

RESEARCH ARTICLE

Anthropogenic risk increases night-time activities and associations in African elephants (*Loxodonta africana*) in the Ruaha-Rungwa ecosystem, Tanzania

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Abstract

Elephants face diverse threats from human activities and use temporal and social strategies to reduce human-induced mortality risk. We used data from camera trap surveys in 2018–2019 ($n = 1625$ independent detection events from 11,751 sampling days) to investigate elephant responses to anthropogenic risk in the Ruaha-Rungwa ecosystem, Tanzania. The study was conducted in one low-risk and three high-risk sites using 26–40 paired camera trap stations per site. Risk influenced the active periods, use of roads and water sources, social associations and behaviour of elephants. Elephants demonstrated significantly more night-time and reduced daytime activity in the high-risk sites relative to the low-risk site. This higher night-time activity in the high-risk sites was observed for both males and females, though it was more pronounced for cow–calf groups than lone males. Foraging events and use of water sources were more frequent at night in the high-risk sites. Elephants used roads as movement routes in the low-risk site but avoided roads in the high-risk sites. Males were significantly more likely to associate with other males and cow–calf groups in the high-risk sites. Fewer occurrences of relaxed behaviours were observed in the high-risk sites compared to the low-risk site. We discuss the potential implications of our findings for elephant survival and reproduction.

KEYWORDS

camera trapping, *Loxodonta africana*, risk response, Ruaha-Rungwa, Tanzania

Résumé

Les éléphants sont confrontés à diverses menaces liées aux activités humaines et utilisent des stratégies temporelles et sociales pour réduire les risques de mortalité provoqués par l'homme. Nous avons utilisé les données des relevés de pièges à caméra de 2018 à 2019 ($n = 1625$ événements de détection indépendants sur 11 751 jours d'échantillonnage) pour étudier les réactions des éléphants aux risques

anthropiques dans l'écosystème de Ruaha-Rungwa, en Tanzanie. L'étude a été menée dans un site à faible risque et dans trois sites à haut risque en utilisant 26 à 40 stations de pièges à caméra appariés par site. En effet, les risques ont influencé les périodes d'activité, l'utilisation des routes et des sources d'eau, les associations sociales et le comportement des éléphants. Par rapport aux sites à faible risque, les éléphants ont montré une activité nocturne nettement plus importante et une activité diurne réduite dans les sites à haut risque. Cette activité nocturne plus importante dans les sites à haut risque a été observée à la fois pour les mâles et les femelles, mais elle était plus prononcée pour les groupes de vaches et de veaux que pour les mâles isolés. Dans les sites à haut risque, les activités de recherche de nourriture et l'utilisation des sources d'eau étaient plus fréquentes la nuit. Dans les sites à faible risque, les éléphants utilisaient les routes comme voies de déplacement, mais les évitaient dans les sites à haut risque. Les mâles étaient nettement plus enclins à s'associer à d'autres mâles et à des groupes de vaches et de veaux dans les sites à haut risque. On a constaté moins d'occurrences de comportements détendus dans les sites à haut risque que dans les sites à faible risque. Nous analysons les implications potentielles de nos résultats pour la survie et la reproduction des éléphants.

1 | INTRODUCTION

Since 2006, African savannah elephants (*Loxodonta africana*) have faced an upsurge in poaching resulting in marked population declines (Schlossberg et al., 2019; Thouless et al., 2016; Wittemyer et al., 2014). Poaching has demographic impacts, including the loss of older males and females and a reduction in the ratio of calves to adult females, resulting in populations consisting of adolescents and young adults (Jones et al., 2018; Poole, 1989). In addition to these direct impacts of poaching, it is important to understand how elephants use behavioural strategies to adapt to risks associated with humans and identify the potential implications of these risk mitigation strategies for elephant survival and reproduction (e.g., Adams et al., 2022; Buchholtz et al., 2021; Gaynor et al., 2018; Ihwagi et al., 2018).

Elephants can identify humans in threatening contexts using visual, olfactory and auditory cues (Bates et al., 2007; McComb et al., 2014). Elephants shift from daytime to crepuscular and nocturnal activity outside protected areas and near protected area boundaries (Gaynor et al., 2018; Graham et al., 2009; Sitati et al., 2003; Wittemyer et al., 2017), allowing them to access areas where they are at higher risk of human encounters and associated threats such as injury or death, especially when they derive energetic benefits (e.g., access to agricultural crops, Chiyo et al., 2011; Smit et al., 2019; Wilkie & Douglas-Hamilton, 2018). Increased nocturnal activity has also been observed in response to poaching (Breuer et al., 2016; Ihwagi et al., 2018). Responses to risk may differ by sex. Males are more likely to engage in 'high-risk, high-reward' crop foraging than females, who tend to move through or avoid areas of high anthropogenic risk to reach foraging or water resources (Boult et al., 2019;

Kangwana, 1993; Sitati et al., 2003). Elephants also use social strategies to mitigate risk by associating with other elephants to share knowledge or dilute mortality risk (e.g., Sitati et al., 2003; Smit et al., 2019). Understanding elephant behavioural responses to risk may help to develop behavioural indicators of anthropogenic pressure (Goldenberg et al., 2017; Ihwagi et al., 2018) and conservation strategies informed by an understanding of elephant behaviour and social structure.

We investigated elephant responses to poaching risk, as inferred from elephant carcass distributions (Beale et al., 2018), in the Ruaha-Rungwa ecosystem of Tanzania. The Ruaha-Rungwa elephant population declined by >50% between 2006 and 2015 due to poaching for the ivory trade (Beale et al., 2018; Thouless et al., 2016; Wasser et al., 2015). This is reflected in a population with a disproportionate number of adolescents and young adults and high levels of tusklessness compared to sites which did not experience poaching (Jones et al., 2018). Ratios of carcasses to live elephants suggested that low-level illegal killing of elephants continued to be a concern during the study period (TAWIRI, 2019). Poaching is likely to have influenced elephant space use and activity patterns in this ecosystem. Elephant mortality risk is distributed unevenly throughout the ecosystem, allowing for comparisons between high- and low-risk sites (Beale et al., 2018). We used camera trap surveys to investigate whether elephants adjust their active period, social associations and behaviour in response to risk.

We hypothesised that anthropogenic risk would influence when elephants were active and how they used roads and water sources. We predicted that elephants would demonstrate greater night-time activity in high-risk areas as a strategy to reduce temporal overlap with humans (e.g., Gaynor et al., 2018; Ihwagi et al., 2018). As

cow-calf groups are thought to be more risk-sensitive than bulls (Sukumar & Gadgil, 1988), we expected female groups to show a greater shift to night-time activity than males in response to risk. We predicted that elephants would visit water sources and use roads as movement corridors predominantly at night in high-risk areas (e.g., Gaynor et al., 2018). We further hypothesised that risk would influence associations and the types of behaviours elephants were engaged in. We predicted that male elephants would be more likely to occur in mixed groups (cow-calf groups with associated mature males) and bull groups in high-risk sites compared to the low-risk site. Finally, we predicted that fewer relaxed behaviours and more stress behaviours would be observed in the high-risk sites compared to the low-risk site.

2 | METHODS

2.1 | Study site

The Ruaha-Rungwa ecosystem is located in south-central Tanzania (Latitude: -7.3, Longitude: 34.4). The study area comprised Ruaha National Park (20,226 km²), Rungwa-Kizigo-Muhesi Game Reserves (17,600 km²) and MBOMIPA Wildlife Management Area (777 km²). For an ecosystem description, see Appendix S1.

Photographic tourism is conducted in the National Park, trophy hunting is permitted in the Game Reserves and both photographic tourism and trophy hunting are allowed in the Wildlife Management Area (WMA). The road network in the ecosystem is designed primarily for ranger access. Only the high-use tourism area and active trophy hunting areas have extensive networks of minor roads, where tourism and hunting vehicle activity is largely restricted to daytime hours.

Camera traps were situated in grids within four sites representing different levels of risk to elephants. We categorised grids as low or high risk based on elephant carcass distribution (Beale et al., 2018), with carcass density used as an indicator of poaching risk, as well as the distribution of illegal human activities (Strampelli et al., 2022; TAWIRI, 2016, 2019). Camera trap surveys were conducted in the dry season of 2018 and 2019.

