African elephant reintegration from captivity to wild living: quantifying the detailed behavioural changes

Tamara Eggeling[1]¶, Tenisha Roos[1]¶*, Victoria L Boult[2], Brett Mitchell[1], TJ Steyn[3]*

[1]Elephant Reintegration Trust, Port Alfred, South Africa
[2]Department of Meteorology, University of Reading, RG6 7BE, UK
[3]Shambala Private Game Reserve, Vaalwater, Limpopo, South Africa

¶Contributed equally to this work
*corresponding authors: tammy@elephantreintegrationtrust.co.za; tenisha@elephantreintegrationtrust.co.za;

Abstract

There is increasing evidence of compromised welfare for captive African savannah elephants managed in confined spaces. With the trend for zoos and captive facilities to close due to public pressure, reflecting ethical concerns, and their limited capacity to manage 'difficult' behaviours, elephants will continue to require rehabilitation into free-ranging areas or living in the wild. During reintegration from captivity into a free-roaming system, management methods need to be carefully considered to ensure the individual's welfare. Elephants have a sophisticated social life and exhibit complex body language, employing a multitude of behavioural signals and gestures to demonstrate their needs or feelings. These detailed signals could be valuable when assessing the welfare status of elephants as any large deviation in behaviour could indicate changes in elephant wellbeing. In this study, a group of African elephants (*Loxodonta africana*) were monitored as they transitioned from captivity to a free-roaming system. To track the impact of reintegration on elephant welfare, we recorded frequencies of behaviours categorized as Ambivalent, Assessing, Frustrated, and Social, and of specific behaviours within each category, across four phases of reintegration into the wild (Stables, Boma, Release and Free). Significant differences in rates between reintegration phases were observed for several categories of behaviour and specific behaviours. Decreased frequencies of Frustrated behaviours and an increase in social behaviours when the elephants were Free were potentially indicative of improved welfare in wild settings. We conclude that monitoring of behaviours is important when assessing elephant welfare and to establish the success of reintegration operations.

Résumé

De plus en plus d'éléments tendent à montrer que le bien-être des éléphants vivant en captivité dans des espaces confinés est compromis. La tendance étant à la fermeture de ces installations — du fait de la pression du public qui manifeste des préoccupations éthiques et en raison des capacités limitées dont elles disposent pour gérer les comportements « difficiles » — les éléphants qui y résident continueront de devoir être réintroduits dans des zones de liberté ou en pleine nature. Les méthodes de gestion de la conservation doivent être soigneusement étudiées afin d'assurer le bien-être des animaux durant le processus de remise en liberté. Les éléphants ont une vie sociale sophistiquée et ils emploient un langage corporel complexe, fait d'une multitude de signaux comportementaux et de gestes leur permettant d'exprimer leurs besoins ou leurs ressentis. Ces signaux élaborés peuvent s'avérer précieux dans l'évaluation de leur niveau de bien-être, tout écart important de comportement indiquant potentiellement des variations dans leur équilibre. Dans cette étude, un groupe d'éléphants d'Afrique (*Loxodonta africana*) a été placé sous surveillance lors de sa remise en liberté après captivité. Afin d'évaluer l'impact de la réintégration sur le bien-être des éléphants, nous avons enregistré des fréquences de comportements, répertoriées dans les catégories suivantes : « ambivalent », « en

recherche de repères », « nerveux » et « sociable », ainsi que les comportements spécifiques au sein de chaque catégorie, sur quatre étapes de réintroduction dans la vie sauvage : « en étable », « en boma » (abri temporaire), « remis en liberté », « libre ». Des différences significatives de taux ont été relevées entre les différentes phases de réintégration pour plusieurs catégories de comportements et de comportements spécifiques. Une baisse de fréquence des comportements « nerveux » ainsi qu'une hausse des comportements « sociables », relevées lorsque les éléphants se retrouvaient « libres », indiquent potentiellement une amélioration du bien-être de ces animaux dans un contexte sauvage. Nous en tirons les conclusions selon lesquelles la surveillance des comportements est importante lors de l'évaluation du bien-être des éléphants, et une observation minutieuse des comportements devrait être mise en place pour des opérations de réintégration réussies.

Introduction

Elephant reintegration is an increasingly relevant concern among animal welfare and conservation organizations, tourists, and tour operators (Doyle 2017; Bansiddhi et al. 2018). Elephant reintegration (or rewilding) refers to the process of facilitating a transition from captive to free roaming, defined as occupancy of an area that is large enough to allow for natural home range size, foraging possibilities, and social interactions with other elephants within a representative age and sex structure (Baker and Winkler 2020). During reintegration from captivity into a free-roaming system, conservation management methods need to be carefully considered to ensure the animals' welfare. Elephants, have a sophisticated social life and exhibit complex body language, employing a multitude of behavioural signals and gestures to demonstrate their needs or feelings. These detailed signals could be valuable when assessing the welfare status of elephants as any large deviation in behaviour could indicate changes in elephant wellbeing.

Although some scientists have questioned the ability of captive elephants to adapt to unfamiliar environments (Doyle 2017; Bansiddhi et al. 2018), numerous successful elephant reintegration operations have been reported in recent years (see for example Evans et al. 2013a, 2013b). This is encouraging since there is increasing evidence of compromised welfare of African elephants managed in captivity (Pretorius et al. 2023). With the trend for these facilities to close due to public pressure in response to ethical concerns and their limited capacity to manage 'difficult' behaviours, elephants will continue to require rehabilitation and reintegration into the wild (Rees 2021). However, fenced reserves that receive captive elephants are not always equipped to facilitate complete reintegration into free-roaming areas due to lack of space and adequate vegetation to allow the elephants to sustain themselves. To address this problem, some partially reintegrated elephants are subsequently translocated to another, larger reserve, sometimes in another province, where they can be fully integrated into a wilder system. The success of reintegration, especially when individuals are translocated to a novel environment (Goldenberg et al. 2022), depends on the behavioural flexibility of the species (Roos et al. 2024). Learning ability and behavioural plasticity are positively associated with animal brain size (Sol and Lefebvre 2000). Elephants have large brains and are recognized as being intelligent, self-aware, and socially complex (Mellor 2019). The combination of these qualities suggests that elephants exhibit unusual potential for successful release and rehabilitation into a novel and natural system.

