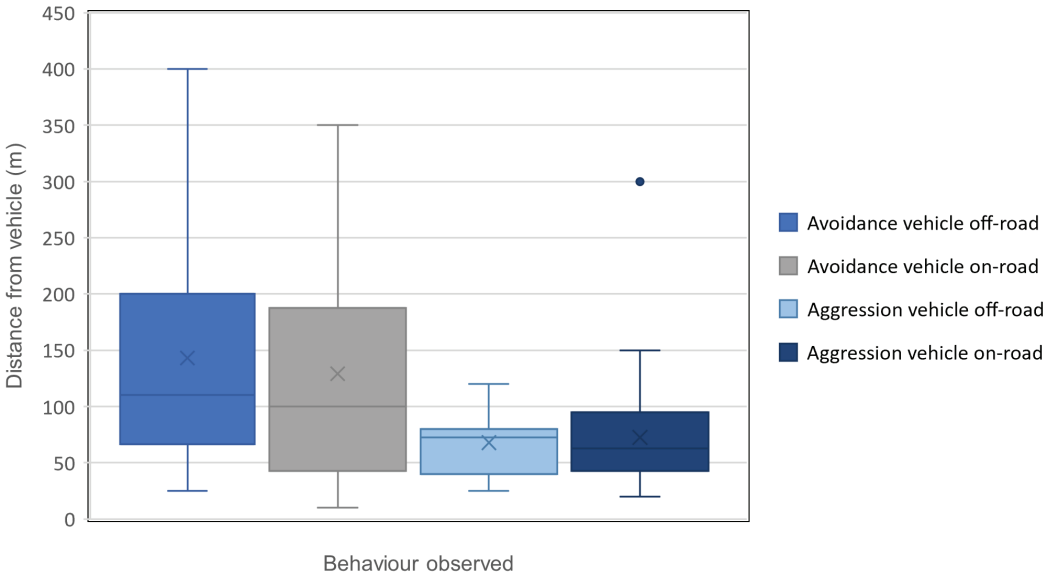

Figure 6. The median distance at which elephant family groups took evasive or aggressive action in response to the presence of vehicles overall, and whether our vehicle was on or off the road. The components of the box-and-whisker plots are the same as in Fig. 5.

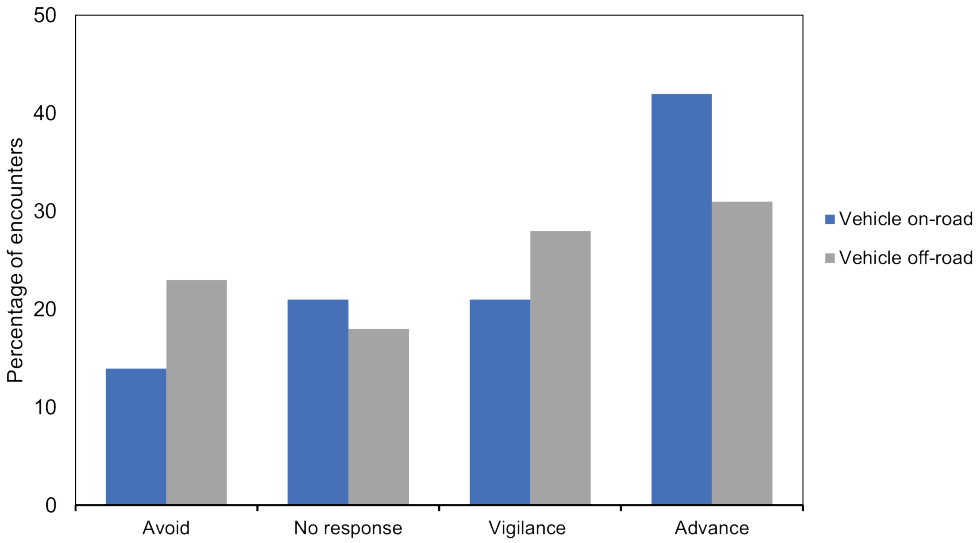

Figure 7. Responses of family groups in on-road and off-road encounters.

