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Lion (*Panthera leo*) diet and cattle depredation on the Kuku Group Ranch Pastoralist area in southern Maasailand, Kenya

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ABSTRACT

Context. African lion (*Panthera leo*) populations are declining throughout Africa, but the problem is particularly acute in southern Kenya, where human–lion conflict is common. **Aims.** Using the Kuku Group Ranch (KGR) in southern Kenya as a case study, we investigated lion diet and the potential drivers of temporal variation in cattle depredation. **Methods.** Using GPS clusters, we investigated the main prey species consumed by lions to determine lion diet. Prey preference of lions in relation to prey availability was then assessed using a Jacobs index to determine whether cattle or wild prey were preferred. We used reported depredation events recorded by verification officers over 36 months (2016–2018) to investigate whether temporal variation in cattle depredation by lions was linked to variation in lag rainfall, normalised difference vegetation index (NDVI) or availability of the most important large non-domestic prey items. **Key results.** Six prey species (cattle, *Bos taurus*; Burchell's zebra, *Equus quagga*; Coke's hartebeest, *Alcelaphus cokeii*; Maasai giraffe, *Giraffa tippelskirchi*; blue wildebeest, *Connochaetes taurinus;* and eland, *Tragelaphus oryx*) made up 92% of the biomass consumed by lions on KGR. Cattle are the most consumed prey item and contribute the second most to consumed biomass after giraffe. However, once prey availability is considered, lions preferred wild prey. Verification officers identified 330 cattle depredation events over 3 years, and we show that the most important predictor of monthly cattle depredation by lions was cumulative rainfall in the preceding 3 months. **Conclusions.** Our results on cattle depredation by lions showed that rainfall and its influence on the environment are important drivers of cattle depredation. Understanding the mechanistic link between lion depredation and rainfall enables us to predict when depredation events may increase and allows hypotheses on the reason why this spike in depredation takes place to be explored. **Implications.** Given that climate-change models indicate that East Africa will experience prolonged and increased seasonal rainfall, we predict that periods when cattle are vulnerable to lion depredation may increase. Therefore, it is imperative to ensure that cattle husbandry is improved during these wetter periods to minimise the risk of conflict and retaliatory killing of lions.

Keywords: carnivore, conservation, human–wildlife conflict, lag-rainfall, NDVI, predator, prey, SMART.

Introduction

Apex carnivore populations, such as the African lion (*Panthera leo*), are declining globally, both in abundance and range (Riggio *et al.* 2013; LeFlore *et al.* 2020; Bauer *et al.* 2022). Lions once ranged from northern Europe to southern Africa but are now confined to <8% of their former range, and populations are estimated to have decreased by 43% since 2000 (Bauer *et al.* 2015). These declines can be linked to anthropogenic pressures and present a key challenge for the conservation of large carnivores (Lindsey *et al.* 2017). Importantly, a large proportion of the lions remaining in Africa occurs outside formally protected areas in mixed-use and human-dominated landscapes that create conflict (Crooks *et al.* 2011; Western *et al.* 2021; Bauer *et al.* 2022). Human–lion conflicts occur frequently and constitute a global challenge (Ripple *et al.* 2016; Broekhuis *et al.* 2017; Montgomery *et al.* 2018; Bauer *et al.* 2022), which is likely to worsen as habitat

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fragmentation increases (Bauer *et al.* 2022). The increasingly fragmented habitats pose a concern because large predators require extensive, intact connected habitats to survive (Sillero-Zubiri and Laurenson 2001; Riggio *et al.* 2013; Sargent *et al.* 2022).

Kenya experiences some of the highest human–carnivore conflict rates in Africa, where the main livelihood of many communities is pastoralism (Beck *et al.* 2019). Agonistic interactions are particularly severe when lions kill cattle (Gebresenbet *et al.* 2018; Mbise *et al.* 2018; van Eeden *et al.* 2018) and often lead to retaliatory killing of lions (Sundararaj *et al.* 2012; Hazzah *et al.* 2014; Ripple *et al.* 2014; Everatt *et al.* 2019). Human–lion conflicts occur most frequently in the areas adjacent to protected areas (Patterson *et al.* 2004; Bauer *et al.* 2022). This relationship poses an important conservation conundrum where protected areas offer lion conservation solutions, but these solutions may be negated if the protected areas are too small, unfenced and/or surrounded by human populations (Woodroffe and Ginsberg 1998). Human conflicts with lions are largely driven by the direct loss of livestock, but have also been found to be driven indirectly by the reduction of wild prey as a result of poaching and competition for natural resources between wild prey and domestic animals (Treves and Karanth 2003; Inskip and Zimmermann 2009).

Lion attacks on livestock (further livestock depredation) can have significant social and economic impacts (Patterson *et al.* 2004; Hemson *et al.* 2009: Schuette *et al.* 2013; Bencin *et al.* 2016; Kissui *et al.* 2019), which need to be negated to ensure lion persistence outside protected areas (Bencin *et al.* 2016). Blackburn *et al.* (2016) showed that in areas where communities gain benefits from wildlife, the survival of lions is greatly improved, but also stated that human–lion conflict-mitigation efforts are critical for the persistence of lions, even more so than reducing livestock grazing intensity or habitat degradation that negatively affect wild prey abundance. Co-existence between humans and wildlife is more likely when adaptation strategies produce and sustain co-benefits for both humans and wildlife, and active guarding strategies have been shown to have the highest percentage of co-benefit outcomes (Ogada *et al.* 2003; Killion *et al.* 2021). However, spatial and temporal variation in livestock predation patterns by lion needs to be understood in the context of existing guarding practises to ensure continuous improvement of guarding measures to minimise livestock loss.

The Tsavo Amboseli landscape sustains viable populations of wildlife species, including lions (Armbruster and Lande 1993), but nearly 250 000 people now live on the borders of protected areas in villages and communally owned areas called group ranches (Patterson *et al.* 2004). Human–lion conflicts are commonplace in these areas (Patterson *et al.* 2004). However, many Maasai communities in Kenya, such as those in the Kuku Group Ranch (KGR), now actively engage in community-based conservation initiatives and refrain from spearing and other means of lethal carnivore control (Bauer *et al.* 2017). Much more emphasis is placed on livestock guarding as the main tool to reduce conflict (Schuette *et al.* 2013; Hazzah *et al.* 2014).