Inevitably, elephants in both captive (Morgan and Tromborg 2007) and wild environments (Szott et al. 2019; Garai et al. 2022) will experience stressors, though the cause and duration (acute or chronic) will differ (Stead 2000). In more natural settings, elephants regularly face a variety of natural stressors associated with finding fodder and water, avoiding predators, disease, injury, and interacting with other elephants (Stead 2000). In captive settings, stressors are related to restricted freedom of choice and lack of opportunity for avoidance of, or flight from discomforts in their environment (Morgan and Tromborg 2007). The consequences of such chronic stress are manifested as increased abnormal behaviour (Carlstead and Brown 2005), increased vigilance behaviours (Carlstead et al. 1993), reduced behavioural complexity (Rutherford et al. 2004) and increased aggression (Bartolomucci et al. 2004).

Various methods have been developed to evaluate animal welfare (Jordan 2005; Boissy et al. 2007). One

such method assesses whether or not the basic welfare needs of an animal are being met according to the 'Five Domains Model' (i.e. nutrition, environment, health, behaviour, and mental state) (Mellor 2017). This approach acts as an effective baseline but is open to interpretation. Dawkins (2008) reports behavioural and physiological abnormalities in apparently healthy animals and suggests that these factors should also be included in welfare assessments. Stressors can lead to repetitive self-directed behaviours (SDBs; Manning et al. 2022) or stereotypic behaviours. These can be considered a form of displacement activity, with no apparent function, and as such are valuable indicators of discomfort (Whitehouse et al. 2022). They are linked to stress and anxiety in primates such as chimpanzees and baboons and have been reported across a range of other species including rats and domestic chickens (Troisi 1999). SDBs and are a potential but still infrequently utilised behavioural marker in elephants, and could include behaviours such as 'brushing face', 'touching face', and 'touching mouth', which are considered useful welfare indicators (Mason and Veasey 2010; Manning et al. 2022). For example, Manning et al. (2023) report decreased frequencies of self-directed touching in captive elephants when tourism numbers declined during the Covid-19 pandemic (Manning et al. 2023). Studies of several successful elephant reintegration operations evaluate the health of elephants (dung, body condition), general behaviour (activity budget), ability to form social bonds, movement patterns, breeding success, and their interaction with surrounding human communities (Evans et al. 2013a, 2013b; Perera et al. 2018). However, despite the recognition of the importance of behaviour, few studies of such conservation management interventions monitor the frequencies of different behaviours (Veasey 2006).

Elephants naturally display a wide range of behaviours in different contexts, under both stressed and unstressed conditions (Poole and Granli 2011). Specific behaviours can act as an indication of an elephant's likely response to stimuli (Poole and Granli 2011). Similar to Garai et al. (2022), we looked at a range of behaviours, grouped into four categories: Social (affection and reassurance), Ambivalent, Frustrated, and Assessing. In a natural system, elephants exhibit social behaviour in the form of play, advertisement or attraction, reassurance, protection, and affection (Poole 2011). Social behaviours considered in this study, included only those that involve interactions with another elephant to demonstrate affection or provide reassurance. Ambivalent behaviours express uncertainty and indecision (Poole and Granli 2011). Frustrated behaviours are associated with displeasure and may occur when key stimuli are absent or in response to physical (tethering) or social barriers (Broom 1985). Assessing behaviours involve paying attention to the environment by smelling, observing, and listening (Poole and Granli 2011). However, behavioural expression is not uniform across individuals (Yasui et al. 2013) and varies by age, sex (Garai et al. 2022, Poole and Granli 2011), personality (Poole 2011) and past experience (Morgan and Tromborg 2007).

The objective of this study was to determine how the transition from captive to wilder living altered the expression of specific behaviours of a group of African elephants. Behaviours that fell within the four behavioural categories (Ambivalent, Assessing, Frustrated, and Social) were assessed to determine changes in their frequencies. We hypothesized that the frequency and array of specific behaviours and behavioural categories would differ across the four phases of transition to wild living, namely Stables, Boma (an enclosure of a specified size), Release, and Free, and that age and sex may further alter elephants' behavioural responses. More specifically, we predicted that reintegration into a wilder environment would lead to a decrease in behaviours associated with Frustration and Ambivalence due to less direct human intervention, less restriction, and more freedom of choice. Furthermore, we predicted an increase in behaviours associated with Assessment as elephants were exposed to environmental stimuli and began to rely on their own senses without human intervention. Additionally, we hypothesized an increase in Social (affective and reassuring) behaviour as interaction forms a crucial part of the daily lives of free-ranging elephants. We propose that such changes would be indicative of improved welfare.

Methodology

Study site

The study was carried out in the Shambala Private Game Reserve (SPGR) located in the Waterberg
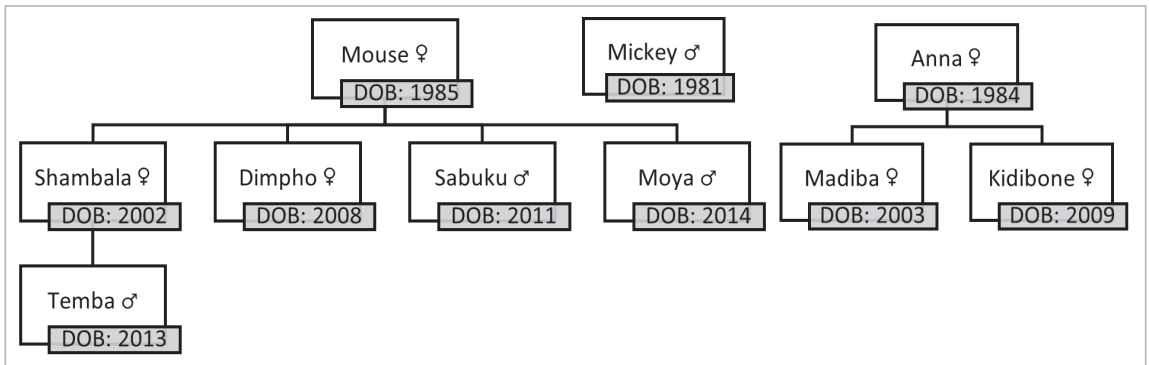
Figure 1. Family tree of study animals on SPGR, showing the date of birth (DOB) and the sex of the elephants.
Anna, Mickey and Mouse came from Sondalani in Zimbabwe and were previously used for riding safaris, Dimpho was previously used for riding safaris within SPGR, but no longer is. Madiba, Moya, Sabuka and Temba were housed in a captive facility at SPGR and now have access to the entire 10,000 ha free release section of SPGR.

