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Delayed physiological acclimatization by African elephants following reintroduction

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Abstract

Managers of reintroduced wildlife commonly encounter behavioral problems post-release that have been linked to physiological condition and elevated stress hormone concentrations. However, there is uncertainty about the generality of a stress response among populations, factors influencing the intensity of the response and the amount of time needed to physiologically acclimatize. We evaluated the relationship of temporal, climatic and social factors to stress hormone concentrations in five African elephant (*Loxodonta africana*) populations following reintroduction. We determined fecal glucocorticoid metabolite concentrations (FGMs) in 1567 fecal samples collected from elephants reintroduced to five fenced reserves with differing reintroduction histories in South Africa during 2000–2006. Variation in FGMs across the five reserves was best explained by the number of years that elapsed since initial release. Compared with FGMs 1 year after release, FGMs were 10% lower 10 years after release and 40% lower 24 years after release. Across all reserves, FGMs were consistently highest in the dry season, although daily and monthly temperature and rainfall were not as important as other factors. FGMs did not vary solely in relationship to reserve size or elephant density. Our findings suggest that regardless of reintroduction site conditions, elephants and likely other species subject to reintroduction require an extended period of time to physiologically acclimatize to their new surroundings. Managers should prepare for prolonged behavioral and physiological consequences of long-term elevated stress responses following reintroduction, such as restricted space use and aggressive behavior.

Introduction

Despite the increasing use of reintroduction as a method of restoring wildlife species to their former range, success is typically low (Griffith *et al*., 1989). The failure of populations to become established post-release has, in part, been linked to a physiological stress response that typically follows the process of capturing, translocating and releasing animals for reintroduction (Armstrong & Seddon, 2008; Dickens, Delehanty & Romero, 2009, 2010). Chronic stress responses have been hypothesized to be a major cause of reintroduction failure by increasing susceptibility to disease, reproductive failure, predation, starvation or dispersal away from the release site (Teixeira *et al*., 2007; Dickens *et al*., 2010). Animals with elevated stress hormone concentrations also can be more prone to aggression (Muller & Wrangham, 2004) or avoidance behaviors (Koolhaas *et al*., 2009). Therefore, a greater understanding of reintroduction practices or environmental factors that influence the physiological stress response could enhance reintroduction success, provide guidelines to mitigate exposure to potential stressors, and help managers be better prepared to manage stress response behaviors.

The reintroduction of African elephants (*Loxodonta africana*) has become an increasingly common and controversial tool to reduce the size of large elephant source populations, and to augment or restore small or extirpated populations (Grobler *et al*., 2008). Whereas reintroductions have been highly successful at restoring elephant populations into portions of their historic range (Garaï *et al*., 2004), behavioral issues have arisen following release that have been linked to elephant physiology. For example, following early attempts to reintroduce elephants in South Africa, aberrant and destructive behaviors were observed, such as the goring of > 100 white rhinoceroses (*Ceratotherium simum*) and several critically endangered black rhinoceroses (*Diceros bicornis*) by young adult male elephants (Slotow, Balfour & Howison, 2001). These attacks, linked with abnormally elevated testosterone levels and prolonged periods of musth in young bulls, were remedied by the introduction of large adult bulls that suppressed the musth patterns in younger bulls (Slotow *et al*., 2000). Problems are not limited to young bulls, because in at least four reintroduced populations normally nonaggressive female elephants have killed people (Slotow *et al.*, 2008). These patterns of female aggression, combined with reclusive behavior, have been linked to elevated glucocorticoid stress hormone concentrations (Jachowski, Millspaugh & Slotow, 2012). To mitigate the occurrence of such physiological and behavioral problems in the future, there is increasing interest in building a more complete understanding of the physiological responses of elephants following reintroduction.