The Ruaha National Park core grid (RNP:LR, low risk) was situated in the high-use tourism zone where the Park's headquarters, three ranger posts and tourism infrastructure are located, and where photographic tourism activity is concentrated. Due to established tourism and ranger presence, this area forms the safest part of the ecosystem for elephants (Beale et al., 2018). The dominant habitat is *Vachellia-Commiphora*.

The Ruaha National Park miombo grid (MIO:HR1, high risk) was located in a 'wilderness zone' in the west of the park in an area dominated by miombo (*Brachystegia-Jubelnardia*) woodland. Tourism activity in wilderness zones is restricted to walking safaris, though no tour operators were present at the time of the study (2018). Due to their low visitation rates, wilderness zone areas within the park were at higher risk of illegal activities than areas with established tourism

presence (Mtahiko, 2007). The MIO:HR1 grid also had higher elephant carcass densities than the Ruaha NP core tourism area in 2013–2015 (Beale et al., 2018).

The MBOMIPA WMA grid (MBO:HR2, high-risk) was located in the Lunda zone of the WMA, where the dominant habitat is *Vachellia-Commiphora*. No tourism activities took place at the time of the study (2018). This area was a hotspot of elephant poaching from 2013 to 2015 (Beale et al., 2018) and the probability of illegal human activity was greater in the WMA than in Ruaha National Park at the time of the study (Strampelli et al., 2022). The grid was also directly adjacent to cultivated and grazed village land.

The Rungwa-Ikiri grid (RUI:HR3, high risk) was located in the Rungwa-Ikiri block of Rungwa Game Reserve, where miombo woodland was dominant. This area experienced elephant poaching between 2013 and 2015 (Beale et al., 2018). Human illegal activity was more prevalent in the Game Reserves than in the National Park (Strampelli et al., 2022). Trophy hunting was actively occurring at the time of the study (2019), although not for elephants.

2.2 | Data collection

We used camera traps to estimate elephant active periods (e.g., Gaynor et al., 2018; Gessner et al., 2014). Elephant active periods have previously been described from camera trap surveys which varied in purpose, layout and duration (Gaynor et al., 2018). Data were collected as part of a multipurpose and multispecies research collaboration, with camera trap survey design initially guided by requirements for spatially explicit capture-recapture density estimation of carnivores (Searle et al., 2021).

A 'grid' was defined as the full complement of camera traps within each of the four survey areas. Grids consisted of between 26 and 44 stations with paired camera traps (Figure 1; Table 1). All surveys were conducted in the dry season to avoid possible confounding effects of seasonality on elephant activity patterns (Barnes, 1983). Camera stations were placed along roads as well as off-road on animal trails. Camera stations were defined as being near water if they were within 1 km of a water source. Grids were situated >30 km apart; as such, it is unlikely that the same elephant(s) would be captured at multiple grids in the same 24-h period. See Appendix S1 for additional information on camera placement and survey design.

Camera trap images were classified using ExifPro Version 2.1 software. We defined independent elephant detection events as images of elephants that were separated by more than 15 min (Gaynor et al., 2018). This definition was based on expert assessment, including examination of camera trap video footage which demonstrated that elephants in the same known group were rarely separated by >15 min at a given location (Gaynor et al., 2018). We noted the start time (the time of the first photograph in an event) and the midpoint for each event. We coded group type for each event as: cow-calf, lone bull, bull group, mixed group of cow-calf plus mature males, or unknown (Table S1), and whether elephants had visited a water source (determined from the presence of moisture

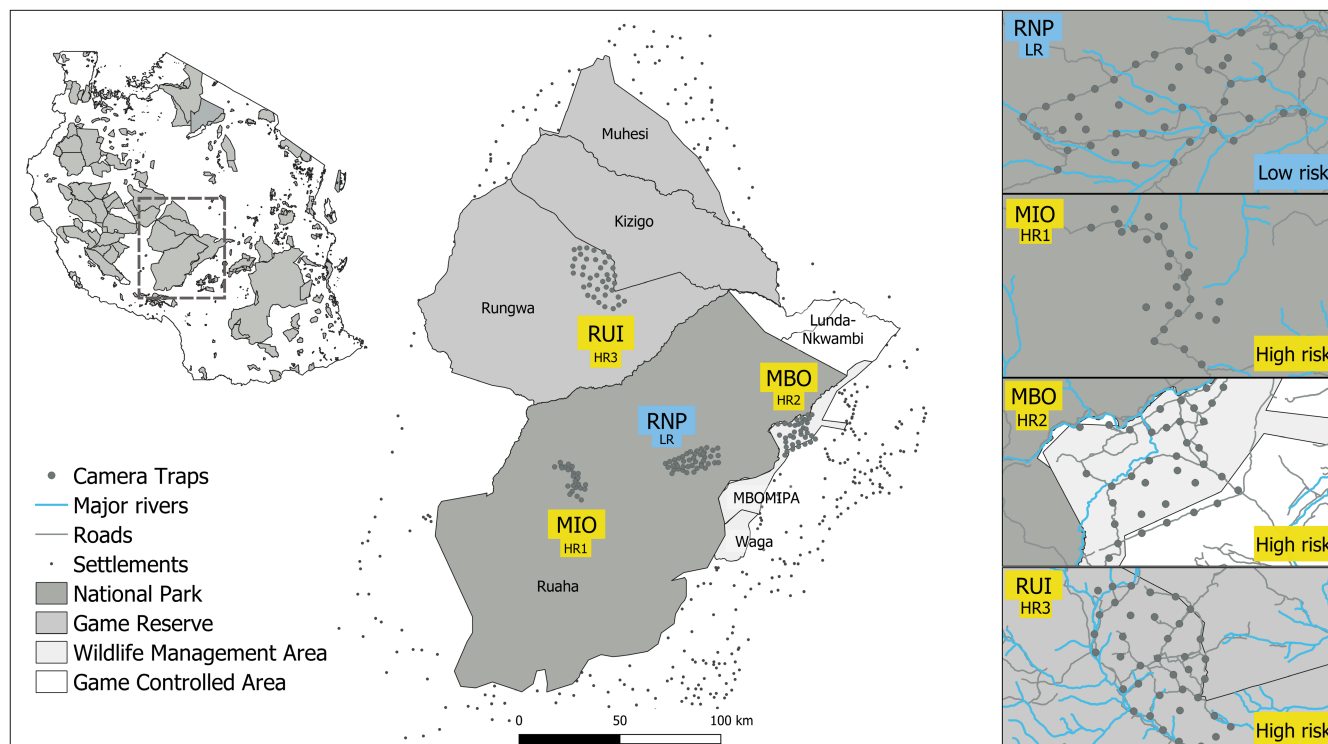


FIGURE 1 Location of the study area in Tanzania (left), study area with camera trap survey grid locations shown (middle) and location of camera traps (grey circles) and risk to elephants shown (right). The RNP:LR grid represents a low-risk area for elephants while the MIO:HR1, MBO:HR2 and RUI:HR3 grids represent high-risk areas.

TABLE 1 Summary of camera trap grid layout, events, and effort, where effort is measured as the total number of active days across all camera stations.

	Ruaha NP core zone (RNP:LR)	Ruaha NP miombo zone (MIO:HR1)	MBOMIPA WMA (MBO:HR2)	Rungwa-Ikiri block (RUI:HR3)
Risk level	Low	High	High	High
No. of camera sites	44 (80 cameras)	26 (52 cameras)	40 (80 cameras)	40 (80 cameras)
Total survey area	223 km ²	152 km ²	270 km ²	555 km ²
Average spacing between camera stations	1.96 km	1.88 km	2.08 km	3.46 km
Camera placement on roads	38 stations on roads, six stations off-road	14 stations on roads, 12 stations off-road	30 stations on roads, 10 stations off-road	32 stations on roads, eight stations off-road
Camera placement near water	17 stations near water	12 stations near water	17 stations near water	19 stations near water
Study period	June–September 2018 (83 days)	September–November 2018 (90 days)	August–November 2018 (70 days)	July–October 2019 (90 days)
Effort (camera trap days)	3508	2187	2681	3375
No. of camera sites with elephant detections	44 (100%)	24 (93%)	32 (80%)	38 (95%)
No. of elephant images	5898	1446	865	1501
No. of elephant detection events	885	166	214	360
RAI	25.2	7.6	8.0	10.7

Note: Relative activity index (RAI) is defined as the number of detection events per 100 sampling days.

on the trunk and/or legs or body). For each detection event, we visually inspected camera trap images to identify which activity types were present (Table S3). An activity type was considered present if at least one individual in the event displayed the activity. More

than one activity type could be present per event. See Appendix S1 for interobserver reliability of group type and activity type scoring. We also scored body condition for adult female elephants from camera trap images and classified images with vehicles and lions to

enable comparisons of elephant, lion and vehicle activity profiles (Appendix S1).