On KGR, cattle are placed in predator-proof bomas at night, whereas a livestock compensation program aims to reduce retaliatory action against lions while promoting the improvement of cattle husbandry (Bauer *et al.* 2017). On the KGR, lions are also actively tracked, allowing the community to avoid high-risk areas when possible (Bauer *et al.* 2017). Cattle are either placed in permanent or temporary bomas. Permanent bomas are better constructed, whereas seasonal bomas are used when cattle have to be moved further away from the permanent settlements because of a lack of sufficient grazing and are less effective in preventing predation by lions (Manoa and Mwaura 2016). Unfortunately, depredation by lion persists despite the herder's best efforts. Depredation rates are not even throughout, and among years (Bauer *et al.* 2017; Robertson *et al.* 2020), suggesting that either herding practise, wild prey availability (Khorozyan *et al.* 2015; Beattie *et al.* 2020) or environmental conditions such as rainfall and vegetative productivity (Beattie *et al.* 2020) may affect depredation rates of cattle.

All four stages of the predation process (search, encounter, engagement and success) vary over time owing to annual and seasonal differences in the landscape (Kittle *et al.* 2022). Livestock and wild prey movements interact directly with predator movement where predators search for prey (MacNulty *et al.* 2007). An encounter between a predator and prey occurs when the movements of the predator and prey interconnect spatiotemporally (Kittle *et al.* 2022). The encounter of prey by lion may vary annually because of changes in prey movements, prey availability and vegetation cover that may affect prey detection. Human–wildlife conflicts may, in turn, increase with increased rainfall and changes in season, especially if the abundance of important wild prey decreases (Kittle *et al.* 2016, 2022) or the condition of wild prey increases to such an extent that it decreases lion hunting success (Owen-Smith 2015). Lions' decision to attack cattle on encounter may also vary seasonally because of changes in the available vegetation cover, given that lions kill predominantly where greater cover exists (Davies *et al.* 2016*a*). Increased cover not only influences hunting success by improving stalking opportunities (Kittle *et al.* 2022), but may also increase the number of engagements and successful attacks because of herders' reduced ability to detect lions prior to and during attacks. Apart from denser vegetation making it more difficult for herders to detect lions, they might also find it more difficult to keep track of their cattle, which then increases attack success because they are not present to drive lions off during an attack.

To better understand observed temporal variation in cattle depredation events by lions at KGR, we first estimated lion diets in KGR and then compared monthly variation in depredation events against corresponding monthly

variation in available prey, lagged rainfall and NDVI. Using ground-truthed GPS clusters, we first identified the most important prey species for lions in the landscape and used the Jacobs' index to assess the prey preference of lions in the KGR. We then explored the potential drivers of depredation on a temporal scale by focusing on changes in rainfall, and NDVI as a proxy for vegetation quality and wild prey over 3 years. Finally, we compared whether patterns of depredation and the drivers varied depending on the husbandry practices (i.e. whether herders were attentive or negligent). Understanding variation in depredation occurrences is important because accurate descriptions of lion diet, prey preference, and cattle depredation in community conservancies can inform and improve lion protection strategies through the reduction of human–lion conflicts.

Materials and methods

Study area

The KGR is a community-owned area covering 1133 km^2 at 2.77554°S, 37.85150°E (Fig. 1). KGR borders Tsavo West National Park to the east and Chyulu Hills National Park to the north and is situated within the 9000 km^2 Amboseli–Tsavo ecosystems. KGR provides residence to approximately 17 000 Maasai and 90 000 heads of livestock (Groom and Harris 2008). The group ranches are livestock production systems, where traditional Maasai occupants jointly own a freehold title to land and both herd and graze their livestock alongside wildlife (Western *et al.* 2009; Bauer *et al.* 2017). Along with the cattle, a range of large antelope species, elephant, (*Loxodonta africana*), and a full carnivore guild roam freely across the KGR. The lion population on the KGR is estimated to be between 20 and 30 lions (Bauer *et al.* 2017), which form part of the Amboseli–Tsavo population, estimated to total approximately 880 individuals (Riggio *et al.* 2013).

The KGR is located in an arid to semi-arid area (Western *et al.* 2009; Bauer *et al.* 2017). Annual rainfall is highly unpredictable (Awere-Gyekye 1996) and varies between 250 and 800 mm annually, with an average of 340 mm (Okello 2005). The area has two rainfall seasons, with a shorter rainfall period from November and December, followed by a more extended period from March to May (Altmann *et al.* 2002). The area experiences significant inter-year variation in the quantity and timing of rain (Phillipson 1975; Altmann *et al.* 2002). Temperatures range from mid-30s°C in February to approximately 20°C in July (Western *et al.* 2009). The KGR comprises heterogeneous landscape that features a transition in vegetation from lowland dry savanna grassland and *Vachelia–Commiphora* forest to an area dominated by a moist, dense cloud forest in the Chyulu Hills (Agnew 1968).

Within the group ranch, the primary occupation of residents is semi-nomadic pastoralism, with most household income being derived from livestock sales (Groom 2007; Bauer *et al.* 2017). Pastoralists reside in manyattas (homesteads), and the landscape is interspersed with permanent and temporary (seasonal) Maasai bomas (Thorn corrals used to protect cattle from predators; Bauer *et al.* 2017). These manyattas are settlements around collectively managed bomas where livestock is kept at night (Groom 2007). There are approximately 1240 bomas located on the group ranch (Bauer *et al.* 2017). This study focused on the eastern part of KGR bordering Tsavo West and Chyulu Hills national parks, where most lions and resultant human–lion conflicts occur (Bauer *et al.* 2017). As part of a livestock protection program called Wildlife Pays (WP), under the KGR Lion Project, the Maasai Wilderness Conservation Trust (MWCT) runs conservation activities on the KGR. MWCT has compensated livestock owners for losses caused by wildlife since 2003, through a predator compensation fund known as WPs (Bauer *et al.* 2017). MWCT further runs seven ranger patrol sectors within this focal area, and the outer boundary of the three most-western patrol sectors demarcated the western boundary of the focal area (Fig. 1*c*).

Data collection

The study used two datasets. First, lion satellite-collar movement data collected between January 2017 and December 2018 was used to identify lion diets. Second, cattle depredation records extracted from the WPs program from January 2016 to December 2018 were used to investigate temporal variation in cattle depredation events as a function of various potential drivers of depredation.

Lion diet

As part of MWCT conservation activities, seven lions (five adult lionesses representing five of the seven prides believed to be present in the area and two adult male lions that roamed between all prides) holding territories across the KGR were fitted with GPS/VHF and satellite transmitter collars (African Wildlife Tracking, Pretoria, South Africa). The collaring operations occurred between 2013 and 2018, with the permission of the Kenya Wildlife Service (KWS) and were completed by a KWS veterinarian. Information on lion diet was obtained by investigating predicted lion-feeding sites (lion GPS clusters; Tambling *et al.* 2010, 2012; Davidson *et al.* 2013) to confirm a lion-feeding event and identify the prey species involved (Sand *et al.* 2005; Tambling *et al.* 2012; Beukes *et al.* 2017).

