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Original research article

Tourism infrastructure and physiological stress in free-ranging impalas (*Aepyceros melampus*) of Serengeti National Park

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A R T I C L E I N F O

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A B S T R A C T

In the developing world, many protected areas (PAs) rely on tourism as a viable source of financial resources for conservation. However, the drive to maximise revenue has led to an increase in tourist numbers and infrastructure developments that often exceed ecological capacity, creating challenges for biodiversity and wildlife populations. To evaluate potential physiological impacts of tourism infrastructure and environmental factors, we measured faecal glucocorticoid metabolites (FGMs), an established indicator of stress in animals, using a validated enzyme immunoassay (EIA). We analysed FGMs from 213 impala *(Aepyceros melampus)* faecal samples collected in Serengeti National Park, Tanzania, between January and February 2025. Our results showed that impalas near lodges exhibited significantly higher FGM levels even without tourist occupancy (i.e., infrastructure), than those near permanent tented camps or seasonal campsites. These findings suggest that large-scale tourism infrastructure is associated with elevated stress in impalas. Future research should focus on identifying the specific features of large tourist facilities that drive physiological stress in wildlife, to better inform tourism development and conservation strategies in PAs.

1. Introduction

Protected areas (PAs) have emerged as increasingly popular tourist destinations worldwide (Balmford et al., 2009; KC, 2022; Petrić and Mandić, 2014; Spenceley and Snyman, 2017). The growing global demand for tourism in PAs is most likely driven by increased interest in nature-based tourism (Baral et al., 2008; Buckley, 2011; Spenceley and Snyman, 2017). PAs, including national parks, are especially suitable areas for biodiversity conservation (KC, 2022). The concept of PAs is regarded as the best approach for conserving flora and fauna across the globe (Pimm et al., 2018). Research indicates that 135,062 terrestrial PAs are identified, encompassing

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12.9% of the global land surface (Venter et al., 2014). Tourists visit PAs mainly for authentic nature experiences. For instance, 8 billion tourist visits in terrestrial PAs have been estimated worldwide each year, generating tourist receipts of USD 600 billion annually (Balmford et al., 2015). The economic viability of tourism as a conservation strategy is well articulated, as it provides essential funding to support conservation initiatives within PAs (Ranke et al., 2023; Wyman et al., 2011). Several studies indicate that many countries, especially those in the developing world, have successfully leveraged tourism to generate financial resources for biodiversity conservation activities in PAs (Balmford et al., 2009; Buckley, 2011; Gereta and Røskaft, 2010; Nielsen and Spenceley, 2010; Nyaupane and Thapa, 2004; Pan et al., 2022). However, there are instances where the pressure to generate funding has led PAs to permit more tourists than they can manage effectively (KC, 2022). This raises important questions about balancing tourism development with the sustainability and integrity of these PAs.

The rapid increase in tourism activities within PAs has posed significant ecological challenges to biodiversity, affecting wildlife populations (Nielsen and Spenceley, 2010; Pan et al., 2022). Numerous studies have documented the detrimental impacts of tourism development in PAs, including wildlife extinction, species decline, avoidance of certain areas, behavioural changes, habitat loss, and wildlife displacement (Buckley, 2011; Muntifering et al., 2021; Nielsen and Spenceley, 2010; Shannon et al., 2017). Infrastructure development to accommodate tourist activities and operations, such as roads and buildings, has substantially damaged flora and fauna (Morrison, 2012; Nyaupane and Thapa, 2004). For instance, research conducted in the Virunga region in Uganda highlighted the effects of tourism on gorilla (*Gorilla beringei beringei*) behaviour (Nielsen and Spenceley, 2010), and records indicate that the critically endangered black rhinoceros (*Diceros bicornis*) at the Palmwag Tourism Concession in Namibia tend to avoid areas with tourist infrastructure (Muntifering et al., 2021). Similarly, the lodges constructed inside Serengeti National Park have altered the movement and distribution of the wildebeest migration (Larsen et al., 2020). The tourist road infrastructure in Kruger National Park of South Africa has changed the behaviour of impala (*Aepyceros melampus*) (Mulero-Pázmány et al., 2016). Tourism development models have also demonstrated a decline in tourist numbers to destinations that suffer from over-tourism and subsequent loss of attractions (Butler, 1980; Butler, 2019). For example, studies show a reduction in tourist visits to natural areas in China that have experienced biodiversity decline due to rapid tourism development (Zhong et al., 2011). Consequently, tourism acts like a double-edged sword in wildlife conservation, offering substantial benefits and notable risks (Buckley and Castley, 2012). Therefore, monitoring the negative impacts of tourism development is crucial for implementing effective mitigation measures that align with conservation objectives (Buckley, 2009; KC, 2022; Morrison, 2012; Spenceley and Snyman, 2017).