Mountain region (Limpopo Province) of South Africa. This 10,000ha fenced reserve falls within the central bushveld bioregion of the savannah biome (Rutherford et al. 2006) and covers most of the elevated plateau west of the slope from the Magaliesberg in the south to the Southpansberg in the north.

The reserve hosts a variety of herbivores such as steenbok (*Raphicerus campestris*), impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*) and white rhinoceros (*Ceratotherium simum*). The predator species present include spotted hyena (*Crocuta crocuta*), lion (*Panthera leo*) and leopard (*Panthera pardus*).

Study animals

SPGR currently hosts 14 elephants, ten of which were previously kept in captivity (Fig. 1). In 2002, SPGR acquired three of these study elephants (one male, Micky, and two females, Mouse and Anna) from a captive elephant facility in Zimbabwe. These elephants were originally captured as calves following culling operations that took place in Gonarezhou National Park (NP), Zimbabwe, in the 1980s. Once at SPGR, these elephants and later some of their offspring (Shambala and Madiba) were used to conduct Elephant Back Safaris, once a day, for 12 years (2004–2016). The rest of the offspring, though not ridden, were held in the same captive conditions. Elephant Back Safaris operated for approximately one hour each morning, and then the elephant handlers guided the elephants out into the reserve to forage for the remaining daylight hours before returning them to their stables at night. The stables consisted of secure holding enclosures designed to separate the elephants from each other and were locked at night. The calves (Temba and Moya) were not separated from their mothers (respectively, Shambala and Mouse) at night. In 2019, two additional calves were born at SPGR (one to Mouse, and the other to Shambala) and in 2022 two subadult bulls were translocated to SPGR. These four individuals were not part of this study as they were not subjected to the reintegration process.

Captivity does not provide a sufficient environment for the social- and space requirements of an elephant. To ensure this group of elephants was afforded this opportunity, a reintegration programme was designed and managed by Brett Mitchell, an elephant expert in the reintegration of captive elephants. He was assisted by experienced elephant handlers who had worked with the elephants for many years. The reintegration programme was designed to ensure the elephants attained full autonomy by reintegrating them into a larger natural system, thereby improving their well-being. The duration of each reintegration phase varied and was adapted to the elephants' requirements, based on the herd's behaviour and speed of adaptation to the new conditions. As each phase was entered, the duration was determined by the elephants' behaviour and adaption to that phase. As soon as the transition was deemed successful, the next phase was started. Table 1 summarises the duration and the description of each of the phases of reintegration.

Table 1. Breakdown of the duration and description of different phases of reintegration of SPGR elephants from captive to wilder living.

Phase	Date	Description
Stables	5–16 Mar 2016	The elephants were not ridden; however, they were managed by the handlers during the day and secured in individual stables at night. Some elephants were tethered during certain times of the day (usually when the handlers were cleaning the stables areas).
Boma	17 Mar–20 May 2016	At night, the elephants roamed freely in an electric fenced 1.7 ha (4.2 acres) open-air boma. During the day, they were allowed to roam freely from the boma on the reserve up to a distance of 5 km (under the supervision of the handlers). The elephants were returned to the boma and closed in at night.
Release	21 May–28 Jun 2016	In the penultimate stage, the boma gate was left open permanently and the elephants were allowed to roam freely on the reserve without any handler supervision. The elephants had complete autonomy within the 10,000 ha fenced reserve. Management interventions were carried out during this phase: Collar checks and removal of a collar that was on Mouse, and, where necessary, redirection by the handlers of unwanted behaviours towards infrastructure and vehicles, to prevent any human–elephant conflict.
Free	22 Jun–10 Jul 2019 28 Jan–15 Feb 2020	The elephants were roaming free for more than three years on the 10,000-hectare fenced reserve. Management interventions were carried out during this phase: Quarterly GnRH (Gonadotropin Releasing Hormone) darting of the adult bull (Micky), and, where necessary, redirection by the handlers of unwanted behaviours towards infrastructure and vehicles, to prevent any human–elephant conflict.

Data collection

Behavioural data were collected over the entire reintegration process (Table 1). However, the duration of observation periods within each phase differed. Specifically, during the Boma, Release, and Free phase, observation periods were adapted in response difficulties associated with restricted access to the elephants. Observations in the first three phases took place continually between 5 March and 28 June 2016. Observations in the Free phase consisted of two data collection periods (22/06/2019–10/07/2019 and 28/01/2020–15/02/2020), when the elephants had been roaming freely on the 10,000 ha reserve for more than three years.

During each phase of the study, multiple video recordings (focal samples of approximately 10 minutes), were taken of each elephant and processed upon completion of all fieldwork (Table 2). Panasonic and Canon cameras were used to film the elephants during the course of this study.

When filming the elephants during the Stables and Boma phases, the researcher maintained a distance of 20 m from the elephant that was being filmed. To ensure the safety of the researcher, an elephant handler was always present. Due to the arrangement of the Stable and Boma systems it was not possible to film the elephants from greater distances. During the Release and Free phases, the elephants were filmed from a game viewing vehicle which they were accustomed to. The vehicle was parked at least 30 m from the elephants to minimize disturbance. Filming during all phases was initiated only when the elephants seemed settled and were not directing attention to the vehicle or the researcher. We aimed to collect an even spread of all individuals during each phase of reintegration; however, due to restrictions imposed by the reserve's road network and topography, this was not always possible during the Release and Free phases. To account for pseudoreplication, we did not process more than one focal sample of each elephant from the same day. The focal samples processed were randomly selected, and

Table 2. The date of birth, sex, age and number of focal samples analysed for each elephant during each phase of the reintegration process. The average gap (number of days) between focal samples is also shown. A = adult; S = subadult; J = juvenile.

