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Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*)

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Abstract

As the human footprint expands worldwide, people and wildlife are coming into greater contact, and areas of human activity may be simultaneously associated with risk and reward for animals. To avoid human threats while exploiting opportunities, animals may adjust their spatiotemporal activity, using areas of anthropogenic disturbance at night when people are less active. We combined four camera trap datasets from Mozambique's Gorongosa National Park to evaluate the effects of roads and settlement on diel activity patterns of elephants (*Loxodonta africana*). We found high rates of elephant activity along the boundary of the park, where elephants can access cultivated crops, and along roads, which serve as movement corridors. However, elephants restricted their activity to the night and crepuscular periods in these areas of human disturbance, seeking refuge in the interior of the park away from roads and settlements during the day. Our findings suggest that a history of killing and antagonism has instilled a fear of humans in this elephant population, with implications for research, tourism and human–elephant coexistence. Our study highlights the utility of camera traps in monitoring human–wildlife conflict and habituation and demonstrates the value of integrating disparate camera trap datasets for comparative analyses on landscape or even continental scales.

Résumé

Alors que la présence humaine s'étend dans le monde entier, les hommes et la faune sauvage ont des contacts de plus en plus fréquents, et les zones d'activités humaines peuvent être associées, pour les animaux, aussi bien à des dangers qu'à des opportunités. Pour éviter les menaces tout en exploitant ces possibilités, les animaux doivent ajuster leurs activités spatio-temporelles en fréquentant les zones de perturbation humaine de nuit, quand les hommes sont moins actifs. Nous avons combiné quatre sets de données provenant de pièges photographiques dans le Parc National de Gorongosa, au Mozambique, pour évaluer les effets des routes et des installations sur les schémas d'activité journalière des éléphants *Loxodonta africana*. Nous avons trouvé un fort taux d'activité des éléphants le long de la limite du parc, où les éléphants peuvent accéder aux cultures, et le long des routes qui servent de corridors de déplacement. Cependant, les éléphants limitaient leurs activités à la nuit et au crépuscule dans les zones de perturbations humaines et cherchaient refuge à l'intérieur du parc, loin des routes et des installations, pendant la journée. Nos résultats laissent penser que des massacres ou des heurts passés ont instillé la crainte des hommes chez cette population d'éléphants, ce qui a des implications pour la recherche, le tourisme et la coexistence hommes-éléphants. Notre recherche montre l'utilité des pièges photographiques pour le suivi des conflits et pour l'habituation hommes-faune sauvage et prouve qu'il est utile d'intégrer différents sets de données de pièges photographiques dans des analyses comparatives à l'échelle de paysages, voire de continents.

KEYWORDS

activity pattern, diel activity, human–wildlife conflict, Mozambique, roads

1 | INTRODUCTION

As the human population grows exponentially and our footprint expands across the globe, people and wildlife are increasingly forced to share space (Hoare & Du Toit, 1999; Jones et al., 2018; Venter et al., 2016). Conservation efforts have bolstered wildlife populations in many African protected areas (Craigie, Baillie, Balmford, & Carbone, 2010), and human development interventions outside of protected areas have promoted the growth of human populations (Wittemyer, Elsen, Bean, Burton, & Brashares, 2008). People and wild animals are therefore coming into contact more frequently in these interfaces along protected areas, and encounters between humans and wildlife can have important implications for animal behaviour, human–wildlife conflict, protected areas management and conservation (Dickman, 2010; Tucker et al., 2018). By simultaneously monitoring the use of both natural and anthropogenic landscapes by wildlife, we can better understand the impacts of humans on wildlife populations and manage for coexistence within shared spaces.

Wild animals often perceive humans as a threat and therefore seek to minimize encounters with people (Frid & Dill, 2002). This perception may sometimes be precipitated by actual risks, such as hunting or persecution (Ndaimani, Murwira, & Kativu, 2014; Setsaas, Holmern, Mwakalebe, Stokke, & Roskaft, 2007). However, animals may also exhibit generalized anti-predator strategies in response to human activity (e.g., tourism, settlement), especially if they have had previous negative experiences with humans (Pangle & Holekamp, 2010; Stankowich, 2008). Despite such perceptions of risk, animals may also seek out areas of human activity that provide accessible or high-quality food resources such as crops, livestock or food waste (Chiyo & Cochrane, 2005; Treves, 2009). Thus, animals sometimes experience trade-offs between forage and perceived risk wherein areas of anthropogenic disturbance are associated with both threats from people and high-quality resources (Brown, Laundré, & Gurung, 1999; Chiyo et al., 2011).

Where wild animals are unable to avoid people in space due to expansive human activity, and especially when animals are drawn to anthropogenic resources, they may instead avoid people in time (Oriol-Cotterill, Macdonald, Valeix, Ekwanga, & Frank, 2015; Rasmussen & Macdonald, 2011). There is growing evidence that mammal species across the planet adjust their diel activity patterns in response to human activities (which occur largely during daylight hours) by becoming more nocturnal (Gaynor, Hojnowski, Carter, & Brashares, 2018). For wide-ranging and behaviourally plastic species, such adjustments may occur at relatively fine-scale spatiotemporal scales (Carter, Shrestha, Karki, Pradhan, & Liu, 2012), where during the daytime animals seek out areas of lower human activity and at night move into human-dominated areas (Barnes et al., 2007; Graham, Hamilton, Adams, & Lee, 2009; Gunn et al., 2014; Valeix et al., 2009).

