



Higher fecal glucocorticoid and triiodothyronine metabolite concentrations are associated with agricultural use in male African savanna elephants

Sandy Oduor^{a,b,c,*}, Janine L. Brown^d, Dennis Kimata^a, Nathaniel N. Gichuki^a, Jenna M. Parker^{c,e}, Suzan Murray^f, Shifra Z. Goldenberg^{c,g}, Nelson Mwangi^{c,h}, Maurice Schutgensⁱ, George Wittemyer^{c,h}

^a Department of Biology, University of Nairobi, P. O. Box 30197-00100, Nairobi, Kenya

^b Department of Reproductive Science, Smithsonian National Zoo and Conservation Biology Institute, Front Royal, VA 22630, USA

^c Save the Elephants, P. O. Box 54667 – 00200, Nairobi, Kenya

^d Center for Species Survival, Smithsonian National Zoo and Conservation Biology Institute, Front Royal, VA 22630, USA

^e School of Natural Resources, Lake Superior State University, Sault Ste. Marie, MI 49783, USA

^f Global Health Program, Smithsonian Conservation Biology Institute, Washington, DC, USA

^g Conservation Science & Wildlife Health, San Diego Zoo Wildlife Alliance, Escondido, CA 92027, USA

^h Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA

ⁱ Conservation Science Department, Space for Giants, P.O. 174 – 10400, Nanyuki, Kenya

ARTICLE INFO

Keywords:

Crop raiding
Fecal glucocorticoid metabolites
Thyroid hormones
Human-elephant conflict
Loxodonta africana

ABSTRACT

Human-wildlife conflict is increasing in frequency and distribution with the accelerating conversion of natural lands to agriculture. These agricultural areas provide valuable resources for wildlife, but also pose risks of conflict with humans. While optimal foraging theory predicts that animals adopt a strategy that maximizes benefits relative to costs, the rewards of foraging on crops come with unclear physiological costs. We investigated how agricultural use by African elephants correlated with ecological conditions as measured by the Normalized Difference Vegetation Index (NDVI) (a measure of vegetation greenness). We also investigated how fecal glucocorticoid metabolite (fGCM) and fecal thyroid metabolite (fTM) concentrations correlated with body condition scores (BCS) and time spent within agricultural areas over different time windows while controlling for ecological conditions as measured by NDVI. Individuals with lower BCSs had higher fGCM concentrations than those with higher scores. Time spent in cultivated areas was negatively correlated with NDVI values. While both fGCM and fTM concentrations were positively correlated with time spent in agricultural areas, those correlations occurred at different time scales. The strongest correlation with fGCM was related to the time spent over the previous 3 days, while for fTM, it was for time spent over the previous 10 days, potentially reflecting differences in physiological response mechanisms related to these two hormones. The association between elephants' dietary choices and habitat use, influenced by their physiological and metabolic states, provides a proximate explanation for human-elephant conflict.

* Corresponding author at: Department of Biology, University of Nairobi, P. O. Box 30197-00100, Nairobi, Kenya.
E-mail address: oduorsandy@gmail.com (S. Oduor).

<https://doi.org/10.1016/j.gecco.2025.e03912>

Received 29 June 2025; Received in revised form 13 October 2025; Accepted 14 October 2025

Available online 15 October 2025

2351-9894/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

The global conversion of natural habitats into cultivated croplands is a major contributor to biodiversity loss (Kehoe et al., 2017; Li et al., 2022; Woodroffe et al., 2005). Undisturbed natural habitats are increasingly being transformed into agriculture, influencing the abundance and quality of food items available to wildlife, with implications for health, reproduction, and survival (Acevedo-Whitehouse and Duffus, 2009; Barker et al., 2019). As natural habitats shrink, wildlife is increasingly forced into people-dominated landscapes, resulting in human-wildlife conflict (Abrahms, 2021; Ma et al., 2024).

While not all animals are drawn to crops, those that are tend to be attracted because crops are often nutrient-dense, high in calories, and concentrated in large, dense patches, requiring less search time than natural habitats (Abbas et al., 2011; Hill, 2017, 2018). Thus, crop foraging is a strategy for optimizing nutritional intake when natural forage may be lower in quality and quantity (Lambert and Rothman, 2015; Vogel et al., 2020). Studies suggest that phenological changes in crop nutrients may influence crop foraging. For example, African savanna elephants (*Loxodonta africana*) were drawn to mature, browning crops in agricultural areas as a primary food source, even when natural vegetation was available, because those crops contained significantly higher digestible energy (Branco et al., 2019). However, crop foraging is risky due to retaliatory attacks by people guarding their farms (Gunaryadi et al., 2017; Mijele et al., 2013; Nyhus et al., 2000). As such, crop access by wildlife can be a high-risk, high-reward endeavor, yet it is unclear how animals balance these risks and rewards in their decisions to use crops. To assess the risks and rewards associated with crop raiding, it is valuable to examine how this behavior correlates with the animals' physiological states.

Conflict with farmers living adjacent or close to protected areas has become a major concern for the conservation of elephants in Africa and Asia (Firdhous, 2020; Gobush et al., 2021). In Africa, crop foraging is predominantly conducted by male elephants (Chiyo et al., 2005), although it can involve both sexes and different age classes (Hahn et al., 2022). While extensive research exists on adaptive foraging strategies in response to seasonal changes, habitat variations, and food nutritional and chemical properties (Gross et al., 2018; Pretorius et al., 2012; Woolley et al., 2009), the physiological impacts of high-risk foraging behaviors, particularly crop raiding, in elephants remain understudied. Analysis of glucocorticoid and nutritional hormones may elucidate the underlying factors influencing crop-raiding behaviors, with the potential to inform management actions aimed at reducing the frequency and severity of crop-raiding incidents.

In vertebrates, the release of glucocorticoid (GC) hormones following exposure to a stressor is partly regulated by activation of the hypothalamic-pituitary-adrenal (HPA) axis and is key to restoring homeostasis by promoting energy metabolism and down-regulating nonessential systems so that an animal can respond appropriately (Boonstra, 2013). However, prolonged exposure to high circulating GC concentrations can negatively affect animal physiology, including suppressing immune function, inhibiting reproduction, and decreasing growth (Busch and Hayward, 2009; Romero and Wingfield, 2015; Sapolsky et al., 2000). The quantification of GC levels can be done noninvasively by measuring GC metabolite concentrations in feces [i.e., fecal glucocorticoid metabolite (fGCM)] and provides an integrated measure over time, depending on gut passage time of the respective metabolite (Palme, 2019; Sheriff et al., 2011). Thus, noninvasive fGCM monitoring could shed light on factors affecting fitness and survival. For example, measures of fGCM helped quantify the long-term negative effects of poaching on reproduction and welfare in populations of African elephants (Foley et al., 2001; Gobush et al., 2008).

Another physiological marker that could help understand high-risk, high-gain foraging strategies is triiodothyronine (T3), the active form of thyroid hormone controlled by the hypothalamic-pituitary-thyroid axis (Behringer et al., 2018). Thyroid hormones play critical roles in regulating metabolic rate, protein synthesis, and glucose availability (Behringer et al., 2018; Pasciu et al., 2022, 2024; Todini, 2007). Just like fGCM, T3 can be measured noninvasively [i.e., fecal triiodothyronine metabolites (fTM)] and is increasingly being employed to assess metabolic status in wildlife (Wasser et al., 2010) and can reflect resource limitations faced by wild populations (Gobush et al., 2014). For instance, fTM concentrations in free-ranging African elephants were positively associated with vegetation quality based on the Normalized Difference Vegetation Index (NDVI), but as temperatures increased, the positive effect of NDVI on fTM concentrations was diminished (Szott et al., 2020). Subsequently, higher fTM concentrations were found in elephants foraging in agropastoral areas compared to other land use types, and lower concentrations during severe drought conditions (Oduor et al., 2024). In wild impala (*Aepyceros melampus*), fTM concentrations were negatively correlated with temperature and NDVI (Hunninck et al., 2020). However, in wild moose (*Alces alces*), individuals with higher energy intake had both higher fTM and fGCM (Jesmer et al., 2017). Still, the combination of fGCM and fTM measures in wildlife can reveal the contribution of different physiological challenges individuals face, including interactions between energy expenditure and intake related to changes in feeding behavior or thermoregulatory needs (Touitou et al., 2021).

This study examined fGCM and fTM as measures of physiological and metabolic stress in GPS-collared male African savanna elephants known for crop raiding in Laikipia County, Kenya, a non-protected savannah region consisting of private, public, and communally-owned ranches (Georgiadis et al., 2007). In the last three decades, Laikipia County has been impacted by climate change, increased human settlements, and expansion of smallholder cultivation (M'mboroki et al., 2018), which has exacerbated human-elephant conflict and increased crop-raiding incidences in the area (Evans and Adams, 2016; Graham et al., 2009). This study aimed to determine how agricultural use and ecological conditions correlated with fGCM and fTM concentrations and body condition in crop-raiding male African elephants. Furthermore, since the excretion time of fTM in African elephants is not well understood and in relation to the potential influence of cumulative experience on hormone levels, we explored the correlation between fecal hormone levels and different time windows of agricultural use. Given that elephants adjust their group sizes based on the level of risk in different areas, with larger groups penetrating deeper into cultivated areas (Songhurst et al., 2016), we included group size in our analysis of agricultural use and measures of endocrine responses. Our findings provide insight into how crop-raiding behavior correlates with the physiological state of African elephants. This could help in improving existing strategies for managing conflicts.

2. Methods

2.1. Study site

This study was carried out in Laikipia County (Fig. 1) between latitudes $0^{\circ} 17' S$ and $0^{\circ} 45' N$ and longitudes $36^{\circ} 15' E$ and $37^{\circ} 20' E$ around Rumuruti, an agropastoral area located in the western part of Laikipia where elephant crop raiding is common (Graham et al., 2010). The area comprises smallholder farms between 0.5 and 2 ha in size, interspersed with natural vegetation. Other land use types within Laikipia include commercial livestock ranches, pastoral communal lands, and private wildlife conservancies (Ihwagi et al., 2015; Kinnaird and O'Brien, 2012). Laikipia has no formal protected area; however, together with the adjacent Samburu County, it is home to the second-largest population of African savanna elephants in Kenya, the largest to roam primarily outside national parks and reserves in Kenya (Waweru et al., 2021). Rainfall is bimodal, with long rains between March and May and short rains between October and December. Temperature ranges between $16^{\circ} C$ and $34^{\circ} C$ (LWF, 2012), with predominant soils being black cotton (Pellic Vertisols) and red sandy loam (Ferric and Chromic Luvisols), Vertisols (Kinyumu et al., 2021).