Name	Date of birth	Sex	Age	Stables		Boma		Release		Free	
				No.	Gap	No.	Gap	No.	Gap	No.	Gap
Anna	1984	F	A	5	1	5	2	5	9	7	3
Dimpho	2008	F	S	5	2	5	2	5	12	3	5
Kidibone	2009	F	J	6	2	4	3	4	8	4	7
Madiba	2003	F	S	5	2	6	3	4	3	4	4
Mickey	1981	M	A	4	1	6	4	5	8	7	5
Mouse	1984	F	A	5	2	5	3	5	8	4	2
Moya	2014	M	J	5	2	3	1	3	9	5	5
Sabuka	2011	M	J	5	2	5	3	5	8	6	5
Shambala	2002	F	S	5	2	4	3	4	10	2	5
Temba	2013	M	J	6	2	3	1	2	11	2	*
Total number of focal samples				**51**		**46**		**42**		**44**	

*One focal sample was taken in 2019 and one in 2020.

we only processed the samples if the elephants were fully visible. The focal samples within each phase were collected throughout the entire period allocated for the study of each of the reintegration phases. At the beginning of each focal sample, the elephant under observation was identified, with each elephant identification linked to date of birth, sex (male or female), and age (juvenile: 2–7 years, subadult: 8–20 years, or adult: >20 years) (Fig. 1).

Behavioural data processing

Prior to the study, an ethogram was compiled based on collected literature and consulted to record specific behavioural frequencies during each focal sample. Specific behaviours were contextualized prior to the study to form various behavioural categories (Table 3). The focal processing phase involved noting the number of occurrences of all specific behaviours exhibited by the observed elephant, continuously, throughout each sample. For analysis, data on the number of occurrences were transformed to show frequency of occurrence (number per minute). All focal recordings were retrospectively coded by a single researcher with considerable experience of observing elephant behaviour between October 2020 and October 2021. This approach eliminated discrepancies between multiple observers in

the coding of the behaviour data and minimized any change in interpretation over time.

For the purposes of this study, selected specific behaviours were chosen for further analysis (Table 3). However, when the behavioural categories were analyzed, all behaviours that fell into the category were considered.

Statistical analysis

We used generalised linear mixed models (GLMMs) to identify relative changes in behavioural frequencies between the four stages of reintegration. The reintegration phase, plus the age and sex of individual elephants, were included as fixed effects in the model. We included the elephant identification as a random intercept since we expected that individual variation might influence behavioural responses to the reintegration process. GLMMs were run for each of the four behavioural categories (Ambivalent, Assessing, Frustrated, and Social) and a subset of the most frequently recorded specific behaviours. All behavioural data were found to violate the assumption of normality (Shapiro-Wilk, $\alpha = 0.05$) and therefore ideally a gamma distribution would have been used for continuous, positive, non-normal distributed data. However, given the limited sample size, a gamma distribution could not converge, and so a Gaussian distribution, which remains robust to non-normal data,

Table 3. Description of the behavioural categories into which the chosen specific behaviours were categorized (Garai et al. 2022; Elephant Voices 2021, 2023). (The authors recognize that elephants in captive facilities form a close bond with their handlers, and this was factored into the rehabilitation programme on an individual-by-individual basis. For instance, the handlers themselves became monitors during the Release and Free phases, however, this was not part of the study design, nor scientifically measured. We understand that each elephant's needs are unique, again this was factored into the reintegration programme).

Behavioural categories	Selected detailed behaviours	Description
Ambivalent: Behaviours that seem inappropriate or irrelevant, often caused by a direct stimulus.	Front foot swing	Lift the front foot slightly and swing back and forth.
	Touch mouth with trunk	Elephant touches its mouth with its own trunk tip.
	Trunk in own mouth	Elephant places the tip of its trunk in its own mouth.
	Trunk twist and twirl	The trunk is folded onto itself, resulting in a twisted trunk that unwinds in a fast action.
	Hanging trunk rotate left and right	Trunk hangs straight while the tip is flicked to the left and right.
	Brushing face	Tip of trunk brushes over face (this is a fast action).
	Touching face	Touch any part of the face, including the ears with the tip of the trunk. Not a fast action.
	Swing trunk through the legs or to the foot	Trunk kept straight while being swung through front feet or touches one of the front feet.
Assessing: Gestures displayed by elephants to gain sensory information about their surroundings.	Smelling down	Trunk held in a relaxed position while the tip of the trunk is curled under and points in the direction of an object of interest.
	Lift trunk to smell	Lifts and holds the trunk up in an S-shape.
	Sudden pause to listen	Sudden, short pause during any activity to listen.
Frustrated: A range of reactions to unpleasant stimuli	Head shake	An abrupt shaking of the head.
	Throwing item	Throwing an object into the air or in the direction of the cause of frustration.
	Trunk swing/ swish	The trunk is swished/swung forward in a fast action.
Social: Behaviours displayed when elephants interact with one another. The behaviour was only noted if the focal elephant was the instigator of the behaviour.	Trunk	Touching another elephant's head, trunk, or body with its trunk.
	Trunk to mouth	Trunk to another elephant's mouth.
	Trunk on back/ head	Trunk on another elephant's back/reach over the head.
	Rub with head/ body	Rubbing against another elephant with its head/body.
	Tusk to body	The elephant gently nudges the other elephant with its tusk.
	Trunk to genitals	The elephant holds its trunk towards the genital area of the other elephant.
	Tusk to head	The elephant gently nudges the other elephant with its tusk.
	Push with head	The elephant pushes the other elephant with its head.
	Push with body	The elephant pushes the other elephant with its body.

was used throughout. Tukey's honest significant test ($\alpha = 0.05$) was used to identify significant differences between the release phases, age, and sex levels while calculating multiple comparisons. All analyses were carried out in R version 4.1.2 using the packages glmmTMB (1.1.7) and multcomp (1.4-18). None of the outliers that were identified and represented in the Fig. 2 were removed from the dataset or excluded from the statistical analysis, as these data points represent the natural variability in elephant behaviour.