African elephants (*Loxodonta africana*) are an ideal species for examining the effects of human activity on spatiotemporal behaviour because of their learning ability, flexible activity patterns, large home range sizes and propensity to exploit anthropogenic resources (Boettiger, Wittemyer, Starfield, & Volrath, 2011; Fullman et al., 2017). Elephants also face diverse threats from humans, including poaching (Ripple et al., 2015; Wasser, 2015; Wittemyer et al., 2014). While some elephant populations can take refuge in protected areas, many also forage in human-dominated environments (Scholssberg, Chase, & Griffin, 2018). However, elephants often leave park boundaries in search of additional resources, resulting in measurable changes in movement patterns (Cook, Henley, & Parrini, 2015; Hunninck et al., 2017) and higher stress levels (Hunninck et al., 2017). The presence of elephants outside of protected areas is frequently a source of human–wildlife conflict in the form of crop damage and threats to safety, which can disrupt human livelihoods and lead to retaliation against elephants (Chase et al., 2016; Chiyo, Cochrane, Naughton, & Basuta, 2005; Graham, Notter, Adams, & Lee, 2010; Hoare, 2000). Elephants are an important flagship species for conservation and are a keystone species in savannah ecosystems (Coppolillo, Gomez, Maisels, & Wallace, 2003; Coverdale et al., 2016; Pringle, 2008). Nonetheless, elephants are also declining across the African continent (Chase et al., 2016). As the human population grows throughout Africa, particularly in areas with high elephant populations (de Boer et al., 2013), it is critical to expand our toolkit for understanding how human disturbance influences the behaviour of this important species. With fine-scale information on the spatiotemporal responses of elephants to human activities, conservation practitioners can better plan for coexistence (Songhurst, McCullouch, & Coulson, 2016).

We used data from multiple camera trap studies throughout Gorongosa National Park in Mozambique to quantify spatiotemporal patterns of elephant activity in close proximity to humans. Camera trap studies have become increasingly common for continuous monitoring and for observational and experimental research, as the cost decreases and software for automating analysis of images becomes more readily available (Burton et al., 2015; Steenweg et al., 2017). Moreover, because camera traps capture all species that pass by (including people) at all times of day, they provide a rich source of data, often beyond the initial study focus (Caravaggi, 2017). Our study was opportunistic in that we took advantage of four unique camera trap projects designed for different monitoring and research purposes by different research teams in the park. The distinct goals of each of these projects led to differences in study design and camera placement, which inadvertently facilitated a larger-scale comparative study.

Our specific objectives were to use the camera trap data to examine the effects of (a) settlement and agriculture just outside of the park and (b) roads used for tourism and research inside the park on elephant diel activity patterns. We expected elephants to be more active in the interior areas of the park during the day and show increased presence in human-dominated areas along the boundary of the park and in the park's buffer zone at night to take advantage of cultivated crops. Due to the recent history of violence against elephants within the national park, both avoidance and aggressive behaviour are common responses to vehicles across elephant families (Poole & Granli, 2018). Therefore, at a finer spatial scale, we expected elephants to avoid the park's roads more strongly during the day, when potential vehicle encounter rates are higher. By elucidating elephant activity patterns in human-altered landscapes, our research highlights the implications of behavioural plasticity for conservation and human–wildlife conflict and coexistence.

2 | METHODS

2.1 | Study site

Gorongosa National Park (GNP) is located in Sofala Province in central Mozambique, at the southern extent of the Great Rift Valley (Latitude: −18.82, Longitude: 34.50). The park encompasses 3,770 km^2 and supports a diversity of large mammal species that occupy a range of habitat types. The study area is characterized by *Acacia–Combretum* savannah woodlands and floodplain grasslands (Stalmans & Beilfuss, 2008). Mean annual rainfall in the valley of GNP is 700–900 mm, with a rainy season that runs from November to March and a dry season from April to October (Stalmans & Beilfuss, 2008). Lake Urema is located in the centre of the park and provides a permanent water source throughout the year, and inundating the floodplains of the valley during the wet season. There are several perennial rivers in GNP, including the Pungue River, which forms the southern border of the park.

During Mozambique's civil war (1977–1992), wildlife populations, including elephants, declined dramatically due to killing for meat and ivory (Daskin, Stalmans, & Pringle, 2016; Vines, 1991). Prior to the war, the park was estimated to have ~2,200 elephants (Tinley, 1977), reduced to <200 individuals by 1994 (Poole & Granli, 2017). Following the end of war, renewed investment in wildlife management has enabled populations to recover, largely through natural population growth. In particular, a public–private partnership between the government of Mozambique and the Gorongosa Restoration Project (Stalmans & Peel, 2016) has facilitated considerable progress towards returning GNP to its former status as one of the most diverse parks in the world. The current elephant population in GNP is estimated to be between 567 (aerial total count, Stalmans & Peel, 2016) and 825 individuals (based on individual registration of adults and a mean ratio of 2.4:1 of immatures to adult female; Poole & Granli, 2018). As a result of their recent history of violence with humans, elephant family groups in GNP exhibit a high rate of aggressive behaviour towards people and are fearful of both humans and vehicles, despite little evidence of elephant poaching at present (Poole & Granli, 2017; 2018).

A variety of human activities occur within GNP, centred on the park's core road network. There is a small but growing tourism operation based in Chitengo, the park's headquarters, and tourist vehicles frequently travel throughout the park for wildlife viewing (multiple times per day during most of the year). Despite their aggression, elephants are a sought-after species for viewing, and tourist vehicles thus regularly seek out areas of high elephant activity. There is also a large amount of research activity in the park, and researchers use the road network as they travel around the park to collect samples, make observations of animals and set up experiments. GNP's park rangers also use the road network, although most of their patrols are in remote, off road areas based out of the park's ranger outposts. The park gates are only open from sunrise to just after sunset, so the vast majority of vehicle activity is restricted to daytime and dusk, with the exception of some ranger activity.

