Pachyderm

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Potential physiological costs of leadership in African elephants: elevated faecal glucocorticoid metabolites in a matriarch

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Introduction

In African elephant (*Loxodonta africana*) societies, matriarchs occupy the highest social rank and play a pivotal role in the survival and cohesion of their family group. Elephants live in fission–fusion societies where adult females and their offspring form the family unit, while males leave the natal group once they reach sexual maturity (Douglas-Hamilton 1972; Poole 1994). The largest, and/or eldest female of the family unit is generally considered the matriarch (Douglas-Hamilton 1972). She possesses crucial knowledge of the area's natural resources and coordinates group movements and defence (Fig. 1) (Poole and Moss 1989; McComb et al. 2001).

We report higher faecal glucocorticoid metabolite (fGCM) concentrations in the matriarch we studied relative to other herd members. Glucocorticoid metabolites (GCs) reflect one component of a suite of physiological and behavioural responses to environmental and social challenges (Sapolsky et al. 2000; Ganswindt et al. 2010). Although GCs are not synonymous with stress, they are a key part of the body's physiological stress response. Activation of the hypothalamic–pituitary–adrenal (HPA) axis during stress triggers the release of several hormones, including GCs (Sapolsky et al. 2000; Ganswindt et al. 2010). During a stress response, elevated GC levels facilitate a shift in energy balance to cope with stressors (MacDougall-Shackleton et al. 2019). We present exploratory observations from a single family group suggesting that the focal matriarch exhibited higher fGCM concentrations than other herd members. These observations are preliminary and, while not permitting generalization, may suggest that the responsibility of leadership, alongside other context-dependent factors, imposes measurable physiological responses in elephants.

Study system and observations

We observed African elephants translocated to a fenced reserve in the semi-arid Nama-Karoo biome of South Africa between 2022 and 2024. In 2004, a family unit of nine elephants was introduced onto the reserve as part of a management intervention strategy to address space limitations in their previous range. In 2010, a single adult male was introduced, and from 2012 onwards, multiple calves were born. The habitat is characterized by low and unpredictable rainfall, sparse woody vegetation—mainly *Vachellia karroo*—and seasonal fluctuations in forage availability (Fig. 1; Cowling et al. 1997). Detailed rainfall data and sampling protocols are provided in Funk et al. (2025a). The focal herd consisted of 18 individuals: seven adult females, two adult males, four juvenile females, and five juvenile males. The current matriarch, known as Zinkwazi, has led the herd since 2018, following the previous matriarch's death from natural causes. The majority of adult females, including the matriarch, have received the porcine zona pellucida vaccine since 2022, and no pregnancies or births have been observed for approximately 10 years.

In the study area, only a single herd resides on the property; however, two adjacent reserves with elephants share boundary fences. Importantly, there are no lions or other natural predators present on the reserve which could influence stressors affecting the elephants.

Between 2022 and 2024, we collected 372 faecal samples from all individuals in the population (9–30 samples per individual, see Table 1) as part of an ongoing monitoring programme. Sampling occurred opportunistically during direct observation to ensure identity of the sample and hormone stability. Faecal samples were placed on ice directly after collection, frozen at the end of each field day and kept frozen until analysis by the Endocrine Research Laboratory of the University of Pretoria, South Africa. Faecal GCs were quantified using a previously established Oxoaetiocholanolone enzyme immunoassay (measuring fGCMs with a 5β-3α-ol-11-one structure). See Ganswindt et al. (2010) for further details on extraction and fGCM analysis. Assay sensitivity was 1.5 ng/g dry faecal mass, and intra-assay coefficients of variance, determined by repeated measurements of high- and low-value quality controls, were 5.57% and 6.58%, respectively, while the corresponding inter-assay coefficients of variance were 9.69% and 12.84%, respectively. Raw fGCM concentrations

Figure 1. The matriarch Zinkwazi, at the front of the herd, coordinates group movement.

are expressed as µg/g dry weight (DW). Data collected adhered to laws and guidelines of South Africa and Canada. Procedures were approved by Memorial University of Newfoundland Animal Welfare Committee (Protocol 23-01-EV). This study adheres to the Animal Behavior Society (ABS) and the Association for the Study of Animal Behaviour (ASAB) Guidelines for the use of animals in research.