Results

We observed significantly higher frequencies of Frustrated behaviour during the Stables phase compared to the Boma ($p < 0.001$) and Release phases ($p = 0.019$) (Fig. 2c; Table 4; Table A1). During the Free and Stables phases, the elephants showed significantly higher frequencies of Social behaviour compared to the Boma and Release phases (Free vs. Boma: $p = 0.006$; Stables vs. Boma: $p = 0.017$; Free vs. Release: $p = 0.007$; Stables vs. Release: $p = 0.019$) (Fig. 2d; Table 4; Table A1).

Subadult elephants showed a significantly higher frequency of Frustrated behaviour than adults ($p = 0.037$). No significant differences were reported between males and females when the frequencies of Ambivalent, Assessing, Frustrated, and Social behaviours were compared.

There were significant differences among the frequencies of specific behaviours in all four behavioural categories. Within the Ambivalent category, the 'Swing trunk through the legs or to

Table 4. Significant differences in frequencies of behavioural categories among phases of the reintegration operation.

Behavioural category	Significant differences in frequency	p-value
Frustrated	Stables > Boma	<0.001
	Stables > Release	0.019
Social	Free > Boma	0.006
	Stables > Boma	0.017
	Free > Release	0.007
	Stables > Release	0.019

the foot' was significantly more frequent during the Stables compared to the Release phase ($p = 0.031$) (Fig. 3A). The 'Touching face' behaviour was more common during the Free compared to the Release phase ($p = 0.005$) (Fig. 3A). Within the Assessing behavioural category, the frequency of 'Sudden pause to listen' occurred at significantly higher rates during the Free compared to the Stables phase ($p = 0.023$) (Fig. 3B). Within the Frustrated behavioural category, the elephants also showed significantly higher rates of 'Head shake' in the Free than during the Boma phase ($p = 0.017$) (Fig. 3C). 'Trunk swing/swish' occurred at significantly higher rates during the Stables compared to the Boma phase ($p = 0.032$) (Fig. 3C). Furthermore, 'Throwing item' only occurred during the Stables phase, and never while in the Boma ($p = 0.024$), Release ($p = 0.026$), or Free ($p = 0.029$) phases (Fig. 3C). Within the Social behavioural category, the elephants showed significantly higher frequencies of 'Trunk to another elephant's mouth' during the Stables phase compared to the Boma ($p = 0.011$), Release ($p = 0.001$), and Free ($p = 0.033$) phases (Fig. 3D). Significantly higher frequencies of 'Push with head' were observed during the Free compared to the Boma ($p = 0.01$) and Release ($p = 0.029$) phases (Fig. 3D) (Table 5; Table A2).

Discussion

Elephants communicate via a rich and complex array of behaviours (Poole and Granli 2011). Studying the occurrence and patterns of usage of specific behaviours in different contexts can improve our understanding of what these different gestures signal or express about the internal emotions or feelings of individuals. Such knowledge increases our awareness of their wellbeing (Mason and Veasey 2010), allowing us to intervene when necessary.

This study assessed whether the different phases (Stables, Boma, Release, and Free) of reintegration (transition from captive to wild living) affected the expression of specific behaviours that fall within four behavioural categories (Ambivalent, Assessing, Frustrated, and Social). We hypothesized that changes in behavioural frequencies and the array thereof would occur during the transition from a captive to a free-roaming environment, as well as between different age and sex groups. Specifically, it was hypothesized that the frequencies of Frustrated and Ambivalent behaviours would decrease and Assessing and Social
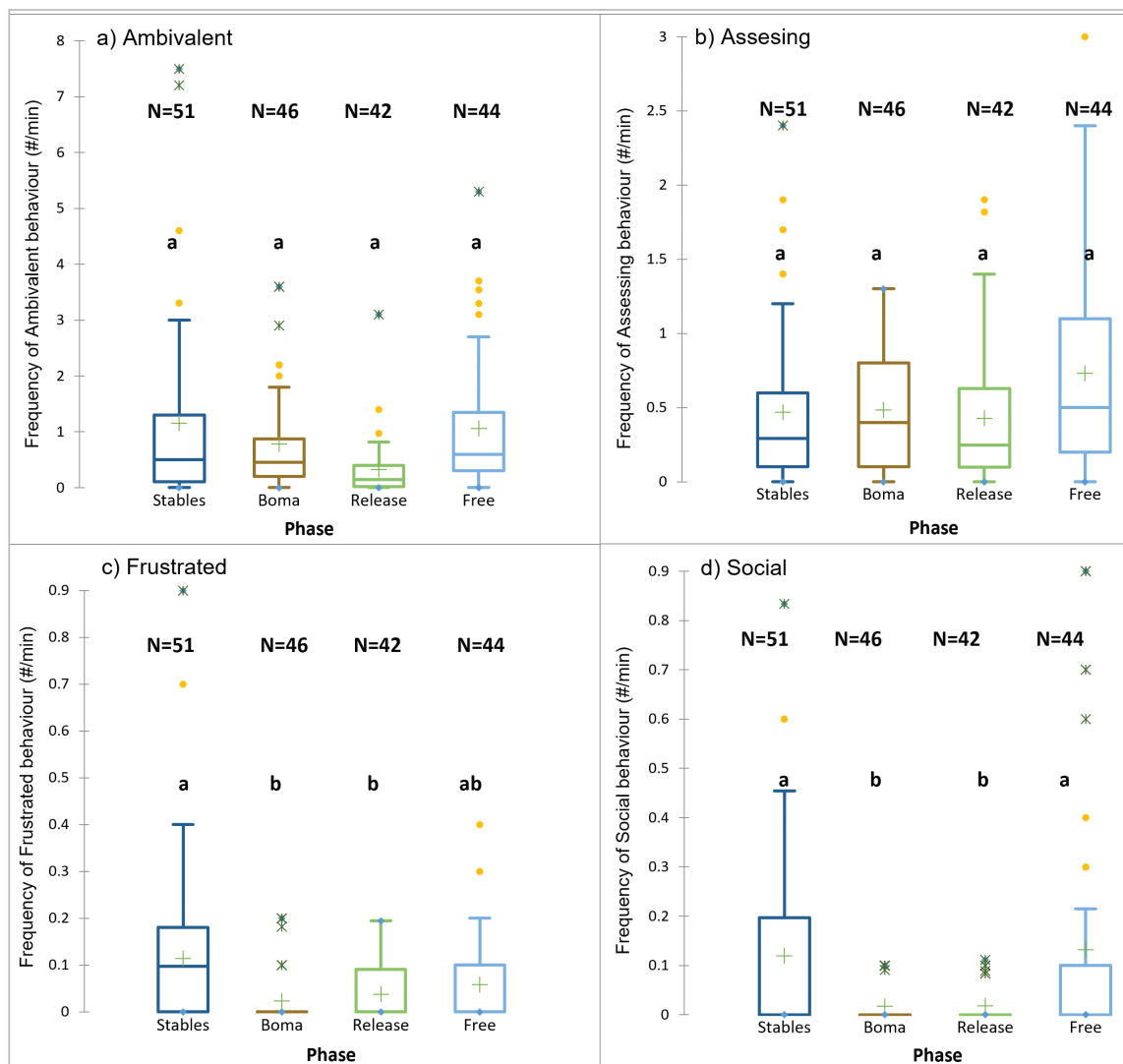
Figure 2. The frequency (no./min) of behaviours in a) Ambivalent, b) Assessing, c) Frustrated, and d) Social behavioural categories expressed by the 10 elephants during the different phases of the reintegration process. N = number of focal samples. The crosses represent means, whereas the central horizontal bars show medians. The first and third quartiles are the lower and upper limits of the box, respectively. The length of the whiskers indicates 1.5 times the interquartile range. The points above the upper limits of the whiskers are outliers. The yellow circles represent outliers >1.5 interquartile ranges from the median, and the dark green stars represent outliers >3 interquartile ranges from the median. Minimum values were zero in all cases and maximum values corresponded to the uppermost outlier. The hashtag symbol (#) indicates no significant difference between different integration phases. Asterisks indicate significant differences as follows: *p < 0.05; **p < 0.01; ***p < 0.001.