GNP is surrounded by a 5,333 km^2 buffer zone, where approximately 200,000 subsistence crop farmers currently reside (Ministério da Terra, 2016). The buffer zone is a mixed-use area, where people are permitted to grow crops, harvest natural resources, raise livestock and conduct controlled burns, along with other livelihood activities. Hunting for bushmeat and trophies is prohibited, and there are no roads with vehicle traffic in the buffer zone study area. Importantly, when asked about the problems they face living close to the national park, residents of the buffer zone overwhelmingly indicate that the primary issue is crop damage by elephants (P. Branco, unpublished data). Most crop foraging occurs along the park's southern border, where GNP's elephants are concentrated (Poole & Granli, 2017; Stalmans & Peel, 2016).

2.2 | Data collection

As scientific activity in GNP has grown, several research projects have deployed camera traps to accomplish various monitoring and research objectives. We combined camera trap data from four projects to quantify elephant activity patterns in relation to human disturbance (Table 1). These projects included a systematic camera grid,

TABLE 1 Summary of camera trap data collected by the four projects included in our analyses

	Elephant voices	Gorongosa lion project	Grid	Human–elephant coexistence
Study purpose	Elephant identification and monitoring	Monitoring of lions and other carnivores	Systematic large mammal survey	Elephant crop foraging and response to deterrents
Camera placement	On elephant river crossing trails	On roads	Game trails off road	On elephant river crossing trails
Study location	Park boundary (park side)	Park interior	Park interior	Park boundary (buffer zone side)
No. of camera sites	5	21	60	13
No. of camera sites with elephant detections	5 (100%)	20 (100%)	60 (100%)	11 (87%)
Study period	May 2015–November 2016 (seasonal)	August 2013–May 2015 (seasonal)	June 2016–July 2017 (continuous)	August 2017–December 2017 (continuous)
Total camera trap-nights	803	2,290	15,599	1,353
No. of elephant detection events (>15 min apart)	406	421	1,022	134

the ElephantVoices project, the Human-Elephant Coexistence (HEC) project and the Gorongosa Lion Project (GLP).

The systematic camera grid (5-km^2 grid cells) was set up to monitor year-round spatiotemporal patterns of large mammal activity and determine landscape-level correlates of occupancy in the core area of the park. To maximize animal detections, cameras faced open areas or small game trails with signs of animal activity, all off of roads.

The ElephantVoices project used cameras to identify individual elephants and groups along the southern boundary of the park and to look at patterns of access from the park to the Pungue River and buffer zone. Camera traps were deployed at five sites on elephant trails off of the Dingue–Dingue Road, which follows the southern boundary of the park. This road is occasionally used by park vehicles, but seldom by tourist or researcher vehicles and therefore has very little vehicle traffic.

The HEC project was aimed at understanding and mitigating crop damage by elephants. HEC cameras were located at 13 elephant crossing locations (>200 m apart) in the park's buffer zone between the Pungue River and agricultural fields. There were 1–3 cameras at each crossing location (<100 m from each other; combined for analysis). Although some camera traps were located near deterrents (e.g., beehive fences) that were constructed halfway through the study period, the cameras were placed in such a way that they photographed the elephants before they encountered these deterrents. Thus, the mitigation experiment does not appear to have affected diel activity patterns, although cameras in that project might have experienced reduced detection rates if elephants were less likely to return to those crossing locations after encountering deterrents.

Finally, the Gorongosa Lion Project used camera traps opportunistically placed on roads to monitor the recovery of the park's lion population. For our analysis of GLP data, we used images from the 21 camera traps that faced roads. All GLP images were uploaded to WildCam Gorongosa, a Zooniverse citizen science platform through which untrained volunteers from around the world identify the species in camera trap images. We downloaded all image records that had been classified as an elephant by at least one of 25 volunteers (n = 6,833). We reviewed all images classified as an elephant by 10% or more of the users and excluded all images that were not elephants.

In total, data were collected from 2013 through 2017, although not all projects spanned this entire period. All projects used Bushnell TrophyCam camera traps with infrared sensors set to be triggered by motion, and detection distances and habitat types were similar across data sets. We reviewed all photographs to identify those with elephants (GLP photographs were first screened by citizen scientists). For all projects, camera traps were deployed within the park's road network in the southern region of GNP, bounded by Lake Urema on the north and the buffer zone in the south (Figure 1). This area of the park corresponds to the area of highest human activity and highest elephant densities, as determined from elephant sightings during seven dry season aerial surveys (2010–2016) that covered all or most of the park area (Stalmans & Peel, 2016). Despite the concentration of human infrastructure, elephants remain in this area as it provides prime habitat and may have historically experienced lower levels of illegal poaching.

2.3 | Data analysis

For each of the four data sets, we identified each independent observation of elephants, defined as an image taken >15 min from any other image. We chose 15 min based on expert assessment; extensive visual observations of elephant groups and examination of camera trap footage indicated that elephants in the same known group were rarely separated by >15 min at a given location. We considered the observation time to be the time of the first photograph. Combining photographs limited pseudoreplication and allowed us to compare relative activity rates across projects, given differences in the number of photographs taken during each trigger event and the delay time between trigger events.