Potential feeding sites (GPS clusters) were identified by analysing the GPS data points to identify a position where three or more consecutive recorded GPS fixes were less than 100 m apart (Tambling *et al.* 2010, 2012; Davidson *et al.* 2013). Clusters of GPS points that could indicate a kill were further identified as those that (a) had a long duration of lion presence, (b) had a high ratio of movement before versus after the cluster and (c) those that formed at night

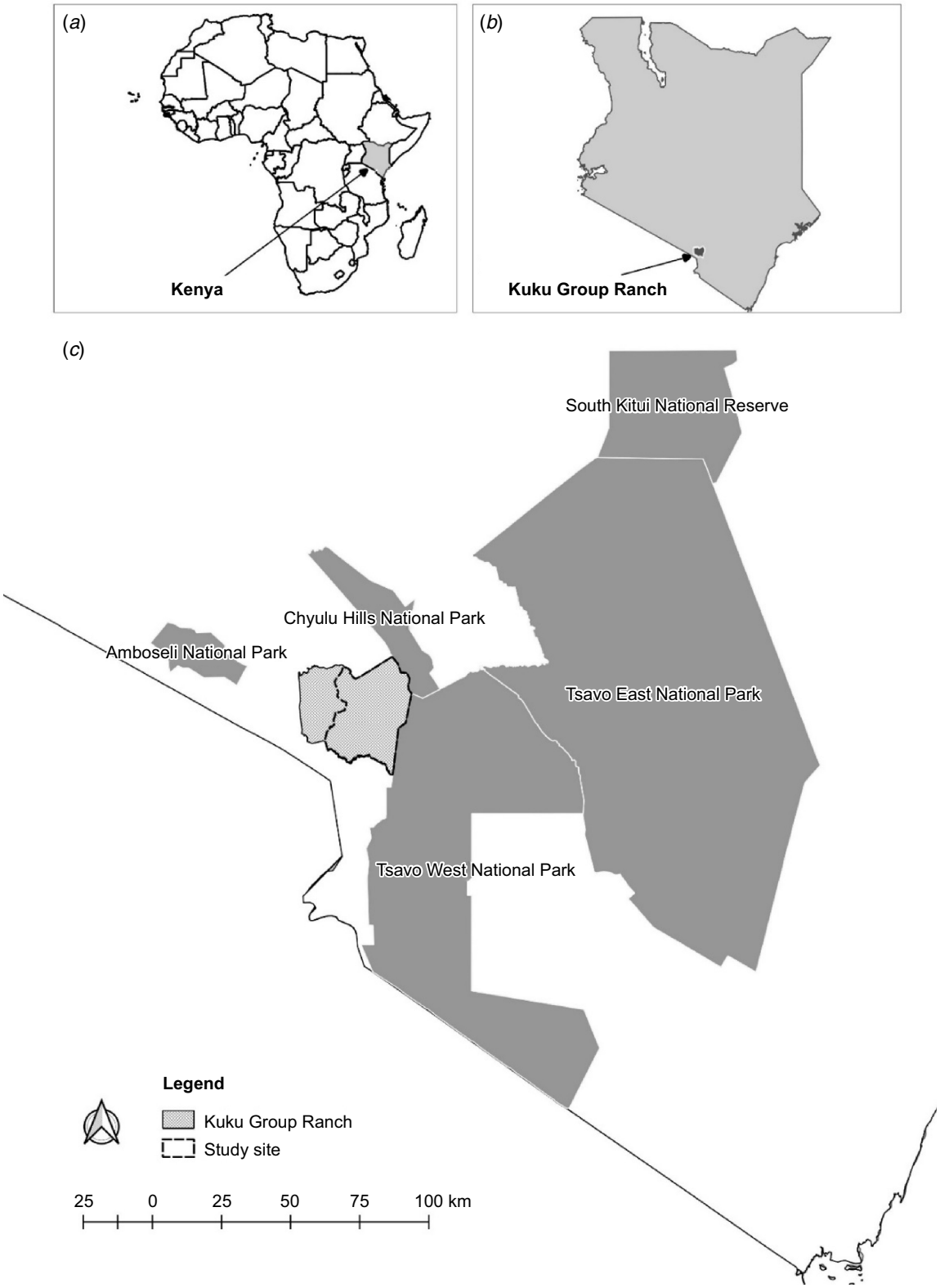

Fig. 1. (*a*) Location of Kenya in the context of Africa, (*b*) location of the Kuku Group Ranch (KGR) in the context of Kenya and (*c*) KGR and the focal study area within the context of the greater Tsavo–Amboseli landscape.

(Tambling *et al.* 2012). On inspection, indicators of feeding sites were signs of a struggle (soil disturbance or trampled vegetation), rumen content, and any other biological signs including hair, bone, jaws, horns, blood, or whole carcasses

(Tambling *et al.* 2012; Davidson *et al.* 2013; Beukes *et al.* 2017). Prey was identified to the species level and included only if there was no uncertainty around the identification on the basis of the biological evidence.

Prey availability

Two data sources were used to estimate prey availability. Bi-annual aerial counts provided information on overall prey availability, whereas ranger foot-patrol data provided more fine-scaled monthly information on wild prey availability in the form of monthly encounter rates. In most studies, prey availability is estimated only from aerial census data, which provides the absolute availability of prey items (Tambling *et al.* 2010). However, as opposed to absolute numbers, prey groups have been argued to be a better measure for assessing predator selection of prey (Fryxell *et al.* 2007). We thus used both encounter rates for different wild prey species groups and absolute abundances (Funston *et al.* 1998; Tambling 2010) as our availability metrics for wild prey species. We were unable to obtain livestock encounter-rate data as Maasai field rangers objected to counting and reporting on fellow KGR residents' cattle in this fashion.

Aerial counts were conducted in May and October 2017 and in May and November 2018, by using the total aerial-count technique of Norton-Griffiths (1978). No estimates of bias or precision error were obtained for the census data, and no adjustments for undercounting were applied (Redfern *et al.* 2002). Encounter rates of wild prey were calculated from ranger patrol records. Seven ranger stations are situated within the focal area from which daily foot patrols are conducted for wildlife monitoring and anti-poaching purposes. Collectively, rangers of the seven patrol sectors cover a minimum of 100 km per day. During patrols, rangers recorded all large mammal species encountered (excluding livestock species), and both the species name and exact location were uploaded on GPS-enabled smartphones by using the Spatial Monitoring and Reporting Tool (SMART; Kavhu and Mpakairi 2021).

Ranger patrol data thus provided monthly accounts of non-domestic large herbivore abundance and encounter rates across the study area and were used to calculate the relative abundance of wild prey on the basis of encounter rates (number of wildlife detected per kilometre walked) of groups of potential prey items. The minimum ranger-patrol effort (distance walked on patrol) needed to produce robust monthly prey encounter rate data was estimated to be 60 km on the basis of a plot generated where the variance around average encounter rates per 100 km was plotted against patrol effort (Supplementary material Fig. S1). Ranger patrol effort surpassed the 60 km threshold in all 36 months of this study.