Past studies of African elephants suggest variations in the duration and intensity of physiological responses to translocation. Pinter-Wollman, Isbell & Hart (2009) observed no difference in stress hormone concentrations in wild elephants that had been translocated to a new area in Kenya (where elephants were already present) in comparison to the resident donor elephant population. In South Africa, in the case of at least two attempts to move elephants to new environments, stress hormone levels increased dramatically during translocation and subsequently declined to baseline conditions within 30 days post-translocation (Millspaugh *et al.*, 2007; Viljoen *et al.*, 2008). However, these studies were limited to populations of captive working elephants (Millspaugh *et al.*, 2007) or wild elephants allowed to navigate back to their original territory (Viljoen *et al.*, 2008). In the case of at least one translocated wild elephant population that was a true reintroduction (i.e. animals released into an area where a population was previously extirpated) into a fenced environment, stress hormone values remained elevated for up to 6 years following reintroduction (Jachowski *et al.*, 2012). Thus, there is uncertainty surrounding the generality of an elevated stress response in translocated elephant populations, and the amount of time needed for reintroduced elephant populations to physiologically acclimatize (i.e. decline from elevated stress hormone levels).

A number of local or site-specific stressors might affect physiological acclimatization following reintroduction. Seasonal climatic conditions frequently have been found to be overriding features influencing the physiological status of large herbivores (Millspaugh *et al.*, 2001; Huber, Palme & Arnold, 2003; Dalmau *et al.*, 2007). For large herbivores in tropical southern Africa, stress hormone values sometimes vary in response to seasonal rainfall patterns and the resulting availability of forage (Chinnadurai *et al.*, 2009). For elephant populations, seasonal limitations in water availability (Foley, Papageorge & Wasser, 2001; Burke, 2005; Woolley *et al.*, 2009) and rainfall (Gobush, Mutayoba & Wasser, 2008), are likely to increase stress hormone concentrations. In addition, high daily maximum temperature has been linked to decreases in stress hormone levels in elephant family groups (Pretorius, 2004; Burke, 2005). Social factors are also known to influence physiological states of vertebrates (McEwen & Wingfield, 2003), particularly in mammalian species that live in groups (Creel, 2001, 2005). Following reintroduction, elephants face a greater likelihood of encountering unrelated family groups or individuals, a social factor that has been linked to increased stress hormone concentrations (Munshi-South *et al.*, 2008). Further, the potential for social stressors is likely greatest in small fenced reserves, where elephant density and the likelihood of interaction is highest post-release.

The objective of this study was to evaluate if temporal, climatic and social factors were related to stress hormone concentrations in African elephants following reintroduction. While the use of stress hormone measures is an increasingly common tool to evaluate animal responses to reintroduction (Teixeira *et al.*, 2007), no previous attempts have been made to compare physiological responses across multiple reintroduced populations of the same species. Further, to our knowledge, there have been no previous examinations of stress hormone responses of wildlife to reintroduction for an extended period of time (> 1–3 years) after release. This study was designed to shed light on the long-term physiological responses of a long-lived social species that could provide key insights into the process of physiological acclimatization to reintroduction.

Methods

Study areas

We studied elephants reintroduced to five fenced reserves in South Africa: Pilanesberg National Park, Phinda Private Game Reserve, iSimangaliso Wetland Park, Mabula Game Reserve and Hluhluwe-Umfolozi Game Reserve (Fig. 1). Most elephants within our five study sites were family groups or individual males translocated from Kruger National Park (Slotow *et al.*, 2005). Reserves differed in climate, size, elephant density and when elephants were first reintroduced (Table 1).