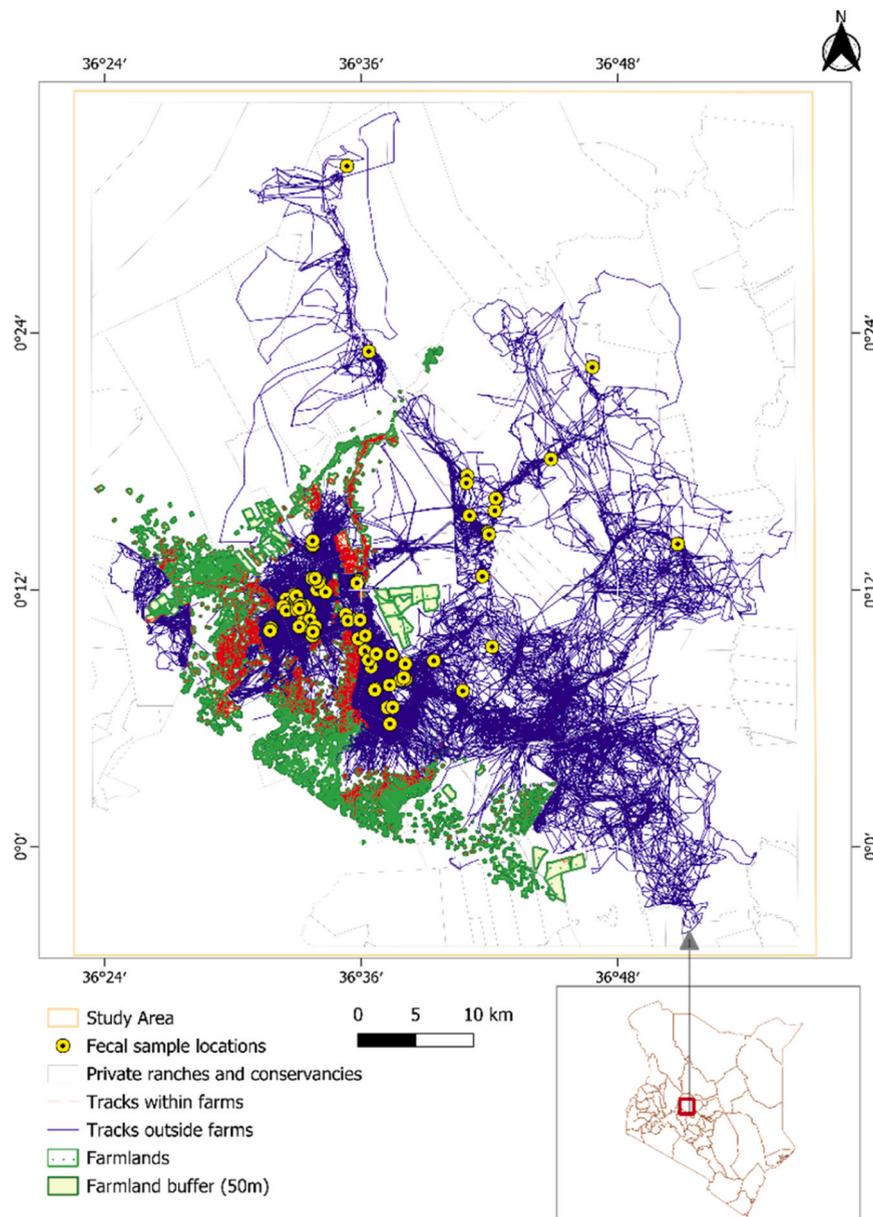


Fig. 1. A map of the study area showing movement tracks of elephants both inside (in red) and outside (in blue) farmland areas (green polygons) between the period June 2022 to February 2024. The yellow points represent locations where samples were collected.

2.2. Fecal sample collection, processing, and analysis

Seven elephant bulls previously identified as fence-breakers/crop-raiders and fitted with GPS collars by the Kenyan-based non-governmental organization (NGO) Space for Giants were targeted for monthly sample collection from June 2022 to February 2024. Due to challenging terrain limiting access to these individuals, sample collection was irregular leading, to variation in the number of samples per elephant. Despite this, dung samples were consistently collected from the same individual over the study period, covering different months and both crop-raiding and non-crop-raiding seasons. This temporal distribution allowed for analysis of hormone levels in relation to recent agricultural area use (see description below). Sample details are summarized in [Table 1](#). A summary of the number of days within agricultural areas each month is shown in [Supplementary Table 1](#). The collars were set to transmit GPS positions hourly to EarthRanger ([Wall et al., 2024](#)) during the first 2 weeks of the month to locate elephants for sampling. When defecation was observed, the time of defecation, time of dung collection, GPS location, body condition score (BCS), and group size (as some collared bulls associated together while others associated with other non-collared bulls with fusion-fission dynamic groupings) were recorded. Subsequent analysis of GPS data allowed quantification of the level of agricultural area use in the last 16 days from the day of sample collection ([Kioko et al., 2017](#); [Morfeld et al., 2014](#)). An individual was considered to have utilized an agricultural area when they spent at least an hour within the agricultural polygon area based on the GPS fixes. The samples were labeled according to individual and date of sample collection and kept in an insulated cooler box with ice packs before being transferred to a $-20\text{ }^{\circ}\text{C}$ freezer within 2 h for storage at the Endocrine Laboratory at Mpala Research Centre until processing and analysis.

Hormones were extracted using an established wet-weight vortexing method ([Edwards et al., 2016](#)). Briefly, samples were thawed, thoroughly mixed, and 0.5 g (± 0.02) extracted by vortexing in 5 mL of 90 % methanol in 16×125 mm glass tubes for 30 min, followed by centrifuging at 700 g for 20 min. The resulting supernatants were decanted into another set of 16×125 mm tubes and dried under air in a warm temperature water bath, reconstituted with 1 mL of assay buffer (Cat. No. X065, Arbor Assays, Ann Arbor, MI USA), sonicated until completely resuspended, and then frozen at $-20\text{ }^{\circ}\text{C}$ until analysis. Concentrations of fGCM and fTM were measured by enzyme immunoassay (EIA) (DetectX® Corticosterone EIA K014, Arbor Assays, Ann Arbor, MI; DetectX® Triiodothyronine EIA K056, Arbor Assays, Ann Arbor, MI) as described by [Oduor et al. \(2020\)](#) and [Szott et al. \(2020\)](#), respectively. The EIA sensitivity for both corticosterone and T3 was 0.90 pg/well (at 90 % binding). Serial dilutions of fecal extracts in assay buffer were tested for parallelism in the corticosterone ($R^2 = 0.982$, $y = 0.90x - 3.75$; $P < 0.05$) and T3 ($R^2 = 0.927$, $y = 0.82x - 28.53$; $P < 0.05$) EIAs. Intra- and inter-assay coefficients of variation were maintained below 10 % and 15 %, respectively, and duplicates over 10 % were reanalyzed. Fecal extracts were diluted 1:10–1:20 and 1:50–1:90 to analyze GC and T3 metabolites, respectively.

2.3. Assessment of the proportion of time spent in agricultural areas

We calculated the proportion of days elephants were in agricultural landscapes across 16-day periods by intersecting each individual's GPS collar data with an agricultural layer derived from digitizing Google Earth imagery. We calculated the minimum convex polygon (MCP) covering all accurate high dilution of position (HDOP < 5) GPS tracking locations from the sampled elephants over the duration of the study to define the overall extent of the study area (See [Fig. 1](#)). Within the MCP, we identified agricultural and non-agricultural areas using high-resolution Google Earth Pro *version 7.3.6* archive images from 20th February 2023 to 5th March 2023 ([Google Earth Pro, 2024](#)). The farmlands were visually identified using image interpretation elements such as shape, texture, tone, and pattern to allocate and then delineated by outlining a coverage polygon as applied by [Campbell and Wynne \(2011\)](#). Once the farmland polygons were digitized, they were merged into a single Keyhole Markup Language (KML) file for mapping in QGIS. We used GPS coordinates of the crop-raiding incidents recorded by SFG monitoring scouts to ground-truth the digitized farmlands and verify the accuracy of the digitized data. The number of days collared elephants entered the digitized farmland polygons over each 16-day

Table 1

A summary of fecal samples collected from GPS-collared male African savanna elephants targeted for monthly collections in Laikipia, Kenya.

Elephant Name	Location of collaring	Age of the elephant at collaring	Date of collaring	Number of samples collected during the study period	Number of days within the agricultural area during the study period	Total number of days considered during the study period	Date of first sample collection	Date of last sample collection
Naledi	Mutara Ranch	24 Years	5-Oct-2017	8	42	611	28-Jun-2022	01-Feb-2024
Tumaini	Kifuko	30–35 years	16-Oct-2020	5	33	426	01-Aug-2022	04-Jul-2023
Uzima	Kieni	45–50 years	16-Oct-2020	17	162	611	09-Jun-2022	08-Jan-2024
Mutara	Haji Musa	40–45 years	18-Feb-2021	16	150	611	13-Jun-2022	01-Feb-2024
Tembea	Muruku	50 years	18-Feb-2021	14	159	611	13-Jul-2022	08-Jan-2024
Jikaze	Muruku	40–45 years	18-Feb-2021	8	75	611	10-Jun-2022	03-Jul-2023
Popote	Muruku	35–40 years	18-Feb-2021	15	154	611	13-Jun-2022	08-Jan-2024

window was calculated by overlaying the GPS tracking data and extracting GPS points within the digitized farmlands using the geometry function in QGIS, from which the proportion of days in agriculture was derived. We considered any individual who spent more than 1 h per day within the digitized agricultural area, based on collar time fixes during the 16-day window, to have utilized the agricultural area. The 16-day window was implemented to align with the 16-day windows of Terra Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI values (Carroll et al., 2004).

In addition, we assessed the number of hours spent over the day in agricultural areas 3, 5, and 10 days before collecting the dung sample by intersecting GPS collar data with our agricultural layer in QGIS to take into account the effects of response and lag times (Wasser et al., 2000; Wasser et al., 1996). Given limited knowledge on thyroid hormone excretion and cumulative exposure effects on hormone excretion in general, we selected 3-, 5-, and 10-day windows to capture potential hormone responses to recent activity in agricultural areas. The 3-day window aligns with the known fGCM lag time, while the 5- and 10-day windows were intended to account for delayed or prolonged physiological responses. Since T3 (and fTM) is not highly dynamic and may take longer to reflect physiological changes, these broader windows also help capture more normalized values and longer-term activity patterns as elephants intensified their use of agricultural areas. Additionally, we calculated the proportion of time each focal bull spent in the agricultural area during the six months prior to sample collection within the study area to determine how crop raiding activity patterns correlated with variations in both fGCM and fTM concentrations. For every individual, we calculated the proportion of fixes in the agricultural area every six months throughout the study period.