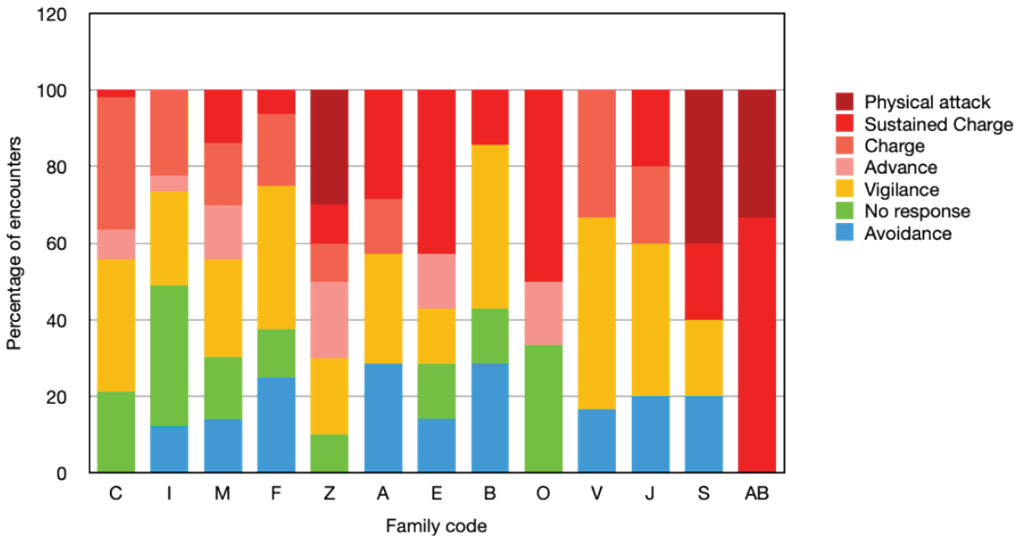

Figure 8. Frequency of different defensive behaviours in encounters with family groups. The number of times each family was observed and behaviour documented is given above each column.

Physical attacks on vehicles

Between 2010 and 2017 there were nine incidents in which an adult female physically attacked a vehicle. The individuals involved and the behaviour observed are summarized in Table 3. Only one of these attacks was carried out by a tusked female. In six of the nine incidents, we were able to identify the attacking elephant from videos and/or photographs that were taken. Three matriarchs carried out the six attacks, each of whom was observed very infrequently during the study: Zira (4 encounters), Stephanie (5) and Akashinga (3). From a tourism and safety perspective, the most problematic individuals were those from families that were encountered rarely because their core area was not in the primary tourist circuit. There have been no reported attacks on vehicles since 2017 (Test Malunga, pers. comm., February 2022).

Age, tusklessness and individual personality

Not all adult females initiated or led Charges; indeed, most did not. Those elephants who did tended to be matriarchs or older females (Fig. 9), the vast majority of whom would have been alive during the war.

Contrary to widely held beliefs by local people, there was no indication that tuskless females were more likely to Charge than two or one tusked females. Among the cohort of females who were born before the war, 24 were tuskless, four were one-tusked and 12 were two-tusked, while of the 21 individuals of this group who were recorded leading Charges 11 were tuskless, four were one-tusked and six were two-tusked ($\chi^2 = 1.01$, df = 2, n = 61, p = 0.60).

We were threatened and Charged regularly and, in many cases, multiple times by the same individual. With time we noticed that some individual elephants adopted idiosyncratic patterns of behaviour, such as exaggerated postures or particular Charging styles; likewise, some families appeared to specialize in particular strategic group manoeuvres and these we viewed as family traditions. In Table 4 we summarize some of these patterns.

Acquisition of behaviour

Older females, in particular those who survived the war, disproportionately took the lead role in defensive behaviour and in initiating and leading charges (Fig. 9). Yet reactions to vehicles involved most family members at some level, at the very least as agitated and sometimes vocal spectators, or more often, as fully engaged participants. Of the charges (n = 16) and advances (n = 9) by Gorongosa females that are publicly documented in *The Elephant Ethogram* at the time of writing, (Poole and Granli 2021) all involved responses by other members of the family. While the most actively engaged were other adult females; juveniles, calves and even infants also participated. Of these 25 charges and advances, 17 involved the entire

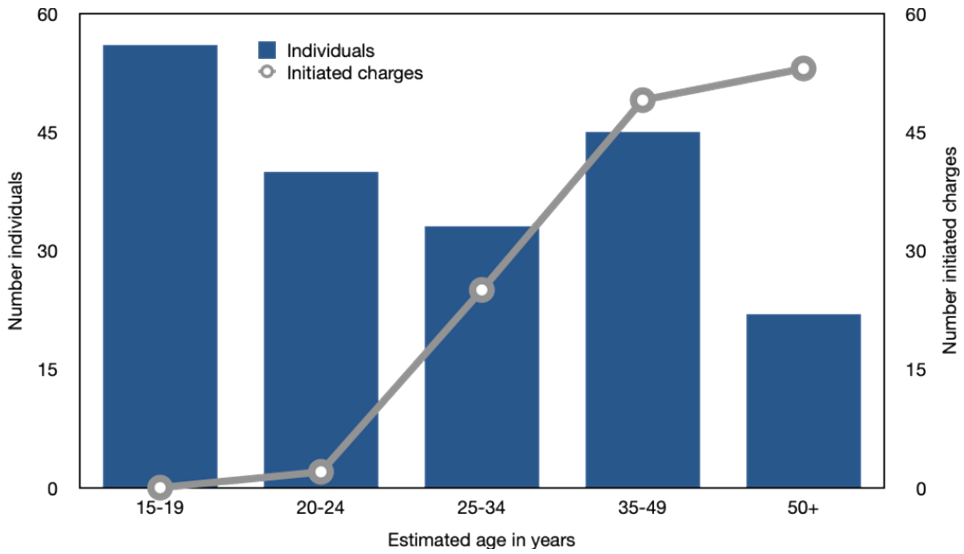

Figure 9. The number of registered females by age class and the number of times individuals of each age class took the lead role in charging.