The effects of anthropogenic activities, including tourism, have drawn research interest due to increased physiological effects on wildlife species (Casas et al., 2016; Hariohay et al., 2023; Larsen et al., 2020; Setsaas et al., 2018). Animal stress is one of the physiological effects arising from either human activities or environmental factors (Marealle et al., 2020). The absence or presence of stress levels in animals is a way of understanding animal welfare (Möstl and Palme, 2002; Tingvold et al., 2013). Glucocorticoids (GCs) are regarded as a classic endocrine response to stress, also known as physiological stress hormones (Hunninck et al., 2020b; Sapolsky et al., 2000). Increased GC levels may be attributed to stressors impairing the animal's physiological function (Sapolsky et al., 2000; Tingvold et al., 2013). Stress levels in animals can be evaluated through behavioural observations (Flølo et al., 2021; Gandiwa et al., 2016; Mulero-Pázmány et al., 2016; Setsaas et al., 2018), biotelemetric methods (Cooke et al., 2004; Whitford and Klimley, 2019) and non-invasive methods for measuring adrenocortical activity (Palme et al., 2005). Among the latter, the faecal glucocorticoid metabolites (FGMs) have been a widely used method by conservation physiologists to understand the physiological stress in animals without causing additional stress (Creel et al., 2013; Hariohay et al., 2023; Lunde et al., 2016; Palme, 2019).

Measuring FGMs is relatively cheap and quick and has the advantage of an easy, non-invasive collection of faecal samples, unlike the use of blood, saliva and urine, which is mostly associated with animal disturbance (Möstl and Palme, 2002; Palme et al., 2005; Schatz and Palme, 2001; Tingvold et al., 2013). FGMs reflect the hypothalamic-pituitary-adrenocortical (HPA) axis activity, providing an integrated measure of stress over time without animal capture (Palme, 2019; Palme et al., 2005). Similarly, FGM levels are less sensitive to short-term fluctuations, offering a more accurate measurement of stress in animals (Hariohay et al., 2023; Tingvold et al., 2013). Equally, FGM levels in animals mirror the true baseline GC levels and the animal stress response, thus considered an invaluable alternative technique to blood sampling in the field (Sheriff et al., 2011). However, animal diet, food availability, sex, and reproductive status have been documented as potential factors that affect the levels of excretion of GCs in animals (Tingvold et al., 2013). Research has demonstrated a spectrum of effects resulting from elevated stress hormone levels in animals, including reduced reproductive success, mortality, and changes in behaviour and physiological state (Geffroy et al., 2017; Hariohay et al., 2023; Lunde et al., 2016; Tingvold et al., 2013). For example, reproduction failure was observed due to high levels of FGMs in captive cheetahs (*Acinonyx jubatus)* in the San Diego Wild Animal Park of California, USA (Jurke et al., 1997). Consequently, glucocorticoid secretion varies across animal group sizes when subjected to stressors (Creel et al., 2013).

In this study, we focused on the impala, a small antelope that is common and widely distributed in African woodlands (Setsaas et al., 2007). Impalas are easy to study and serve as an indicator species when examining impacts of anthropogenic activities in PAs (Fyumagwa et al., 2017). Several studies have examined the FGM levels in antelopes to understand the physiological condition, including impala and greater kudu (*Tragelaphus strepsiceros*) in Ruaha-Rungwe ecosystem (Hariohay et al., 2023), impala in Serengeti National Park (Lunde et al., 2016), roan antelope (*Hippotragus equinus*) at the Lapalala Wilderness Nature Reserve (Kamgang et al., 2022), impala and blue wildebeest (*Connochaetes taurinus*) at the Laoalala Wilderness and Welgevonden Game Reserve of South Africa (Chizzola et al., 2018), scimitar-horned oryx (*Oryx dammah*) at the Smithsonian Conservation Biology Institute in Front Royal, USA (Stabach et al., 2020), and mountain gazelles (*Gazella gazella*) at Hatay Mountain Gazelle Wildlife Development Area in the Hatay Province of Turkey (Karaer et al., 2024). The studies are vital in understanding the ecological and management issues in respective conservation areas (Sheriff et al., 2011).