2.4. Assessment of body condition

A visual BCS for each elephant bull was assigned on the day of sample collection based on fat deposition patterns around the ribs, backbone, lumbar, and pelvic regions using a modified scale described by Morfeld et al. (2014). An individual was scored as BCS = 1 (emaciated - ribs, scapular blade, pelvic bone, lumbar depression, and vertebral ridge of the backbone visible); BCS = 2 (thin - individual ribs less distinguishable; scapular blade, pelvic bone, lumbar depression, and vertebral ridge visible); BCS = 3 (ideal - individual ribs and scapular blade not visible; pelvic bone, lumbar depression and vertebral ridge visible but less distinguishable); BCS = 4 (overweight - ribs, scapular bone, pelvic bone, and lumbar depression not visible; vertebral ridge less distinguishable); or BCS = 5 (obese - ribs, scapular bone, pelvic bone, lumbar depression, and vertebral ridge not visible). No elephants were BCS = 1 or BCS = 5, so those scores were excluded from the analysis.

2.5. Assessment of NDVI

NDVI is a ratio of the near-infrared and red reflectance spectral bands that are reflected from the earth's surface, captured by the sensor from an Earth observation satellite and scaled between -1 (no vegetation) and 1 (Pettorelli et al., 2005). Although NDVI can be affected by vegetation type, NDVI values reflect seasonal variation in the ecological conditions of the area (i.e., Afrotropical savanna), whereby NDVI values increase in the wet season and decline during the dry season. As such, NDVI reflects seasonal shifts in the ecosystem. We assessed ecological conditions within the digitized polygon of agricultural and non-agricultural areas (as defined above) by calculating average, 16-day composite NDVI values from the MOD13Q1 Version 6.1 (MODIS_061_MOD13Q1), which provides NDVI data at a 250 m spatial resolution. To derive NDVI values for the GPS locations of the tracked elephants, we calculated average NDVI values for 3-, 5-, and 10-day time windows prior to each dung sample collection using Sentinel-2 satellite (Sentinel-2). This product provides finer temporal scale NDVI values at a 10 m spatial resolution than the MODIS satellite, but is more susceptible to gaps caused by cloud cover (Drusch et al., 2012). We addressed cloud-related gaps in Sentinel-2 NDVI data by masking clouds with the Scene Classification Layer (SCL) and creating monthly maximum value composites. Then, we applied interpolation to fill missing values in Google Earth Engine (GEE) (Main-Knorn et al., 2017). We used Sentinel NDVI for this latter analysis, given the finer temporal and spatial resolution of the data. To better understand the temporal resolution of the analyzed hormones, we analyzed the average NDVI hormone relationship at 3, 5, and 10 days. The different time scales were to account for variation in both hormones as they intensified their use of agricultural areas. We matched extracted average NDVI to GPS fixes for each temporal resolution analyzed (i.e., 3-, 5-, and 10-day timescales). This best aligned with the temporal windows used in our analyses. Average NDVI data were retrieved and analyzed in GEE (<https://earthengine.google.com>) (Crego et al., 2021).

2.6. Statistical analysis

To investigate correlates of the proportion of days in agricultural areas during 16-day periods, we developed multiple generalized linear mixed models (GLMMs) with beta probability distribution and logit link with zero inflation using the *glmmTMB* package R version 4.4.1 (Brooks et al., 2017). We investigated two covariates of the response variable, proportion of days in agricultural area, namely 1) NDVI value of the agricultural and agricultural areas traversed by the elephants in the study area, and 2) group size. We included elephant bull ID ($N = 7$) as a random effect in the model, given that repeated samples were collected from the same individual. In addition, we constructed multiple GLMMs with a Gaussian distribution using the *glmmTMB* package R version 4.4.1 (Brooks et al., 2017) to investigate correlates of fGCM and fTM concentrations, which were log-transformed to improve model fit. We included the following covariates in the model: 1) hours spent in agricultural areas 3, 5, and 10 days before sample collection, 2) average NDVI values of locations used by collared elephants 3, 5, and 10 days before sample collection, 3) BCS, 4) proportion of time in agricultural area over six months period prior to sampling, and 5) group size. We also included elephant bull ID as a random effect.

For both GLMMs with either a beta or Gaussian distribution, we conducted model selection using Akaike's Information Criterion

adjusted for small sample size to identify the most parsimonious models (Supplementary Table 2 for proportion of days in agriculture, Supplementary Table 3 for fGCM concentrations, and Supplementary Table 4 for fTM concentrations) (Burnham and Anderson, 2004). We checked for model misspecification issues (i.e., dispersion and uniformity) for the GLMM with a beta distribution using the DHARMA package in R version 4.4.1 (Hartig, 2016). For the GLMM with a Gaussian distribution, we evaluated model assumptions using diagnostic residual plots, including normality and heteroscedasticity. Additionally, we assessed the fit of our final models by calculating variation explained by the fixed effects only (i.e., marginal R^2) and the variation explained by both fixed and random effects (i.e., conditional R^2) using the *performance* package in R version 4.4.1 (Lüdtke et al., 2021). If no variation was explained by the random effect in our final model, we created a simpler model without random effects and compared it to our best model with random effects using Akaike's Information Criterion adjusted for small sample size. We compared the mean concentrations expressed as \pm standard deviation (SD) of fGCM and fTM across different BCS and Elephant IDs using a one-way analysis of variance (ANOVA) and used Tukey HSD for pairwise comparison of the significant effects. All statistical analyses were performed in R version 4.4.1 (R Development Core Team, 2024).

3. Results

3.1. Descriptive results

The proportion of days in an agricultural area within the 16-day window ($n = 83$ samples) averaged (\pm SD) 0.20 ± 0.20 and ranged from 0 to 0.75. Some bulls regularly used these areas, spending about 28 % of their tracked time there, while others used them sparingly, with only 4 % of their time in agricultural landscapes. However, time spent in agriculture was not significantly correlated with either fGCM concentrations ($R^2 = 0.13$, $p = 0.22$) or fTM concentrations ($R^2 = 0.18$, $p = 0.79$). Concentrations of fGCM ($n = 83$) averaged 31.45 ± 43.41 ng/g and ranged from 6.63 to 338.55 ng/g. Mean fGCM concentrations per individual bull ranged from 17.23 ± 5.21 ng/g to 57.17 ± 88.82 ng/g but did not differ significantly (ANOVA: $F_{6, 76} = 1.92$, $p = 0.09$). Concentrations of fTM ($n = 83$) averaged 384.95 ± 365.57 ng/g and ranged from 73.00 to 2485.29 ng/g. Mean fTM concentrations per individual bull ranged from 211.28 ± 141.61 ng/g to 547.48 ± 785.76 ng/g but did not differ significantly (ANOVA: $F_{6, 76} = 0.95$, $p = 0.47$). Concentrations of fTM for individuals did not differ significantly between individual BCS, with BCS = 3 having higher concentrations (506.34 ± 529.65 ng/g, $n = 25$) compared to individuals with BCS = 2 (373.72 ± 281.13 ng/g, $n = 39$) or BCS = 4 (248.29 ± 165.77 ng/g, $n = 19$) (ANOVA: $F_{2, 80} = 2.85$, $p = 0.06$).

3.2. Proportion of days in agriculture

The top model for the proportion of days in agriculture consisted of landscape-wide NDVI (Table 2). The proportion of days in agriculture was negatively correlated with landscape-wide NDVI, such that the proportion of days in agriculture decreased from 0.36 [95 % confidence interval (CI) = 0.26–0.48] during low NDVI value to 0.07 (CI = 0.02–0.18) at the highest NDVI value (Fig. 2).

3.3. Concentrations of fGCM and fTM

The top model for fGCM concentrations consisted of the average NDVI value derived from GPS-tracked locations three days before sample collection, hours spent in farmland 3 days before sample collection, and BCS (Table 3, Fig. 3). Concentrations of fGCM were positively correlated with hours spent in agriculture 3 days before sample collection, such that the mean fGCM concentrations increased from 10.65 ng/g (CI = 9.01–12.58 ng/g) during the least time spent in an agricultural area to 54.54 ng/g (CI = 35.16–84.59 ng/g) during the most time spent in an agricultural area. Mean fGCM concentrations were significantly higher among different BCSs ($\chi^2(2) = 13.03$, $p < 0.05$). A post hoc Tukey HSD test indicated that individuals with BCS = 4 were significantly lower than those with BCS = 3 (estimate = 0.36, CI = 0.10–0.62) ($p < 0.05$) or BCS = 2 (0.43, CI = 0.12–0.75) ($p < 0.05$). However, individuals with BCS = 2 did not significantly differ from those with BCS = 3 (0.07, CI = – 0.18 to 0.34) ($p = 0.78$). The mean fGCM concentrations decreased from 18.16 ng/g (CI = 14.54–22.68 ng/g) during periods with the lowest NDVI values derived from GPS-

Table 2

Results from the top mixed-effects generalized linear model (GLMM) with a zero-inflated beta distribution explaining the variation in the proportion of days in agriculture by crop-raiding male African savanna elephants.

Proportion of days in agriculture ~ Landscape-wide NDVI + (1 Elephant ID)					
Predictors	Estimate	Std. Error	CI	Z value	P value
Intercept	– 1.24	0.15	– 1.61 to – 0.96	– 8.23	< 0.001
Landscape-wide NDVI	– 0.34	0.13	– 0.59 to – 0.09	– 2.64	0.008
Zero-inflation model					
Intercept (zero-inflation)	– 1.68	0.30	– 2.32 to – 1.13	– 5.58	< 0.001
Random effect					
Elephant ID	0.04	0.21			
Number of elephants	7				
Observation	83				
Marginal R^2 /Conditional R^2	0.02	0.03			

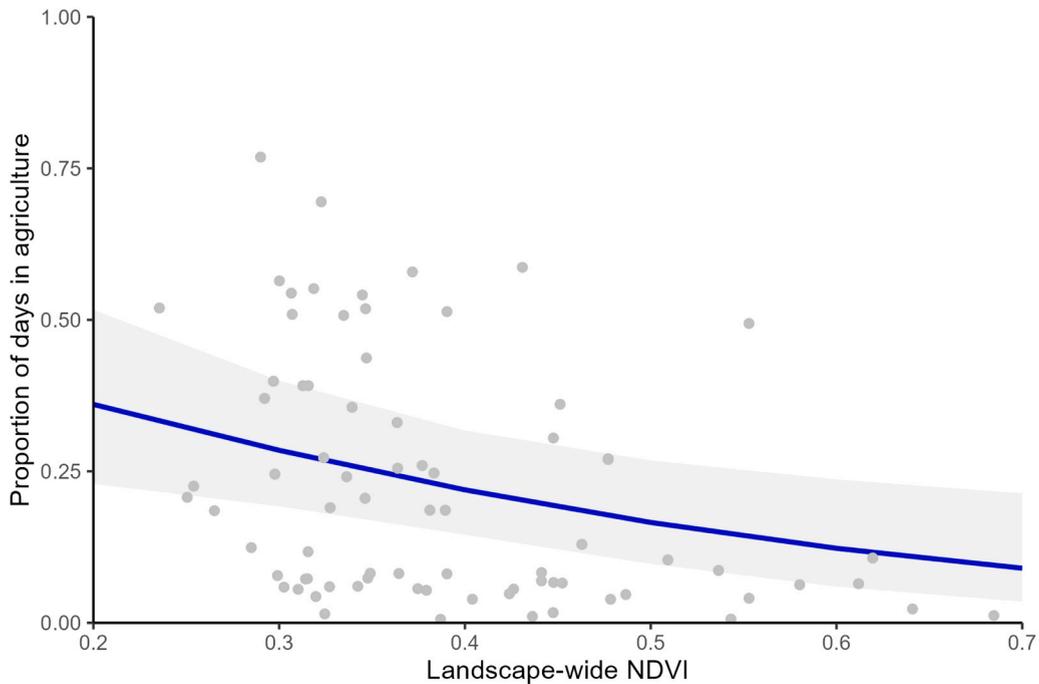


Fig. 2. Model effect plots showing the relationship between the proportion of days male African savanna elephants spent in agriculture and landscape-wide NDVI. The blue line represents the model fit, while the shaded area represents a 95 % confidence interval.