Ethics approval for this study was granted by the University of Stirling General University Ethics Panel and the Animal Welfare and Ethical Review Body.

2.3 | Data analysis

To visualise elephant active periods over 24h, we used the *overlap* package in R version 1.4.1106 to generate smoothed nonparametric kernel density distributions of independent elephant events (Ridout & Linkie, 2009). We used event start times following Gaynor et al. (2018), as distributions using event start times and mid times were identical (Table S4; Figure S1). Since the Sun's position in the sky ('sun time'), rather than clock time (the time on a 24-h clock), has biological and environmental meaning, we accounted for geographic and temporal variation in the times of sunrise and sunset over the study area and study period by using the *SunTime* function to convert clock times to sun times (Nouvellet et al., 2012).

We compared 24-h activity profiles for all elephant events and calculated the coefficient of overlapping between the low-risk site and each of the high-risk sites. The coefficient of overlapping represents the total percentage of area that is shared by two activity distributions. We determined if two activity distributions were significantly different using the *activity* package (Rowcliffe et al., 2014). We also compared the activity distributions and coefficient of overlapping between the low-risk and each of the high-risk grids for cow-calf group and lone bull events (Table S5).

To examine the effect of diel period, grid (a proxy for risk), group type, water and roads on the number of elephant observations, we summed the number of elephant events for each group type and diel period by camera trap station (Smit, 2021a). Sample sizes for bull groups and mixed groups were too small to analyse independently (Table S5). We combined lone bull and bull group events into a single category of male events, as these two group types reflect male decision-making. We combined cow-calf and mixed group events into a single category of female events, as these two group types reflect primarily female decision-making. Each camera trap station was either near or far from water, on- or off-road and in one of four grids (RNP:LR, MIO:HR1, MBO:HR2, RUI:HR3). Events were assigned to four diel periods: dawn (0.5 h), day (12h), dusk (0.5 h) and night (11h). Dawn and dusk were considered separately from day and night because they represent transition periods in brightness and temperature. Sunrise, sunset and twilight times were extracted from timeanddate.com. We excluded the dawn and dusk diel periods (comprising 5% of detection events) from subsequent analysis to reduce zero inflation resulting from small sample sizes.

Data exploration was done following the eight-step protocol in Zuur et al. (2010) and exposed heterogeneity and overdispersion of the elephant event count data. To model the number of elephant events as a function of the covariates, a Negative Binomial Generalised Linear Mixed Model (GLMM) with a log link function

was used. The log link function ensures positive fitted values, and the negative binomial distribution is typically used for overdispersed count data. Fixed covariates were *diel period* (categorical with two levels, with *Day* as the reference level), *water* (categorical with two levels, with *No* as the reference level), *road* (categorical with two levels, with *Off* as the reference level), *grid* (categorical with four levels, with *RNP:LR* as the reference level) and *group type* (categorical with two levels, with *Male* as the reference level). To account for repeated measures from cameras, camera station was used as a random intercept. We fit a global model with all biologically possible interactions informed by our hypotheses, including two-way and three-way interactions between *diel*, *group*, *water*, *road* and *grid*. Those interactions which did not contribute to model fit were removed during model selection. To account for differences in camera trap sampling effort and differences in the duration of the day and night diel periods, the number of sampling hours was included as an offset in the model. For confirmatory purposes, we also fit the top random intercept-only model with *diel* and *group* as random slopes. Models were fit using maximum likelihood estimation using the package *lme4* (Bates et al., 2015).

Model selection was done using AIC, whereby all models within $\Delta AIC 6$ were considered top models (Richards, 2008). We expressed model coefficients as incident rate ratios (IRRs) to compare the incidence rates of events between different levels of a categorical variable. IRRs were visualised using the package *sjPlot* (Lüdtke, 2020).

We examined whether there was a difference in the relative frequency of female and male events across the four grids using a chi-square test of homogeneity. We also used chi-square goodness-of-fit tests to determine if there was a significant difference in the number of (1) lone bull versus bull group events and (2) lone bull versus mixed group events between the low-risk grid and each of the three high-risk grids. We applied the Bonferroni correction to correct for multiple comparisons ($\alpha = 0.05 / 3 = 0.017$).

We investigated whether the range and frequency of elephant activity types detected by camera traps varied between the low- and high-risk sites. Activity types were grouped into three broad categories of (1) energy acquisition and movement behaviours, (2) relaxed behaviours and (3) stress behaviours (Tables S2 and S3). Events were classified as either day (07:00–18:59h) or night (19:00–06:59h). We compared the number of diurnal and nocturnal occurrences of energy acquisition and movement behaviours and visits to water sources between the low- and high-risk grids using chi-square goodness-of-fit tests. All probability tests were two-tailed and set to $p < 0.05$.

Finally, we compared adult female body condition scores between sites and generated elephant, lion and vehicle activity profiles for each site (Appendix S1).

3 | RESULTS

Camera traps detected 1625 unique elephant events (Smit, 2021b) over 11,751 camera trap days (Table 1). In the low-risk site, elephant activity was predominantly diurnal, with a peak around dusk.

Elephant activity profiles for the three high-risk sites differed in the location of activity peaks, but all had reduced diurnal activity and increased nocturnal activity and were significantly different from the activity distribution for the low-risk site. Activity profiles for the high-risk sites had compressed peaks of elephant activity, while elephant activity was more evenly spread over the 24-h period in the low-risk site (Figure 2).

Activity profiles for cow-calf groups and lone bulls (Figure 2) demonstrated increased nocturnal activity in the high-risk sites relative to the low-risk site. For cow-calf groups, 79% of events were nocturnal in the high-risk sites compared to 45% in the low-risk site. For lone bulls, 81% of events were nocturnal in the high-risk sites compared to 59% in the low-risk site. Overlap between the cow-calf distributions in the low- and high-risk sites was lower