family (including small calves) following the initiator in the charge or advance. In the instances they did not follow the leader they remained bunched and vigilant awaiting her return. During Group-Advances and Group-Charges calves rushed at the vehicle alongside their mothers (e.g. Fig. 10d), whereas when a single female charged, her calves remained Bunched with the rest of the family.

Vigilant behaviour was typically initiated by an adult female and quickly adopted by other members of the family, who were either also aware of the perceived threat or were alerted by the behaviour of the initiator or by other family members. We found that once one elephant exhibited vigilant behaviour all other adult females present followed suit, while the likelihood of immature elephants responding depended on their age (Fig. 11). Older juveniles were significantly more likely to exhibit vigilant behaviour in response to adult behaviour than were younger juveniles ($\chi^2 = 25.24$, df = 2, n = 101, $p < 0.001$). Ninety percent of adolescents/juveniles responded appropriately (n = 40), 68% of calves (n = 37), while only 29% of infants (n = 24) responded with appropriate vigilant behaviour, suggesting that individuals gradually acquired knowledge about danger in a social context.

Response to vehicles over time

To see whether the degree of aggressive behaviour declined with exposure to vehicles, we examined the behaviour of three families whose range fell in the core tourist area and had been observed most frequently (C, I and M). While all three families showed a negative correlation (C family: Spearman Rank Correlation $r_s = –0.216$, $p = 0.123$, n = 52; M family: $r_s = –0.198$, $p = 0.240$, n = 37), only the I family showed a significant decline in aggressive behaviour over time ($r_s = –0.438$, $p = 0.003$, n = 43). These results, however, reflect the behaviour of the family as a whole, while aggression was typically instigated and carried out by specific individuals who might or might not have been present when other family members were sighted. Each of these families contained an individual, or individuals, who stood out from the rest as being most likely to instigate and carry out aggressive behaviour. These were: *Corajosa*, *iJunia* (matriarch), and *Mwana Nzo*. When we included only the observations and behaviour of the families when these individuals were known to be present we found that both *Corajosa* and *iJunia* exhibited a significant decline in the degree of aggressive behaviour over time (*Corajosa*: $r_s = –0.407$, $p = 0.039$, n = 26; *iJunia*: $r_s = –0.577$, $p = 0.015$, n = 17), while *Mwana Nzo* did not ($r_s = –0.251$, $p = 0.236$, n = 24).

Table 3. Recorded physical attacks by elephants on vehicles, including those of the authors (pax = passengers)

Date	Occupants	On/off-road	Age, sex, tusks	Elephant	Notes
2010	Guide, ~5 pax	On	Adult female, tuskless	Zira	Charged and Head-Butted side and bonnet of Land Cruiser and knocked it onto its side into a ditch.
2012	Film crew, 6 pax	On, but drove off around fallen tree	Adult female, tuskless	Unknown, no photos	Dusk, did not see elephants in forest. As filmmaker drove around fallen tree female Charged and Head-Butted front fender and blew tyre off rim; she paused as warning shot was fired by ranger; Charged again and Head-Butted bonnet and roll cage, pushed Land Rover back into tree. Stood-Guard over vehicle and Charged again while tyre being changed.
2013	Building contractors, 2 pax	On	Adult female, 2 tusks	Unknown, no photos	Charged pickup and pushed tusk through passenger window and seat, and back through pickup cab window.
2013	Park manager, Film crew, 4 pax	On	Adult female, tuskless	Zira	Waiting on road as manager drove Hilux around bend. Charged from 15–20 m and Head-Butted bonnet and smashed front windscreen. Stepped back and Head-Butted vehicle again. For the third time Head-Butted driver's side and tried to push Hilux off road. Backed up 15–20 m, then turned and departed.
2016	Guide, 5–6 pax	On	Adult female, tuskless	Zira	20+ elephants Group-Charge, rumble and trumpet which alerted matriarch, Zira, who ran to them from 120 m away. Paused in trees behind family and then initiated attack with a Perpendicular-Walk and a 50 m Charge followed half-way by family. Head-Butted back of open Land Cruiser several times. A tourist jumped out of vehicle and hid in bushes.
2016	Scientists, (DG, JD), 3 pax	Off	Adult female tuskless	Stephanie	Charged from 80 m, paused at 20 m, Charged again. Head-Butted bonnet and left fender and smashed window, tried to flip Land Cruiser.
2016	Scientists, 3 pax	On	Adult female, tuskless	Unknown, no photos	Charged from 100 m, paused 1 m from car, walked around it, went back into forest. Returned Charging then shuffled toward vehicle, got down onto knees and Head-Butted the bonnet of the vehicle three times lasting about five seconds. Stood-Guard for 30 minutes and then Charged again chasing car down road for 15 seconds.
2017	Scientists, 2 pax (JP, PG)	On	Adult female tuskless	Akashinga	Solitary Charge from 200 m, paused on road in front of the open Land Cruiser before crossing track to the other side. Hid behind tree peering out with one eye and then the other. Charged again, from 25 m then shuffled toward the Land Cruiser, lowered body and head and Head-Butted bonnet and right fender for ten seconds. Put trunk under vehicle as if to flip. Sustained Charge of 300 m as we drove away.
2017	Guide, ~5 pax	Off	Adult female tuskless	Stephanie	Driving off road. Family group seen running then Stephanie charged from 70 m with family following. Paused at 20 m. Led family away, engaged in Rear-Guard, retreated to 70 m. Charged with family following and Head-Butted side of open Land Cruiser for 20 seconds; got head inside vehicle with tourists, damaged middle back seat of vehicle and was in contact with several people who sustained bruises from her or from falling out of vehicle on other side.