Cattle depredation

As part of the WPs programme, verification officers (VOs) are employed to respond to all livestock depredation events on a motorcycle and investigate each claim in detail by stating the livestock species lost in the husbandry context, commonly referred to as the 'loss type'. Loss types include poor bomas, good bomas, negligent herding and non-negligent herding. These loss types were defined by ensuring that VOs are trained according to a standard protocol to ensure consistent reporting. The carcass condition and circumstances around the depredation event assist in the classification of a depredation event as either non-negligent or negligent (Bauer *et al.* 2017).

Non-negligent husbandry practises are generally recorded when appropriate defences are applied, such as keeping livestock in a boma of at least 1.2 m high and 1.2 m wide at night and ensuring that cattle are well attended to during the day. Good herding by livestock owners entails rapid response, which leads to the recovery of an almost intact carcass. Negligent husbandry is recorded when depredation occurs on livestock that is unattended by a herder during the day or night or where depredation occurs within substandard bomas. The WP program has been running for over 10 years, and community members are aware of the compensation program and actively participate in it because of the monetary rewards. It is thus assumed that reporting levels, verification, and data capture in the field by VOs have been constant over the study period (Bauer *et al.* 2017). The actual number of reported cattle depredations for each month between January 2016 and December 2018 was used to investigate differences in depredation frequencies between months over the 36 months.

Environmental variables

Environmental variables that could explain variation in monthly cattle depredation events by lions were identified and dealt with, and are listed below.

Lag-rainfall data. Rainfall affects the condition, availability and vulnerability of lion prey because of its effect on forage availability and surface-water availability that varies seasonally in savanna areas (Owen-Smith 2015). The effect of rainfall on prey condition and movement is not immediate but rather cumulative, especially in this area experiencing high variability in the quantity and timing of rainfall (Fig. S2), because soil moisture needs to accumulate to trigger vegetation growth (Shinoda 1995) and seasonal pans and rivers need time to fill. Lag-rainfall is thus used here to explore the delayed effect of rainfall on surface-water availability, vegetation productivity and predation (Patterson *et al.* 2004), with months with a higher lag-rainfall likely having greater grass biomass and vegetative cover. Rainfall was recorded within the study area at the Chyulu Hills Conservation & Research Centre (CCRC), situated on the eastern border of the study area. The monthly rainfall for 2016–2018 was obtained from MWCT rainfall-data records. Lag-rainfall was calculated by determining the average rainfall for the current and preceding 2-month rainfall

figures (Ogutu and Owen-Smith 2005). For example, the lagged rainfall for March 2016 was the average rainfall received during January, February, and March 2016 (Fig. S3).

Monthly normalised difference vegetation index (NDVI) values. NDVI is a measure of greenness that gives a coarse measure of vegetation quality (Winnie *et al.* 2008; Beattie *et al.* 2020) that can be used to explore a potential relationship among vegetation quality, wild prey catchability and associated cattle depredation rates. During the dormant season when plant growth ceases and NDVI declines, wild herbivores are forced to seek food more widely, losing fitness and potentially exposing themselves to areas of increased predation risk (Owen-Smith 2015). In contrast, when NDVI increases, forage quality is higher, which could lead to greater body condition and, consequentially, lower chance of wild prey being killed by lions (Ng'weno *et al.* 2019). As such, when wild prey is harder to catch, lions may switch their focus to potentially easier prey such as cattle.

The NDVI of the vegetation within the study site was assessed using geospatial techniques in Google Earth Engine (GEE; Martín-Ortega *et al.* 2020; Kumari *et al.* 2021). The relative vegetative productivity in the study for each of the 36 months of 2016–2018 was calculated by averaging NDVI values recorded at 911 points by using GEE for each month. The position of 911 points was obtained from cattle depredation locations reported between 2011 and 2018. Effectively, these averaged NDVI data provide a proxy for relative vegetative quality for each month across the study site (Kundu *et al.* 2018).

Data analysis

All statistical procedures were conducted in R software, ver. 3.1.2 (R Core Team 2017).

Lion diet

Lion diet was expressed as relative proportions of the total number of prey species identified through GPS cluster investigation of large-bodied prey species (Tambling *et al.* 2012). For all confirmed feeding events, the relative contribution and frequency of occurrence of each prey species were calculated and then converted into biomass estimates by using the average adult female body weight for each species (Cumming and Cumming 2003; Radloff and Du Toit 2004; Davidson *et al.* 2013). We considered prey species the size of Thompson's gazelle (*Eudorcas thomsonii*) and smaller (≤50 kg) as small prey, and the rest as large prey (>50 kg).

Prey availability

The absolute number of wildlife and livestock prey species greater than 50 kg present in the focal area of KGR was estimated by calculating the average number of prey available per species by using the total large-herbivore count values from the four uncorrected aerial counts. The proportional large prey species availability (for both wild herbivores and cattle) was then calculated from these average count values, and this availability was used in the preference analysis.

Wild prey species encounter rates as a measure of monthly wild prey availability were estimated by expressing ranger sightings of wildlife groups per month per 100 km walked. The monthly encounter rate of wildlife groups per 100 km was calculated by dividing the pooled number of groups encountered by all rangers during a month by the pooled kilometres patrolled and multiplying this by 100. Total ranger effort (kilometres patrolled) was calculated per month by summing the total distance walked by all ranger patrol groups in any given month. The monthly comparison of the encounter rates of the four wild prey species contributing most to the prey biomass consumed by lions at KGR was determined for 2016–2018.

Prey selection

Prey selection and measurement of prey preference (D) were calculated using the Jacobs' index for all comparisons (Jacobs 1974; Hayward and Kerley 2005). In Jacobs' index, r is the proportion of the overall number of prey consumed by lions in the dietary sample, and p is the proportional availability (see below) of that species for the study area (Jacobs 1974; Hayward and Kerley 2005). The Jacobs index allows for assessing prey selection when different relative abundances of prey are compared (Jacobs 1974). The resulting value falls between +1 and −1, with zero indicating no selection, +1 indicating maximum preference, and −1 indicating maximum avoidance. Confirmed lion feeding events obtained from GPS cluster data provided r, and p was derived from the average of the aerial game counts and the encounter rates were obtained from SMART patrol data.

$$D = \frac{r - p}{r + p - 2rp}.$$

Modelling monthly depredation events

The frequency and occurrence of cattle depredation within the KGR were extracted from the WPs data for each month from 2016 to 2018 (n = 330 depredation events). To assess the relative importance of temporal drivers of lion depredation on cattle, we modelled the monthly depredation rate as a function of various predictor variables for the same month. We considered the role that lagged rainfall, NDVI, important prey availability and interaction of important prey and NDVI played in driving the monthly depredation events over the 36 months of our study period.