Table 3

Results from the top mixed-effects GLMM with a Gaussian distribution explaining variation in fGCM concentrations in crop-raiding male African savanna elephants. The reference category for body condition scores is 4.

fGCM ~ hours in farmland 3 days before sampling + NDVI 3 days before sampling + BCS + (1 Elephant ID)					
Predictors	Estimate	Std. Error	CI	Z value	P value
Intercept	2.80	0.10	2.61–2.99	28.76	< 0.001
Hours spent in farmland 3 days before sampling	0.49	0.05	0.38–0.59	9.14	< 0.001
NDVI 3 days before sampling	– 0.05	0.04	– 0.13 to 0.02	– 1.34	0.180
BCS = 3	0.36	0.11	0.14 to 0.58	3.21	0.001
BCS = 2	0.43	0.13	0.17 –to 0.70	3.24	0.001
Random effect		Variance	Std. dev		
Elephant ID		0.003	0.056		
Residual		0.126	0.355		
Number of elephants		7			
Observation		83			
Marginal R ² /Conditional R ²		0.73/0.74			

tracked locations three days before sample collection to 13.23 ng/g (CI = 8.93–19.59 ng/g) during the same timeframe, although this effect was not significant.

The top model for fTM concentrations comprised the average NDVI value derived from GPS-tracked locations 10 days before sample collection, hours spent in agriculture 10 days before sample collection, BCS, and group size (Table 4, Fig. 4). Concentrations of fTM were negatively correlated with the average NDVI value derived from GPS-tracked locations 10 days before sample collection, such that mean fTM concentrations decreased from 569.43 ng/g (CI = 352.08–920.96 ng/g) during the periods with the lowest NDVI values to 111.00 ng/g (CI = 56.67–217.44 ng/g) during the periods with the highest NDVI values. The mean concentrations of fTM were positively correlated with hours spent in agriculture 10 days before sample collection such that fTM concentrations increased from 227.57 ng/g (CI = 172.01–301.09 ng/g) during the period they least spent in an agricultural area to 573.90 ng/g (CI = 326.70–1008.15 ng/g) during the periods with most time spent within an agricultural area. Individuals with BCS = 2 (238.64 ng/g, CI = 194.46–292.87 ng/g) showed lower fTM concentrations compared to those with BCS = 3 (348.35 ng/g, CI = 276.95–438.15 ng/g) or BCS = 4 (338.14 ng/g, CI = 241.68–473.10 ng/g), although this effect was not significant. Concentrations of fTM were negatively correlated with group size, with fTM concentrations decreasing from 358.24 ng/g (CI = 257.27–498.83 ng/g) when individuals were in smaller groups to 198.74 ng/g (92.35–427.69 ng/g) for individuals in larger groups although this effect did not significantly differ.

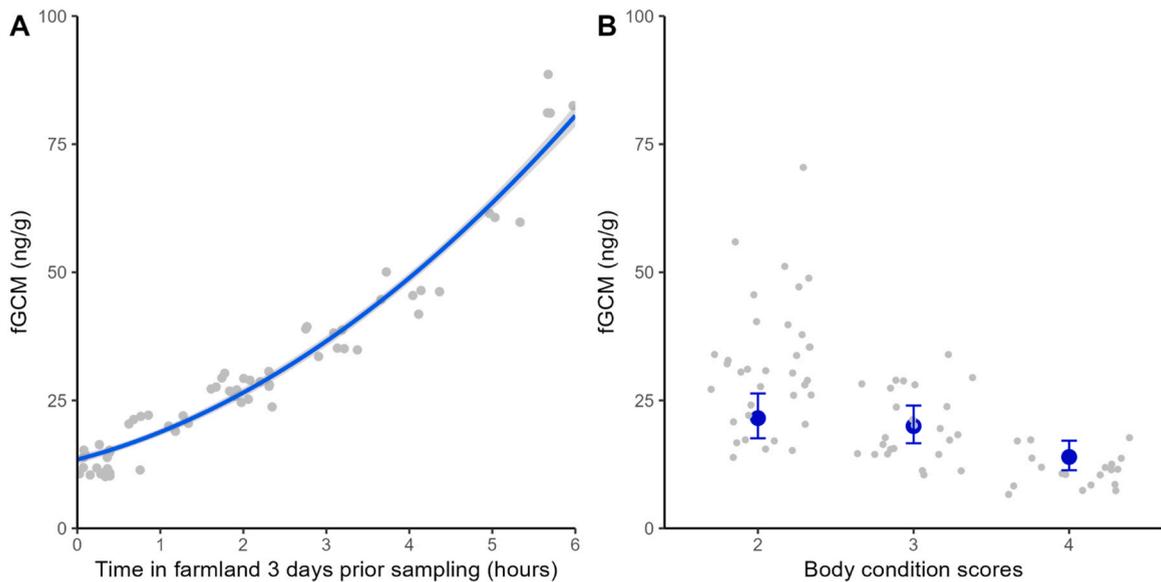


Fig. 3. Model effect plot showing the relationship between fGCM concentrations in male African savanna elephants and (A) time spent in farmland during the 3 days leading up to sample collection and (B) body condition scores. The blue line on the left side represents the regression line, while the shaded area represents a 95 % confidence interval. The error bars on the right side represent the mean (blue dots) with both upper and lower intervals. The grey dots represent the fitted raw data points. The Y-axis is truncated at 100 ng/g to aid in the interpretation of the results.

Table 4

Results from generalized linear model (GLM) with a Gaussian distribution explaining variation in fT3 concentrations in crop-raiding male African savanna elephants. The reference category for body condition scores is 4.

fT3m ~ hours in farmland 10 days before sampling + NDVI 10 days before sampling + BCS + group size					
Predictors	Estimate	Std. Error	CI	Z value	P value
Intercept	5.82	0.17	5.49 – 6.16	33.99	< 0.001
Hours spent in farmland 10 days before sampling	0.30	0.09	0.13 – 0.47	3.44	0.001
NDVI 10 days before sampling	– 0.24	0.07	– 0.38 – – 0.10	– 3.44	0.001
BCS = 3	0.03	0.21	– 0.39 – 0.45	0.14	0.888
BCS = 2	– 0.35	0.22	– 0.79 – 0.09	– 1.55	0.121
Group size	– 0.11	0.07	– 0.24 – 0.02	– 1.64	0.100
Observations	83				
R ² /R ² adjusted	0.35/0.30				

4. Discussion

We assessed how agricultural use, ecological conditions, and BCS correlated with adrenal and thyroid hormone concentrations in fecal samples collected from habitually crop-raiding male African savanna elephants within Laikipia County, Kenya. Our findings showed strong relationships between agricultural use, fGCM and fTM concentrations, and NDVI. Unlike other studies that based the assessment of crop raiding on the presence of feces in agricultural fields (Ahlering et al., 2011; Malcolm et al., 2014; Pokharel et al., 2019) or assessed behavioral drivers of crop raiding (Chiyo et al., 2012; Hahn et al., 2024; Naha et al., 2020; Songhurst and Coulson, 2014; Walton et al., 2021), we used location data from GPS collars to determine the time individuals spent in agricultural areas directly. We also investigated the time frame of agricultural use that most strongly correlated with fGCM and fTM concentrations, showing time-lag differences between fGCM and fTM excretion patterns. Our results provide insight into how individual physiology and habitat choice are related, with potential implications for devising mitigation strategies for human-elephant conflicts and developing those strategies.

Determining the time delay between stimuli and corresponding physiological responses and between hormone secretion and excretion is crucial for accurately interpreting endocrine data. In this study, the strongest positive correlation between fGCM concentrations and time in agricultural fields was observed on a 3-day rather than a 5- or 10-day scale. This time frame aligns with the known gut-passage time for this hormone and likely reflects the period during which elephants mobilize energy to cope with or respond to challenges encountered in agricultural areas. Lag times of 24–60 h between blood hormone secretion (estradiol, progesterone, T3) and fecal excretion (Wasser et al., 2000; Wasser et al., 1996) align with our predictor model for a 3-day time scale.