Data analysis

We analysed fGCM concentrations in a Bayesian framework, using RStudio version 2025.05.0+496 (R Core Team 2020). We fitted a model using the 'brms' package (Bürkner 2017), with fGCM concentrations as the response variable. The age/sex category and age in years were predictor variables. We included individual identity as a random effect. Weakly informative priors were set to normal (0,1); for the model centred on zero, we set adult females as the reference level for the age/sex category. We accounted for variation in the number of samples per individual by setting the total fGCM samples per individual as an offset variable. We ran four chains for 2,500 iterations and confirmed convergence of the chains, i.e. all R-hat = 1.00.

We used the posterior predictive check function (Gabry et al. 2019) to assess the model performance and the 'DHARMa' package (Hartig 2017) to test for dispersion issues. No issues with model fit or dispersion were detected (See Fig. 3a, b). We set credible intervals (CI) to 95%, providing interpretatively familiar bounds to frequentist analyses (McElreath 2020). We estimated the probability of direction (PD) for each effect, ranging from 50% to 100%, and used the posterior distributions to determine the certainty of the effect's direction (positive or negative; Makowski et al. 2019). A PD of ~97.5%, ~99.5% and ~99.95% may be considered to indicate weak, moderate and strong

Table 1. Descriptive statistics of fGCM concentrations between individuals

ID	Age/sex	fGCM_Min	fGCM_Max	fGCM_Average	fGCM_SD	Total samples	Notes
Duzi	MJ	0.15	0.72	0.34	0.12377276	22	
Inanda	MJ	0.15	0.65	0.30	0.12102091	19	
Kariega	FJ	0.19	0.81	0.45	0.20236636	9	
Komati	MJ	0.13	1.18	0.38	0.20423101	23	Maximum levels recorded two days following large puncture wound
Levubu	FJ	0.27	0.50	0.39	0.08459275	12	
Mbizana	MJ	0.18	0.68	0.34	0.12437017	17	
Mdumbe	MA	0.18	0.55	0.31	0.08740191	28	
Nahoon	FA	0.18	0.74	0.40	0.1333076	17	
Ntombe	FJ	0.25	0.78	0.39	0.13402181	15	
Rex	MA	0.21	0.71	0.40	0.11273889	30	
Sabie	FA	0.20	0.81	0.41	0.12516677	30	
Storm	FA	0.29	0.80	0.44	0.16270125	18	
Sunday	FA	0.15	0.40	0.28	0.0569221	21	
Toti	FA	0.14	0.64	0.31	0.1094568	30	
Tugela	FA	0.14	0.53	0.33	0.10441294	18	
Umfolozi	MJ	0.21	0.51	0.34	0.08401558	17	
Umgeni	FJ	0.12	0.45	0.29	0.08337565	21	
Zinkwazi	FA	0.29	0.76	0.46	0.13300389	26	Matriarch

fGCM concentrations are in µg/g dry weight. MJ: male juvenile; FJ: female juvenile; MA: male adult; FA: female adult; fGCM: faecal glucocorticoid metabolites.

Table 2. Posterior estimates of fGCM concentrations. SE: Standard error of the estimate, CI: credible interval, Bulk ESS: bulk effective sample size estimate, Tail ESS: tail effective sample size estimate, PD: probability of direction. N = 372. R^2 marginal = 0.436, R^2 conditional = 0.146.

Effect	Parameter	Estimate	SE	l–95% CI	u–95% CI	Bulk ESS	Tail ESS	PD
Population-level effects	Intercept (adult females)	–2.78	0.33	–3.44	–2.14	2452	2547	100%
	Juvenile females	0.50	0.26	–0.02	1.01	2529	2249	97.26%
	Adult males	–0.25	0.23	–0.69	0.20	3680	3201	87.50%
	Juvenile males	0.13	0.26	–0.38	0.63	2336	2264	69.44%
	Age (years)	0.00	0.01	–0.02	0.02	2746	2696	61.18
Group-level effects	Sd (individual ID)	0.29	0.07	0.20	0.45	1740	2439	--