Serengeti National Park in Tanzania is a globally recognised PA. Serengeti has experienced a substantial increase in tourist numbers, driving the need for more infrastructure. In 2014, the park hosted approximately 15 permanent visitor accommodation facilities; by 2024, this number had grown to around 50, with an additional 25 facilities under various stages of development (TANAPA, 2025). Likewise, the number of non-permanent visitor accommodation facilities (camping sites) rose from 98 sites in 2014–218 sites in 2024 (TANAPA, 2025). While tourism is a key driver of economic and conservation benefits, the rapid proliferation of infrastructure raises concerns about its ecological impacts. Studies have documented potential adverse effects of tourism infrastructure on wildlife (Larsen et al., 2020), yet limited research has explored the indirect negative impacts of tourist accommodations and operations on impalas in the park. Understanding this dynamic is critical for balancing tourism growth with long-term conservation goals in Serengeti and other PAs. This could be realized through formulating responsive mitigation plans that promote tourism without harming biodiversity (Gössling, 1999; Gutiérrez et al., 2017; Mejía and Brandt, 2015).

The present study aimed to assess the temporal increase in tourist accommodation facilities in Serengeti and evaluate FGM levels of impalas around the facilities. Through assessing impala populations exposed to varying proximities and types of tourist accommodation facilities, we sought to determine whether accommodation facilities are associated with elevated physiological stress responses in impala. Previous scholars have indicated that human activities have been shown to affect FGM levels in impala (Hariohay et al., 2023; Lunde et al., 2016). Equally, research indicates the presence of a high number of tourists tends to elevate FGM levels in animals (Karaer et al., 2023; Pirovino et al., 2011). Specifically, we predicted that (1) FGM levels in impala are positively related to the number of tourists present; and (2) more infrastructure-demanding types of accommodation (i.e., lodges) will lead to higher FGM levels in impala compared to, e.g., seasonal campsites. In this study, we also took forage quality, measured as normalised vegetation index (NDVI) (Oduor et al., 2020), group sizes of impala (Hennessy et al., 2009; Marealle et al., 2020), Land Surface Temperature (LST) - an environmental factor, time of the day the sample was collected, behaviour and age group (Hariohay et al., 2023; Hunninck et al., 2020a) into account. Examining the link between anthropogenic activities (tourism), environmental quality, and the physiological condition of impalas in Serengeti is important to understand animal welfare and suggest measures that will enhance sustainable tourism practices and wildlife conservation.

2. Methodology

2.1. Study area

The study was conducted in Serengeti National Park, located in Northern Tanzania and covers an area of 14,700 square kilometres (Fig. 1). Serengeti is a world heritage site and a man and biosphere reserve. The park is renowned for its diverse wildlife, hosting millions of ungulates, including wildebeests (*Connochaetes taurinus)* and plain zebras (*Equus burchelli)* supporting a high density of predators, such as lions (*Panthera leo)* cheetahs (*Acinonyx jubatus)* and hyenas (*Crocuta crocuta)* (Sinclair et al., 2007).

2.2. Study species

The impala is a medium-sized antelope found across eastern and southern Africa, including the Serengeti. The population of impala in the Serengeti Ecosystem is estimated to be more than 85,000 (TAWIRI, 2025). This animal is readily recognised by its reddish-brown