Field sampling and stress hormone analyses

Trained employees of the reserves and students/staff from the University of KwaZulu-Natal collected fecal samples in the field during elephant monitoring surveys in each of the five reserves. They attempted to collect samples from all family groups in each reserve on nearly consecutive days (Table 1). To avoid pseudoreplication, they avoided collecting multiple samples from the same individual elephant on the same day by using a combination of visual observation, GPS collar tracking data and comparing bolus size, a method commonly used to differentiate sex and age classes in elephants (Morrison *et al.*, 2005; Burke *et al.*, 2008; Woolley *et al.*, 2008). For each fecal sample, time of collection, approximate age of the sample and location of collection, and whenever possible identification of the individual or family group that deposited the sample was recorded. Samples were only collected if < 72 h had passed since deposition following identification, collection and processing protocols detailed elsewhere (see Millspaugh *et al.*, 2003; Burke, 2005). Fecal glucocorticoid metabolite concentrations (FGMs) were extracted from the feces using corticosterone I^{125} radioimmunoassay kits (MP Biomedicals, Solon, OH, USA) following established protocols that have been validated for elephants (see Wasser *et al.*, 2000; Millspaugh *et al.*, 2007). Assay accuracy and precision were confirmed by conducting a standard assay validation, including assessment of parallelism, recovery of exogenous analyte, intra- and inter-assay precision, and assay sensitivity (Jeffcoate, 1981; O'Fegan, 2000; Millspaugh *et al.*, 2007). Inter-assay variation for 21 assays was 8.1% and average intra-assay variation was 4.4%.

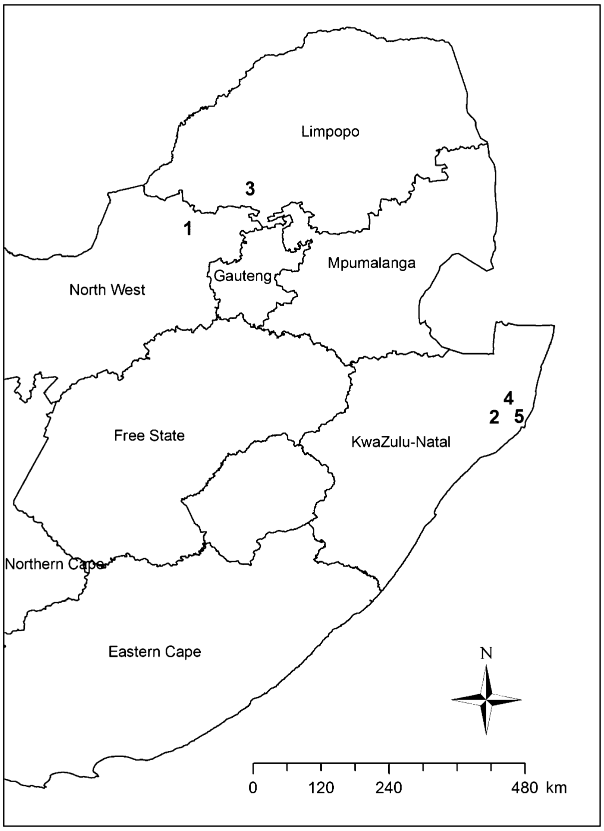

Figure 1 Location of the five reserves (1, Pilanesberg National Park; 2, Hluhluwe-Umfolozi Game Reserve; 3, Mabula Game Reserve; 4, Phinda Private Game Reserve, 5, iSimangaliso Wetland Park) monitored during this study within provinces of eastern South Africa.

Statistical analyses

We first used a repeated measures analysis of variance to test whether FGM concentrations differed by reserve and season. Given that multiple samples were collected from populations on individual days, we treated day as the repeated effect. We classified seasons based on temperature and rainfall, where the wet season occurred from November to April, and the dry season occurred from May to October (Burke, 2005; Shannon *et al.*, 2006).

To evaluate support for the hypothesized influence of time since release, temperature, rainfall, reserve size and elephant density on FGMs, we used linear mixed models [SAS PROC MIXED (Littell *et al.*, 2006)] and an information-theoretic framework (Burnham & Anderson, 2002). We calculated time since release as the amount of time that had elapsed between the first release of elephants into the reserve and the time of inference for the FGM sample. We estimated the maximum daily temperature and daily rainfall at the reserve level based on data provided by the nearest South African Weather Service remote weather station (http://www.weathersa.co.za/) within or adjacent to each reserve. We also calculated average maximum temperature and rainfall at monthly intervals. We included the following two interactions. First, because the effects of limited rainfall (and lower water availability) are likely to be exacerbated by increases in temperature, we included an interaction between daily temperature and rainfall as well as monthly temperature and rainfall. Second, because smaller reserves could result in elephants maintaining increased FGMs due to the greater probability of coming into close proximity to stressors such as roads or human disturbance (Burke, 2005) or unrelated family groups or individuals