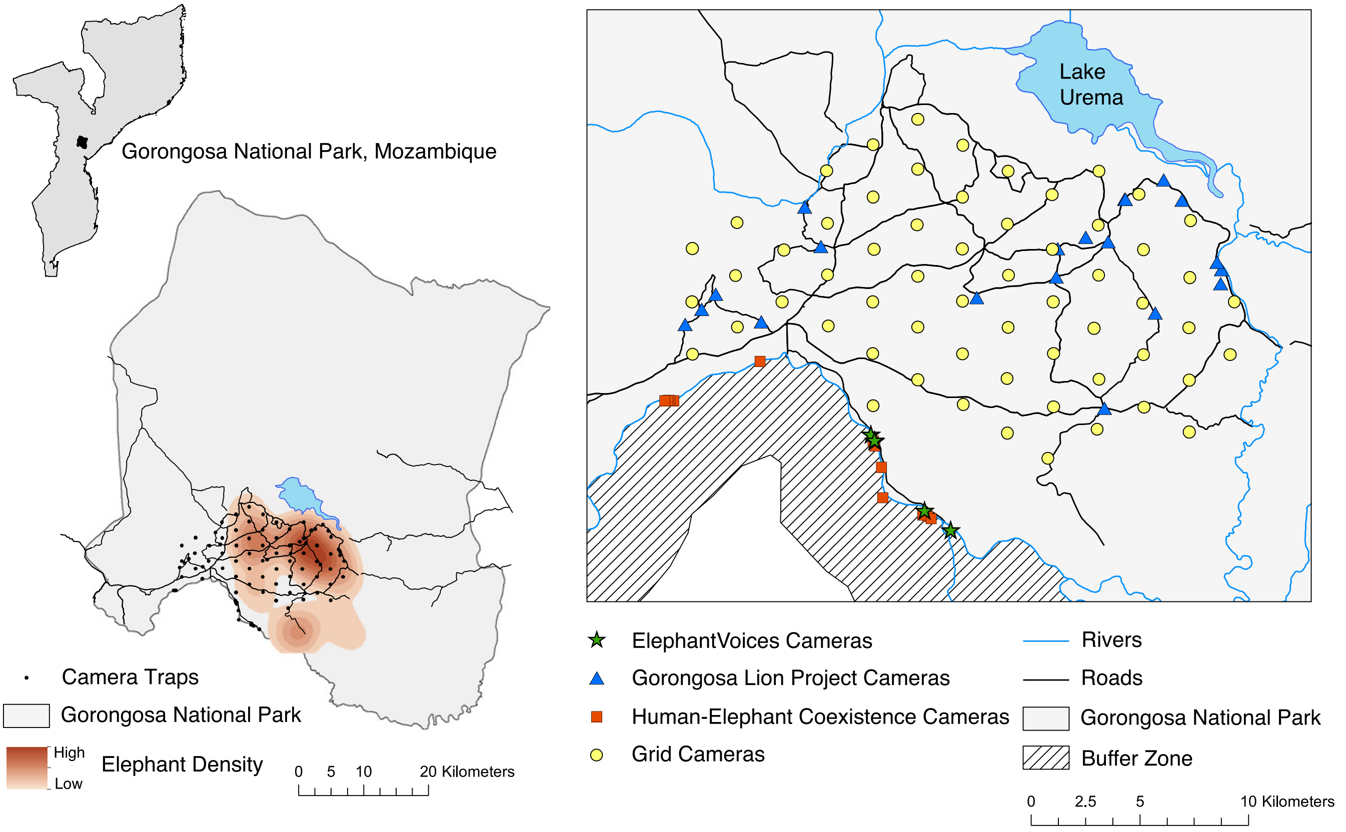

FIGURE 1 Map of the study area in the southern portion of Gorongosa National Park, Mozambique, showing locations of camera traps from all four projects in relation to roads and the park boundary. The smoothed kernel density of elephants in the park was calculated in ArcGIS using the location of elephants (weighted by group size) recorded during seven aerial surveys of the park from 2000 to 2016, during the dry season (208 records of 1,932 elephants) [Colour figure can be viewed at wileyonlinelibrary.com]

To quantify differences in elephant activity between the core and exterior of the park, we compared the grid dataset (interior) with the combined ElephantVoices and HEC datasets (edge). To evaluate the effects of roads on elephant diel activity patterns, we compared a subset of the grid dataset (off roads) with the GLP dataset (on roads). To control for non-random placement of GLP cameras across habitat types and areas of the park, we included only the 13 grid cameras (of the 60 cameras) that were located within the same 5-km^2 grid cell as a GLP camera.

We used kernel density estimation to model diel activity patterns of elephants, as described by Ridout and Linkie (2009). We converted the times of each observation to radians to account for the circularity of the temporal data. To account for seasonal differences in sunset and sunrise time, we scaled the times so that $\pi/2$ corresponded to sunrise and $3\pi/2$ corresponded to sunset. Based on the distribution of observation across the 24-hr cycle, we generated a smoothed non-parametric kernel density distribution of elephant activity for each project.

We compared pairs of density distributions (interior versus edge of park, on versus off road) by calculating the temporal overlap value, d-hat. The value d-hat represents the area under the curve formed by taking the minimum of the two activity density distributions at each time point. A value of 0 indicates no temporal overlap, whereas a value of 1 indicates complete overlap. We used the d-hat4 formula for estimating overlap, as recommended by Ridout and Linkie (2009) for sample sizes >50, and calculated an approximate 95% bootstrap confidence intervals. We used the *overlap* package in R for these analyses (Ridout & Linkie, 2009). Although there was an uneven survey effort across projects, the sample size was >100 detections for all datasets and considered to be sufficiently large for these analyses (Ridout & Linkie, 2009).

We used counts of elephant observations at each of the 99 camera sites to further examine patterns of elephant activity in response to human disturbance. We determined the time period of each observation based on the sunrise and sunset times on the day of the observation. We defined four diel time periods: dawn (30-min period before sunrise), day (sunrise to sunset), dusk (30-min period after sunset) and night (between dusk and dawn). We also combined dawn and dusk detections to determine the total number of crepuscular detections.