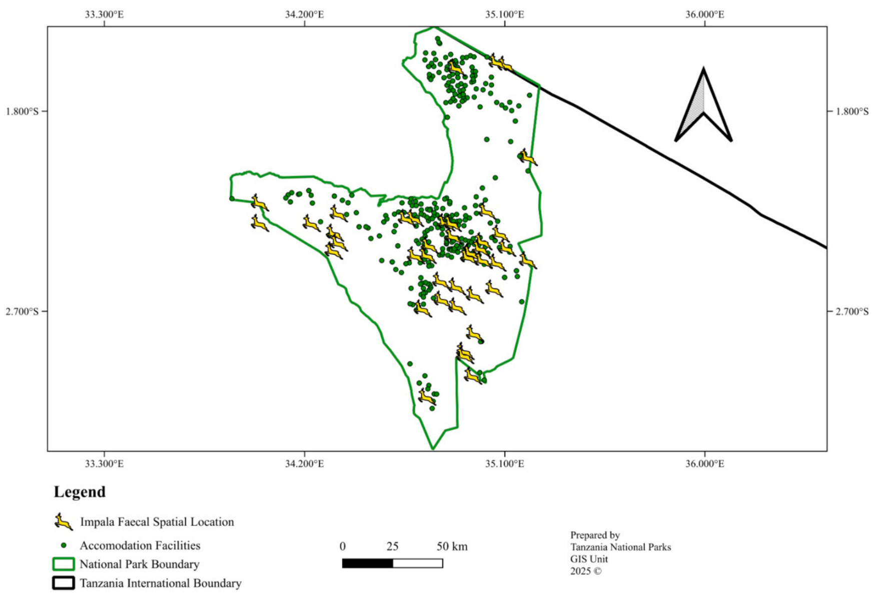

Fig. 1. Location of impala faecal samples collected in Serengeti National Park. The base map shows the location of various accommodation facilities across the study area.

coat, lighter flanks, white underparts, and black stripes on rump and tail, and sexual dimorphism is evident as only males possess horns up to 90 cm long, whereas females are hornless (Jarman and Jarman, 1979). Adult males stand 75–95 cm at the shoulder and weigh 45–76 kg, while females are smaller at 40–53 kg and can leap up to 10 m and 3 m high (Estes, 2012). Impalas are social animals forming large herds through observing distinctive social groups of female herds, male/bachelor herds and solitary males (Estes, 2012; Murray, 1982). The dominant male leads the female herds, and other males attempt to mate with females but are fought against by the territorial male (Sinclair et al., 2000). They have a short synchronised breeding season lasting between 2 and 3 weeks (Murray, 1982). Research indicates impalas in the Serengeti-Mara ecosystem have asynchronous birth, an adaptation to avoid predation, with fewer births recorded in wet season and peak births in the dry season (Ogutu et al., 2008; Sinclair et al., 2000). Impalas are mixed feeders, grazing grasses in the wet season and browsing shrubs in the dry season, thriving in areas with water (Jarman and Jarman, 1979; Murray, 1982). Impalas are non-migratory animals moving within a small home range in search of forage availability (Jarman and Jarman, 1979). They mostly prefer succulent food with a high crude protein content (Monro, 1980). Impalas are prey for large carnivores, and their population dynamics often mirror the health of savanna ecosystems (Hayward and Kerley, 2008). Because of their strong physiological responses to anthropogenic disturbances, including tourism activities, impalas serve as an important indicator species for understanding the effects of tourism growth and environmental variability on wildlife physiology (Hariohay et al., 2023; Lunde et al., 2016).

2.3. Faecal sample collection

We collected faecal samples (n = 213) comprised of 39 males and 174 females from January to February 2025 (Table S1). This period is the wet season in the Serengeti, with high-quality forage availability, thereby minimising potential nutritional stress (Sinclair et al., 2000). Equally, the park receives a high number of tourist visits at this time, thus a favourable period to assess whether stress levels in impalas are associated with tourism. Fresh faecal pellets from individually sighted impalas were collected from the ground. Groups (individuals found together displaying similar behavioural activity) were observed from a vehicle, and when respective individuals defecated, their details were recorded and the defecation site marked with a range finder (i.e., locating the exact spot of defecation). The site was then inspected by foot, and faecal samples were collected by hand with gloves. Gloves were changed after each sample collection. The procedure was applied with confidence by previous studies (Hariohay et al., 2023; Hunninck et al., 2020a; Palme, 2005). Samples were placed in labelled zip-lock bags, immediately stored in an ice-cooled box, and transported to the laboratory within eight hours to be frozen until analysis (Palme, 2005).