Table 4. (a) Typical and idiosyncratic defensive behaviours of some adult females (and see Fig. 10). (b) Defensive family traditions. An explanation of capitalized behavioural terms can be found on *The Elephant Ethogram*

Family (no. of individuals)	Name (age class)	Leadership status (when applicable)	Tusks	No. of sightings (no. of times as leader of aggression)	Typical defensive behaviour (% aggressive incidents in which behaviour observed)
	a. Examples of individual or idiosyncratic defensive behaviour				
I (30–35)	*Iphigenia* (4)	Led sub-group	2	13 (6)	Highly dramatized Perpendicular-Walk with Chin-Up (100%; Fig. 10b), Stood-Guard, Charged in short bursts.
	Iria (4)	Led sub-group	0	38 (1)	Peaceful, relaxed female. Very little reaction from her and her sub-group when approached beyond some vigilance (97% of sightings).
C (35–40)	*Camilla* (4)		0	22 (3)	Placed herself between family and vehicle and Stood-Guard over vehicle for long periods. Threatened us if we made a move (66%); engaged in short Charges (100%).
	Corajosa (3)		0	33 (15)	Uppity agitator. Charged frequently and incited others present (100%).
M (34–40)	*Provocadora* (5)	Matriarch (previously)	2	13 (5)	Instigator, until her death in 2014. Initiated aggression with purposeful Perpendicular-Walk signalling to *Valente*, *Mwana Nzo* and *Marcela* (see below) to take over with a coordinated Group-Advance or Group-Charge (80%).
O (10)	*One Tusk* (5)	Matriarch	1	10 (5)	Engaged in sustained solitary Charges (80%) up to several hundred meters; returned at run to vocalize and 'High-Five' (see Fig. 10 legend) with waiting family.
A (20–25)	*Ambuscadora* (4)		2	4 (3)	Ambusher. Burst out of the forest at high speed, sustained Charges of up to several hundred meters (100%), gave Trumpet-Blasts and punched ground with audible Trunk-Bounces (75%).
S (15)	*Stephanie* (5)	Matriarch	0	5 (3)	Very aggressive; engaged in sustained Charges (100%). Once led wall of 25 elephants in sustained 100 m Charge (Fig. 10d). Damaged two vehicles following sustained Charges (See Table 3).
ab (20–25)	*Akashinga* (4)	Matriarch	0	3 (3)	Very aggressive (100%). Charged from long distance (>150 m; 66%) and chased vehicles for up to 300 m (66%). Charged and then lowered head, pounded ground with Trunk-Bounces (66%); once came within <1 m of hitting vehicle, and on another occasion Head-Butted a vehicle (see Table 3).
Z (25–30)	*Zira* (5)	Matriarch	0	4 (4)	Very aggressive. (100%) Attacked three vehicles (see Table 3) and almost hit the vehicle on a fourth occasion.
	b. Examples of defensive family traditions				
M (34–40)	*Valente* (5)	Matriarch (current)	2	37 (10)	In response to *Provocadora*'s instigation (see above) and, after her death, of their own volition, these three engaged in highly coordinated and sustained Group-Advances and Charges (91% of 11 sightings when aggression occurred and all three were noted as present); one lasted eight minutes during which they alternatively shared the lead, as if in relay race. Typically, the entire family of 34 individuals participated. Often Coalitions began with, and successful.
	Mwana Nzo (4)		0	35 (14)	
	Marcela (4)		2	20 (8)	Group-Advances/Charges were celebrated with, loud vocalizations and 'High-Fiving' between the lead females (n = 9; Fig. 10c). *Mwana Nzo* was notorious. She was most vigilant, typically took lead alerting *Valente* of trouble. She was backed up by *Valente* and *Marcela*.
I (30–35)	*iJunia* (5)	Matriarch	0	27 (6)	Presumed mother and daughter look-alikes who postured, gestured with heads and trunks, and moved in such remarkable synchrony as if choreographed (100% of four sightings when aggression occurred, and both were present; Fig. 10b). Toward the end of the study a third, younger female participated.
	Isabella (4)		0	21 (4)	