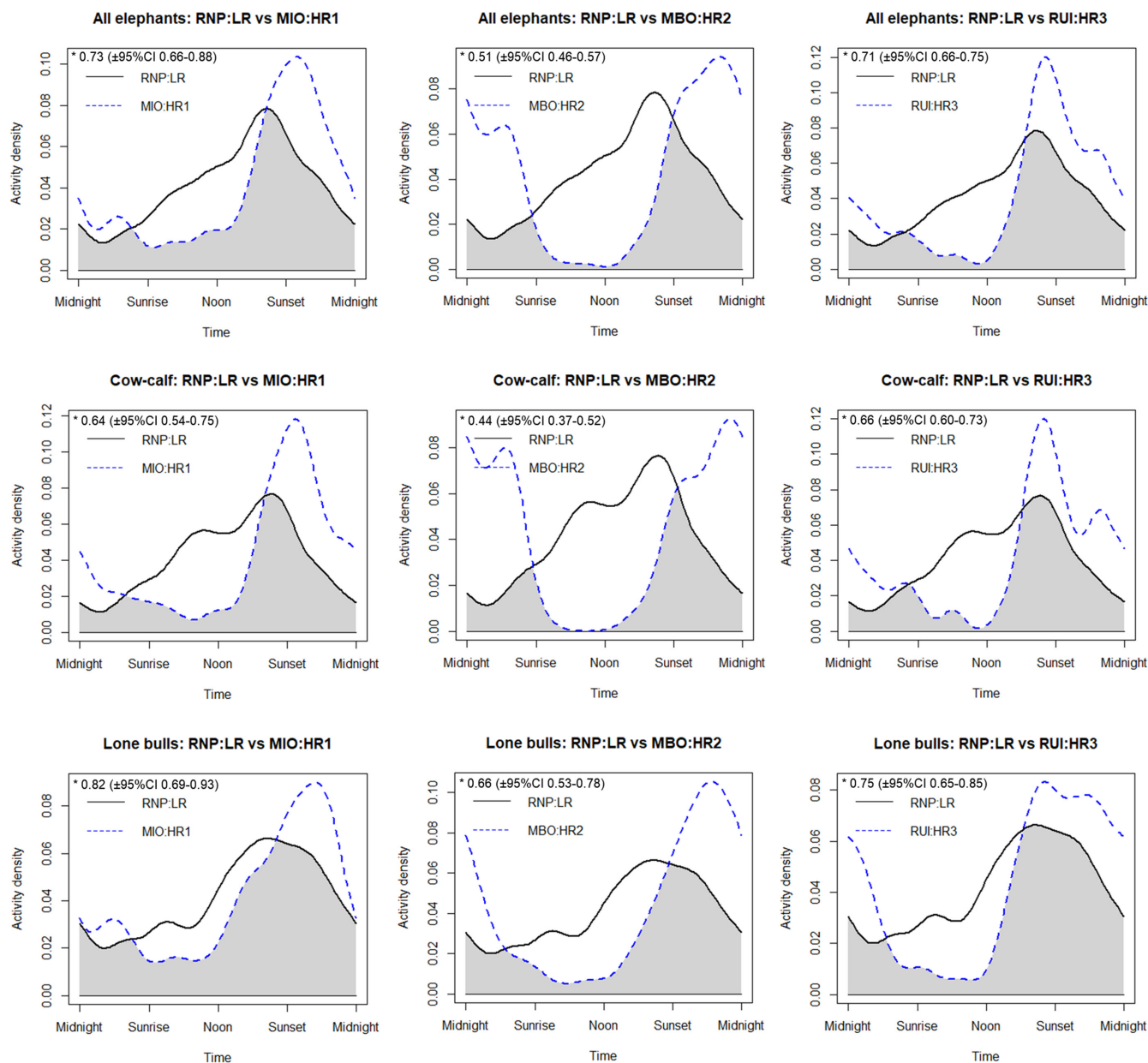


FIGURE 2 Elephant activity profiles for all events (top row) in the low-risk RNP:LR grid ($n = 885$ events) and three high-risk grids: MIO:HR1 ($n = 166$ events), MBO:HR2 ($n = 214$ events) and RUI:HR3 ($n = 360$ events); cow-calf events (middle row) in the low-risk RNP:LR grid ($n = 453$ events) and three high-risk grids: MIO:HR1 ($n = 60$ events), MBO:HR2 ($n = 104$ events) and RUI:HR2 ($n = 170$ events); and lone bull events (bottom row) in the low-risk RNP:LR grid ($n = 207$ events) and three high-risk grids: MIO:HR1 ($n = 35$ events), MBO:HR2 ($n = 41$ events) and RUI:HR3 ($n = 59$ events). Note the y-axes are not the same. The density of elephant events over a 24-h period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between the two distributions and is equivalent to the coefficient of overlapping. The coefficient of overlapping and 95% confidence interval is indicated for each pair of activity distributions. An asterisk indicates the two distributions are significantly different.

than the overlap between lone bull distributions in the low- and high-risk sites.

There was a significant difference in the number of diurnal and nocturnal feeding events between the low-risk site and the high-risk sites, $X^2(1, N = 345) = 8.3, p < 0.005$; Figure 3. In the low-risk site, 46% of feeding events occurred during the day and 54% at night, compared to 33% and 67%, respectively, for the high-risk sites. There was also a significant difference in the number of diurnal and nocturnal moving events between the low-risk grid and the high-risk grids, $X^2(1, N = 1549) = 174.0, p < 0.005$. In the low-risk site, 48% of moving events occurred during the day and 52% at night, compared to 23% and 77%, respectively, for the high-risk sites. There was a significant difference in the number of diurnal and nocturnal visits to water sources between the low-risk sites and the high-risk sites, $X^2(1, N = 413) = 33.8, p < 0.005$. In the low-risk site, 45% of water source visits occurred during the day and 55% at night, compared to 18% and 82%, respectively, for the high-risk sites.

The effect of diel period, grid, group type, water and roads on the number of elephant events was modelled using GLMM. Four models were within ΔAIC of 6 (Table S7; Figure S3). The top random intercept-only model with the lowest AIC included the term

water and interactions *diel* \times *grid*, *road* \times *grid* and *diel* \times *group* (Figure 4; Table S6). The random slopes model (Figure S6; Table S8) had the same fixed effects structure as the intercept-only model. The top model included an interaction between diel period and grid, such that night had a positive effect on elephant event counts for the three high-risk grids. Water and roads had a significant positive effect on the number of elephant events. There was an interaction between road and grid, such that in the high-risk MIO:HR1 and RUI:HR3 grids, roads had a significant negative effect on elephant event counts. We did not find a significant interaction between group type and diel period.

Model validation showed mixed results (Figures S4 and S5). The top model had normally distributed residuals, though some heterogeneity was evident in the deviance residuals by grid and diel period. The top model was overdispersed (dispersion parameter 3.4).

Cow-calf groups (787 events) and lone bulls (342 events) were the most frequently detected group types. There was no significant difference in the relative frequency of female (cow-calf and mixed groups) and male (lone bull and bull group) events between the four grids, $X^2(3, N = 1327) = 4.9, p > 0.1$ (Figure S2). Male associations differed between the low-risk and high-risk grids (Figure 5). There

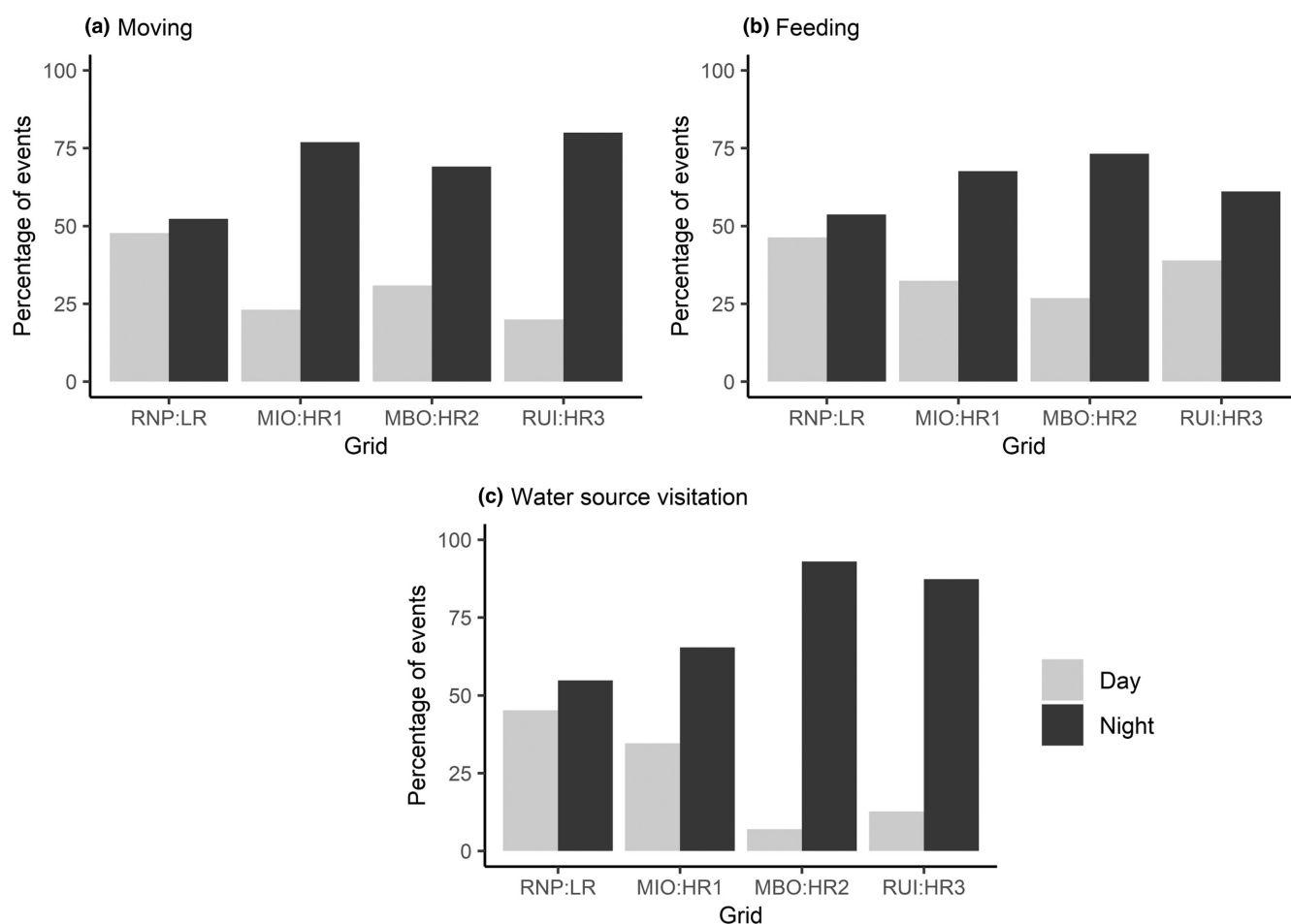


FIGURE 3 Percentage of daytime and night-time (a) moving events ($n = 1549$), (b) feeding events ($n = 345$) and (c) visits to water sources by grid ($n = 413$). The RNP:LR grid represents a low-risk area for elephants while the MIO:HR1, MBO:HR2 and RUI:HR3 grids represent high-risk areas.