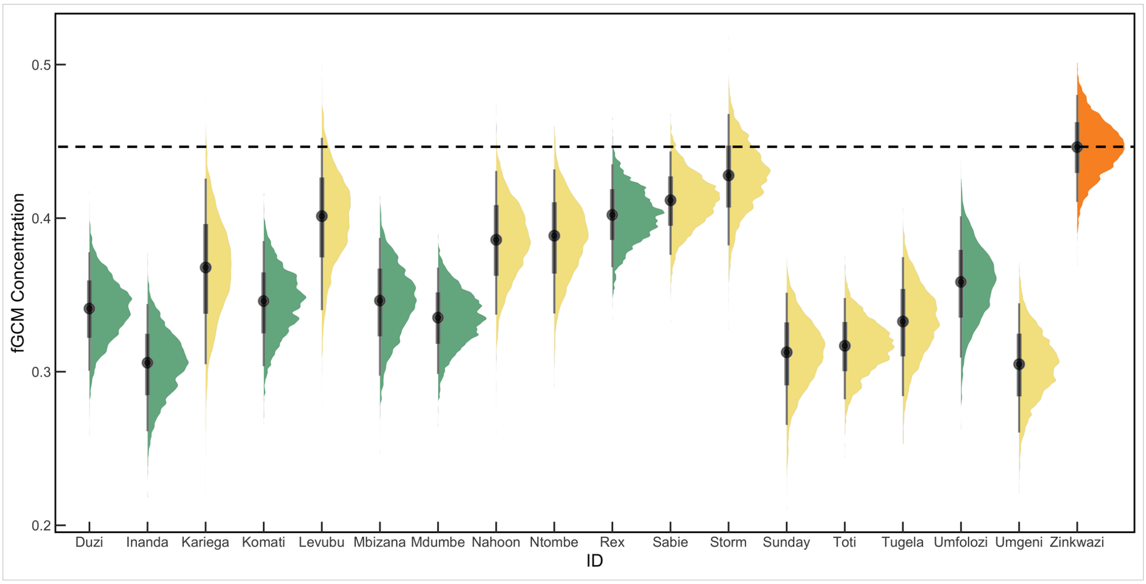

Figure 2. Posterior expectations from the Bayesian model showing predicted fGCM concentrations (µg/g dry weight) for each elephant in the herd. The shape of each shaded distribution represents the posterior probability density of predicted fGCM concentrations, where broader horizontal sections indicate values with higher probability. Yellow distributions represent females, green distributions represent males, and orange represents the matriarch, Zinkwazi.

The central dot indicates the mean predicted fGCM concentration for each individual. The thick vertical line represents the 66% credible interval, while the thin vertical line represents the 95% credible interval around the posterior estimate. The dotted horizontal line indicates the matriarch Zinkwazi's mean predicted fGCM concentration from the posterior distribution. fGCM: faecal glucocorticoid metabolites.

evidence for an effect, respectively (Colquhoun 2014). Data and code supporting the findings of this study are available at https://github.com/krfunk/fGCM-Karoo-Elephants-Note/tree/main.

Results

Based on the raw data (Table 1), Zinkwazi had the highest average fGCM levels of all herd members. Demographic variables such as age/sex category and age in years (PD = 61.18%) were not predictive of fGCM concentrations (Table 2). Juvenile females (PD = 97.25%), juvenile males (PD = 69.44%), and adult males (PD = 87.50%) were not predicted to be different from the adult female reference category. However, our model identified variation at the group level effects (estimate = 0.29, lower CI = 0.20, upper CI = 0.45), indicating inter-individual differences in responses to predictors. As such, we extracted individual posterior draws from our Bayesian model, which indicates that the matriarch, Zinkwazi, is predicted to have a higher fGCM concentration on average compared to other herd members (Fig. 2).

Discussion

Individual level fGCM concentrations varied within the herd, with the matriarch showing the highest mean value among family members. Mean fGCM concentrations across all monitored individuals were comparable to baseline values reported for other African elephant populations, monitored using the same approach (Carlin et al. 2020; Pretorius et al. 2023). The comparatively higher fGCM levels found for the matriarch raise the possibility that leadership entails cognitive, social, and energetic demands that may contribute to chronic elevations in glucocorticoid levels. However, given the exploratory nature of this study and its focus on a single matriarch within a single, fenced population, these results should be interpreted with caution and in the context of the specific ecological constraints of this population.