Figure 10. Some females adopted idiosyncratic defensive behaviours and some families appeared to have defensive traditions. (a) *Iphigenia* adopts an exaggerated Perpendicular-Walk; (b) *iJunia* and daughter, *Isabella*, move in synchrony; (c) *Valente* and *Mwana Nzo* engage in a 'High-Five' (heads raised, open mouths, trunks entwined in victory) after a Group-Charge and as they prepare again to see us off; (d) *Stephanie* and *Berta* lead a sustained Group-Charge as calves and infants join in (© *Joyce Poole*)

Comparison with other poached populations

The four heavily poached populations surveyed in 1989 (in Kenya, Tanzania and Uganda) differed from each other and from the Gorongosa population in their response to our vehicle (Fig. 12). In the open habitat of Uganda's Queen Elizabeth NP, the majority of the population moved in one semi-permanent aggregation of 170 elephants (observed for four days) and permitted close approach (~30–40 m). In Tanzania's Mikumi NP, where the habitat was generally denser, many of the remaining elephants sought safety near the lodge and Park headquarters in small fragmented and orphan groups. They permitted approach to a median distance of 150 m (IQ range 97–200). In the mixed open savannah bushland of Tsavo East NP and Tsavo West NP in Kenya, elephants were more likely to Retreat-from or Panic-Run from vehicles sometimes from up to a kilometre away. In both populations the median distance we observed elephants was 200 m (IQ range: Tsavo East NP 150–350; Tsavo West NP 100–500). While the response pattern of Tsavo East NP and Tsavo West NP was similar, the groups in Tsavo West NP were twice as likely to Panic-Run than those in Tsavo East NP. At the time of the 1989 survey, heavy poaching was ongoing in Mikumi NP and in Tsavo NPs and had only recently declined in Queen Elizabeth NP. The Gorongosa elephants lived in the densest habitat and were the most likely to respond aggressively to vehicles, despite poaching having ended decades previously.

Discussion

In 1972, prior to the Mozambican civil war, 22,000 tourists visited GNP. Those who lived there or visited Gorongosa NP at that time agreed that the

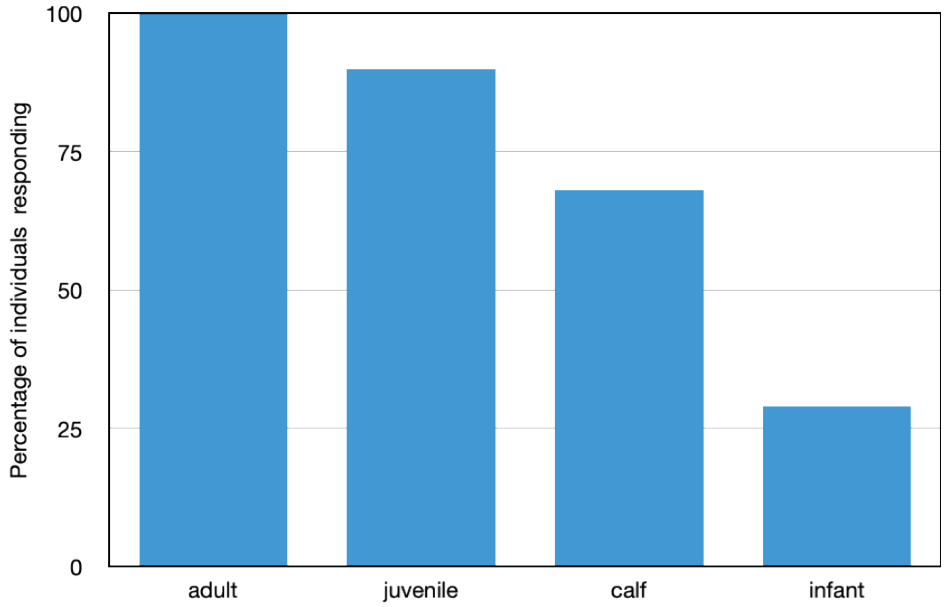

Figure 11. Frequency of vigilant behaviour by differently aged family members in response to adult female behaviour; scored from 22 videos illustrating the following stationary vigilant behaviours: Head-Swinging, Chin-Up, Periscope-Trunk, Standing-Tall. The number of individuals observed in the videos are listed above each column.