Table 1 Reserve attributes as well as periods of time, total number and rate of collection of fecal samples from African elephants in five reserves investigated in this study

Reserve	Reserve size (km^2)	Year elephants first reintroduced	Elephant density (per km^2)	Period sampling occurred	Number of samples collected	Samples collected per day (SE)
Pilanesberg National Park	560	1981	0.32[a]	August 2000–February 2005	706	0.43 (0.03)
Hluhluwe-Umfolozi Game Reserve	960	1981	0.47[b]	March 2002–August 2002	67	0.37 (0.06)
Mabula Game Reserve	85	1992	0.12[c]	March 2002–September 2002	194	0.92 (0.14)
Phinda Private Game Reserve	180	1992	0.54[d]	March 2003–April 2003 and September 2003–June 2005	195	0.27 (0.03)
iSimangaliso Wetland Park	602	2000	0.07[e]	August 2001–August 2002 and September 2005–November 2006	405	0.52 (0.05)

[a] Shannon *et al.*, 2008.

[b] Based on 2009 estimate (D. Druce, Hluhluwe-Umfolozi Game Reserve, pers. comm.).

[c] Pretorius, 2004.

[d] Druce, Pretorius & Slotow, 2008; Lagendijk *et al.*, 2011.

[e] van Aarde *et al.*, 2008.

Table 2 Support for models based on time since release, social and environmental reserve-specific attributes explaining observed FGM concentrations of African elephants in five reserves in South Africa between 2000 and 2006

Model	log (*l*)	*K*	ΔAIC$_c$	AIC$_c$ weight	σ^2_{model} [a]	Absolute variation explained
Time since release + average monthly rainfall × average monthly temperature	1524	8	0	0.8134	0.0005	97%
Average monthly rainfall × average monthly temperature	1529	7	2.948	0.1863	0.0118	29%
Average monthly temperature	1546	5	16.032	0.0003	0.0126	25%
Time since release + maximum daily temperature	1557	6	28.798	0.0000	0.0016	90%
Time since release + maximum daily temperature × total daily rainfall	1556	8	32.318	0.0000	0.0016	90%
Maximum daily temperature × total daily rainfall	1564	7	38.115	0.0000	0.0140	16%
Average monthly rainfall	1574	5	44.186	0.0000	0.0192	15%
Time since release	1586	5	56.011	0.0000	0.0025	85%
Time since release + size of reserve	1585	6	56.963	0.0000	0.0017	90%
Time since release + total daily rainfall	1586	6	57.775	0.0000	0.0025	85%
Density of elephants in reserve	1593	5	62.681	0.0000	0.0091	45%
Intercept only model	1595	4	63.584	0.0000	0.0167	–
Total daily rainfall	1595	5	65.357	0.0000	0.0167	0%
Size of reserve	1595	5	65.564	0.0000	0.0166	0%
Maximum daily temperature	1731	5	201.302	0.0000	0.0228	37%

[a] σ^2_{model} = covariance parameter estimate.

(Munshi-South *et al.*, 2008), we included a fixed effect of reserve size and calculated the density of elephants within each reserve during our study. Prior to model fitting, we standardized our continuous covariates and tested our response variable (FGM) for normality.

Within our mixed models, the day of sample collection was the repeated effect, the reserve sampled was a random effect, and all other independent variables hypothesized to influence FGMs were fixed effects. We fitted models that individually evaluated the effect of each hypothesized factor, as well as models that contained combinations of the two types of factors hypothesized to influence FGMs: reserve-specific conditions (i.e. reserve size, elephant density and time since release) and climatic factors (i.e. daily and monthly rainfall and temperature; Table 2). We used restricted maximum likelihood (REML) to select the most appropriate covariance structure to the data based on the lowest Akaike information criteria for small sample size (AIC$_c$) scores (Littell *et al.*, 2006), which we identified to be compound symmetry. Therefore, we fit all subsequent models with a compound symmetry structure. Because REML, AIC$_c$ values are not comparable across models with different fixed effects, we used a maximum likelihood approach to rank models using ΔAIC$_c$ (Diggle, Liang & Zeger, 1994).