We collected samples within a distance of 1 km from tourist accommodation areas, mostly, lodges (n = 46 samples), permanent tented camps (n = 86 samples), seasonal campsites (n = 71 samples), public campsites (n = 5 samples), and cottages (n = 2 samples), due to a stable impala home range around these facilities. We sampled 41 groups of impalas around 29 accommodation facilities in the park during the day. To avoid collecting samples from the same group more than once, we avoided all facilities where samples had previously been collected. The number of samples collected per group varied depending on group size and on individuals defecating within 25 min of the first defecation in the group (see Table S1). The group sizes ranged from 4 to 156 impalas (Table S1). Samples were collected from adult (n = 211) and sub-adult (n = 2) individual impalas only, and samples that were observed with urine contamination were not collected, as urine can bias the FGM levels (Sheriff et al., 2011). Reproductive status may influence FGM concentrations (Grotta-Neto et al., 2024). While pregnancy-related effects on FGM concentrations cannot be definitively excluded, available evidence from sheep (*Ovis aries)*, cow (*Bos taurus)*, and red deer (*Cervus elaphus)* suggests that pregnancy does not necessarily result in elevated baseline glucocorticoid levels (Edwards and Boonstra, 2018). Samples were collected within the time frame, and reproductive status should be unrelated to the distance from tourism facilities, and would therefore only contribute to noise in the analyses. For each sample, we recorded the sample number, date, location (global positioning system (GPS) coordinate), sex (male/female), age (adult/sub adult) based on horn length and shape (males), and body proportions, group size, time of day (between 0600hrs and 1900hrs), and distance from the accommodation facility (measured using a range finder Leica Rangemaster 900) and behaviour in the group. Due to the small number (n = 7) of faecal samples collected around public campsite and cottage accommodation facilities, we excluded this data from the statistical analyses.

2.4. Behavioural data collection

The behavioural patterns expressed by animals have an effect on the animal's physiological condition (Pirovino et al., 2011). To account for the potential influence of behavioural states on FGM concentrations, systematic behavioural observations were conducted for not less than 10 min before sample collection. We observed the behavioural activity of the impala focal group, the primary behaviour documented included walking (moving within the group range), resting (stationary behaviour of either lying on the ground or standing in an active posture) and feeding (grazing or browsing activity). Once the focal individual defecated, behaviour was recorded. Observers were trained to ensure consistency in behavioural data categorization. We also used binoculars for observations, especially when the group was moving. Moreover, the behavioural variable was incorporated into statistical models to test any effect on FGM concentration.

2.5. Forage quality (NDVI) and Land surface temperature (LST)

The forage quality was measured using the normalised difference vegetation index (NDVI) data. NDVI values reflect the productivity of the vegetation cover and are regarded as an estimate of the greenness of the land cover (Pettorelli et al., 2011). NDVI is used to predict the animal physiological conditions (Oduor et al., 2020). Since we could not obtain the ambient temperatures due to the unavailability of weather stations across, we used the land surface temperature (LST) data (Hariohay et al., 2023). The NDVI and LST data were generated from Earth Explorer (https://earthexplorer.usgs.gov/), an open-source website developed by the U.S.A. We utilised Landsat 8 Operational Land Imager (OLI) and Thermal Infrared Sensor (TIRS) data to derive the NDVI and LST for the Serengeti National Park. We computed NDVI as the difference between Near Infra-Red (Band 5) and Red (Band 4) reflectance values.

2.6. Extraction and analysis of FGMs

The extraction process of the FGM was conducted at the Serengeti Wildlife Research Centre veterinary laboratory, located inside the Serengeti. Before processing, the fresh faecal samples were thawed, and then pellets were mixed by hand to ensure no variation within each sample that could bias the results. From each mixed wet faecal sample, we weighed 0.5 gm (+ or - 2) and mixed it thoroughly with 5 mL of 80% methanol in a centrifuge tube of Nunc®, 10 mL (Palme, 2005). The samples were shaken for one minute and then centrifuged for 20 min at 1200xg Unico Power Spin TM LX. We then pipetted 1 mL from each sample into a 2 mL microtube. Further, we kept the samples in vials for 14 days until they dried at room temperature. The dried down extracts were shipped to the University of Veterinary Medicine in Vienna, Austria. FGMs were analysed with an 11-oxoaetiocholanolone enzyme immunoassay (EIA) as described in detail before (Möstl et al., 2002). The EIA measures metabolites with a 5β-3α-ol-11-one structure and has been successfully validated for impala (Chizzola et al., 2018).