elephants were calm and unaggressive. In 1977 Mozambique entered a 15-year civil war during which hostilities raged in and around Gorongosa NP and >90% of the elephant population were killed by soldiers hunting for meat and ivory with automatic weapons. After the war until about 2016 there was subsistence bushmeat snaring in Gorongosa NP. Despite human activity, however, records indicate that human-induced elephant mortality was relatively low (Poole and Granli 2022).

Nineteen years after the war ended, when we began our study, the elephants were highly aggressive. The war had imposed a 'landscape of fear' for elephants causing them to abandon huge areas of the Park (Stalmans and Peel 2020) and to adjust their behaviour, avoiding roads where they might expect to encounter humans (Gaynor et al 2018). Elephants often appeared vigilant in photographs captured by our trail cameras placed along the Pungue River (Fig. 1), where they might expect to meet people.

We found aggressive behaviour towards vehicles to be common, although almost exclusively among females and family groups. Several factors affected whether a family in Gorongosa NP charged, including the distance between the vehicle and the elephants, whether the vehicle was on or off the road, and the age and personality of the matriarch or other lead females. The closer the vehicle, the more likely family groups were to act with aggression. Furthermore, they were more likely to respond aggressively if a vehicle was on the road, and to retreat if it was off the road. The vehicle's speed, the noise it or its occupants created, and the respectfulness of their approach, may also have been factors. Furthermore, the response of some drivers to depart in haste when threatened may also have stimulated elephants to charge and chase vehicles.

The dense vegetation in Gorongosa NP meant that the presence of elephants was often not detected until a vehicle was upon them. Since elephants were more likely to respond with aggression when vehicles were on roads and in close proximity, the lack of visibility meant that one could come upon elephants unexpectedly, some of whom became confrontational. We know from our camera trap study (Gaynor et al. 2018) that, generally, elephants actively avoided roads during game drive hours when they expected vehicles to be present. We also know from our audio recordings from Amboseli (JP), and from our observations of elephants in Tsavo West NP, that elephants can detect

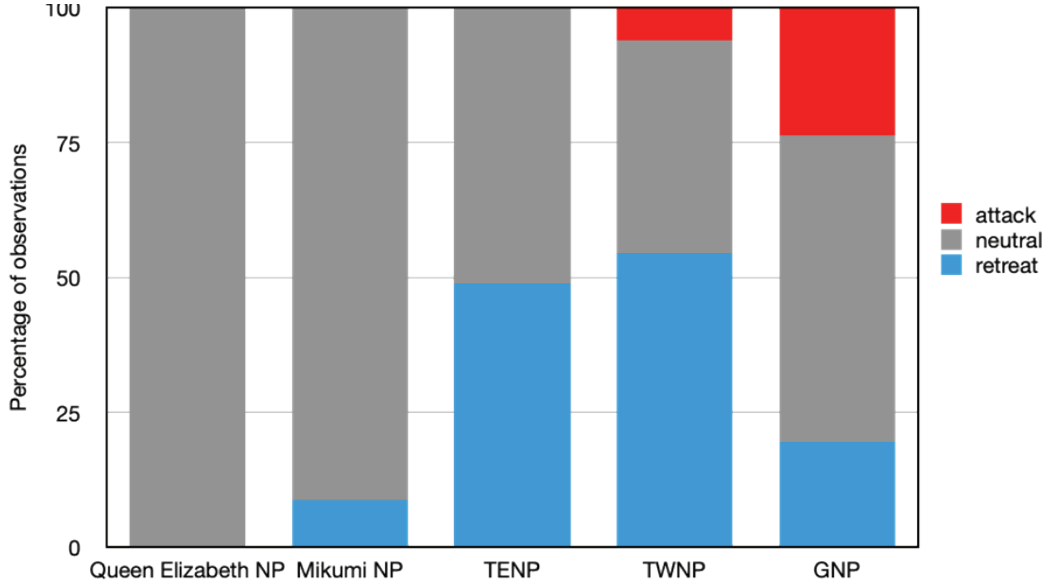

Figure 12. Responses of elephant groups to vehicles in several heavily poached populations illustrating the distinctive patterns of response. The numbers at the top of each column refer to the number of groups observed (parentheses = total number of elephants observed).

the sound of vehicles from up to 1.5 km away. This begs the question: If elephants could hear or feel us coming, why didn't they move further away so as to avoid confrontation? While we were likely unaware of the departure of some elephants due to the dense habitat, aggressive behaviour was remarkably prevalent given the elephants' ability to avoid us if they wanted to. It is quite possible, even probable, that some individuals were seeking confrontation. Indeed, our data showing that elephants were more likely to attack when vehicles were on the road suggest that some individuals may have been waiting for us.