We tested for possible collinearity among our predictor variables by investigating variance inflation factors (VIF) for all predictor variables (Zuur *et al.* 2010; Davies *et al.* 2016*a*; Western *et al.* 2021). Our resulting models had no

variables with VIF > 2, which suggests a limited correlation among our predictor variables (Zuur *et al.* 2010; Davies *et al.* 2016*b*; Western *et al.* 2021). In addition, no correlations between variables exceeded 0.7. Given that our dataset is collected in sequential months, these data may be correlated over time. To investigate possible temporal autocorrelation in our dataset, we plotted an autocorrelation function over the 36-month dataset, with some suggestion of temporal autocorrelation being detected. To account for this autocorrelation in our modelling approach, we included a first-order autocorrelation structure in our modelling process.

Further investigation of the resulting autocorrelation function from these models that account for temporal autocorrelation showed that the serial autocorrelation in our dataset had been removed. For the modelling process, we fitted monthly depredation events as a function of various predictor variables by using linear models fitted through generalised least squares in the package 'nlme' (Pinheiro *et al.* 2022). To select our most parsimonious and best drivers of depredation, we used a forward step-selection process where we modelled each covariate individually and then retained the covariate that resulted in the lowest Akaike information criterion (AIC; Akaike 1974) score while adding additional variables in subsequent iterations of the model process. We stopped this iterative process when adding covariates to the model no longer resulted in a decrease in the AIC score.

The above modelling approach was applied to three different sets of depredation data. The first analysis investigated overall monthly depredation irrespective of husbandry practice at the time of the lion attack (i.e. negligent and non-negligent herding practise). In contrast, the second and third analyses separated the depredation events into the number of kills per month under negligent and non-negligent herding circumstances respectively. Model validity was assessed using diagnostic checks with model residuals, showing an even spread and no clear outliers influencing the data.

To visually assess the influence of important predictor variables on the probability of an increase or decrease in cattle depredation events for a given month, the median marginal probability of cattle depredation was plotted as a function of the range of observed predictor variables used in this study (Elith *et al.* 2005). These plots were constructed by fixing the predicted cattle depredation as a function of the variable that varied across its observed range and, for each value, predicting the observed probability of cattle depredation from the best candidate model while maintaining all other predictor variables (fixed) at their original input values (Elith *et al.* 2005).

Finally, we investigated whether the main contributor to non-negligent predation was depredation events from bomas or those that took place while cattle were being herded by conducting a correlation analysis between total non-negligent depredation and boma predation events, and total non-negligent depredation and herding depredation events respectively.

Results

Lion diet

We identified 2386 lion GPS clusters from the collared lion movement over the 2-year study period in the focal area. Two hundred and five (8.6%) sites were identified as highly probable feeding locations and ground-truthed. Field investigation of the 205 sites resulted in the discovery of 119 feeding events for which the prey could be identified to species level, with 112 (94%) of these prey items being large-bodied prey species (>50 kg) comprising nine different species (Table 1). Six species, namely cattle (*Bos taurinus*, 24%), Burchell's zebra (*Equus quagga*, 20%), Coke's hartebeest (*Alcelaphus cokeii*, 18%), Maasai giraffe (*Giraffa tippelskirchi*, 12%), blue wildebeest (*Connochaetes gnu*, 8%), and eland (*Tragelaphus oryx*, 9%), made up 91% of all the identified prey larger than 50 kg (Table 1). Maasai giraffe (29%) contributed most to biomass consumed, followed by cattle (23%).

Prey availability

Between 2017 and 2018, the most common large mammal species counted during the aerial census were cattle (74%). Wildlife made up only 26% of the large prey available, with Burchell's zebra (11%) and Maasai giraffe (7%) being the most common wild prey species recorded (Table 2). During the study period, between 2017 and 2018, the average daily patrol distance was 174 km, with a minimum of 114 km and a maximum of 242 km. The four wild prey species identified to contribute most to lion prey biomass, namely Maasai giraffe, Burchell's zebra, eland and Coke's hartebeest, are also the four wild prey species most encountered during ranger patrols (Fig. 2). The Maasai giraffe was the most encountered animal, followed by the Burchell's zebra. Coke's hartebeest and eland were encountered equally often across the study area (Fig. 2).

Prey selection

Although lions consumed more cattle than any other prey species during our study, they showed a greater preference for wild prey (Fig. 3). Cattle were the least sought-after species of all the available large prey species, despite their high numbers and biomass availability within the study site (Fig. 3).

Cattle depredation

In total, 330 cattle depredation events were recorded through the WPs program in the study area over the 36-month study period. Of the 330 events, 176 (141 negligent herding;

Table 1. Location data obtained from the satellite collars of seven lions during January 2017–December 2018 led to the discovery of 112 lion feeding sites of prey species bigger than 50 kg.

Prey species	Number of times identified	Percentage contribution (%)	Adult female mass (kg)	Biomass consumed (kg)	% Biomass contribution to diet (kg)
Cattle (*Bos taurus*)	27	24.11	306	8262	22.80
Plain's zebra (*Equus quagga burchellii*)	23	20.54	302	6946	19.16
Cokes' hartebeest (*Alcelaphus cokeii*)	20	17.86	135	2700	7.45
Maasai giraffe (*Giraffa camelopardalis tippelskirchi*)	13	11.61	828	10 764	29.70
Eland (*Tragelaphus oryx*)	11	9.82	450	4950	13.66
Blue wildebeest (*Connochaetes taurinus*)	9	8.04	180	1620	4.47
Warthog (*Phacochoerus africanus*)	5	4.46	57	285	0.79
Maasai ostrich (*Struthio camelus massaicus*)	3	2.68	68	204	0.56
Buffalo (*Syncerus caffer*)	1	0.89	513	513	1.42
Total	112			36 244	

Data are the number and percentage contributions of the respective large-bodied prey species; also included are the biomass of each species (Cumming and Cumming 2003; Radloff and Du Toit 2004; Davidson *et al.* 2013), and the cumulative proportional contribution of the biomass to the lion diet.

Table 2. The large terrestrial wildlife and cattle that were recorded in the Kuku Group Ranch study site during aerial census counts conducted in 2017 and 2018.