Based on this count data, we calculated a Relative Activity Index (RAI) for elephants at each camera. Daily RAI (RAI_D) was equal to the total number of observations divided by the number of trap-nights (based on the dates of deployment). We calculated mean RAI_D for each treatment (interior versus edge of park, on versus off road). We also calculated an hourly RAI (RAI_H) for each of the four diel time periods, defined as the number of independent detections per trap-hour (day: 12 hr, night: 11 hr; dawn and dusk: 0.5 hr each).

We used generalized linear models to examine the effects of roads and settlement on elephant observation counts. For all models, we used a negative binomial distribution to account for the overdispersion of the count data. We then used Wald chi-square tests, with the ANOVA function in the *car* R package, to test the significance of the fixed effects on elephant activity (Fox & Weisberg, 2011). To compare overall numbers of elephant detections across projects and human disturbances, we ran separate models with fixed effects of road treatment (on versus off) and settlement (park interior versus boundary), in which the dependent variable was the overall count of elephant observations, and the unit of analysis was the camera site. We controlled for differences in camera trap sampling effort by including effort (number of trap-nights) as an offset in the model. To examine temporal differences, we also ran separate models for each project and treatment, in which we included time period as a fixed effect, camera site as a random effect and effort (number of trap-hours) as an offset.

We did not conduct any spatially explicit analyses, given the differences in spacing of the camera traps. While the grid cameras were systematically deployed and >2 km apart, the other cameras were all opportunistically placed.

3 | RESULTS

The four projects generated a total of 1,983 independent elephant detection events, over a total of 19,904 trap-nights. Elephants were detected at 93 of the 99 camera sites. The number of elephant observations differed across the four datasets ($\chi^2 = 47$, $df = 3$, $p < 0.0001$, Figure S1). Elephant RAI_D (mean ± *SD*) was highest for the ElephantVoices project (0.47 ± 0.17), followed by the GLP (0.23 ± 0.27) and the HEC cameras (0.10 ± 0.08). RAI_D was lowest on the grid cameras (0.06 ± 0.09).

Distinct diel patterns of activity were evident among elephants in each of the four datasets (Figure 2). Elephant activity was higher at night and during crepuscular periods than during the day for the ElephantVoices and HEC datasets (EV $\chi^2 = 175$, $df = 2$, $p < 0.0001$; HEC $\chi^2 = 61$, $df = 2$, $p < 0.0001$), with sharp peaks in activity just after sunset, and less pronounced peaks just before sunrise. In the grid dataset, elephant activity was highest during crepuscular periods, intermediate during the day and lowest at night ($\chi^2 = 37$, $df = 2$, $p < 0.0001$). Elephant activity at GLP cameras was highest during crepuscular periods and the night and lower during the day, though there was no significant difference between time periods ($\chi^2 = 5$, $df = 2$, $p = 0.09$).

Inside the park, elephants were active throughout the 24 period, though there were significant differences across diel periods with most activity occurring during the day ($\chi^2 = 37$, $df = 2$, $p < 0.0001$). In contrast, elephants showed crepuscular activity patterns at the park edge, with significant differences across diel periods ($\chi^2 = 233$, $df = 2$, $p < 0.0001$). The overlap coefficient of the activity distributions of elephants in the interior versus the edge of the park was 0.46 (±95% CI 0.40–0.48), representing the percentage of the total area under the activity density curves that is shared by the inside and outside park activity distributions (Figure 3). Mean RAI was higher at the boundary of the park (0.203 ± *SD* 0.200) than in the interior of the park (0.062 ± *SD* 0.087; Figure 5). There was a significant effect of settlement proximity on elephant observation counts ($\chi^2 = 27$, $df = 1$, $p < 0.0001$).

Elephant diel activity patterns on versus off of roads differed (Figure 4). On roads, elephants showed a peak in activity before sunrise, a reduction in activity during the daytime and an increase in activity again at sunset and into the early hours of the morning, although differences across diel categories were not significant ($\chi^2 = 5$, $df = 2$, $p = 0.09$). Off of roads, elephants were more active during the middle of the day and late afternoon, with significant differences across diel periods ($\chi^2 = 9$, $df = 2$, $p = 0.01$). The overlap coefficient of the activity distributions of elephants on versus off road in the park was 0.79 (95% CI: 0.73–0.84). In the core of the

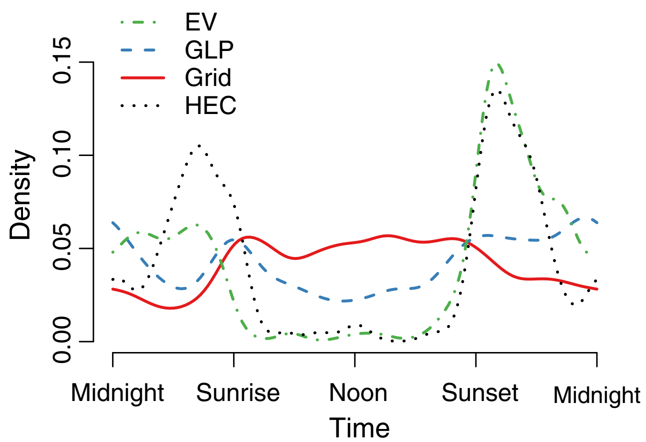

FIGURE 2 Diel distribution of elephant activity for each project [Colour figure can be viewed at wileyonlinelibrary.com]