It is also possible that elephants just did not want to move. Examining the situation from an elephant's perspective, since they knew when vehicles were approaching, they may have assumed that *we also knew that they were present*. If so, they may have wondered why we were being so provocative. While this is pure conjecture, when dealing with an intelligent social animal capable of empathy (Bates et al. 2008), reasoning and coordinated planning (Poole 2011), it is unwise to discount such possibilities when searching for solutions to conservation problems.

Although eight of the nine attacks on vehicles were by tuskless females, the widely held belief that tuskless females are more aggressive than tusked females was not born out by the overall data on aggression. Among the older cohort of females who were born before the war there was no indication that tuskless females were more likely to Charge than two-tusked or one-tusked females.

Personality, idiosyncratic behaviour, and family traditions (Fragaszy and Perry 2003; Whiten 2017), where two or more individuals from the same family engaged in distinctive defensive behaviour that persisted through time, all played a role in the overall culture of aggression that characterized the Gorongosa population post-civil war. Some individual females were more aggressive than others. Others adopted specific idiosyncratic defensive behaviours, or routines, that were repeated and could be expected of them. For example, extreme postures or actions (e.g. exaggerated Perpendicular-Walk, exaggerated Standing-Tall), manner of Charging (e.g. ambush, sustained lone Charge, Charge in short bursts), Standing-Guard over the vehicle, attempting to cut it off by taking short cuts, or by using a Perpendicular-Walk to instigate other members of the family to mob the vehicle (Poole and Granli 2021 and *The Elephant Ethogram*). Family traditions included, for example, highly synchronized "mirroring" of movement among closely bonded members of a family; engaging in

'High-Fiving' during initiation and conclusion of highly coordinated and strategic mobbing; and the tendency of others to hold back while their leader engaged in a sustained lone Charge. The existence of family traditions, that persisted over time and involved the addition of new practitioners, suggests that elephants are learning distinctive defensive behaviour from one another (i.e. via social learning). Such behaviours are likely to be established through the example of older females.

Young Gorongosa elephants learned defensive behaviour in the context of their families. While older females disproportionately took the principal role in initiating and leading Advances and Charges, 68% of these events involved the entire family following the initiator. During Group-Advances and Group-Charges, calves rushed at the vehicle alongside older females. While very young elephants likely learned to view vehicles as a threat in this social context, it is also true that they might have simply been running to stay close to their mothers without being cognizant that they were engaging in mobbing. However, the fact that calves remained with other members of the family when their mother engaged in a lone Charge, suggests learned behaviour, as did the acquisition of vigilant behaviour directed at vehicles.

Vigilant behaviour was typically initiated by an adult female and quickly adopted by other members of her family, who were either also aware of the perceived threat or were alerted to it by her or others' behaviour. We found that once one elephant exhibited vigilant behaviour, all other adult females (100%) present followed suit, while the likelihood that immature elephants did so depended on their age, with infants and calves sometimes apparently unaware of the concerns of their elders, attempting to suckle as their mothers threatened the vehicle. Ninety percent of juveniles and adolescents, 68% of calves and only 29% of infants engaged in vigilant behaviours when adults were vigilant.

The increase in the expression of vigilant behaviour with age supports the argument that young elephants learn from their elders to be aggressive toward vehicles. The pattern of aggression we observed among Gorongosa elephant families led by survivors of civil war is a long-term consequence of the trauma these individuals experienced as calves. With these individuals now acting as role models (Bates et al. 2010), the participation of their daughters and granddaughters is evidence of the transfer of behaviour across generations and families creating an elephant culture of aggression. Thirty years after the end of the war, during which the levels of recorded human induced mortality have been very low (Poole and Granli 2022), infant elephants are still learning to respond to vehicles with aggression.

Our data suggest that while the level of aggression exhibited towards vehicles by well-known families and particular individuals is decreasing, change is extremely slow. The process of habituation is hampered by several factors including: relatively few visitors to the Park, only a small part of the Park being accessible by road, and the core tourist section being subject to annual flooding and closed to traffic for a third of the year. Thus, the opportunity for individual elephants to learn that vehicles no longer present a threat is low, even for the minority of families whose core range lies in the vicinity of the primary road network (Poole and Granli 2022).

As we document in this paper, elephant behaviour toward humans varies among populations, presumably due to environmental differences and unique historical experiences, and because individuals learn from one another in a social context. In other words, we argue, elephant populations develop different culturally learned behavioural variants. Of relevance to conservation are questions such as: How long does it take for such behavioural variants to become established, or be modified, and through what transformative processes? Furthermore, are there management interventions we can adopt to facilitate change in a desired direction?