Prey species	May 2017	October 2017	June 2018	November 2018	Average	Average % contribution
Wildlife						
Buffalo	0	0	35	35	17.5	0.2
Eland	268	115	197	245	206.25	2.6
Maasai giraffe	750	343	427	814	583.5	7.2
Coke's hartebeest	180	61	194	390	206.25	2.5
Maasai ostrich	39	10	14	19	20.5	0.3
Warthog	3	0	4	4	2.75	0.0
Blue wildebeest	244	23	190	256	178.25	2.1
Burchell's zebra	1088	326	937	1340	922.75	11.3
Total	2572	878	1998	3103	2137.75	26.2
Cattle	6610	4668	5182	6340	5700	73.8
Wildlife + cattle	9182	5546	7180	9443	7837.8	

35 negligent bomas) were categorised as negligent and 154 (126 non-negligent herding; 28 non-negligent bomas) as non-negligent depredation events. On average, 110 cattle depredation events were found per year, but this varied among years (77 in 2016, 162 in 2017 and 91 in 2018). The average number of depredation events by lion per month was nine, but again this varied considerably, both within a year and among months within the 3 years (range 1–25 predation events per month), with all months showing substantial differences, apart from August, which had consistently low predation levels throughout the study period. The maximum number of depredation events recorded was in July 2016 (n = 25), whereas, generally, January, May, and December had the highest incidences of cattle depredation.

Modelling-predicted drivers of depredation

The top model for overall depredation included lag-rainfall and important prey (Table 3). An increase in lag-rainfall increased the levels of depredation (β = 2.92, s.e. = 1.16), with an increase in lag-rainfall of 150 mm resulting in an almost doubling of the number of predicted depredation events per month (Fig. 4*a*). In contrast, the relative probability of cattle depredation declined with an increase in the availability of the most important prey, but this effect was weak (β = −1.18, s.e. = 1.24; Fig. 4*b*). None of the modelled predictor variables was present in the top models for negligent predation, and the intercept-only model was the best model.

The top model for non-negligent predation included only lag-rainfall (Table 3). An increase in lag-rainfall resulted in an increase in the levels of cattle depredation under

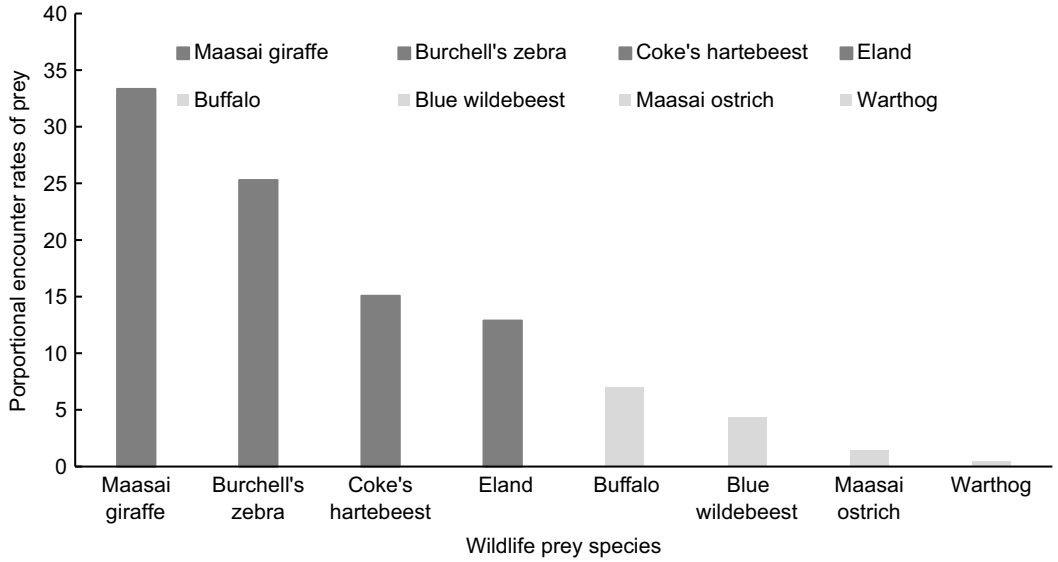

Fig. 2. The proportional encounter rate of the eight most common large prey items consumed by lions as recorded during ranger patrols conducted in the KGR study area between 2016 and 2018. The four wild prey species contributing the greatest portion of biomass to lions' diet are highlighted in dark grey. The *y*-axis represents the proportional encounter of the respective prey species as calculated from the encounter rate of each species per 100 km walked per month.

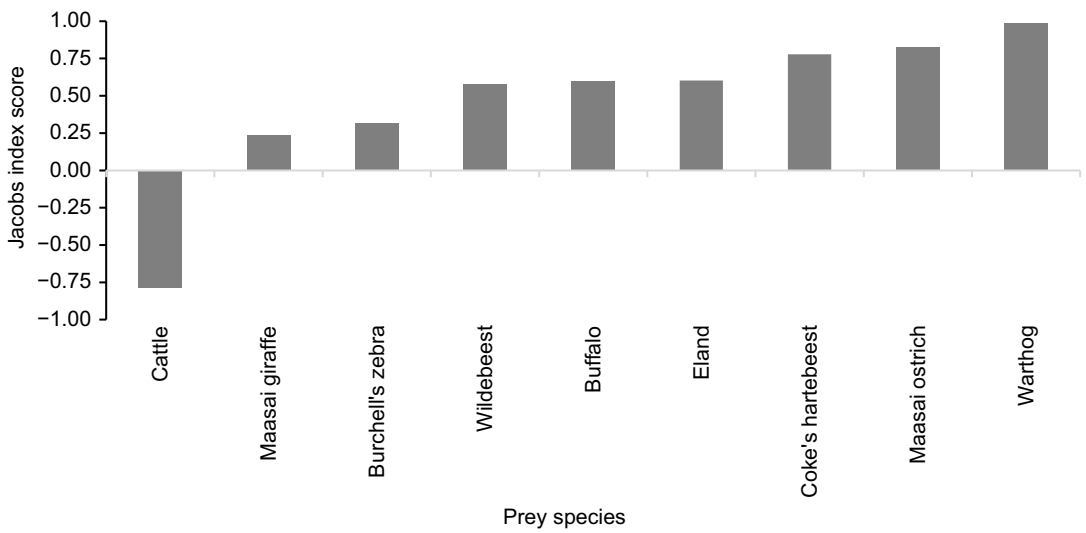

Fig. 3. Prey preference calculated using prey records obtained from GPS cluster analysis (confirmed feeding events) and aerial census data.

non-negligent herding practises on the KGR, with an increase in lag-rainfall of 150 mm resulting in an almost doubling of the number of predicted depredation events per month (Fig. 5). The non-negligent model results were most likely reflecting the pattern that exists for cattle lost while herding because the total non-negligent depredation was correlated with non-negligent depredation events during herding (correlation coefficient 0.96 [0.92–0.98]) to a greater degree than for non-negligent depredation events in bomas (correlation coefficient 0.58 [0.32–0.77]).

Discussion

Cattle are the most consumed prey item on KGR and contribute a large proportion of the biomass consumed.

Table 3. Model results for overall and non-negligent cattle predation at the Kuku Group Ranch, Kenya.