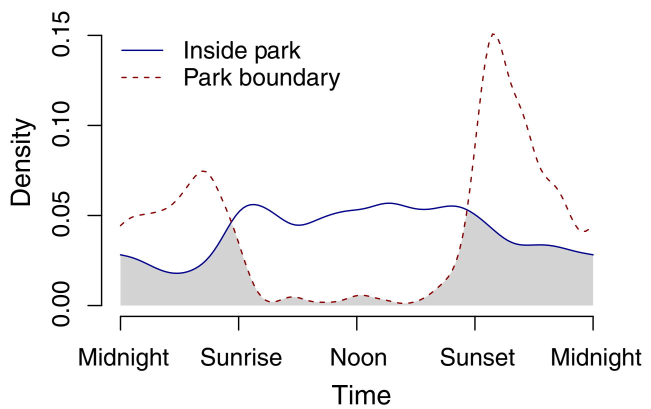

FIGURE 3 Diel distribution of elephant activity inside the park (grid dataset) versus at the park boundary (ElephantVoices and HEC datasets). The grey region shows the overlap between the two distributions, and its area represents the overlap value (d-hat) [Colour figure can be viewed at wileyonlinelibrary.com]

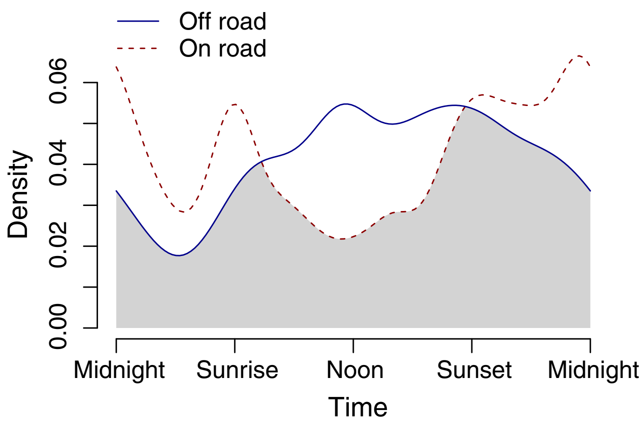

FIGURE 4 Diel distribution of elephant diel activity on roads (GLP dataset) versus off roads (grid data, subset to include only cameras in proximity to GLP cameras) inside Gorongosa National Park. The grey region shows the overlap between the two distributions, and its area represents the overlap value (d-hat) [Colour figure can be viewed at wileyonlinelibrary.com]

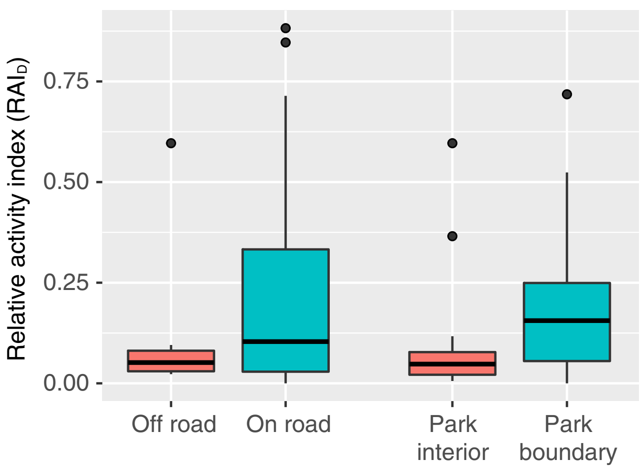

FIGURE 5 The Relative Activity Index of elephants (independent detections per camera trap-night), for cameras off road (subset grid dataset) and on road (GLP dataset), and for cameras inside the park (grid dataset) and at the park boundary (ElephantVoices and HEC datasets). The dark horizontal line indicates the median RAI across camera sites, the boxes represent lower and upper quartiles, and the whiskers represent minima and maxima (excluding outliers, which are shown as points) [Colour figure can be viewed at wileyonlinelibrary.com]

park, there was no significant effect of roads on elephant observation counts (χ^2 = 3, *df* = 1, *p* = 0.09). Mean RAI at cameras on roads was 0.24 (±*SD* 0.29), and mean RAI at cameras off road was 0.10 (±*SD* 0.16; Figure 5).

4 | DISCUSSION

Our findings suggest that elephants in Gorongosa National Park adjust the timing and location of their activity to avoid encounters with vehicles in the park and with people living in the buffer zone. Despite a likely fear of humans, however, this population of elephants did not entirely avoid areas of human disturbance; elephants exploited agricultural areas as food and water sources and used roads as movement corridors. By adjusting the timing of their movements at multiple spatial scales, elephants were able to navigate a landscape of multiple anthropogenic activities and opportunities while minimizing direct contact with people.

Although elephants in the park were more likely to be detected on roads than on trails, our study suggests that they adjusted the timing of their movement on roads to avoid vehicle encounters. We found that elephants were more active during the day than during the night on the grid cameras, which were placed away from roads, whereas elephants were more active at crepuscular and nocturnal periods on the GLP cameras that were placed on the road system. Elephants appear to be reducing their use of roads during areas of peak vehicle traffic, which are restricted to daytime and dusk periods. Such fine-scale temporal avoidance of vehicles has also been observed among Asian elephants (*Elephas maximus*; Katugaha, de Silva, & Santiapillai, 1999). Our finding could also be attributed in part to the non-random distribution of GLP (road) cameras.

Previous studies have reported that elephants avoid roads in places where they experience persecution, such as the Congo Basin, where road avoidance by elephants restricts their habitat access, home range size and movement ability (Blake et al., 2008). The elephant population of GNP was heavily poached during Mozambique's civil war, which may account for their avoidance of vehicles (Poole & Granli, 2018). Many elephants in GNP exhibit distress, flight and aggression in the presence of vehicles, and their response to vehicles has the potential to hinder tourism and elephant research in GNP. There is evidence that some elephants are slowly becoming habituated to the presence of vehicles, and in the assumed absence of direct threats to elephants inside the park, this habituation may continue to increase (Poole & Granli, 2018). The continued use of camera traps throughout GNP will enable us to document and monitor potential changes in behaviour through time, and inform ongoing efforts to habituate the park's elephants to human presence.