Matriarchs in elephant societies bear primary responsibility for group cohesion and decision making, which requires constant vigilance and responsiveness to environmental and social cues (McComb et al. 2001). For instance, elephant families with older matriarchs are more adept at discriminating between familiar and unfamiliar individuals and at responding appropriately (McComb et al. 2001). In the Nama-Karoo, where water and forage are often patchily distributed (Cowling et al. 1997), the costs of leadership may be amplified. The matriarch's experience and knowledge are crucial in guiding the group to distant or transient resources. Such challenges could plausibly increase both cognitive workload and energy expenditure compared to other herd members. Therefore, the constraints of a semi-arid environment combined with the efforts of leadership may lead to elevated fGCM levels of the matriarch.

Higher fGCM concentrations may also be associated with social dynamics within the herd. The matriarch arbitrates interactions among other herd members and often intervenes during social tension. In fenced reserves, where space is finite and resources may be locally depleted, social competition may be exacerbated, thereby potentially increasing the GC concentrations of the matriarch. Comparative evidence from other taxa supports the idea that occupying dominant or leadership positions can be physiologically demanding. For example, alpha male chimpanzees (*Pan troglodytes*) exhibit increased GC levels during periods of heightened social tension and competition (Muller and Wrangham 2004; Wittig et al. 2016). Similarly, in meerkats (*Suricata suricatta*), dominant females exhibit higher GC levels compared to subordinates, especially during social instability or when regulating subordinate reproduction (Young et al. 2006). Among elephants, previous research has linked elevated fGCM concentrations to anthropogenic disturbance (Tingvold et al. 2013; Oduor et al. 2024), reproductive activity (Freeman et al. 2013), lack of social support (Parker et al. 2022), or translocation history (Viljoen et al. 2008), and these factors could serve as alternative or confounding explanations not explored here. However, few studies of elephants have considered leadership as an intrinsic source of physiological strain. These observations broaden the interpretation of stress physiology in elephants to include the demands of maintaining social cohesion and decision making, in addition to previously established context-specific stressors.

Of note, no pregnancies occurred among individuals during the study period, and elevated fGCM levels in Zinkwazi are unlikely to be driven by reproductive or energetically demanding life stages. This removes one potential confounding factor when interpreting fGCM levels in females and strengthens the inference that environmental demands, leadership responsibilities, and social factors may be possible contributing factors. However, this study did not consider the potential direct and indirect effects of fertility control on fGCM concentrations (Funk et al. 2025b). Given that the majority of adult females in this population, including the matriarch, have been treated with immunocontraception, the effects of fertility control may also contribute to variation in fGCM concentrations. These relationships are currently being examined in detail and will be presented in future work (Funk et al. 2026).

These observations, however, are limited as they come from a single, fenced population. This group is unable to fuse with unrelated groups, meaning we did not capture potential physiological responses to intergroup encounters or intergroup competition over shared resources. Similarly, without data from larger, unfenced systems, we cannot determine whether the comparatively higher fGCM levels in this matriarch are generalizable or context specific; these individual averages must also be interpreted considering other sources of GC variability. For instance, ecological and social factors known to influence GC production, such as seasonality, rainfall, temperature, and group interactions, were not explicitly modelled in this exploratory analysis. Physiological variables, such as individual body condition, were also not considered here (but see Funk et al. 2025a). However, the raw data and preliminary analysis indicate that elevated fGCM levels of elephant matriarchs warrant further investigation.

Conclusions

These results suggest that the cost of leadership in elephant societies may have measurable physiological effects that warrant further comparative investigation. The elevated fGCM concentrations observed in the matriarch, Zinkwazi, suggest that the responsibilities of leadership may impose sustained physiological demands. Downstream consequences of heightened GC levels, such as survival and reproductive success, are also worth examining. Future work comparing matriarchs across reserves, ecological contexts, and management strategies would help clarify whether leadership itself heightens GC levels or whether these results reflect the unique ecological and social features of this semi-arid fenced environment. From a conservation perspective, matriarchal GC levels may have implications for population management and the wellbeing of elephant populations. Understanding such costs is essential, as the wellbeing of a matriarch influences group stability, decision making, and the transmission of ecological knowledge (McComb et al. 2001).

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