By contrast, fTM concentrations exhibited the strongest positive correlation with time spent in agricultural areas when measured in samples collected after 10 days, rather than after 3 or 5 days. While there is no information in the literature on the gut passage time of

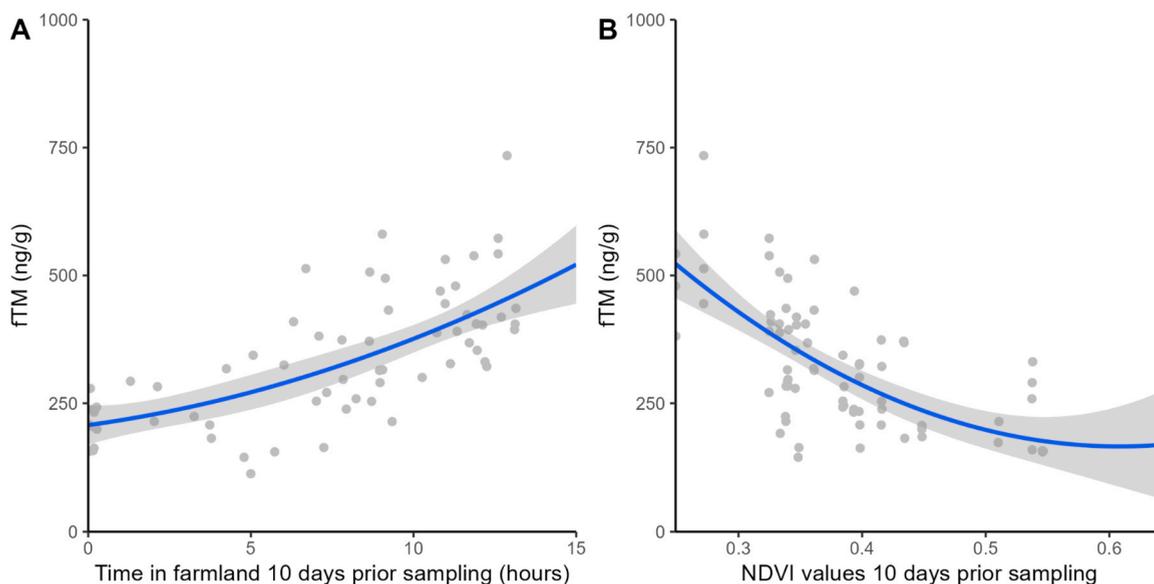


Fig. 4. Model effect plot showing the relationship between fT3m concentrations in male African savanna elephants and (A) time spent in farmland during the 10 days before sampling and (B) average NDVI values over the 10 days before sampling. The blue line represents the regression line, while the shaded area represents a 95 % confidence interval. The grey dots represent the fitted raw data points. The Y-axis is truncated at 1000 ng/g to aid in the interpretation of the results.

thyroid hormones in elephants, studies in other species have found it to range between 24 and 48 h, with variations across species. The longer lag time observed between agricultural use and fTM excretion in elephants may therefore reflect differences in the physiological drivers of the two hormones, such as acute versus chronic responses and the physiological lag in metabolizing and storing energy from increased food intake associated with repeated crop-raiding events. In contrast to GCs, T3 levels typically show less sensitivity to daily fluctuations (Wasser et al., 2010) or short-term nutritional changes (Eales, 1988). Instead, T3 concentrations are more responsive to long-term factors such as the extent and duration of energy deficits and the animal's condition before food limitation (Hornick et al., 2000; Kelly, 2000).

The positive correlation between time spent in agricultural fields and fGCM concentrations suggests the risks associated with using these areas could induce a physiological response in elephants. Agricultural use primarily occurs at night, potentially reflecting a 'landscape of fear' adaptation (Brown et al., 1999; Corde et al., 2024; Gunn et al., 2014). This behavior suggests a temporary adjustment in elephant activity patterns to minimize human encounters (Naha et al., 2020; Troup et al., 2020), which may elicit a greater physiological stress response. Farmers in the area incur losses from crop foraging, experience delays in compensation from government authorities, and employ various methods to deter elephants. These methods sometimes result in physical harm or even mortality to the elephant (Evans, 2015; Thouless, 1994; Van Eden et al., 2016). Consequently, crop raiding is a risky activity, likely driving the observed positive correlation between agricultural use and fGCM concentrations.

Our results also showed that fTM concentrations were higher as elephants spent more time in agricultural areas. Wildlife may prefer crops because of their high nutritional value and essential mineral content (McLennan and Ganzhorn, 2017; Riley et al., 2013; Rode et al., 2006). Research on Asian elephants in India suggested that elephants are drawn to crops because of the higher nitrogen content and lower carbon-to-nitrogen ratio compared to natural vegetation, making them a more attractive protein source (Pokharel et al., 2019). While links between fTM and crop raiding are lacking in the literature, our previous study found higher fTM concentrations among elephants in agropastoral landscapes than in other areas, potentially reflecting a higher dietary intake (Oduor et al., 2024). Conversely, during periods of nutritional deficit, animals lower their metabolic rate to conserve energy, resulting in decreased T3 levels (Flier et al., 2000). For example, lower fTM concentrations were observed in yellow baboons (*Papio cynocephalus*) (Gesquiere et al., 2024), Barbary macaques (*Macaca sylvanus*) (Cristóbal-Azkarate et al., 2016), and mantled howler monkeys (*Alouatta palliata*) (Dias et al., 2017) in response to reduced caloric intake. Similarly, in previous work on African savanna elephants in the Laikipia-Samburu system, lower fTM concentrations were found during drought periods (Oduor et al., 2024). However, in the Serengeti ecosystem, fTM concentrations were inversely related to NDVI in impalas (*Aepyceros melampus*) (Hunninck et al., 2020). These contrasting findings in impalas highlight the complexity of thyroid hormone responses across species and ecosystems, emphasizing the need for species-specific studies to understand relationships among environmental factors, nutritional status, and thyroid function in wildlife.

While we found no significant effect of fTM concentrations on BCS in elephants, other researchers have found this in other species. For example, in free-ranging island foxes (*Urocyon littoralis*), higher fTM concentrations were observed among individuals with higher BCSs in southern California's Channel Islands National Park (CINP) (Kozłowski et al., 2020). In sheep, feeding restriction reduced plasma T3 concentrations and other metabolic markers in animals with lower BCSs (Caldeira et al., 2007). Lower nutritional status

during periods of reduced forage quality could be driving African elephants to seek crops in agricultural areas that are more nutrient-dense; however, the nonsignificant difference between fTM concentrations and BCS could reflect limited sample size or the inherent lag between changes in dietary intake and alterations in body composition.

African elephants live in a seasonal environment with varying forage and nutritional quality (Shannon et al., 2013), both of which can influence metabolic activity and, consequently, thyroid hormone levels. In our study, fTM concentrations were inversely related to NDVI, indicating higher metabolic activity during periods of low vegetation greenness. During low NDVI periods, elephants often expand their ranges into agricultural areas to exploit energy-dense crops (Chiyo et al., 2005; Mukenka et al., 2019; Osborn, 2004; Vogel et al., 2020; Webber et al., 2011). While these crops provide supplemental nutrients, crop raiding typically occurs when natural forage is limited and is associated with greater energetic expenditure and exposure to human disturbance. These factors can increase metabolic rates and, consequently, thyroid activity. As such, increased use of agricultural areas when the surrounding NDVI was low could result in higher fTM concentrations. In Mozambique, crop-raiding elephants similarly increased their preference for crops during the brown-down stages (Branco et al., 2019). Although cultivated crops contain higher levels of protein and certain minerals, such as sodium and phosphorus, compared to natural vegetation (Chiyo et al., 2005; Rode et al., 2006), the observed increase in fTM concentrations during periods of intensified agricultural use might be related to elevated metabolic demands and nutritional stress associated with foraging effort and energy imbalance rather than direct dietary effects. Conversely, during high NDVI periods, abundant natural forage improves energy balance, reducing metabolic demand, thyroid activity, and fTM concentrations.

Although we found an inverse relationship between BCS and fGCM concentrations, the inverse relationship between NDVI and fGCM concentrations was not significant in this study, the latter of which contrasts with previous studies in other savannah elephants (Oduor et al., 2020, 2024). Fluctuations in environmental conditions can influence resource availability and foraging behavior of elephants, with consequences for overall body conditions. Pokharel et al. (2017) found higher fGCM concentrations in Asian elephants with lower BCS in the Mysore and Nilgiri Elephant Reserves in southern India. In Myanmar, Mumby et al. (2015) observed fGCM concentrations correlated with seasonal changes in the body weight of Asian elephants. While GC indirectly responds to changes in food availability, crop-raiding elephants oscillate between the use of agricultural areas and natural vegetation depending on their net energy balance. This could have potentially influenced any relationship between fGCM concentrations and NDVI in our study. However, in tourist elephants in Thailand, higher fGCM concentrations were associated with higher body mass (i.e., BCS = 4 and 5) and alterations in lipid and sugar metabolism (Norkaew et al., 2018). Low BCSs are more of a problem for wild elephants, which have higher fGCM (Tang et al., 2024; Wato et al., 2016), whereas in captivity, obesity (i.e., high BCSs).

Male elephants have been observed to form larger groups during crop raiding, which was assumed to reduce individual risks (Chiyo et al., 2012). Crop raiding is considered a high-risk foraging behavior (Chiyo et al., 2011), and individuals detected by farmers risk injury or death. However, contrary to our expectations, group size had no significant influence on agricultural use. One limitation of our study was the relatively small number of focal bull elephants ($N = 7$), which may have reduced our ability to detect statistically significant effects of group size on agricultural use. General monitoring that would capture larger sample sizes is needed to more accurately assess the relationship between group size and crop-raiding behavior in male elephants. Based on our study results, we recommend strengthening existing mitigation strategies to address crop-raiding behavior in male elephants. Specifically, installing smart GPS collars with geo-fence technology on known fence-breakers and crop-raiders could help mobilize resources more effectively in response to crop-raiding incidents, especially during the dry season when such incidents are more frequent. Additionally, there is a pressing need to develop a comprehensive land use plan for heterogeneous areas shared by wildlife and human communities. We also recommend further studies to better understand how elephants maximize their net energy intake – for example, by assessing how digestible energy correlates with fTM concentrations as they move between agricultural areas and natural vegetation. Higher levels of digestible energy beyond the maintenance requirement are beneficial to male elephants as they confer a reproductive advantage by supporting the energetically demanding state of musth (Rasmussen et al., 2008; Sukumar, 1990).

5. Conclusions

Given the link between physiology and fitness, understanding the biological factors that drive African elephants to use agricultural areas is important. Our study helps to untangle how variation in the use of natural vegetation and agricultural areas with differing forage quality influences fGCM and fTM concentrations and body condition in free-ranging African elephants. Our results suggest that elephants increase their time in agricultural areas when natural habitats have low NDVI values. As BCS improves, agricultural use decreases, and these risk-reward decisions appear to be reflected in fGCM and fTM concentrations. With natural habitats increasingly being replaced by agriculture and negatively affected by recurrent droughts due to climate change (Frank, 2016), elephants are likely to intensify their use of agricultural areas to meet energetic demands, potentially escalating conflicts. Hormonal measurements can provide physiological indicators of an individual's energy balance while navigating risky landscapes and potentially indicate conditions facilitating conflict. Our findings highlight the value of endocrine biomarkers in monitoring wildlife behavior across human-modified landscapes with fluctuating resources, revealing the risks animals take to maximize their energy and nutritional intake.

CRediT authorship contribution statement

Suzan Murray: Writing – review & editing, Funding acquisition. **Goldenberg Shifra:** Writing – review & editing, Funding acquisition. **Nelson Mwangi:** Writing – review & editing, Formal analysis. **Maurice Schutgens:** Writing – review & editing, Funding acquisition. **George Wittemyer:** Writing – review & editing, Validation, Supervision. **Sandy Oduor:** Writing – original draft, Project

administration, Investigation, Formal analysis, Data curation, Conceptualization. **Brown Janine:** Writing – review & editing, Supervision, Methodology, Funding acquisition. **Dennis Kimata:** Writing – review & editing, Supervision. **Gichuki Nathaniel:** Writing – review & editing, Supervision. **Parker Jenna:** Writing – review & editing, Data curation.