Despite their tendency to avoid vehicles, cameras placed on the road system (GLP cameras) still detected similar overall levels of elephant activity than cameras placed off of roads (grid cameras). This suggests that despite perceived risk from vehicles, elephants use low-traffic unpaved roads (Granados, Weladji, & Loomis, 2012) as movement corridors, as has been documented for many other large mammal species (Abrahms et al., 2016). In fact, many of the roads in Gorongosa National Park originated as elephant trails. Elephants sometimes respond vocally to the sound of vehicles (Poole, 2017), doing so in one documented case from up to 3 km away (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005), and, therefore, may choose to reactively avoid vehicles when they encounter them, rather than proactively avoid roads altogether.

Elephants in GNP are far more likely to be active in and around human settlements during the night, when people are generally less active. Our findings are consistent with the results of GPS telemetry studies that found that elephants utilize settled areas most often at night (Cook et al., 2015; Graham et al., 2009) and have relatively higher nocturnal movement speeds in response to poaching (Ihwagi et al., 2018) or human settlement (Galanti, Preatoni, Martinoli, Wauters, & Tosi, 2006). In GNP, elephants cross park boundaries to forage in maize fields in the communities along the Pungue River (P. Branco, unpublished data). The overall higher activity rates at the boundary of the park as compared to the interior can be attributed to study design and elephant movement patterns. The cameras on the boundary of the park were placed on elephant paths with the goal of capturing elephants, and as elephants have been found to show strong site fidelity to crossing paths, these cameras had high detection rates (Von erhardt, 2014).

By entering the settled areas of the buffer zone mainly at night, elephants reduce the risk of direct contact with people and maximize their crop foraging opportunities, as has been reported in similar studies in Kenya (Graham et al., 2010) and Tanzania (Gunn et al., 2014). Direct encounters with humans can pose a risk to elephants, which may be chased away or harassed by people defending their fields, and can also pose a risk to people (Moss, 2001; Sitati, Walpole, Smith, & Leader-Williams, 2003). However, although nocturnal activity among elephants in settled areas benefits elephants by reducing direct contact with people, this activity pattern makes it more difficult for local farmers to protect their crops, resulting in high rates of crop damage (Parker, Osborn, Hoare, & Niskanen, 2007). Camera traps set up in strategic locations, like those used by the ElephantVoices and Human-Elephant Coexistence projects in GNP, can be used to document, monitor and potentially mitigate crop foraging and conflict. Such efforts will be increasingly important, as elephants in GNP are expanding their range and are beginning to raid crops in other areas of the buffer zone.

In addition to implications for tourism and human–wildlife conflict, behavioural responses of animals to human disturbance can have important consequences for wildlife populations and their conservation. When animals perceive risk from people, they may avoid areas of human activity, and these behavioural adjustments may alter foraging and reproduction and have costly consequences for individual fitness and survival (Sawyer, Korfanta, Nielson, Monteith, & Strickland, 2017). Avoidance of human activity may also decrease the effective amount of habitat available for wild animals (Eldegard, Lyngved, & Hjeljord, 2012; Gibeau, Clevenger, & Herrero, 2002). For wide-ranging species like elephants, avoidance of humans in both space and time may increase movement distances and travel costs (Graham et al., 2009). However, such effects likely are context-dependent. For example, as we found in this study, animals such as elephants may sometimes be able to exploit anthropogenic infrastructure and resources, which could compensate for increased costs of movement in anthropogenic landscapes (Chiyo et al., 2011). Future research is needed to understand the costs and benefits of spatiotemporal responses to human activity and their implications for conservation at the human–wildlife interface (Goldenberg, Douglas-Hamilton, Daballen, & Wittemyer, 2017; Songhurst et al., 2016).

Our study demonstrates the utility of camera traps as an alternative to telemetry for studying spatiotemporal activity patterns of wildlife. While camera traps do not yield fine-scale spatial data, they provide insight into the 24-hr activity patterns and can be systematically deployed to facilitate spatial analysis. Our results also highlight the value of integrating datasets for comparative analyses. We compared different regions of a study system to examine the dynamics of elephant behaviour in and around a national park. Similar analyses could be conducted at larger scales to compare different systems or even regions throughout the African continent, highlighting similarities and differences in drivers of animal activity. As the use of camera traps throughout Africa grows, there will be opportunities to integrate disparate datasets to improve our understanding of the continent's wildlife and address conservation challenges.

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REFERENCES

Abrahms, B., Jordan, N. R., Golabek, K. A., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2016). Lessons from integrating behaviour and resource selection: Activity-specific responses of African wild dogs to roads. *Animal Conservation*, *19*, 247–255. https://doi.org/10.1111/acv.12235

Barnes, R., Dubiure, U. F., Danquah, E., Boafo, Y., Nandjui, A., Hema, E. M., & Manford, M. (2007). Crop-raiding elephants and the moon. *African Journal of Ecology*, *45*, 112–115. https://doi.org/10.1111/j.1365-2028.2006.00689.x

Blake, S., Deem, S. L., Strindberg, S., Maisels, F., Momont, L., Isia, I.-B., … Kock, M. D. (2008). Roadless wilderness area determines forest elephant movements in the Congo Basin. *PLoS ONE*, *3*(10), e3546. https://doi.org/10.1371/journal.pone.0003546

Boettiger, A. N., Wittemyer, G., Starfield, R., & Volrath, F. (2011). Inferring ecological and behavioral drivers of African elephant movement using a linear filtering approach. *Ecology*, *92*(8), 1648–1657. https://doi.org/10.1890/10-0106.1

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., … Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685.