behaviours would increase in a wilder environment (Free phase). Our investigation showed significant differences among the phases of reintegration and ages for some behavioural categories and detailed behaviours.

The elephants, particularly juveniles, exhibited significantly higher rates of Frustrated behaviours during the confinement of the Stables phase compared to Boma and Release phases, suggesting that they were stressed by the captive environment. The increased levels of Frustrated behaviours during the Stables phase could be attributed to restricted movement and choice of social companions, as well as the lack of ability to escape pressure (Wiepkema and Koolhaas 1993; Morgan and Tromborg 2007). During the Stables phase, some elephants exhibited

Table 5. Significant differences in frequencies of specific behaviours among phases of the reintegration operation.

Behavioural category	Specific behaviour	Significant differences in frequency	p-values
Ambivalent	Swing trunk through the legs or to the foot	Stables > Release	0.031
	Touching face	Free > Release	0.005
Assessing	Sudden pause to listen	Free > Stables	0.023
Frustrated	Head shake	Free > Boma	0.017
	Trunk swing/swish	Stables > Boma	0.032
	Throwing item	Only occurred in the Stables phase	≈0.03
Social	Trunk to another elephant's mouth	Stables > Boma	0.011
		Stables > Release	0.001
		Stables > Free	0.033
	Push with head	Free > Boma	0.01
		Free > Release	0.029

Ambivalent behaviours up to eight times per minute. These frequencies were high compared to other phases and are higher than those reported for wild elephants (2–6 times per 10 minutes) (Garai et al. 2022). Furthermore, the higher frequency of Frustrated behaviour shown by juveniles and subadults suggests that older elephants may possess more developed skills in regulating their emotions, or be better acclimatized to captivity after living for many years in confinement.

An important factor to consider is the source of uncertainty and stress during each phase. When confined to their stables, the needs to search for food and water and to avoid predators were eliminated. This suggests that uncertainty was most likely related to the elephants' inability to escape other stressors (Morgan and Tromborg 2007), such as boredom, physical confinement that prevented elephants from interacting with or moving away from other group members, and restricted access to food and water.

Interestingly, elephants showed similar frequencies of Assessing behaviour during the Stables, Boma, and Release phases. A large, but insignificant, increase was observed during the Free phase, within which some elephants exhibited Assessing behaviours up to three times per minute. This increase could be attributed to increased exposure to natural stimuli and aligns with what is expected for wild elephants (Garai et al. 2022). When observations were made during the Free phase, the elephants had been roaming independently for more than three years, so it is probable that they had begun to recognize the need

for assessing their environment as they were no longer guided and protected by the handlers. In line with this, we also expected the frequency of Assessing behaviours to increase during the Release phase, but this was not the case. This could be because, initially after release, elephants spent more time in familiar areas and only began to roam more widely across the reserve in the Free phase.

Social behaviours were significantly more frequent and diverse in the Stables and Free phases compared to the Boma and Release phases. The lower frequencies observed during the Boma and Release phases could be attributed to the novelty of the environment, elephants' increased drive to investigate, and the freedom to explore away from the rest of the group. The Boma phase was the beginning of their life as a herd in the wild. However, the presence of their handlers may have altered the behaviour of the elephants, and they might have found familiarity or reassurance by being near the handlers. Another explanation could be that, during the Stables phase, the elephants were kept adjacent to each other in small enclosures, thus increasing the opportunity for social interactions.

The results showed differences between the array and frequencies of specific behaviours expressed by the elephants during the different phases of reintegration. This was expected as the elephants were exposed to different levels of freedom and environmental stimuli during the four phases. One Ambivalent behaviour that stood out was 'Swing trunk though legs or to foot', with some elephants exhibiting this behaviour up to 5–6 times per minute during the Stables phase, suggesting that repeated self-directed behaviours (SDBs) can represent a form of stereotypic behaviour

Figure 3. Strip plot showing the means (cross) and medians (blue line) of the most frequently recorded detailed behaviours within the categories A) Ambivalent, B) Assessing, C) Frustrated, and D) Social during the four reintegration phases. N = number of focal samples. The hashtag symbol (#) indicates no significant difference between different integration phases. Asterisks indicate significant differences as follows: *p < 0.05; **p < 0.01; ***p < 0.001.

(Elzanowski and Sergiel 2006) with no obvious goal or function (Mason 1991).