Funding

This work was supported by the 1st Booster Rufford Grant (Grant no. 40012-B) and Save the Elephants. S. Oduor was supported by funding from the Smithsonian Conservation Biology Institute's Research Endocrinology and Global Health Programs. San Diego Zoo Wildlife Alliance (SDZWA) provided funding for lab assistance and equipment.

Conflict of interest

The authors have no conflict of interest to declare.

Declaration of Competing Interest

The authors have no conflict of interest to declare.

Acknowledgments

We sincerely acknowledge Charles Kinyua and Reuben Mungai from Space for Giants, who assisted the team with tracking the elephants and sample collection. We also thank the staff of Kenya Wildlife Service (KWS), Rumuruti station, and Mpala Research Centre who provided security to the team during sample collection. We thank Ephantus Wambui who assisted with sample processing at the Endocrine Lab, Mpala Research Centre. Lastly, we would like to thank Purity Milgo, who assisted with generating a map for the study area. Permission to conduct this study was granted by the Wildlife Research and Training Institute (Permit no. WRTI-0110-11-21) and the National Commission for Science, Technology & Innovation (Permit no. NACOSTI/P/21/4067).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03912](https://doi.org/10.1016/j.gecco.2025.e03912).

Data availability

Data will be made available on request.

References

- Abbas, F., Morellet, N., Hewison, A.J.M., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault, J.-M., Daufresne, T., Aulagnier, S., Verheyden, H., 2011. Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. *Oecologia* 167, 401–411. <https://doi.org/10.1007/s00442-011-1994-0>.
- Abrahms, B., 2021. Human-wildlife conflict under climate change. *Science* 373, 484–485. <https://doi.org/10.1126/science.abj4216>.
- Acevedo-Whitehouse, K., Duffus, A.L.J., 2009. Effects of environmental change on wildlife health. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 3429–3438. <https://doi.org/10.1098/rstb.2009.0128>.
- Ahlering, M.A., Millsbaugh, J.J., Woods, R.J., Western, D., Eggert, L.S., 2011. Elevated levels of stress hormones in crop-raiding male elephants. *Anim. Conserv.* 14, 124–130. <https://doi.org/10.1111/j.1469-1795.2010.00400.x>.
- Barker, K.J., Mitchell, M.S., Proffitt, K.M., 2019. Native forage mediates influence of irrigated agriculture on migratory behaviour of elk. *J. Anim. Ecol.* 88, 1100–1110. <https://doi.org/10.1111/1365-2656.12991>.
- Behringer, V., Deimel, C., Hohmann, G., Negrey, J., Schaeb, F.S., Deschner, T., 2018. Applications for non-invasive thyroid hormone measurements in mammalian ecology, growth, and maintenance. *Horm. Behav.* 105, 66–85. <https://doi.org/10.1016/j.yhbeh.2018.07.011>.
- Boonstra, R., 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Funct. Ecol.* 27, 11–23. <https://doi.org/10.1111/1365-2435.12008>.
- Branco, P.S., Merkle, J.A., Pringle, R.M., Pansu, J., Potter, A.B., Reynolds, A., Stalmans, M., Long, R.A., 2019. Determinants of elephant foraging behaviour in a coupled human-natural system: is brown the new green? *J. Anim. Ecol.* 88, 780–792. <https://doi.org/10.1111/1365-2656.12971>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 400. <https://doi.org/10.32614/RJ-2017-066>.
- Brown, J.S., Laundré, J.W., Gurung, M., 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399. <https://doi.org/10.2307/1383287>.
- Burnham, K.P., Anderson, D.R., 2004. Model selection and multimodel inference. A practical information-theoretic approach 2.
- Busch, D.S., Hayward, L.S., 2009. Stress in a conservation context: a discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biol. Conserv.* 142, 2844–2853. <https://doi.org/10.1016/j.biocon.2009.08.013>.
- Caldeira, R.M., Belo, A.T., Santos, C.C., Vazques, M.I., Portugal, A.V., 2007. The effect of long-term feed restriction and over-nutrition on body condition score, blood metabolites and hormonal profiles in ewes. *Small Rumin. Res.* 68, 242–255. <https://doi.org/10.1016/j.smallrumres.2005.08.026>.
- Campbell, J., Wynne, R., 2011. History and scope of remote sensing. *Introd. Remote Sens.* 3–30.
- Carroll, M., DiMiceli, C., Sohlberg, R., Townshend, J., 2004. 250m MODIS Normalized Difference Vegetation Index. University of Maryland, College Park, Maryland.

- Chiyo, P.I., Cochrane, E.P., Naughton, L., Basuta, G.I., 2005. Temporal patterns of crop raiding by elephants: a response to changes in forage quality or crop availability? *Afr. J. Ecol.* 43, 48–55. <https://doi.org/10.1111/j.1365-2028.2004.00544.x>.
- Chiyo, P.I., Lee, P.C., Moss, C.J., Archie, E.A., Hollister-Smith, J.A., Alberts, S.C., 2011. No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants. *Behav. Ecol.* 22, 552–558. <https://doi.org/10.1093/beheco/arr016>.
- Chiyo, P.I., Moss, C.J., Alberts, S.C., 2012. The influence of life history milestones and association networks on crop-raiding behavior in male African elephants. *PLoS One* 7, e31382. <https://doi.org/10.1371/journal.pone.0031382>.
- Corde, S.C., Von Hagen, R.L., Kasaine, S., Mutwiva, U.N., Amakobe, B., Githiru, M., Schulte, B.A., 2024. Lunar phase as a dynamic landscape of fear factor affecting elephant crop raiding potential. *Ethol. Ecol. Evol.* 36, 295–308. <https://doi.org/10.1080/03949370.2023.2263406>.
- Crego, R.D., Masolele, M.M., Connette, G., Stabach, J.A., 2021. Enhancing animal movement analyses: spatiotemporal matching of animal positions with remotely sensed data using google earth engine and R. *Remote Sens.* 13, 4154.
- Cristóbal-Azkarate, J., Maréchal, L., Semple, S., Majolo, B., MacLarnon, A., 2016. Metabolic strategies in wild male barbary macaques: evidence from faecal measurement of thyroid hormone. *Biol. Lett.* 12, 20160168. <https://doi.org/10.1098/rsbl.2016.0168>.
- Dias, P.A.D., Coyohua-Fuentes, A., Canales-Espinosa, D., Chavira-Ramírez, R., Rangel-Negrín, A., 2017. Hormonal correlates of energetic condition in mantled howler monkeys. *Horm. Behav.* 94, 13–20. <https://doi.org/10.1016/j.yhbeh.2017.06.003>.
- Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., Martimort, P., Meygret, A., Spoto, F., Sy, O., Marchese, F., Bargellini, P., 2012. Sentinel-2: ESA's optical high-resolution mission for GMES operational services. *Remote Sens. Environ.* 120, 25–36. <https://doi.org/10.1016/j.rse.2011.11.026>.
- Eales, J.G., 1988. The influence of nutritional state on thyroid function in various vertebrates. *Am. Zool.* 28, 351–362. <https://doi.org/10.1093/icb/28.2.351>.
- Edwards, K.L., Trotter, J., Jones, M., Brown, J.L., Steinmetz, H.W., Walker, S.L., 2016. Investigating temporary acyclicity in a captive group of asian elephants (*Elephas maximus*): relationship between management, adrenal activity and social factors. *Gen. Comp. Endocrinol.* 225, 104–116. <https://doi.org/10.1016/j.ygcen.2015.09.011>.
- Evans, L.A., 2015. *Fencing the Front Line: The Separation of Elephants and Cultivation with Electrified Fences*. University of Cambridge.
- Evans, L.A., Adams, W.M., 2016. Fencing elephants: the hidden politics of wildlife fencing in Laikipia, Kenya. *Land Use Policy* 51, 215–228. <https://doi.org/10.1016/j.landusepol.2015.11.008>.
- Firdhous, M.F.M., 2020. IoT-enhanced smart laser fence for reducing human elephant conflicts. In: *2020 5th International Conference on Information Technology Research (ICITR)*, pp. 1–5.
- Flier, J.S., Harris, M., Hollenberg, A.N., 2000. Leptin, nutrition, and the thyroid: the why, the wherefore, and the wiring. *J. Clin. Invest.* 105, 859–861.
- Foley, C.A.H., Papageorge, S., Wasser, S.K., 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conserv. Biol.* 15, 1134–1142. <https://doi.org/10.1046/j.1523-1739.2001.0150041134.x>.
- Frank, L., 2016. *Effects of Drought on the Relationships Between Herbivores and Vegetation Types in the Laikipia-Samburu Ecosystem*. University of Twente.
- Georgiadis, N.J., Olwero, J.G.N., Ojwang', G., Romanach, S.S., 2007. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biol. Conserv.* 137, 461–472. <https://doi.org/10.1016/j.biocon.2007.03.005>.
- Gesquiere, L.R., Adjangba, C., Wango, T.L., Oudu, V.K., Mututua, R.S., Warutere, J.K., Siodi, I.L.I., Campos, F.A., Archie, E.A., Markham, A.C., Alberts, S.C., 2024. Thyroid hormone concentrations in female baboons: metabolic consequences of living in a highly seasonal environment. *Horm. Behav.* 161, 105505. <https://doi.org/10.1016/j.yhbeh.2024.105505>.
- Gobush, K., Edwards, C., Balfour, D., Wittemyer, G., Maisels, F., Taylor, R., 2021. *Loxodonta africana*. The IUCN Red List of threatened species 2021: e.T181008073A181022663.
- Gobush, K.S., Mutayoba, B.M., Wasser, S.K., 2008. Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Conserv. Biol.* 22, 1590–1599. <https://doi.org/10.1111/j.1523-1739.2008.01035.x>.
- Gobush, K.S., Booth, R.K., Wasser, S.K., 2014. Validation and application of noninvasive glucocorticoid and thyroid hormone measures in free-ranging Hawaiian monk seals. *Gen. Comp. Endocrinol.* 195, 174–182. <https://doi.org/10.1016/j.ygcen.2013.10.020>.
- Google Earth Pro, 2024. Rumuruti Region, Laikipia County, Kenya. 0° 5'9.32"N, 36°34'6.84"E, Eye Alt 73.48 km. Borders and Labels; Places Layers. NOAA, DigitalGlobe.
- Graham, M.D., Douglas-Hamilton, I., Adams, W.M., Lee, P.C., 2009. The movement of African elephants in a human-dominated land-use mosaic. *Anim. Conserv.* 12, 445–455. <https://doi.org/10.1111/j.1469-1795.2009.00272.x>.
- Graham, M.D., Notter, B., Adams, W.M., Lee, P.C., Ochieng, T.N., 2010. Patterns of crop-raiding by elephants, *Loxodonta africana*, in Laikipia, Kenya, and the management of human–elephant conflict. *Syst. Biodivers.* 8, 435–445. <https://doi.org/10.1080/14722000.2010.533716>.
- Gross, E.M., Lahkar, B.P., Subedi, N., Nyirenda, V.R., Lichtenfeld, L.L., Jakoby, O., 2018. Seasonality, crop type and crop phenology influence crop damage by wildlife herbivores in Africa and Asia. *Biodivers. Conserv.* 27, 2029–2050. <https://doi.org/10.1007/s10531-018-1523-0>.
- Gunaryadi, D., Sugiyono, Hedges, S., 2017. Community-based human–elephant conflict mitigation: the value of an evidence-based approach in promoting the uptake of effective methods. *PLoS One* 12, e0173742. <https://doi.org/10.1371/journal.pone.0173742>.
- Gunn, J., Hawkins, D., Barnes, R.F.W., Mofulu, F., Grant, R.A., Norton, G.W., 2014. The influence of lunar cycles on crop-raiding elephants; evidence for risk avoidance. *Afr. J. Ecol.* 52, 129–137. <https://doi.org/10.1111/aje.12091>.
- Hahn, N.R., Wall, J., Denninger-Snyder, K., Goss, M., Sairouwa, W., Mbise, N., Estes, A.B., Ndambuki, S., Mjingo, E.E., Douglas-Hamilton, I., Wittemyer, G., 2022. Risk perception and tolerance shape variation in agricultural use for a transboundary elephant population. *J. Anim. Ecol.* 91, 112–123. <https://doi.org/10.1111/1365-2656.13605>.
- Hahn, N.R., Wall, J., Denninger-Snyder, K., Tiedeman, K., Sairouwa, W., Goss, M., Ndambuki, S., Eblate, E., Mbise, N., Wittemyer, G., 2024. Crop use structures resource selection strategies for African elephants in a human-dominated landscape. *Ecol. Evol.* 14, e11574. <https://doi.org/10.1002/ece3.11574>.
- Hartig F (2016) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. CRAN: Contributed Packages.
- Hill, C.M., 2017. Primate crop feeding behavior, crop protection, and conservation. *Int. J. Primatol.* 38, 385–400. <https://doi.org/10.1007/s10764-017-9951-3>.
- Hill, C.M., 2018. Crop foraging, crop losses, and crop raiding. *Annu. Rev. Anthr.* 47, 377–394. <https://doi.org/10.1146/annurev-anthro-102317-050022>.
- Hornick, J.L., Van Eenaeme, C., Gérard, O., Dufresne, I., Istasse, L., 2000. Mechanisms of reduced and compensatory growth. *Domest. Anim. Endocrinol.* 19, 121–132. [https://doi.org/10.1016/S0739-7240\(00\)00072-2](https://doi.org/10.1016/S0739-7240(00)00072-2).
- Hunninck, L., Jackson, C.R., May, R., Røskaft, E., Palme, R., Sheriff, M.J., 2020. Triiodothyronine (T3) levels fluctuate in response to ambient temperature rather than nutritional status in a wild tropical ungulate. *Conserv. Physiol.* 8 (1), coaa105. <https://doi.org/10.1093/conphys/coaa105>.
- Ihwagi, F.W., Wang, T., Wittemyer, G., Skidmore, A.K., Toxopeus, A.G., Ngene, S., King, J., Worden, J., Omondi, P., Douglas-Hamilton, I., 2015. Using poaching levels and elephant distribution to assess the conservation efficacy of private, communal and government land in Northern Kenya. *PLoS One* 10, e0139079. <https://doi.org/10.1371/journal.pone.0139079>.
- Jesmer, B.R., Goheen, J.R., Monteith, K.L., Kauffman, M.J., 2017. State-dependent behavior alters endocrine–energy relationship: implications for conservation and management. *Ecol. Appl.* 27, 2303–2312. <https://doi.org/10.1002/eap.1608>.
- Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H., Kuemmerle, T., 2017. Biodiversity at risk under future cropland expansion and intensification. *Nat. Ecol. Evol.* 1, 1129–1135. <https://doi.org/10.1038/s41559-017-0234-3>.
- Kelly, G., 2000. Peripheral metabolism of thyroid hormones: a review. *Alter. Med. Rev.* 306.
- Kinnaird, M.F., O'Brien, T.G., 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. *Conserv. Biol.* 26, 1026–1039. <https://doi.org/10.1111/j.1523-1739.2012.01942.x>.
- Kinyumu, D.M., Kamiri, H.W., Mathenge, P., 2021. Adoption and adaptation of conservation agriculture practices in Laikipia, Kenya. *East Afr. Agric. For. J.* 85, 8–8.
- Kioko, J., Taylor, K., Milne, H.J., Hayes, K.Z., Kiffner, C., 2017. Temporal gland secretion in African elephants (*Loxodonta africana*). *Mamm. Biol.* 82, 34–40. <https://doi.org/10.1016/j.mambio.2016.07.005>.