We compared model performance within both stages of analysis by calculating the per cent of variation explained. To calculate the per cent of variation explained, we used maximum likelihood covariance parameter estimates for each model in each stage by using the formula:

$$\%\ \text{variation explained} = \left| \left(\frac{\sigma^2_{\text{process}} - \sigma^2_{\text{residual}}}{\sigma^2_{\text{process}}} \right) \times 100 \right|$$

where σ^2 process = variance component estimate for the intercept-only model, and the σ^2 residual = variance component estimate for the model in question (Doherty *et al.*, 2010).

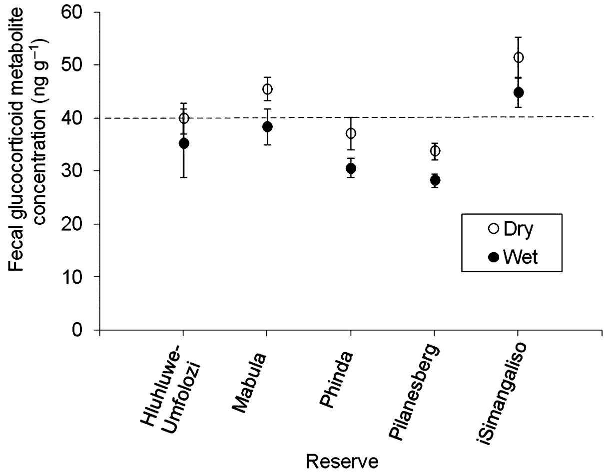

Figure 2 Mean (with 95% confidence intervals) seasonal fecal glucocorticoid metabolite (FGM) concentrations of elephants by reserve. FGM values > 40 ng g^{-1} (dashed line) are typical of elephants in an elevated physiological state (Wasser *et al.*, 2000; Jachowski *et al.*, 2012).

Results

We collected and assayed 1567 samples from the five reserves between 2000 and 2006. FGMs were 23% higher during the dry season than the wet season ($F_{1,1560} = 30.55$, $P < 0.0001$). Elephant FGMs differed among reserves ($F_{4,93} = 41.66$, $P < 0.0001$; Fig. 2). Samples originating from iSimangaliso (during both seasons) and Mabula (during the dry season) were typically > 40 ng g^{-1}, indicative of an elevated physiological state (Wasser *et al.*, 2000; Jachowski *et al.*, 2012). By contrast, samples from Phinda and Pilanesberg tended to have FGMs 16–45% lower, and on average below 40 ng g^{-1}, indicative of elephant populations in basal physiological condition (Wasser *et al.*, 2000; Jachowski *et al.*, 2012).

Variation in FGM concentrations across the five reserves was best explained by the number of years that elapsed since initial release and the interaction of monthly average maximum temperature and average monthly rainfall (Table 2). All models containing time since release explained > 85% of the variation (Table 2), where FGMs were predicted to decrease by 1.18% each year following release (Fig. 3). FGMs for elephants in iSimangaliso 1 year after release ($\bar{x} = 48.47$, SD = 26.32, range = 9.87–123.70) were 10% greater than values for elephants in Phinda and Hluhluwe-Umfolozi reserves 10 years after release ($\bar{x} = 43.41$, SD = 14.17, range = 19.28–91.35), and were 40% greater than values in Pilanesberg 24 years following release ($\bar{x} = 27.00$, SD = 6.65, range = 17.13–42.06; Fig. 4). In addition, the variability of FGMs decreased over time, where the coefficient of variation in FGMs in elephants in iSimangaliso 1 year following reintroduction (0.5429) was nearly twice as high as in elephants in Pilanesburg 24 years following reintroduction (0.2462; Fig. 4).