The array of Frustrated behaviours also differed across the four phases. 'Throwing item' was only observed in the Stables phase. This behaviour can be interpreted as an escalation of the 'Trunk swish/swing' behaviour and may have been common in the Stables phase due to physical restrictions (tethering) experienced. 'Throwing item' can also act as a warning signal and can become dangerous in certain situations (Poole and Granli 2011). The significant increase in 'Sudden pause to listen' (freezing) during the Free compared to the Stables phase was encouraging, possibly indicating an increased engagement with the environment and an increasing occurrence of auditory or seismic communication among individuals (Langbauer et al. 1989). It was also to be expected that the increased access to novel areas and environmental stimuli would result in heightened levels of awareness. During the Stables phase, the adults were sometimes constrained (tethered) and interactions between adults and other group members included reassurance behaviours in the form of 'Trunk to another elephant's mouth' and 'Trunk to body' of conspecifics. This was not seen at such elevated levels in the Boma, Release, or Free phases, when individuals exhibited more physically affectionate social interaction behaviours like 'Push with the head' and 'Rub with head' (social rubbing).

In this study we observed higher levels of stress and uncertainty during the Stables phase in the form of increased reassurance behaviour amongst stablemates, as well as high frequencies of self-directed touching in the form of 'Swing trunk to leg or foot' behaviour. The behaviours indicating uncertainty were mostly observed when the elephants could not escape circumstances such as being tethered or confined to the Stables without the freedom to express natural movement. We would expect significantly greater disparities between captive and free phases when elephants are initially held in more restrictive captive environments. In cases where reintegration is not a feasible option, the next most appropriate system is a genuine sanctuary. Such a captive setting represents a considerable improvement on a stable system that separates bonded individuals and is designed to ensure that the elephants experience the highest standards of welfare and complete freedom to make decisions within their (restricted) environment. This can be achieved by the creation of either single or multiple areas that are large enough to allow bonded individuals or mother and offspring to have the freedom to choose where to sleep or with whom to associate. This would reduce stress-related behaviours during captivity.

Conclusions

The results of the study suggest that the frequency and array of specific behaviours and behavioural categories differed between different phases of reintegration, although not all differences were significant. The results showed decreased frequencies of Frustrated behaviours and an increase in Social behaviours when the elephants were Free, possibly indicative of improved welfare in wild settings.

Although additional research including longer observation periods, more reintegrated individuals, larger behavioural sample size, and direct comparisons with wild elephants on the same reserve would be required to draw more concrete conclusions, the preliminary results presented here suggest that reintegration is a vital management tool to improve the welfare of captive elephants.

It would also be important to determine the timing of different phases of the reintegration process to accommodate elephants from different captivity systems. For example, elephants subjected to very restricted forms of captivity or those being reintegrated into reserves in faraway locations may require longer periods of adjustment between phases.

We acknowledge that the captive system to which these study elephants were subjected may be viewed as a more conducive to their welfare and freedom of movement compared to more restrictive captive management systems. Nevertheless, our research underscores that even these relatively improved circumstances do not allow expression of the natural behaviours observed in fully wild elephants.

Acknowledgements

References

Baker L and Winkler R. 2020. Asian elephant rescue, rehabilitation and rewilding. *Animal Sentience* 28 (1). doi:10.51291/2377-7478.1506

Bansiddhi et al. 2018. Changing trends in elephant camp management in northern Thailand and implications for welfare. *PeerJ* 6: e5996. doi:10.7717/peerj.599

Bartolomucci A, Pederzani T, Sacerdote P, Panerai AE, Parmigiani S, Palanza P. 2004. Behavioral and physiological characterization of male mice under chronic psychosocial stress. *Psychoneuroendocrinology* 29 (7): 899–910. doi:10.1016/j.psyneuen.2003.08.003

Boissy A, Manteuffel G, Jensen MB, Moe RO, Spruijt B, Keeling LJ, Winckler C, Forkman B, Dimitrov I, Langbein J,Bakken M, Veissier I, Auber A. 2007. Assessment of positive emotions in animals to improve their welfare. *Physiology and Behaviour* 92 (3): 375–397. doi:10.1016/j.physbeh.2007.02.003

Broom DM. 1985. Stress, welfare and the state of equilibrium. In: Wegner RM (Ed). *Proceedings of the Second European Symposium on Poultry Welfare*. World Poultry Science Association, Celle, Germany, pp. 72–81.

Carlstead K and Brown JL. 2005. Relationships between patterns of faecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. *Zoo Biology* 24 (3): 215–232. doi:10.1002/zoo.20050

Carlstead K, Brown JL, Strawn W. 1993. Behavioural and physiological correlates of stress in laboratory cats. *Applied Animal Behaviour Science* 38 (2): 143–158. doi:10.1016/0168-1591(93)90062-T

Dawkins MS. 2008. The science of animal suffering. *Ethology* 114 (10): 937–945. doi:10.1111/j.1439-0310.2008.01557.x

Doyle C. 2017. Captive wildlife sanctuaries: definition, ethical considerations and public perception. *Animal Studies Journal* 6 (2): 55–85. https://ro.uow.edu.au/asj/vol6/iss2/5

Elephant Voices. 2023. Ethogram table. https://www.elephantvoices.org/elephant-ethogram/ethogram-table/overview.html [Accessed Aug 112023]

Elzanowski A and Sergiel L. 2006. Stereotypic behaviour of a female Asiatic elephant (*Elephas maximus*) in a zoo. *Journal of Applied Animal Welfare Science* 9 (3): 223–232. doi:10.1207/s15327604jaws0903_4

Evans K, Moore R, Harris S. 2013a. The social and ecological integration of captive-raised adolescent male African elephants (*Loxodonta africana*) into a wild population. *PLoS One* 8 (2): e55933. doi:10.1371/journal.pone.0055933

Evans K, Moore RJ, Harris S. 2013b. The release of a captive-raised female African elephant (*Loxodonta africana*) in the Okavango Delta, Botswana. *Animals* 3 (2): 370–385. doi:10.3390/ani3020370

Garai ME, Roos T, Eggeling T, Ganswindt A, Pretorius Y, Henley M. 2022. Developing welfare parameters for African elephants (*Loxodonta africana*) in fenced reserves in South Africa. *PLoS One* 17 (3): e0264931. doi:10.1371/journal.pone.0264931