- Kozłowski, C.P., Clawitter, H., Guglielmino, A., Schamel, J., Baker, S., Franklin, A.D., Powell, D., Coonan, T.J., Asa, C.S., 2020. Factors affecting glucocorticoid and thyroid hormone production of island foxes. *J. Wildl. Manag.* 84, 505–514. <https://doi.org/10.1002/jwmg.21808>.
- Lambert, J.E., Rothman, J.M., 2015. Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. *Annu. Rev. Anthropol.* 44, 493–512. <https://doi.org/10.1146/annurev-anthro-102313-025928>.
- Li, G., Fang, C., Li, Y., Wang, Z., Sun, S., He, S., Qi, W., Bao, C., Ma, H., Fan, Y., Feng, Y., Liu, X., 2022. Global impacts of future urban expansion on terrestrial vertebrate diversity. *Nat. Commun.* 13, 1628. <https://doi.org/10.1038/s41467-022-29324-2>.
- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* 6.
- LWF, 2012. *A Wildlife Conservation Strategy for Laikipia County (2012–2030)*, 1st Edition. Laikipia Wildlife Forum, Nanyuki, Kenya.
- M'mboroki, K.G., Wandiga, S., Oriaso, S.O., 2018. Climate change impacts detection in dry forested ecosystem as indicated by vegetation cover change in —Laikipia, of Kenya. *Environ. Monit. Assess.* 190, 255. <https://doi.org/10.1007/s10661-018-6630-6>.
- Ma, D., Abrahms, B., Allgeier, J., Newbold, T., Weeks, B.C., Carter, N.H., 2024. Global expansion of human-wildlife overlap in the 21st century. *Sci. Adv.* 10, eadp7706. <https://doi.org/10.1126/sciadv.adp7706>.
- Main-Knorn, M., Pflug, B., Louis, J., Debaecker, V., Müller-Wilm, U., Gascon, F., 2017. Sen2Cor for Sentinel-2. SPIE.
- Malcolm, K.D., McShea, W.J., Garshelis, D.L., Luo, S.-J., Van Deelen, T.R., Liu, F., Li, S., Miao, L., Wang, D., Brown, J.L., 2014. Increased stress in asiatic black bears relates to food limitation, crop raiding, and foraging beyond nature reserve boundaries in China. *Glob. Ecol. Conserv.* 2, 267–276. <https://doi.org/10.1016/j.gecco.2014.09.010>.
- McLennan, M.R., Ganzhorn, J.U., 2017. Nutritional characteristics of wild and cultivated foods for chimpanzees (*Pan troglodytes*) in agricultural landscapes. *Int. J. Primatol.* 38, 122–150. <https://doi.org/10.1007/s10764-016-9940-y>.
- Mijele, D., Obanda, V., Omondi, P., Soriguer, R.C., Gakuya, F., Otiende, M., Hongo, P., Alasaad, S., 2013. Spatio-temporal distribution of injured elephants in masai mara and the putative negative and positive roles of the local community. *PLoS One* 8, e71179. <https://doi.org/10.1371/journal.pone.0071179>.
- Morfeld, K.A., Lehnhardt, J., Alligood, C., Bolling, J., Brown, J.L., 2014. Development of a body condition scoring index for female African elephants validated by ultrasound measurements of subcutaneous fat. *PLoS One* 9, e93802. <https://doi.org/10.1371/journal.pone.0093802>.
- Mukeka, J.M., Ogutu, J.O., Kanga, E., Roskaft, E., 2019. Human-wildlife conflicts and their correlates in Narok County, Kenya. *Glob. Ecol. Conserv.* 18, e00620. <https://doi.org/10.1016/j.gecco.2019.e00620>.
- Mumby, H.S., Mar, K.U., Thitarum, C., Courtiol, A., Towiboon, P., Min-Oo, Z., Htut-Aung, Y., Brown, J.L., Lummaa, V., 2015. Stress and body condition are associated with climate and demography in Asian elephants. *Conserv. Physiol.* 3 (1), cov030. <https://doi.org/10.1093/conphys/cov030>.
- Naha, D., Dash, S.K., Chettri, A., Roy, A., Sathyakumar, S., 2020. Elephants in the neighborhood: patterns of crop-raiding by Asian elephants within a fragmented landscape of eastern India. *PeerJ* 8, e9399. <https://doi.org/10.7717/peerj.9399>.
- Norkaew, T., Brown, J.L., Bansiddhi, P., Somgird, C., Thitarum, C., Punyapornwithaya, V., Punturee, K., Vongchan, P., Somboon, N., Khonmee, J., 2018. Body condition and adrenal glucocorticoid activity affects metabolic marker and lipid profiles in captive female elephants in Thailand. *PLoS One* 13, e0204965. <https://doi.org/10.1371/journal.pone.0204965>.
- Nyhus, P.J., Tilson, R., Sumianto, 2000. Crop-raiding elephants and conservation implications at Way Kambas National Park, Sumatra, Indonesia. *Oryx* 34, 262–274. <https://doi.org/10.1046/j.1365-3008.2000.00132.x>.
- Oduor, S., Brown, J., Macharia, G.M., Boisseau, N., Murray, P., 2020. Differing physiological and behavioral responses to anthropogenic factors between resident and non-resident African elephants at Mpala Ranch, Laikipia County, Kenya. *PeerJ* 8, e10010.
- Oduor, S., Gichuki, N.N., Brown, J.L., Parker, J., Kimata, D., Murray, S., Goldenberg, S.Z., Schutgens, M., Wittemyer, G., 2024. Adrenal and metabolic hormones demonstrate risk–reward trade-offs for African elephants foraging in human-dominated landscapes. *Conserv. Physiol.* 12 (1), coae051. <https://doi.org/10.1093/conphys/coae051>.
- Osborn, F.V., 2004. Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe. *Afr. J. Ecol.* 42, 322–327. <https://doi.org/10.1111/j.1365-2028.2004.00531.x>.
- Palme, R., 2019. Non-invasive measurement of glucocorticoids: advances and problems. *Physiol. Behav.* 199, 229–243. <https://doi.org/10.1016/j.physbeh.2018.11.021>.
- Pasciu, V., Nieddu, M., Baralla, E., Muzzeddu, M., Porcu, C., Sotgiu, F.D., Berlinguer, F., 2022. Non-invasive assay for measurement of fecal triiodothyronine (T3) metabolite levels in European mouflon (*Ovis aries musimon*). *Front. Vet. Sci.* 9, 851794. <https://doi.org/10.3389/fvets.2022.851794>.
- Pasciu, V., Nieddu, M., Sotgiu, F.D., Baralla, E., Berlinguer, F., 2024. Fecal thyroid hormone metabolites in wild ungulates: a mini-review. *Front. Vet. Sci.* 11, 1407479. <https://doi.org/10.3389/fvets.2024.1407479>.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20, 503–510. <https://doi.org/10.1016/j.tree.2005.05.011>.
- Pokharel, S.S., Seshagiri, P.B., Sukumar, R., 2017. Assessment of season-dependent body condition scores in relation to faecal glucocorticoid metabolites in free-ranging Asian elephants. *Conserv. Physiol.* 5 (1), cox039. <https://doi.org/10.1093/conphys/cox039>.
- Pokharel, S.S., Singh, B., Seshagiri, P.B., Sukumar, R., 2019. Lower levels of glucocorticoids in crop-raiders: diet quality as a potential 'pacifier' against stress in free-ranging Asian elephants in a human-production habitat. *Anim. Conserv.* 22, 177–188. <https://doi.org/10.1111/acv.12450>.
- Pretorius, Y., Stigter, J.D., de Boer, W.F., van Wieren, S.E., de Jong, C.B., de Knegt, H.J., Grant, C.C., Heitkönig, I., Knox, N., Kogi, E., Mwakiwa, E., Peel, M.J.S., Skidmore, A.K., Slotow, R., van der Waal, C., van Langevelde, F., Prins, H.H.T., 2012. Diet selection of African elephant over time shows changing optimization currency. *Oikos* 121, 2110–2120. <https://doi.org/10.1111/j.1600-0706.2012.19680.x>.
- R Development Core Team, 2024. *R: A Language and Environment for Statistical Computing*. The R Foundation for Statistical Computing, Vienna.
- Rasmussen, H.B., Okello, J.B.A., Wittemyer, G., Siegmund, H.R., Arctander, P., Vollrath, F., Douglas-Hamilton, I., 2008. Age- and tactic-related paternity success in male African elephants. *Behav. Ecol.* 19, 9–15. <https://doi.org/10.1093/beheco/arm093>.
- Riley, E.P., Tolbert, B., Farida, W.R., 2013. Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques. *Curr. Zool.* 59, 160–169. <https://doi.org/10.1093/czoolo/59.2.160>.
- Rode, K.D., Chiyo, P.I., Chapman, C.A., McDowell, L.R., 2006. Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *J. Trop. Ecol.* 22, 441–449. <https://doi.org/10.1017/S0266467406003233>.
- Romero, L.M., Wingfield, J.C., 2015. *Tempests, Poxes, Predators, and People: Stress in Wild Animals and How They Cope*. Oxford University Press.
- Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* 21, 55–89. <https://doi.org/10.1210/edrv.21.1.0389>.
- Shannon, G., Mackey, R.L., Slotow, R., 2013. Diet selection and seasonal dietary switch of a large sexually dimorphic herbivore. *Acta Oecol.* 46, 48–55. <https://doi.org/10.1016/j.actao.2012.10.013>.
- Sheriff, M.J., Dantzer, B., Delehanty, B., Palme, R., Boonstra, R., 2011. Measuring stress in wildlife: techniques for quantifying glucocorticoids. *Oecologia* 166, 869–887. <https://doi.org/10.1007/s00442-011-1943-y>.
- Songhurst, A., Coulson, T., 2014. Exploring the effects of spatial autocorrelation when identifying key drivers of wildlife crop-raiding. *Ecol. Evol.* 4, 582–593. <https://doi.org/10.1002/ece3.837>.
- Songhurst, A., McCulloch, G., Coulson, T., 2016. Finding pathways to human–elephant coexistence: a risky business. *Oryx* 50, 713–720. <https://doi.org/10.1017/S003065315000344>.
- Sukumar, R., 1990. Ecology of the Asian elephant in Southern India. II. Feeding habits and crop raiding patterns. *J. Trop. Ecol.* 6, 33–53.
- Szott, I.D., Pretorius, Y., Ganswindt, A., Koyama, N.F., 2020. Normalized difference vegetation index, temperature and age affect faecal thyroid hormone concentrations in free-ranging African elephants. *Conserv. Physiol.* 8 (1), coaa010. <https://doi.org/10.1093/conphys/coaa010>.
- Tang, Y., Jia, T., Zhou, F., Wang, L., Chen, Z., Zhang, L., 2024. Obesity prevalence and associated factors in captive Asian elephants (*Elephas maximus*) in China: a body condition assessment study. *Animals* 14, 3571.