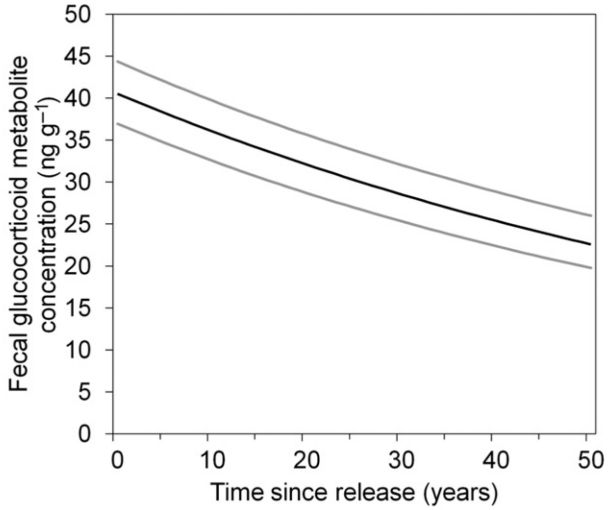

Figure 3 Predicted response of fecal glucocorticoid metabolite concentrations in elephants as a function of time elapsed since initial release based on the top-ranked across-population level model. Gray lines indicated 95% confidence intervals.

Despite observing an overall effect of season on FGMs across all reserves, when the effect of time since release was removed, daily and monthly rainfall and temperature patterns did not explain a large amount of observed variation in FGMs (Table 2). The interaction of monthly average maximum temperature and total rainfall, while a component of the most supported model, individually explained only 29 and 15% of the variation in FGMs, respectively (Table 2). Based on our top-ranked model, we predicted a 3.49% decrease in FGMs for every 20-mm increase in monthly rainfall (Fig. 5), and a 0.03% decrease in FGMs for every one degree increase in average maximum monthly temperature. Maximum daily temperature and rainfall were even poorer predictors of FGMs, explaining 0–16% of the variation and were not retained in our top-ranked model.

We failed to find support for a direct effect of reserve size or elephant density on FGMs (Table 2). In contrast to our hypothesized negative relationship between reserve size and elephant FGMs, reserve size alone explained 0.36% of the observed variation. One of the largest reintroduction sites (iSimangaliso) was also the most recently initiated, and its elephants consistently had the highest FGMs (Fig. 2). With the exception of Mabula, elephant density was inversely correlated to time since release for the reintroduced populations we studied. Therefore, despite remaining lower than the density of elephants at the donor site [Kruger National Park, 0.63 elephants per km^2; (van Aarde *et al.*, 2008)] and receiving a low amount of model support (Table 2), elephant density explained 45% of the observed variation in FGM concentrations.