In Pilanesberg NP, South Africa, for example, the unwanted behavioural variant involving the killing of rhinos by young males in musth was halted by the introduction of higher-ranking male role models (Slotow et al. 2000).

In Amboseli NP, despite increasing human, livestock and elephant numbers, there is now more tolerance between people and elephants encouraged by an intervention implemented through the Amboseli Trust for Elephants that involves consolation payments for livestock killed in exchange for a pledge not to retaliate by spearing (Sayialel and Moss 2011).

In Gorongosa NP, we recognized that the culture of aggression was caused by the elephants' traumatic history. As a Park management intervention, we

collectively promoted consistent respectful interactions with elephants to allay their fears and to build trust (Poole et al 2023). Although we have documented a decline in the frequency of severe aggression, with no physical attacks on vehicles since 2017, and a decline in the frequency of charging behaviour among specific individuals, we cannot prove that this is a direct result of our management intervention. As long as hostilities do not resume, however, we believe that the elephants' culture of aggression will gradually abate as the number of responsible visitors increases and the road network is expanded, and as elephants learn from one another that vehicles are not a threat.

Elephants have been killed by humans at least since the Palaeolithic era (Agam and Barkai 2018). We would argue that the elaborate, flexible, and strategic behaviours and gestural and vocal communication exhibited by elephants in their complex anti-predator reactions (Poole and Granli 2021) are likely an adaptive response shaped, in part, by confronting these cunning human predators over millennia.

In recent centuries, however, the use of modern weapons and sophisticated technology in the targeted mass killings of elephants has resulted in populations that exhibit hyper-aggression, extreme fear, abnormal behaviour and impaired decision making (Bradshaw et al. 2005; Slotow et al. 2000, 2008; Shannon et al. 2013). Furthermore, because elephants learn in a social context, particular behavioural responses to traumatic events or historical experiences can be transmitted through groups to give rise to culturally learned behaviours that persist over time and generations. Our assessment is that witnessing the slaughter of other elephants during the Mozambican civil war caused the aggressive and fearful patterns of behaviour, giving rise to the different family traditions and the population level cultural variant that we observed among the Gorongosa elephants.

Our findings indicate that the flexibility of elephant behaviour (Poole and Granli 2021) combined with their ability to learn in a social context (Bates et al. 2010; Chiyo et al. 2012), can result in distinct culturally learned behavioural variants in response to a range of anthropogenic threats and differing environmental circumstances. Such variants are exemplified by the behavioural patterns we observed in Gorongosa NP, Queen Elizabeth NP, Mikumi NP, Tsavo East NP, Tsavo West NP and Maasai Mara NR and further supported by studies in Amboseli NP (Bates et al. 2007; McComb et al. 2014), Pilanesberg NP (Slotow et al. 2000) and elsewhere.

Behavioural variants can have implications for elephant conservation and management, with potentially negative ramifications for human–elephant co-existence as well as for revenue streams from tourism. Furthermore, elephants who put considerable time into avoiding or attacking humans are using energy that could otherwise be spent on survival and reproduction (Brakes et al. 2021). Since cultural variants may affect the viability of populations, our ability to recognize and adapt management interventions to them (Sayialel and Moss 2011; Slotow et al 2000; Poole et al 2023) will impact the results of conservation efforts focused on this endangered species (Brakes et al. 2021).

While the elephants of Gorongosa NP are, at least numerically, on the road to recovery (Poole and Granli 2022), many populations of traumatized elephants are less fortunate. Given rapid environmental change, increasing contact between elephants and people, and the extreme losses caused by poaching and armed conflict, a better understanding of the role culture plays in the response of elephants to people is urgently needed. Conservation and management strategies may have to be adapted to meet the changing cultures of specific elephant populations.

Acknowledgements

We thank the Government of Mozambique for permission to work in Gorongosa NP. We are grateful to our colleagues Marc Stalmans, Tonecas Paolo, Mike Marchington, Rui Branco and the many scientists and guides who photographed and recorded elephant groups for us. GNP Communications Director Vasco Galante, and Tourism Manager Test Malunga helpfully provided us with records of the numbers of tourists and vehicles entering the park. Special thanks to Lucy Bates and two anonymous reviewers for their helpful comments and to Suzannah Goss and Andrew Halliday for their careful editorial work, which improved the manuscript. We gratefully acknowledge support from the Elephant Crisis Fund, National Geographic,

WildiZe Foundation, Crystal Springs Foundation, The Elephant Sanctuary, the Marshall Frankel Foundation, the Aall Foundation, the Oakland Zoo, the Gorongosa Project and USAID.

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