2.7. Statistical analysis

We used generalized linear mixed models (GLMMs) using the glmmTMB package v.1.1.11 v (Brooks et al., 2017) in R (R Core Team, 2024) with the FGM (ng/g) as a response variable. We log-transformed the response variable, ensuring normally distributed residuals. Our analysis included the following fixed effects: (i) tourist occupancy (TO), (ii) type of accommodation facility (ACT) and (iii) distance from the accommodation (DA). Similar to previous studies, we included (iv) normalised difference vegetation index (NDVI), (v) land surface temperature (LST), (vi) sex (SX), (vii) age (AG), (viii) group size (GS) and (ix) impala behaviour (IB), and (x) time of day (TD) as other fixed effects accounting for the variation in FGM levels, and (xi) group ID (GID) as a random effect to account for non-independence within the groups (Hariohay et al., 2023; Hunninck et al., 2020b; Lunde et al., 2016; Setsaas et al., 2018). First, we tested the full model **[FGM ~ TO * ACT + DA + SX + AG + IB + GS + NDVI + LST * TD + (1 | GID)]**, which included fixed effects, see model output in Table S2. Note the interaction between TO and ACT, and between LST and TD. The demographic variables and DA did not contribute to explaining any variation. Thus, we simplified to model **[FGM ~ TO * ACT + NDVI + IB + GS + LST * TD + (1 | GID)]** (i.e. excluding sex, age and the effect of the distance from the accommodation). The model performed equally well ($\chi^2 = 0.50$, $df = 3$, $p = 0.92$) and was considered the most parsimonious model to be discussed. We assessed diagnostics of the selected model using the DHARMa package (Hartig, 2022). Ensuring no violations of model assumptions (*KS test:* $p = 0.22$; *dispersion test:* $p = 0.74$).

Table 1
Model estimates from the generalized linear mixed model, explaining the variation in impala faecal glucocorticoid metabolite (FGM [ng/g]) levels. Bold text represents significant results.

Conditional model:				
	Estimate	*SE*	*z =*	*P*
(Intercept)	0.15	3.76	0.04	0.968
Tourist occupancy	-0.00	0.05	-0.35	0.729
Accommodation type (ref: Lodge)				
Accommodation type (Permanent tented camp)	**-1.41**	**0.39**	**-3.57**	**< 0.001*******
Accommodation type (Seasonal campsite)	**-1.12**	**0.35**	**-3.23**	**0.001****
Impala behaviour (ref: Feeding)				
Impala behaviour (Resting)	0.37	0.20	1.79	0.072
Impala behaviour (Walking)	**1.52**	**0.41**	**3.69**	**< 0.001*******
Group size	**-0.01**	**0.00**	**-2.87**	**0.004****
Normalised difference vegetation index	**-4.77**	**2.08**	**-2.30**	**0.022***
Land surface temperature	**0.21**	**0.09**	**2.15**	**0.031***
Time of day	**0.67**	**0.29**	**2.34**	**0.019***
Tourist occupancy: Accommodation type (ref: Lodge)				
Tourist occupancy: Accommodation type (Permanent tented camp)	**0.02**	**0.01**	**2.59**	**0.009****
Tourist occupancy: Accommodation type (Seasonal campsite)	0.03	0.02	1.48	0.138
Land surface temperature: Time of day	**-0.02**	**0.01**	**-2.35**	**0.019***
Random effects	*Variance*	*Std. dev.*		
Group ID (Intercept)	0.14	0.37		
Residual	0.49	0.70		

Significant differences are indicated in bold. Significance levels; '*' $p < 0.05$; '**' $p < 0.01$; '***' $p < 0.001$;

3. Results

We found that FGM concentrations were significantly lower in impalas around permanent tented camps (β = −1.41, SE=0.39, $p < 0.001$), and seasonal campsites (β = −1.12, SE=0.35, p = 0.001) compared to those found around the lodges in Serengeti National Park (Table 1). We recorded significant differences in the effect of tourist occupancy apparent from the interaction between accommodation facility and tourist occupancy, tourist occupancy have a stronger positive effect on impala FGM level in permanent tented camps ($\beta = 0.02$, SE=0.01, $p = 0.009$; Table 1; Fig. 2). Further, we found expected significant effects of NDVI, behaviour, group size and LST*TD on FGM levels (Table 1).