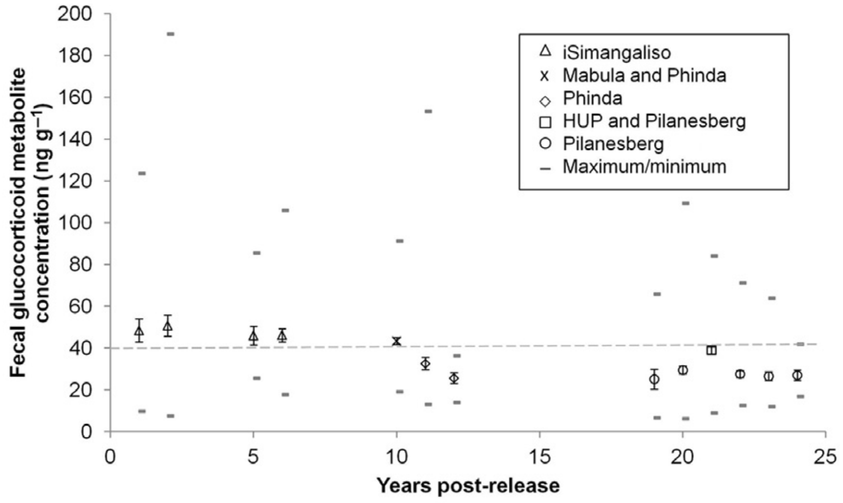

Figure 4 Mean and 95% confidence intervals, as well as maximum and minimum (dashes) values of fecal glucocorticoid metabolite concentrations by year following release into Pilanesberg National Park, Hluhluwe-Umfolozi (HUP) Game Reserve, Mabula Game Reserve, Phinda Private Game Reserve and iSimangaliso Wetland Park. FGM values > 40 ng g^{-1} (dashed line) are typical of elephants in an elevated physiological state (Wasser *et al.*, 2000; Jachowski *et al.*, 2012).

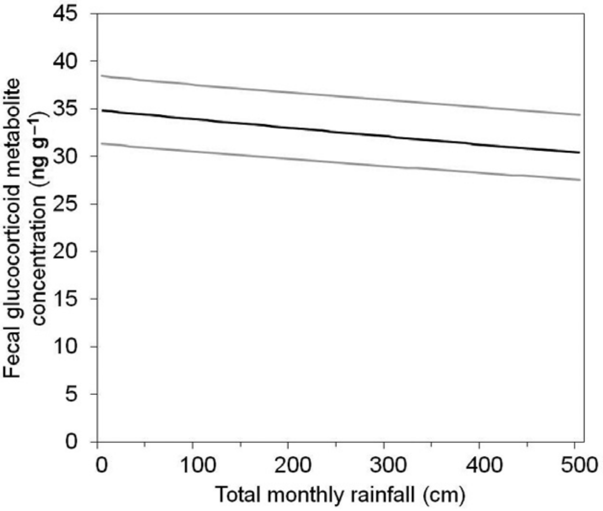

Figure 5 Predicted response of fecal glucocorticoid metabolite concentrations in elephants as a function of the total monthly rainfall based on top-ranked population level model.

Discussion

Our study shows that physiological acclimatization can require an extended period of time for wild elephants following reintroduction into fenced reserves. Elevated stress responses are not uncommon following wildlife reintroduction (Teixeira *et al.*, 2007), but previously little was known about how long stress hormones remain elevated post-release (Dickens *et al.*, 2010). Generally, the duration of elevated stress response following release has been linked to the sensitivity of a species, the intensity and duration of stressors, and the number of stressors encountered (Dickens *et al.*, 2010). Within the reserves we studied, elephant FGMs have been shown to vary in relationship to fluctuations in the availability of key nutrients in their forage (Woolley *et al.*, 2009), human disturbance both in the form of tourism (Pretorius, 2004; Burke, 2005) and hunting (Burke *et al.*, 2008), as well as stochastic events such as catastrophic fires (Woolley *et al.*, 2008). However, regardless of the presence of acute, reserve-specific stressors, our data suggest that a relatively long-term (> 10 years), population-level, elevated stress response is likely to occur following reintroduction.

Elevated stress hormones can have multiple pathological and behavioral consequences that should be of concern to managers (Romero, 2004). While pathological implications of elevated stress hormone concentrations in elephants are not well understood, elephants in an elevated physiological state can exhibit refuge behavior (Woolley *et al.*, 2008; Jachowski *et al.*, 2012) that in turn could limit tourist viewing opportunities (one of the primary reasons for reintroducing elephants), lead to aggressive elephant behavior when encountering humans (Jachowski *et al.*, 2012), and potentially cause extensive habitat modification (Skarpe *et al.*, 2004; Lagendijk *et al.*, 2011). In contrast to environmental and seasonal stressors that can be difficult to manage, human disturbance is known to elicit a physiological stress response (Pretorius, 2004; Burke, 2005), and can be more easily managed. Therefore, to mitigate human–elephant conflict, we suggest that managers ensure that reintroduced elephants have access to refugia away from human disturbance, and limit human access to refugia to avoid potential aggressive encounters (Jachowski *et al.*, 2012).