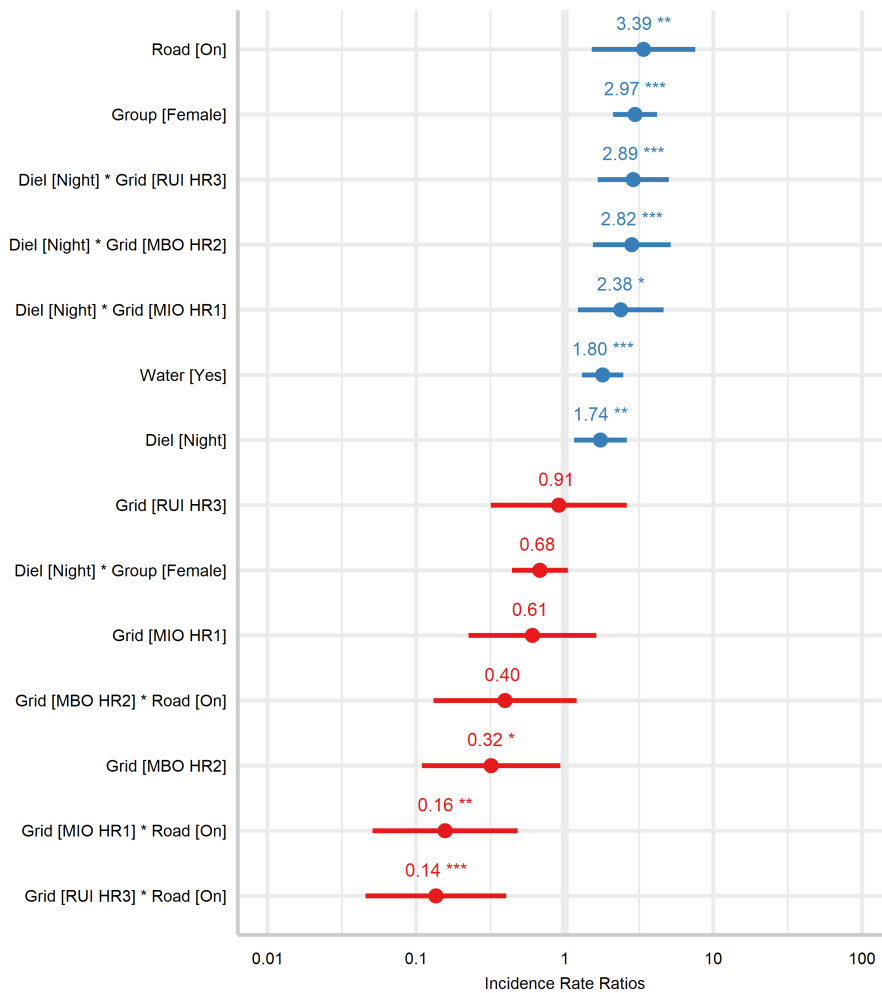


FIGURE 4 Elephant event incident rate ratios (dots) and 95% confidence intervals (bars) for model parameters. To express model coefficients as incident rate ratios, we raised the natural log to the power of each coefficient. The terms GridMBO HR2, RoadOn, WaterYes, GroupFemale, DielNight:GridMBO HR2, DielNight:GridMIO HR1, DielNight:GridRUI HR2, RoadOn:GridMIO HR1 and RoadOn:GridRUI HR3 were statistically significant. Red indicates that a term has a negative effect on incident rates, while blue indicates that a term has a positive effect on incident rates. The RNP LR grid represents a low-risk area for elephants while the MIO HR1, MBO HR2 and RUI HR2 grids represent high-risk areas.

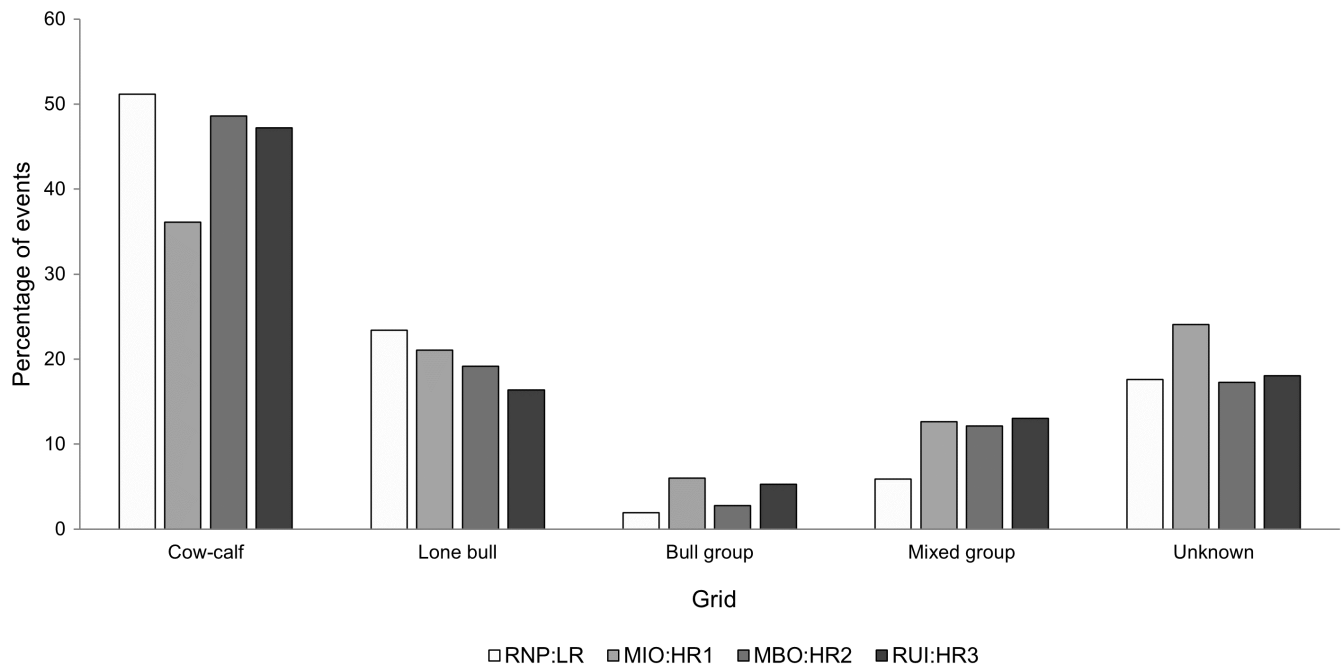


FIGURE 5 Percentage of events for each group type by grid. The RNP:LR grid ($n = 885$ events) represents a low-risk area for elephants while the MIO:HR1 ($n = 166$ events), MBO:HR2 ($n = 214$ events) and RUI:HR3 ($n = 360$ events) grids represent high-risk areas.

were significantly more bull group events than lone bull events in two of the high-risk grids (MIO:HR1, RUI:HR3) than in the low-risk grid: RNP:LR versus MIO:HR1, $X^2(1, N = 45) = 12.4, p < 0.005$ and RNP:LR versus RUI:HR3, $X^2(1, N = 78) = 28.4, p < 0.005$. There were also significantly more mixed group events than lone bull events in the three high-risk grids than in the low-risk grid: RNP:LR versus MIO:HR1, $X^2(1, N = 56) = 10.7, p < 0.005$, RNP:LR versus MBO:HR2, $X^2(1, N = 67) = 14.8, p < 0.005$ and RNP:LR versus RUI:HR3, $X^2(1, N = 106) = 39.2, p < 0.005$.