4. Discussion

We investigated the relationship between impala FGM levels and tourism occupancy in accommodation facilities in Serengeti National Park. We recorded lower FGM levels in impala groups around permanent tented camps and the seasonal campsites compared to the lodges. Furthermore, we found larger facilities, such as lodges, were associated with increased stress levels even when there were no visitors.

4.1. *Effect of the type of accommodation facility and its interaction with tourist occupancy on FGM levels*

We predicted that the FGM level would be higher in large tourist facilities such as lodges. Our results show that impalas near permanent tented camps and seasonal campsites had significantly lower FGM levels compared to those near lodges. The observed difference in stress levels may be attributed to the infrastructure size of lodges. We also found that the effect of tourist occupancy was greater in permanent tented camps and seasonal campsites than in lodges, apparent from a significant interaction between tourist occupancy and accommodation type. This finding is in line with a study conducted by (Karaer et al., 2024) who recorded higher FGM levels of mountain gazelles during the peak tourist season. Thus, our results indicated that when the permanent tented camps and seasonal campsites exceeded the occupancy limits set by TANAPA of 50 and 20 tourists, respectively (TANAPA, 2019), they may have a larger negative effect on impala physiology than lodges. In total, this suggests that infrastructure puts pressure on the PAs through increased stress levels in wildlife, corroborating previous research (Larsen et al., 2020). Moreover, increasing tourist numbers in less infrastructure demanding facilities is also discouraged according to our findings. Studies have shown that mass tourism has detrimental effects on wild animal physiology and behaviour, which leads to a decline in reproduction capacity and survival rate (Geffroy et al., 2017; Shannon et al., 2017). Therefore, it is encouraged to maintain the occupancy limits set by TANAPA for the permanent tented camps and seasonal campsites to minimise stress levels of impala resulting from tourism pressure. Stress negatively affects the performance of individual animals' physical health and population size (Karaer et al., 2023). Equally, we suggest that further studies should be conducted to understand specific factors associated with an increase in stress levels of impalas around the lodges in PAs. However, exploration of more economically viable sustainable tourism options that will complement wildlife conservation should be encouraged to aid revenues for conservation, such as pricing mechanisms (KC, 2022; Leung et al., 2018).

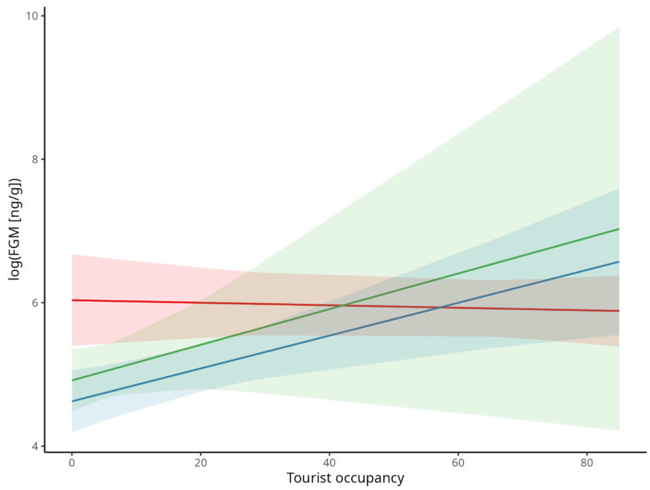

Fig. 2. Predicted changes in FGM levels in impala due to tourist occupancy (number of individuals) in different accommodation facility types, in Serengeti National Park (see Table 1 for model estimates and accounting effects). In the absence of tourists, lodges are predicted to constitute a large baseline effect on impala stress levels, likely due to extensive infrastructure. Red line (lodge), blue line (permanent tented camp) and green line (seasonal campsite).

4.2. Effect of forage quality on FGM levels

We found that the FGM levels of the observed impalas decreased with the increase in NDVI (a measure of forage quality) as predicted. The negative relationship suggests that nutrient-rich pastures buffer the stress levels of the impalas by providing better forage quality. Data was collected during the rainy season (January-February), the period when vegetation in Serengeti National Park is green with high productivity, perhaps leading to generally high NDVI values. Previous studies show that access to adequate forage mitigates physiological stress in animals; for instance, higher vegetation quality lowered the FGM levels of non-resident elephants (*Loxodonta africana*) in Mpala Ranch in Kenya (Oduor et al., 2020). Furthermore, there is strong evidence of a decrease in impala FGM concentration with the increase in NDVI that was observed in the Serengeti Ecosystem (Hunninck et al., 2020a).