Variable	B	s.e. (β)	t-value	P
Overall cattle depredation model results				
Lag-rainfall	2.92	1.16	2.5	0.0174
Important prey	−1.18	1.24	−0.95	0.3512
Non-negligent cattle depredation model results				
Lag-rainfall	1.19	0.53	2.26	0.0304

However, lions on KGR prefer wild prey once prey availability is taken into account. Lion first needs to find prey whereafter they then decide whether it is worth pursuing on the basis of (a) prey size, (b) ease of approach (stalking cover) and (c) danger of personal injury (Kittle *et al.* 2022). With cattle abundance being consistently more than double that of wild prey, finding cattle should not be a problem for lions at KGR, suggesting that the availability of wild prey, herding practise or changing environmental conditions act as possible drivers for the apparent lack of cattle preference and variation in cattle depredation over time. However, despite the importance of wild prey to lion diets, variation in wild prey abundance had little impact on depredation. Instead, lag-rainfall was identified as the most important driver of depredation, pointing towards changes in herding practice and/or environmental conditions during the wettest periods being responsible for the variation in cattle depredation per month.

Over the 36-month study period, cattle depredation increased with an increase in lag-rainfall. If we break this down into the negligent and non-negligent forms of depredation, the relationship with lag-rainfall remains for non-negligent depredation but falls away for negligent

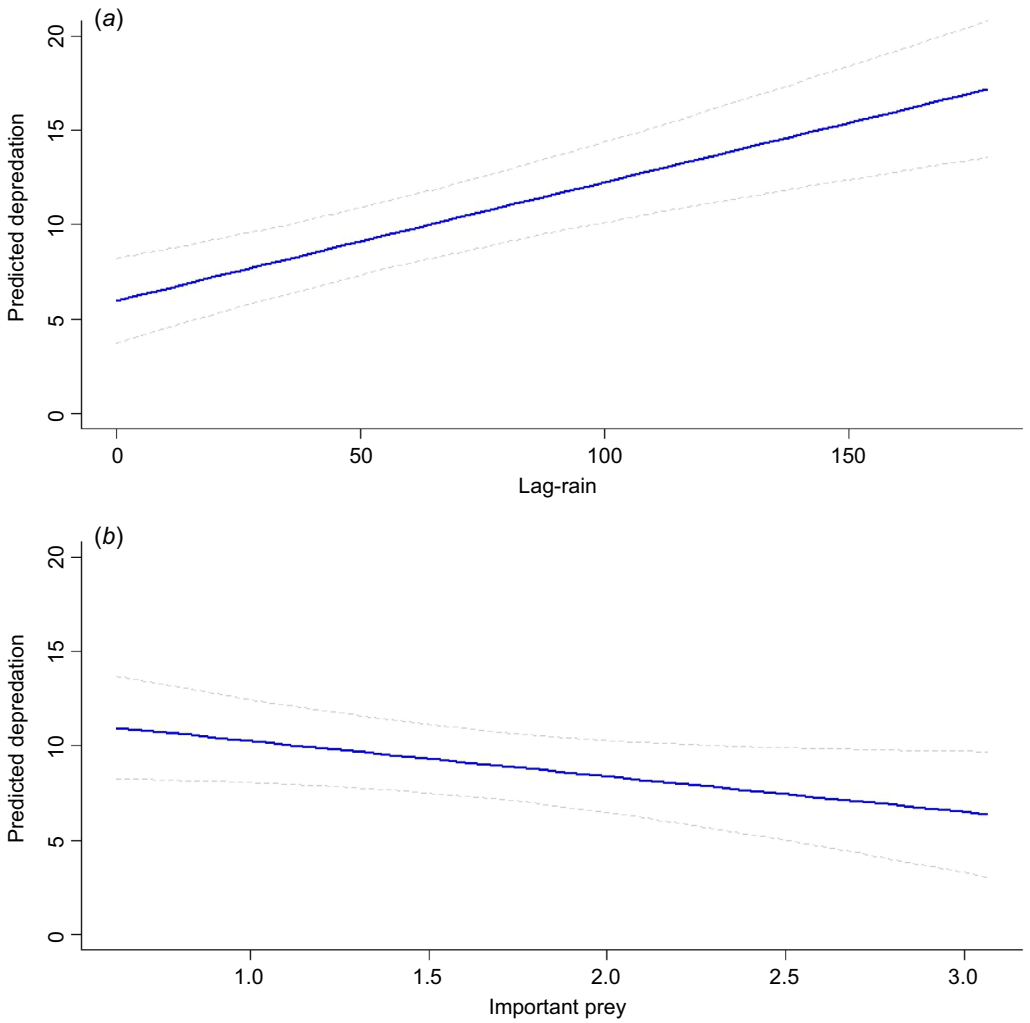

Fig. 4. General linear modelling indicated (*a*) a positive relationship between overall monthly cattle predation effects by lions and the monthly lag-rainfall recorded between 2016 and 2018 and (*b*) a negative relationship between monthly cattle predation effects by lions and the monthly encounter rate of the four prey species contributing most to lion diet, including Maasai giraffe, Burchell's zebra, eland, and Coke's hartebeest.

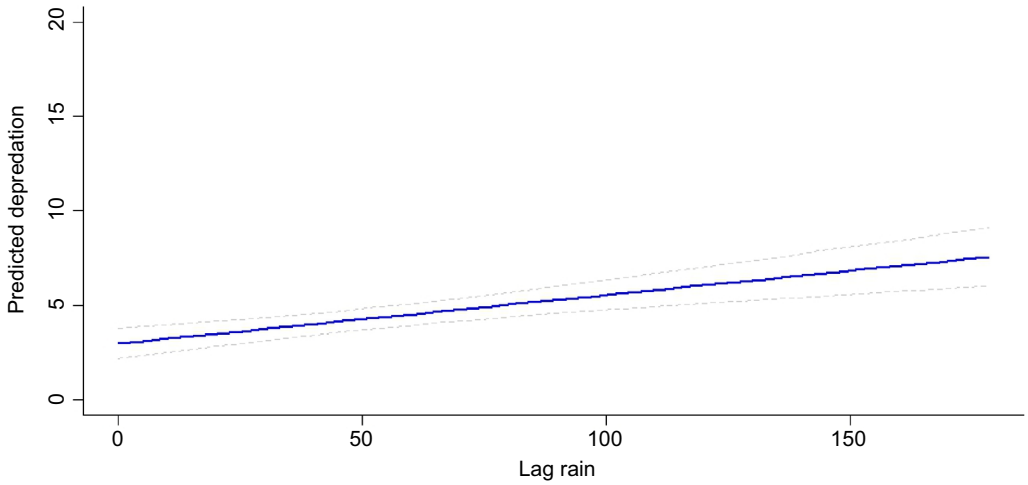

Fig. 5. For non-negligent depredation, general linear modelling indicated a positive relationship between monthly cattle predation effects by lions and the monthly lag-rainfall recorded between 2016 and 2018.

depredation. This finding suggests that lions opportunistically take advantage of poor herding irrespective of the environmental conditions. However, in contrast, some mechanism allows lions to increase their success at catching cattle after it has rained, even when herders are implementing good husbandry practices.