A total of 14 activity types were identified from camera trap images (Table 2 and Table S2). Movement and energy acquisition activities were dominant in camera trap detections of elephants. A greater diversity of activity types was observed for the low-risk site (14 types) compared to the high-risk sites (6–7 types). Relaxed behaviours were observed in 4% of elephant events from the low-risk site and in 0.8% of events from the high-risk sites. A single instance of play was recorded from the high-risk sites, compared to 11 instances of play in the low-risk site. Running, a stress behaviour, was recorded in 1.6% of events in the low-risk site and in 2.6% of events in the high-risk sites.

TABLE 2 Activity types observed from unique camera trap events of elephants for each grid.

Activity type (% of events)	RNP:LR <i>n</i> = 885	MIO:HR1 <i>n</i> = 166	MBO:HR2 <i>n</i> = 214	RUI:HR3 <i>n</i> = 360
Energy acquisition and movement behaviours				
Walking	94.2	91.0	86.0	95.0
Feeding while walking	19.9	14.5	30.4	12.8
Feeding while standing	4.5	6.0	0.0	2.2
Drinking	0.6	1.2	0.0	0.0
Relaxed behaviours				
Dusting	2.3	0.0	0.0	0.0
Wallowing	0.1	0.0	0.0	0.0
Lying	0.7	0.0	0.5	0.0
Suckling	0.3	0.0	1.4	0.6
Social play	0.2	0.0	0.0	0.0
Object play	0.9	0.0	0.0	0.3
Lone play	0.1	0.0	0.0	0.0
Explore object	0.1	0.0	0.0	0.0
Stress behaviours				
Running	1.6	5.4	1.9	1.9
Other behaviours				
Pause	11.2	16.3	2.3	8.1

Note: The RNP:LR grid represents a low-risk area for elephants while the MIO:HR1, MBO:HR2 and RUI:HR3 grids represent high-risk areas. More than one activity type may be observed per event. For activity type definitions, see Table S2. Total *n* = 1625 events.

Although mean body condition scores were slightly lower for the three high-risk grids, most adult females assessed were in normal condition across the four grids (Tables S9 and S10). There was more overlap in elephant and vehicle activity curves (Figure S13) and less overlap between elephant and lion activity curves (Figure S14) in the low-risk site than in the high-risk sites.

4 | DISCUSSION

The African elephant has experienced widespread population declines over recent decades and was recently up-listed from *Vulnerable* to *Endangered* by the IUCN (Gobush et al., 2021). Understanding the longer term impacts of anthropogenic pressure on elephant behaviour can help to reveal the consequences for at-risk populations. We provide evidence of temporal and social adaptations to risk for elephants and shed light on differences in risk response among males and females.

We found that elephants were more nocturnal in the high-risk sites, in line with findings of previous studies that elephants increase night-time activity in response to risk. Elephants tend to crop forage (Sitati et al., 2003; Smit et al., 2019) and move through areas outside of formally protected areas at night as a strategy to reduce temporal overlap with humans (Galanti et al., 2006; Gaynor et al., 2018; Graham et al., 2009; Lewis, 1986; Wittemyer et al., 2007), and increased night-time movements in response to poaching in the Samburu-Laikipia ecosystem in Kenya (Ihwagi et al., 2018). In addition to risk, elephant active periods may be influenced by environmental temperatures (Mole et al., 2016) and the quality and distribution of forage and water resources (e.g., Guy, 1976). Average maximum daily temperatures in the study area varied with elevation and time of year (range 27–33°C). Temperature increased over the course of the dry season, but as two of the high-risk sites were at higher elevation (MIO:HR1 at 1350m asl and RUI:HR3 at 1200m asl) than the low-risk RNP:LR site (800m asl), maximum daytime temperatures during the survey periods were comparable for these sites. As the RNP:LR and MBO:HR2 sites were both in *Vachellia-Commiphora* habitat, it is unlikely that the observed difference in elephant diel activity patterns was due to variation in habitat quality. The MIO:HR1 and RUI:HR3 sites were in more marginal miombo woodland habitat. As there was no low-risk miombo site, it is uncertain to what extent habitat contributed to the observed activity patterns. However, risk was likely a more important driver of elephant activity patterns than habitat at the MIO:HR1 and RUI:HR3 sites. This is supported by the fact that, contrary to what would be expected for more marginal habitats in which elephants spend more time feeding and moving to meet energetic requirements (Mramba et al., 2019), elephant activity profiles were more compressed in these two high-risk miombo sites than in the low-risk site in more productive habitat.

Consistent with previous studies, we found that cow-calf groups were more risk-sensitive than bulls (Sukumar & Gadgil, 1988). In Samburu-Laikipia, both male and female elephants moved more at night when poaching levels were high, but the relationship between

poaching levels and increased night-time movement was stronger for females than for males (Ihwagi et al., 2018). In the current study, both male and female elephants were more nocturnal in the high-risk sites, but the increase in night-time activity relative to the low-risk site was more pronounced for cow-calf groups than lone bulls (Figure S7). However, we did not find an interaction between group type, grid and diel period because the risk-induced shift to night-time activity occurred for both male and female groups and was similar in magnitude with the different male and female group types pooled (Figure S8).

Elephants visited water sources more at night in the high-risk sites compared to the low-risk site. Although cameras near water had a marginally higher proportion of nocturnal events than did cameras far from water in the high-risk sites, we did not find a significant interaction between water, grid and diel period because the shift to night-time activity in response to risk occurred both near and far from water (Figure S9). This pattern was consistent across male and female groups (Figure S11). Water is a key resource for elephants: family groups typically drink at least once a day with lactating females requiring water for milk production (Chamaillé-Jammes et al., 2013; Wyatt & Eltringham, 1974). Previous studies observed that elephant use of water sources peaked during the middle of the day (Leggett, 2009) or at dusk (Guy, 1976) in the dry season. In our study, elephants visited water sources primarily at night in the high-risk sites. Similarly, in Gorongosa National Park, Mozambique, elephants visited a risky water source (a river along the park boundary) almost exclusively at dusk and during the night (Poole & Granli, 2017), suggesting that risk influences the timing of elephant use of water sources.

Elephants used roads in the low-risk site but avoided roads in the high-risk sites. While elephant use of roads was more nocturnal in the high-risk sites than in the low-risk site (Figure S10), there was no interaction between road, grid and diel period as the shift to nocturnal activity in the high-risk sites occurred on- as well as off-road. This pattern was consistent for male and female groups (Figure S12). There was greater overlap between elephant and vehicle activity profiles in the low-risk site than in the high-risk sites (Figure S13), suggesting that nocturnal use of roads in the high-risk sites enabled elephants to avoid vehicles. Our findings contribute to evidence that elephant use of roads varies with risk: where elephants are well protected, elephants may use roads for ease of movement (Granados et al., 2012), while in areas of higher risk, elephants may avoid roads (Blake et al., 2008) or time their use of roads to reduce interactions with humans and vehicles (Gaynor et al., 2018; *Elephas maximus*, Katugaha et al., 1999).

Camera traps detected significantly more mixed and bull groups in the high-risk sites compared to the low-risk site, contributing to evidence that anthropogenic risk is a driver of male associations (e.g., Chiyo et al., 2014; Srinivasaiah et al., 2019). While female elephants live in family groups composed of related adult females and their offspring, males disperse from their natal family group at an average age of 14 years (Lee et al., 2011). Independent males associate with other males for social partners and to reduce mortality risk, as observed in

our study and elsewhere (Allen et al., 2020; Chiyo et al., 2014; Lee et al., 2011; Sitati et al., 2003). Males may also form associations to take advantage of the knowledge of other males (Allen et al., 2020; Chiyo et al., 2014; Srinivasaiah et al., 2019), potentially to problem solve. Males also associate with cow-calf groups for companionship, knowledge, access to reproductive females and, as observed in this study, to dilute mortality risk (Chiyo et al., 2014).