4.3. Effect of impala behaviour on FGM levels

Human activities are associated with negative interactions with wild animal behaviour (Setsaas et al., 2018). We recorded different FGM levels that were associated with the observed impala behaviour. Specifically, we found that individual impalas that were walking were significantly more likely to be associated with increased FGM levels compared to those that were feeding. The findings may indicate that behaviour during the collection period could represent general activity levels for a long time period, thereby representing a useful covariate for the stress level in impala. However, we could not establish clear reasons that have led to variations in FGM concentration in different behaviour patterns, perhaps due to the likelihood of large variation in behaviour during FGM accumulation. Therefore, more studies should be conducted to understand FGM levels in relation to impala behaviour.

4.4. Effect of group size on FGM levels

We found the FGM levels were significantly lower in larger impala groups than in small groups, consistent with our prediction. Similar to previous findings, group size appears to buffer disturbance, leading to lower FGM levels (Hariohay et al., 2023). Research indicates that the individual predation risk is generally lower for larger groups (Roberts, 1996). Equally, large groups benefit from collective vigilance, which reduces the perceived risk of predation and other disturbances, while also allowing more time for foraging and energy allocation to reproduction (Creel et al., 2014). Although, (Lunde et al., 2016) argued that predators in the Serengeti are unlikely to elevate FGM levels in impala, our results may imply that group living still confers stress-reducing benefits. Stress in animals has been widely recognised as a factor that lowers reproductive rates (Edwards et al., 2019). Thus, the negative association between group size and FGM levels suggest that larger herds may support improved impala populations. However, negative impacts of group size, notably disease transmission, have been recorded (Edwards et al., 2019). Therefore, future research should examine whether group size directly contributes to proportionally higher survival and reproduction in free-ranging impalas.

4.5. Effect of LST on FGM levels

Our results suggest that LST may influence FGM levels in impala, but the effect is time-dependent. Although we recorded variation in FGM concentration across the day, the short-term nature of our sampling limits the strength of our data for inferring physiological stress responses. In particular, the apparent association between LST and FGM levels, such as the increase during the morning hours and the decline in the late afternoon, may reflect sampling dynamics rather than a true shift in FGM levels. This pattern may be associated with behavioural adaptation strategies, with animals resting or feeding in shaded areas in the late afternoon to cope with thermal stress (Fuller et al., 2016; Hunninck et al., 2020a). Therefore, we recommend future studies with a longer temporal scale covering different seasons to understand the effect of LST on FGM variation across different times of the day.

5. Conclusion

We found that impalas in areas around lodges were significantly more likely to have higher FGM levels compared to those found around permanent tented camps and seasonal campsites. Interestingly, higher tourist occupancy in permanent tented camps and seasonal camp sites had a larger effect than in lodges, but exceeded lodges only when occupancy exceeded the permitted numbers for such facilities. Our results highlight the negative ecological impacts of large tourist infrastructure, which may also subject impala to higher stress levels and likely several other species. This study also underscores the importance of tourist occupancy limits in permanent tented camps and seasonal campsites set by TANAPA, as these limits would have an even greater impact than in lodges at high tourist numbers. We encourage research on the effect of infrastructure located outside PA borders, and strategies to alleviate tourism pressure on sensitive areas, such as the iconic Serengeti National Park.

CRediT authorship contribution statement

Eivin Røskaft: Writing – review & editing, Visualization, Validation, Supervision, Methodology, Conceptualization. **Kwaslema Malle Hariohay:** Writing – review & editing, Visualization, Methodology, Conceptualization. **Rupert Palme:** Writing – review & editing, Validation, Methodology. **Augustine Arukwe:** Writing – review & editing, Supervision, Conceptualization. **Franco Peniel Mbise:** Writing – review & editing, Validation, Methodology, Conceptualization. **Beatrice Modest Kessy:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Peter Sjolte Ranke:** Writing –

review & editing, Visualization, Validation, Supervision, Methodology, Formal analysis, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04130.

Data availability

Data will be made available on request.

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