Goldenberg SZ, Chege SM, Mwangi N, Craig I, Daballen D, Douglas-Hamilton I, Lamberski N, Lenaipa M, Lendira R, Lesowapir C. 2022. Social integration of translocated wildlife: a case study of rehabilitated and released elephant calves in northern Kenya. *Mammalian Biology* 102: 1299–1314. https://doi.org/10.1007/s42991-022-00285-9

Jordan B. 2005. Science-based assessment of animal welfare: wild and captive animals. *Revue scientifique et technique (International Office of Epizootics)* 24 (2): 515–528. https://doi.org/10.20506/rst.24.2.1588

Langbauer WR Jr, Payne KB, Charif RA, Thomas EM. 1989. Responses of captive African elephants to playback of low-frequency calls. *Canadian Journal of Zoology* 67: 2,604–2,607. https://doi.org/10.1139/z89-368

Manning P, Dawson E, Tholander C, Bonato M. 2023. The effect of COVID-19 lockdown restrictions on self-directed behaviour, activity budgets, movement patterns, and spatial use in semi-captive African elephants (*Loxodonta africana*). *Applied Animal Behaviour Science* 266: 106007. doi:10.1016/j.applanim.2023.106007

Manning P, Hauff L, Padfield C, Olivier L, Ganswindt A, Young D. 2022. Can stress and anxiety be assessed in African elephants (*Loxodonta africana*) using self-directed behaviour? *Applied Animal Behaviour Science* 256: 105746. doi:10.1016/j.applanim.2022.105746

Mason, GJ. 1991. Stereotypies: a critical review. *Animal Behaviour* 41 (6): 1015–1037. doi: 10.1016/S0003-3472(05)80640-2

Mason GJ and Veasey JS. 2010. How should the psychological well-being of zoo elephants be objectively investigated? *Zoo Biology* 29 (2): 237–255. doi:10.1002/zoo.20256

Mellor DJ. 2019. Welfare-aligned sentience: enhanced capacities to experience, interact, anticipate, choose and survive. *Animals* 9 (7): 440. doi:10.3390/ani9070440

Mellor DJ. 2017. Operational details of the Five Domains Model and its key applications to the assessment and management of animal welfare. *Animals* 7: 60. doi:10.3390/ani7080060

Morgan KN and Tromborg CT. 2007. Sources of stress in captivity. *Applied Animal Behaviour Science* 102 (3–4): 262–302. doi:10.1016/j.applanim.2006.05.032

Perera BV, Jayawardena BADS, Prasad GAT, Silva-Flecher A. 2018. Back to the wild—rehabilitation of orphan Asian elephant calves in Sri Lanka. In: Soorae PS (Ed). *Global reintroduction perspectives: 2018. Case studies from around the globe*. IUCN/SSC Reintroduction Specialist Group and Environment Agency, Abu Dhabi, pp. 170–173.

Poole J and Granli P. 2011. Signals, gestures, and behaviour of African elephants. In: Moss CJ, Croze HJ, Lee PC (Eds). *The Amboseli Elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago, pp. 109–124.

Poole JH. 2011. The behavioral context of African elephant acoustic communication. In: Moss CJ, Croze HJ, Lee PC (Eds). *The Amboseli elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago, pp. 126–159.

Pretorius Y, Eggeling T, Ganswindt A. 2023. Identifying potential measures of stress and disturbance during a captive to wild African elephant reintegration. *PLoS One* 18 (10): e0291293. doi: 10.1371/journal.pone.0291293

Rees PA. 2021. The future of elephants in captivity. In: *Elephants under human care*. Elsevier, Amsterdam, pp. 313–27. doi:10.1016/B978-0-12-816208-8.00011-7

Roos T, Purdon A, Boult V, Delsink A, Mitchell B, Kilian PJ. 2024. Movement patterns of two reintegrated African elephant (*Loxodonta africana*) herds: transitioning from captivity to free-living. *PeerJ* 12: e17535. doi:10.7717/peerj.17535

Rutherford K, Haskell M, Glasbey C, Jones R, Lawrence A. 2004. Fractal analysis of animal behaviour as an indicator of animal welfare. *Animal welfare* 13 (S1): S99–S103. doi:10.1017/S0962728600014433

Rutherford MC, Mucina L, Lötter MC, Bredenkamp GJ, Smit JHL, Scott-Shaw CR, Hoara DB, Goodman PS, Bezuidenhout H, Scott L. 2006. Savannah Biome. In: Mucina L, Rutherford MC (Eds). *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia, Pretoria. pp. 438–539.

Sol D and Lefebvre L. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* 90: 599–605. https://doi.org/10.1006/anbe.2001.1953

Stead SK. 2000. The assessment of stress in captive juvenile African elephants (*Loxodonta Africana*). MSc Thesis. University of Pretoria, Pretoria, https://repository.up.ac.za/bitstream/handle/2263/29337/dissertation.pdf?sequence=1

Szott ID, Pretorius Y, Koyama NF. 2019. Behavioural changes in African elephants in response to wildlife tourism. *Journal of Zoology* 308 (3): 164–174. doi:10.1111/jzo.12661

Troisi A. 1999. Ethological research in clinical psychiatry: the study of nonverbal behavior during interviews. *Neuroscience & Biobehavioral Reviews* 23 (7): 905–913. doi:10.1016/S0149-7634(99)00024-X

Veasey J. 2006. Concepts in the care and welfare of captive elephants. *International Zoo Yearbook* 40: 63–79. https://doi.org/10.1111/j.1748-1090.2006.00063.x

Whitehouse J, Milward SJ, Parker MO, Kavanagh E, Waller BM. 2022. Signal value of stress behaviour. *Evolution and Human Behavior* 43 (4): 325–333. doi:10.1016/j.evolhumbehav.2022.04.001

Wiepkema PR and Koolhaas JM. 1993. Stress and animal welfare. *Animal welfare* 2 (3): 195–218. doi:10.1017/S0962728600015876

Yasui S, Konno A, Tanaka M, Idani G, Ludwig A, Lieckfeldt D, Inoue-Murayama M. 2013. Personality assessment and its association with genetic factors in captive Asian and African elephants. *Zoo Biology* 32 (1): 70–78. doi:10.1002/zoo.21045