Camera traps detected fewer occurrences of relaxed behaviours and more occurrences of stress behaviours in the high-risk sites than in the low-risk site. Although sample sizes were small, we suggest that elephants may engage less frequently in relaxed behaviours such as play in areas of higher risk (e.g., Lee & Moss, 2014), with potential implications for learning and acquisition of social experience (Lee & Moss, 1999). This is an important area for further research through observational studies.

It is now clear that elephants adjust their active period in response to risk and we demonstrate that this can be a generalised response over large areas (e.g., 555 km² for the high-risk RUI:HR3 grid). We further demonstrate that this risk response is not limited to the boundaries of protected areas (as in Gaynor et al., 2018) or in areas without formal protection status (e.g., Graham et al., 2009), but that it can occur inside protected areas where on-the-ground protection and tourism presence are low, and where elephants have experienced poaching. Our findings suggest that focused protection efforts and strategic distribution of tourism investments could help to make a larger part of the ecosystem safe for elephants.

Our study was conducted after the peak poaching period—although some illegal killing of elephants continued to occur (TAWIRI, 2019)—suggesting that elephants may maintain risk responses for a prolonged period, even after their environment has become more secure. This has been observed for African forest elephants (*Loxodonta cyclotis*) in Central Africa (Breuer et al., 2016) and savannah elephants in Gorongosa, where elephants continued to be wary of and aggressive to humans long after the cessation of intensive poaching during the country's 15-year civil war (Poole & Granli, 2018).

Elephant movement and activity patterns have implications for foraging, survival and reproduction. The costs of risk-induced shifts in movement and energy acquisition activities are not fully understood, nor do we understand if risk-induced activity shifts result in a compression of the activity budget of elephants. With the caveat that camera traps are not appropriate for estimating activity budgets, we did find that the active period of elephants was compressed in the high-risk sites relative to the low-risk site. If risk-induced shifts in the timing and total time available for energy acquisition activities affect maternal food intake by limiting foraging duration or efficiency, this could potentially result in early calf mortality, poor growth rates and reduced lifetime fitness, as has been observed for droughts (Lee et al., 2013). Mean body condition scores for adult female elephants were lower in the three high-risk sites than in the low-risk site, but females in all four sites had normal body condition overall (Table S9). We encourage other studies to explore the impact of activity shifts on condition by optimising camera placement for body condition

assessment. In addition, increased nocturnal activity in response to risk potentially exposes elephant calves to greater predation risk, as we found greater overlap in the active periods of elephants and lions in the high-risk sites than in the low-risk site (Figure S14).

Human activities can profoundly influence elephant society, and the impacts of humans extend beyond direct effects on elephant population size and structure. Our study indicates that anthropogenic risk affects elephant decisions about when they move, when they forage and access water sources, how they use roads and whom they associate with, resulting in potential 'indirect' impacts on survival and reproduction. Importantly, however, our findings suggest that human presence in the form of tourism can contribute to making areas safer for elephants (e.g., Beale et al., 2018; Smit et al., 2017). Furthermore, the ability of elephants to make behavioural adjustments in response to risk might allow them to persist in increasingly human-modified landscapes. Understanding the broader impacts of human activities on elephants can help to design conservation strategies informed by elephant behaviour, movement decisions and social requirements.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Stirling Online Research Repository (STORRE) at <http://hdl.handle.net/11667/182> and <http://hdl.handle.net/11667/183>.

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REFERENCES

Adams, T. S. F., Leggett, K. E. A., Chase, M. J., & Tucker, M. A. (2022). Who is adjusting to whom?: Differences in elephant diel activity in wildlife corridors across different human-modified landscapes. *Frontiers in Conservation Science*, 3, 872472. <https://doi.org/10.3389/fcsc.2022.872472>

- Allen, C. R., Brent, L. J., Motsentwa, T., Weiss, M. N., & Croft, D. P. (2020). Importance of old bulls: Leaders and followers in collective movements of all-male groups in African savannah elephants (*Loxodonta africana*). *Scientific Reports*, 10(1), 1–9.
- Barnes, R. F. W. (1983). Elephant behaviour in a semi-arid environment. *African Journal of Ecology*, 21(3), 185–196.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bates, L. A., Sayialel, K. N., Njiraini, N. W., Moss, C. J., Poole, J. H., & Byrne, R. W. (2007). Elephants classify human ethnic groups by odor and garment color. *Current Biology*, 17(22), 1938–1942.
- Beale, C. M., Hauenstein, S., Mduma, S., Frederick, H., Jones, T., Bracebridge, C., Maliti, H., Kija, H., & Kohi, E. M. (2018). Spatial analysis of aerial survey data reveals correlates of elephant carcasses within a heavily poached ecosystem. *Biological Conservation*, 218, 258–267.
- Blake, S., Deem, S. L., Strindberg, S., Maisels, F., Momont, L., Isia, I.-B., Douglas-Hamilton, I., Karesh, W. B., & Kock, M. D. (2008). Roadless wilderness area determines forest elephant movements in The Congo Basin. *PLoS One*, 3(10), e3546.
- Boult, V. L., Sibly, R. M., Quaife, T., Fishlock, V., Moss, C., & Lee, P. C. (2019). Modelling large herbivore movement decisions: Beyond food availability as a predictor of ranging patterns. *African Journal of Ecology*, 57(1), 10–19.
- Breuer, T., Maisels, F., & Fishlock, V. (2016). The consequences of poaching and anthropogenic change for forest elephants. *Conservation Biology*, 30(5), 1019–1026.
- Buchholtz, E. K., Spragg, S., Songhurst, A., Stronza, A., McCulloch, G., & Fitzgerald, L. A. (2021). Anthropogenic impact on wildlife resource use: Spatial and temporal shifts in elephants' access to water. *African Journal of Ecology*, 59(3), 614–623.
- Chamaillé-Jammes, S., Mtare, G., Makuwe, E., & Fritz, H. (2013). African elephants adjust speed in response to surface-water constraint on foraging during the dry-season. *PLoS One*, 8(3), e59164.
- Chiyo, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J., & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. *Animal Behaviour*, 81(6), 1093–1099.
- Chiyo, P. I., Wilson, J. W., Archie, E. A., Lee, P. C., Moss, C. J., & Alberts, S. C. (2014). The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants. *Behavioral Ecology*, 25(6), 1494–1504.
- Galanti, V., Preatoni, D., Martinoli, A., Wauter, L. A., & Tosi, G. (2006). Space and habitat use of the African elephant in the Tarangire-Manyara ecosystem, Tanzania: Implications for conservation. *Mammalian Biology*, 71(2), 99–114.
- Gaynor, K. M., Branco, P. S., Long, R. A., Gonçalves, D., Granli, P., & Poole, J. (2018). Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*). *African Journal of Ecology*, 56(4), 872–881.
- Gessner, J., Buchwald, R., & Wittemyer, G. (2014). Assessing species occurrence and species-specific use patterns of Bais (forest clearings) in Central Africa with camera traps. *African Journal of Ecology*, 52(1), 59–68.
- Gobush, K. S., Edwards, C. T. T., Balfour, D., Wittemyer, G., Maisels, F., & Taylor, R. D. (2021). *Loxodonta africana*. The IUCN Red List of Threatened Species 2021: eT181008073A181022663.
- Goldenberg, S. Z., Douglas-Hamilton, I., Daballen, D., & Wittemyer, G. (2017). Challenges of using behavior to monitor anthropogenic impacts on wildlife: A case study on illegal killing of African elephants. *Animal Conservation*, 20(3), 215–224.
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated landscape mosaic. *Animal Conservation*, 12(5), 445–455.