Cattle's higher susceptibility to lion predation in wetter periods could be driven by wild prey being in better condition (making them harder to catch), as well as the wild prey being more dispersed across the landscape as a consequence of increased surface water and available quality forage (making them harder to find; Mills *et al.* 1995; Patterson *et al.* 2004; Owen-Smith and Mills 2008; Owen-Smith 2015). If wild prey is harder to find or catch following rainfall, lions may be driven to predate on relatively easier-to-catch cattle. Alternatively, increased rain may lead to greater cover that assists lions, not only in their stalking but also in avoiding detection by herders while hunting (Ogutu and Dublin 2004; Beattie *et al.* 2020) and potentially also after a kill has been made. Vegetative cover has been shown to be another important landscape feature for ambush predators such as lions (Hopcraft *et al.* 2005; Davies *et al.* 2016*a*), and is something that needs to be assessed at a fine scale at cattle depredation sites in future studies (Miller *et al.* 2015).

It is possible that a delay in cattle-carcass detection by herders may encourage decisions to engage with cattle as the probability of acquiring sufficient food from the carcass improves. A lion might perceive herders as kleptoparasites depriving them of kills, in a similar fashion as non-human kleptoparasites have been found to influence cheetah (*Acinonyx jubatus*) prey selection (Hayward *et al.* 2006). Non-negligent predation is occurring while the cattle are being herded and not when they are in bomas. Thus, although the specific mechanism that allows lions to increase their depredation during these wetter periods still needs to be investigated, knowledge of this pattern can allow pro-active herding and husbandry to be employed to reduce depredation during wet periods.

When modelling depredation as a function of NDVI, we expected that higher NDVI values would lead to an increased incidence of cattle depredation (Beattie *et al.* 2020) because wild prey would be in better condition (Ng'weno *et al.* 2019), and thus be harder to catch. However, our results showed that in our site, NDVI had little impact on cattle depredation. Over our study period, NDVI remained relatively constant across months and years when compared with other variables measured (Fig. S4) and this lack of variation may be masking any influence that NDVI could have on the relationship with cattle depredation. For example, in Manyara Ranch Conservancy, a multi-use area in northern Tanzania, seasonal variation in vegetative productivity was a strong predictor of livestock depredation risk (Beattie *et al.* 2020) and NDVI (i.e. vegetation quality) may be more important during periods or locations where vegetation quality varies more than it did during our study.

Two of the many threats affecting lion populations and their abundance across Africa are cattle depredation, which leads to the retaliatory killing of lions, and the depletion of wild prey (Western *et al.* 2021; Bauer *et al.* 2022). Although wild prey availability was not identified as a strong driver of cattle depredation in this study, it is important in other areas in Kenya and the Tsavo–Amboseli landscape (Dolrenry *et al.* 2020; Western *et al.* 2021; Bauer *et al.* 2022). That wild prey availability was not a strong driver of cattle depredations may indicate that the KGR still has enough wild prey to support the resident lion population. Furthermore, there was little variation in the relative encounter rates of wild prey over the 36 months (Fig. S5), suggesting an adequate and stable wild prey base.

Given that there may be sufficient wild prey that remains in the KGR year-round and that wild prey are generally preferred over cattle, an important consideration in this landscape is to

ensure that wild prey numbers do not decline. If wild prey numbers do decline, we may move past a threshold where the predation pressure on cattle increases (Khorozyan *et al.* 2015). Wild prey has been found to be important elsewhere in Kenya (Dolrenry *et al.* 2020; Western *et al.* 2021), and a more detailed assessment of wild prey availability may be needed to fully understand their role in cattle depredation. For example, perhaps the ratio of wild prey to cattle in a month may be a more informative metric than are relative encounter rates, and this should be considered an additional metric to be measured in future studies. We did not measure the wild prey-to-cattle ratios for this study because of the cultural resistance of Maasai rangers to count cattle numbers. Measuring this ratio may be beneficial for future studies but would require that social norms be challenged.

There are few options to address cattle depredation and conflicts, but the common understanding in lion–livestock conflict scenarios is that improved cattle husbandry can limit the predation risk of livestock by lions (Loveridge *et al.* 2017). However, herding practices that are already likely to reduce the lion predation of cattle on the KGR, given that cattle are not preferred (Fig. 3), do not prevent the observed increase in depredation events during periods of high lag-rainfall.

Cattle herders in the KGR should be aware that the risk of predation increases at times of high lag-rainfall, and they should be extra vigilant (Fig. S6). To improve vigilance levels and herding practices, the cattle owners in the KGR could employ only adult or professional herders to guard cattle during these times of elevated rainfall. These more experienced livestock guarders are generally used when cattle are moved long distances. The use of guard dogs can also deter lion predation on livestock both while grazing and in protective bomas (Ogada *et al.* 2003; Treves and Karanth 2003). The KGR community should investigate this intervention, bearing in mind that dogs can also harass and kill wildlife, and potentially transmit wildlife diseases (Smith *et al.* 2020). The number of herders deployed to guard cattle during these peak predation periods can also be increased. By using exclusively adult herders, engaging the Maasai warriors and the potential deployment of guard dogs, better husbandry can potentially reduce cattle depredation on the KGR.

The findings outlined in this study can provide insights into similar mixed-use areas where humans and wildlife co-exist in Africa and contribute to the discussions around the requirements of cattle owners, wild prey populations, and lions in the Tsavo–Amboseli ecosystem and KGR. Lag-rainfall as the strongest predictor of cattle depredation has potentially long-term repercussions for lion conservation on the KGR, assuming various climate-change scenarios. Climate models for the Horn of Africa, which experiences two rainfall periods or seasons per year, indicate that East Africa will experience increased rainfall during the shorter rains under future climate-change predictions (Rowell *et al.* 2015; Dunning *et al.* 2018). More recent modelling has further predicted that short rains are projected to end over a week later, with a significant increase in seasonal rainfall (Wainwright *et al.* 2021). Both of these findings suggest greater lag-rainfall during the shorter rainfall period, and thus, along with the longer rainfall period, mean two possible periods where lions may focus their hunting on cattle. Given the dire need to conserve lion conservation strongholds, the burgeoning human population and increasingly variable and changing climates, integrated, proactive solutions are required to reduce human–wildlife conflicts. This reality is likely to be the same across many landscapes experiencing depredation from large carnivores (Di Minin *et al.* 2021). Our results showed that there may be key temporal variations in risk that can be considered to develop proactive solutions to human–wildlife conflicts. Thus, a holistic view that incorporates both spatial and temporal variation in risk can and should be used to develop local and regional conservation plans to ensure the long-term conservation of large predators.

Supplementary material

Supplementary material is available online.

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