- Thouless, C.R., 1994. Conflict between humans and elephants on private land in Northern Kenya. *Oryx* 28, 119–127. <https://doi.org/10.1017/S0030605300028428>.
- Todini, L., 2007. Thyroid hormones in small ruminants: effects of endogenous, environmental and nutritional factors. *Animal* 1, 997–1008. <https://doi.org/10.1017/S1751731107000262>.
- Touitou, S., Heistermann, M., Schülke, O., Ostner, J., 2021. Triiodothyronine and cortisol levels in the face of energetic challenges from reproduction, thermoregulation and food intake in female macaques. *Horm. Behav.* 131, 104968. <https://doi.org/10.1016/j.yhbeh.2021.104968>.
- Troup, G., Doran, B., Au, J., King, L.E., Douglas-Hamilton, I., Heinsohn, R., 2020. Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. *Anim. Behav.* 168, 97–108. <https://doi.org/10.1016/j.anbehav.2020.08.009>.
- Van Eden, M., Ellis, E., Bruyere, B.L., 2016. The influence of human–elephant conflict on electric fence management and perception among different rural communities in Laikipia County, Kenya. *Hum. Dimens Wildl.* 21, 283–296. <https://doi.org/10.1080/10871209.2016.1149746>.
- Vogel, S.M., Blumenthal, S.A., de Boer, W.F., Masake, M., Newton, I., Songhurst, A.C., McCulloch, G., Stronza, A., Henley, M.D., Coulson, T., 2020. Timing of dietary switching by savannah elephants in relation to crop consumption. *Biol. Conserv.* 249, 108703. <https://doi.org/10.1016/j.biocon.2020.108703>.
- Wall, J., Lefcourt, J., Jones, C., Doehring, C., O'Neill, D., Schneider, D., Steward, J., Krautwurst, J., Wong, T., Jones, B., Goodfellow, K., Schmitt, T., Gobush, K., Douglas-Hamilton, I., Pope, F., Schmidt, E., Palmer, J., Stokes, E., Reid, A., Elbroch, L.M., Kulits, P., Villeneuve, C., Matsanza, V., Clinning, G., van Oort, J., Denninger Snyder, K., Peter Daati, A., Gold, W., Cunliffe, S., Craig, B., Cork, B., Burden, G., Goss, M., Hahn, N., Carroll, S., Gitonga, E., Rao, R., Stabach, J.A., Dulude-de Broin, F., Omondi, P., Wittemyer, G., 2024. EarthRanger: an open-source platform for ecosystem monitoring, research and management. *Methods Ecol. Evol.* 00, 1–12. <https://doi.org/10.1111/2041-210X.14399>.
- Walton, B.J., Findlay, L.J., Hill, R.A., 2021. Insights into short- and long-term crop-foraging strategies in a chacma baboon (*Papio ursinus*) from GPS and accelerometer data. *Ecol. Evol.* 11, 990–1001. <https://doi.org/10.1002/ece3.7114>.
- Wasser, S.K., Papageorge, S., Foley, C., Brown, J.L., 1996. Excretory fate of estradiol and progesterone in the African elephant (*Loxodonta africana*) and patterns of fecal steroid concentrations throughout the estrous cycle. *Gen. Comp. Endocrinol.* 102, 255–262. <https://doi.org/10.1006/gcen.1996.0067>.
- Wasser, S.K., Hunt, K.E., Brown, J.L., Cooper, K., Crockett, C.M., Bechert, U., Millspaugh, J.J., Larson, S., Monfort, S.L., 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen. Comp. Endocrinol.* 120, 260–275. <https://doi.org/10.1006/gcen.2000.7557>.
- Wasser, S.K., Azkarate, J.C., Booth, R.K., Hayward, L., Hunt, K., Ayres, K., Vynne, C., Gobush, K., Canales-Espinosa, D., Rodríguez-Luna, E., 2010. Non-invasive measurement of thyroid hormone in feces of a diverse array of avian and mammalian species. *Gen. Comp. Endocrinol.* 168, 1–7. <https://doi.org/10.1016/j.ygcen.2010.04.004>.
- Wato, Y.A., Heitkönig, I.M.A., van Wieren, S.E., Wahungu, G., Prins, H.H.T., van Langevelde, F., 2016. Prolonged drought results in starvation of African elephant (*Loxodonta africana*). *Biol. Conserv.* 203, 89–96. <https://doi.org/10.1016/j.biocon.2016.09.007>.
- Waweru, J., Omondi, P., Ngene, S.M., Mukeka, J., Wanyonyi, E., Ngoru, B., Mwiu, S., Muteti, D., Lala, F., Kariuki, L., Ihwagi, F.W., Kiambi, S., Khyale, C., Bundotich, G., Omengo, F., Hongo, F., Maina, P., Muchiri, F., Omar, M., Nyunja, J., Edebe, J., Mathenge, J., Anyona, G., Ngesa, C., Gathua, J., Njino, L.W., Njenga, G., Wandera, A., Mutisya, S., Njeri, R., Kimanzi, D., Imboma, T., Wambugu, J., Mwinami, T., Kaka, A., Kanga, E., 2021. National Wildlife Census 2021 Report. Wildlife Research & Training Institute (WRTI) and Kenya Wildlife Service (KWS).
- Webber, C.E., Sereivathana, T., Maltby, M.P., Lee, P.C., 2011. Elephant crop-raiding and human–elephant conflict in Cambodia: crop selection and seasonal timings of raids. *Oryx* 45, 243–251. <https://doi.org/10.1017/S0030605310000335>.
- Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. *People and Wildlife, Conflict or Co-existence?* Cambridge University Press.
- Woolley, L.-A., Millspaugh, J.J., Woods, R.J., Van Rensburg, S.J., Page, B.R., Slotow, R., 2009. Intraspecific strategic responses of African elephants to temporal variation in forage quality. *J. Wildl. Manag.* 73, 827–835. <https://doi.org/10.2193/2008-412>.