- Granados, A., Weladji, R. B., & Loomis, M. R. (2012). Movement and occurrence of two elephant herds in a human-dominated landscape, the Benoue wildlife conservation area. Cameroon. *Tropical Conservation Science*, 5(2), 150–162.
- Guy, P. R. (1976). Diurnal activity patterns of elephant in the Sengwa area, Rhodesia. *African Journal of Ecology*, 14(4), 285–295.
- Ihwagi, F. W., Thouless, C., Wang, T., Skidmore, A. K., Omondi, P., & Douglas-Hamilton, I. (2018). Night-day speed ratio of elephants as indicator of poaching levels. *Ecological Indicators*, 84, 38–44.
- Jones, T., Cusack, J. J., Pozo, R. A., Smit, J., Mkuburo, L., Baran, P., Lobora, A., Mduma, S., & Foley, C. (2018). Age structure as an indicator of poaching pressure: Insights from rapid assessments of elephant populations across space and time. *Ecological Indicators*, 88, 115–125.
- Kangwana, K. F. (1993). *Elephants and maasai: Conflict and conservation in Amboseli, Kenya*. [Doctoral Dissertation, University of Cambridge].
- Katugaha, H. I. E., de Silva, M., & Santiapillai, C. (1999). A long-term study on the dynamics of the elephant (*Elephas maximus*) population in Ruhuna National Park, Sri Lanka. *Biological Conservation*, 89(1), 51–59.
- Lee, P. C., Bussière, L. F., Webber, C. E., Poole, J. H., & Moss, C. J. (2013). Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (*Loxodonta africana*). *Biology Letters*, 9(2), 20130011.
- Lee, P. C., & Moss, C. J. (1999). The social context for learning and behavioural development among wild African elephants. In H. O. Box, K. R. Gibson, & A. K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 102–125). Cambridge University Press.
- Lee, P. C., & Moss, C. J. (2014). African elephant play, competence and social complexity. *Animal Behavior and Cognition*, 1(2), 144–156.
- Lee, P. C., Poole, J. H., Njiraini, N., Sayialel, C. N., & Moss, C. (2011). Male social dynamics: Independence and beyond. In C. J. Moss, H. Croze, & P. C. Lee (Eds.), *The Amboseli elephants: A long-term perspective on a long-lived mammal*. University of Chicago Press.
- Leggett, K. (2009). Diurnal activities of the desert-dwelling elephants in northwestern Namibia. *Pachyderm*, 45, 20–33.
- Lewis, D. M. (1986). Disturbance effects on elephant feeding: Evidence for compression in Luangwa Valley, Zambia. *African Journal of Ecology*, 24(4), 227–241.
- Lüdecke, D. (2020). *sjPlot: Data visualization for statistics in social science*. R package version 2.8.5. <https://CRAN.R-project.org/package=sjPlot>
- McComb, K., Shannon, G., Sayialel, K. N., & Moss, C. (2014). Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. *Proceedings of the National Academy of Sciences*, 111(14), 5433–5438.
- Mole, M. A., Rodrigues D'Araujo, S., Van Aarde, R. J., Mitchell, D., & Fuller, A. (2016). Coping with heat: Behavioural and physiological responses of savanna elephants in their natural habitat. *Conservation Physiology*, 4(1), cow044.
- Mramba, R. P., Andreassen, H. P., Mlingi, V., & Skarpe, C. (2019). Activity patterns of African elephants in nutrient-rich and nutrient-poor savannas. *Mammalian Biology*, 94, 18–24.
- Mtahiko, M. G. G. (2007). Tanzania wilderness areas. In A. Watson, J. Sproull, & L. Dean (Eds.), *Science and stewardship to protect and sustain wilderness values: Eighth World Wilderness Congress symposium*. September 30–October 6, 2005; Anchorage, AK. Proceedings RMRS-P-49 (Vol. 49, pp. 239–243). US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Nouvellet, P., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2012). Noisy clocks and silent sunrises: Measurement methods of daily activity pattern. *Journal of Zoology*, 286(3), 179–184.
- Poole, J. H. (1989). The effects of poaching on the age structures and social and reproductive patterns of selected East African elephant populations. In *The ivory trade and the future of the African elephant Volume II technical reports*. The Ivory Trade Review Group.
- Poole, J. H., & Granli, P. (2017). *ElephantVoices 2016 report to the Gorongosa restoration project*. ElephantVoices.
- Poole, J. H., & Granli, P. (2018). *ElephantVoices 2017 report to the Gorongosa restoration project*. ElephantVoices.
- Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, 45(1), 218–227.
- Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3), 322–337.
- Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5(11), 1170–1179.
- Schlossberg, S., Chase, M. J., & Sutcliffe, R. (2019). Evidence of a growing elephant poaching problem in Botswana. *Current Biology*, 29(13), 2222–2228.
- Searle, C. E., Smit, J., Strampelli, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., Loveridge, A. J., & Dickman, A. J. (2021). Leopard population density varies across habitats and management strategies in a mixed-use Tanzanian landscape. *Biological Conservation*, 257, 109120.
- Sitati, N. W., Walpole, M. J., Smith, R. J., & Leader-Williams, N. (2003). Predicting spatial aspects of human–elephant conflict. *Journal of Applied Ecology*, 40(4), 667–677.
- Smit, J., Pozo, R. A., Cusack, J. J., Nowak, K., & Jones, T. (2019). Using camera traps to study the age–sex structure and behaviour of crop-using elephants *Loxodonta africana* in Udzungwa Mountains National Park, Tanzania. *Oryx*, 53(2), 368–376.
- Smit, J. B. (2021a). *Elephant event counts, Ruaha-Rungwa 2018–2019*. Stirling Online Research Repository (STORRE). [Dataset]. <http://hdl.handle.net/11667/183>
- Smit, J. B. (2021b). *Elephant camera trap detection events, Ruaha-Rungwa 2018–2019*. Stirling Online Research Repository (STORRE). [Dataset]. <http://hdl.handle.net/11667/182>
- Smit, J. B., Mkuburo, L., Sembosi, S., Lihwa, F., Banham, P., & Jones, T. (2017). Using hotspot analysis to investigate seasonal and sex-based differences in the distribution of elephants (*Loxodonta africana*) in Ruaha National Park, Tanzania. In *Proceedings of the Tanzania Wildlife Research Institute (TAWIRI) conference Arusha* (7 December 2017). Tanzania Wildlife Research Institute.
- Srinivasaiah, N., Kumar, V., Vaidyanathan, S., Sukumar, R., & Sinha, A. (2019). All-male groups in Asian elephants: A novel, adaptive social strategy in increasingly anthropogenic landscapes of southern India. *Scientific Reports*, 9(1), 1–11.
- Strampelli, P., Henschel, P., Searle, C. E., Macdonald, D. W., & Dickman, A. J. (2022). Habitat use of and threats to African large carnivores in a mixed-use landscape. *Conservation Biology*, e13943. <https://doi.org/10.1111/cobi.13943>
- Sukumar, R., & Gadgil, M. (1988). Male–female differences in foraging on crops by Asian elephants. *Animal Behaviour*, 36(4), 1233–1235.
- TAWIRI. (2016). *Wildlife census in Ruaha-Rungwa ecosystem, dry season, 2015*. Tanzania Wildlife Research Institute.
- TAWIRI. (2019). *Aerial wildlife survey of large animals and human activities in the Katavi-Rukwa and Ruaha-Rungwa ecosystems, dry season, 2018*. Tanzania Wildlife Research Institute.
- Thouless, C. R., Dublin, H. T., Blanc, J. J., Skinner, D. P., Daniel, T. E., Taylor, R. D., Maisels, F., Frederick, H. L., & Bouche, P. (2016). African elephant status report 2016: An update from the African elephant database. In J. J. Blanc & R. F. Barnes (Eds.), *Occasional paper series of the IUCN species survival commission*, No. 60. IUCN/SSC Africa elephant specialist group, IUCN.
- Wasser, S. K., Brown, L., Mailand, C., Mondol, S., Clark, W., Laurie, C., & Weir, B. S. (2015). Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science*, 349(6243), 84–87.

- Wilkie, R., & Douglas-Hamilton, I. (2018). High-resolution tracking technology reveals distinct patterns in nocturnal crop raiding behaviour of an African elephant (*Loxodonta africana*) in Amboseli, Kenya. *Pachyderm*, 59, 41–48.
- Wittemyer, G., Getz, W. M., Vollrath, F., & Douglas-Hamilton, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: A contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, 61(12), 1919–1931.
- Wittemyer, G., Keating, L. M., Vollrath, F., & Douglas-Hamilton, I. (2017). Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. *Ecography*, 40(5), 598–605.
- Wittemyer, G., Northrup, J. M., Blanc, J., Douglas-Hamilton, I., Omondi, P., & Burnham, K. P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences*, 111(36), 13117–13121.
- Wyatt, J. R., & Eltringham, S. K. (1974). The daily activity of the elephant in the Rwenzori National Park, Uganda. *African Journal of Ecology*, 12(4), 273–289.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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