During physiological acclimatization, seasonal patterns in the availability of water and forage likely influence elephant FGMs similar to other large vertebrate species. Within a given reserve, short-term elevations in stress hormones have been observed in response to acute environmental stressors (Burke *et al.*, 2008; Woolley *et al.*, 2008), including daily maximum temperature and rainfall (Burke, 2005). Such reserve-specific environmental conditions are likely important in evaluating FGMs at the individual or population level over short periods of time, but our study shows that variation in FGMs across multiple populations over an extended period of time is better explained by translocation history. Nevertheless, during physiological acclimatization, FGMs varied in response to longer term monthly patterns of rainfall and maximum temperature that were representative of wet and dry season conditions. Seasonal differences in stress hormone concentrations are commonly observed in herbivores (Millspaugh *et al.*, 2001; Chinnadurai *et al.*, 2009). Although the mechanism underlying such seasonal variations in tropical systems remains unclear, the heightened FGM concentrations observed in elephants and other large herbivores in South Africa during the dry season is likely due to variations in water availability and forage quality (Chinnadurai *et al.*, 2009). In contrast to previous findings that suggest elephant FGMs are elevated seasonally in response to decreases in water availability (Foley *et al.*, 2001), elephants reintroduced to fenced reserves typically have year-round access to natural or man-made water sources. Therefore, it is likely that the seasonal variations in FGM concentrations we observed were due primarily to lower forage quality (Woolley *et al.*, 2009) or lower forage water content that delays gut passage time and allows glucocorticoids to accumulate in feces (Morrow *et al.*, 2002) during the dry season.

Our findings suggest that at a population scale, differences in FGMs related to social stressors were likely of less importance than the overriding factor of acclimatization time post-release. Persistent social stressors that are likely to be represented at the population level in fenced reserves, such as overcrowding and more frequent interactions with unrelated family groups (Munshi-South *et al.*, 2008), were not likely to have been major factors during our study (where < 25 years had elapsed since release) because of a combination of lag time in elephant population growth and proactive population control (Pretorius, 2004; Druce, Mackey & Slotow, 2011). Further, the consistent practice of translocating entire family groups, a practice initiated across South Africa in 1993, likely helped maintain the social structure and group size needed to ameliorate group-specific social FGM responses as seen in disturbed wild populations (Gobush *et al.*, 2008).

Failure to observe long-term elevated physiological stress responses in previous studies of vertebrate reintroductions is likely attributed to lack of long-term monitoring and fundamental differences between translocation and reintroduction. Previous studies of elephant physiological responses to translocation that found only short-term (0–30-day) elevations in FGMs were limited to translocations where individuals were allowed to return to their home range (e.g. Viljoen *et al*., 2008) or where resident populations were already present at the release site (e.g. Pinter-Wollman *et al*., 2009). By contrast, elephants reintroduced into fenced reserves during this study were restricted in their ability to navigate back to their original territory and there was no resident population with which to interact following release. Therefore, the discrepancy we observed from previous translocation studies is potentially attributed to a key difference between the practice of reintroduction from other types of translocation, where in true reintroductions, individuals are moved to a portion of their historic range where conspecifics are no longer present (Armstrong & Seddon, 2008). This suggests that while previous assessments have summarized physiological responses of wildlife to translocation and reintroduction collectively given exposure to similar stressors (e.g. capture, handling, and release into new environment; Teixeira *et al*., 2007; Dickens *et al*., 2010), those considering reintroductions likely need to be particularly concerned about the potential for long-term elevated physiological stress responses following release.

For elephants and other species subject to reintroduction, because the establishment phase following release is critical to overall success or failure (Armstrong & Seddon, 2008), it is important to identify the amount of time needed for animals to acclimatize following release. In addition to monitoring stress hormone concentrations for extended periods post-release, there is a need to better understand behavioral and pathological consequences associated with sustained elevated physiological states (Dickens *et al*., 2010). In this case, and likely other vertebrate reintroduction programs, such information can be used to guide decisions that mitigate human–wildlife conflict and facilitate long-term reintroduction success.

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