Caravaggi, A. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122. https://doi.org/10.1002/rse2.48

Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M. B., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences*, *109*(38), 15360–15365. https://doi.org/10.1073/pnas.1210490109

Chase, M. J., Schlossberg, S., Griffin, C. R., Bouché, P. J. C., Djene, S. W., Elkan, P. W., … Sutcliffe, R. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, *4*, e2354. https://doi.org/10.7717/peerj.2354

Chiyo, P. I., & Cochrane, E. P. (2005). Population structure and behaviour of crop-raiding elephants in Kibale National Park, Uganda. *African Journal of Ecology*, *43*, 233–241. https://doi.org/10.1111/j.1365-2028.2005.00577.x

Chiyo, P. I., Cochrane, E. P., Naughton, L., & Basuta, G. I. (2005). Temporal patterns of crop raiding by elephants: A response to changes in forage quality or crop availability? *African Journal of Ecology*, *43*, 48–55. https://doi.org/10.1111/j.1365-2028.2004.00544.x

Chiyo, P. I., Lee, P. C., Moss, C. J., Archie, E. A., Hollister-Smith, J. A., & Alberts, S. C. (2011). No risk, no gain: Effects of crop raiding and genetic diversity on body size in male elephants. *Behavioral Ecology*, *22*, 552–558. https://doi.org/10.1093/beheco/arr016

Cook, R. M., Henley, M. D., & Parrini, F. (2015). Elephant movement patterns in relation to human inhabitants in and around the Great Limpopo Transfrontier Park. *Koedoe*, *57*(1), 1–7. https://doi.org/10.4102/koedoe.v57i1.1298

Coppolillo, P., Gomez, H., Maisels, F., & Wallace, R. (2003). Selection criteria for suites of landscape species as a basis for site-based conservation. *Biological Conservation*, *115*, 491–430.

Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A., Goheen, J. R., … Pringle, R. M. (2016). Elephants in the understory: Opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology*, *97*(11), 3219–3230. https://doi.org/10.1002/ecy.1557

Craigie, I. D., Baillie, J., Balmford, A., & Carbone, C. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, *143*, 2221–2228. https://doi.org/10.1016/j.biocon.2010.06.007

Daskin, J. H., Stalmans, M., & Pringle, R. M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology*, *104*, 79–89. https://doi.org/10.1111/1365-2745.12483

De Boer, W. F., van Langevelde, F., Prins, H. H. T., de Ruiter, P. C., Blanc, J., Vis, M. J. P., … Hamilton, I. D. (2013). Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. *Biological Conservation*, *159*, 468–476. https://doi.org/10.1016/j.biocon.2012.10.015

Dickman, A. J. (2010). Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, *13*(5), 458–466. https://doi.org/10.1111/j.1469-1795.2010.00368.x

Eldegard, K., Lyngved, J. T., & Hjeljord, O. (2012). Coping in a human-dominated landscape: Trade-off between foraging and keeping away from roads by moose (*Alces alces*). *European Journal of Wildlife Research*, *58*(6), 969–979. https://doi.org/10.1007/s10344-012-0640-4

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*, 2nd ed. Thousand Oaks, CA: Sage.

Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11. https://doi.org/10.5751/ES-00404-060111

Fullman, T. J., Kiker, G. A., Gaylard, A., Southworth, J., Waylen, P., & Kerley, G. I. (2017). Elephants respond to resource trade-offs in an aseasonal system through daily and annual variability in resource selection. *Koedoe*, *59*(1), a1326. https://doi.org/10.4102/koedoe.v59i1.1326

Galanti, V., Preatoni, D., Martinoli, A., Wauters, 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. https://doi.org/10.1016/j.mambio.2005.10.001

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*, 1232–1235. https://doi.org/10.1126/science.aar7121

Gibeau, M. L., Clevenger, A. P., & Herrero, S. (2002). Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation*, *103*, 227–236. https://doi.org/10.1016/S0006-3207(01)00131-8

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*, 215–224. https://doi.org/10.1111/acv.12309

Graham, M. D., Hamilton, I. D., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, *12*, 445–455. https://doi.org/10.1111/j.1469-1795.2009.00272.x

Graham, M. D., Notter, B., Adams, W. M., & Lee, P. C. (2010). Patterns of crop-raiding by elephants, *Loxodonta africana*, in Laikipia, Kenya, and the management of human–elephant conflict. *Systematics and Biodiversity*, *8*(4), 435–445.

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.

Gunn, J., Hawkins, D., Barnes, R. F. W., Mofulu, F., Grant, R. A., & Norton, G. W. (2014). The influence of lunar cycles on crop-raiding elephants; evidence for risk avoidance. *African Journal of Ecology*, *52*, 129–137. https://doi.org/10.1111/aje.12091

Hoare, R. (2000). African elephants and humans in conflict: The outlook for co-existence. *Oryx*, *34*(01), 34. https://doi.org/10.1017/S0030605300030878

Hoare, R. E., & Du Toit, J. T. (1999). Coexistence between people and elephants in African savannas. *Conservation Biology*, *13*(3), 633–639. https://doi.org/10.1046/j.1523-1739.1999.98035.x

Hunninck, L., Ringstad, I. H., Jackson, C. R., May, R., Fossøy, F., Uiseb, K., … Røskaft, E. (2017). Being stressed outside the park—Conservation of African elephants (*Loxodonta africana*) in Namibia. *Conservation Physiology*, *5*(1), cox067. https://doi.org/10.1093/conphys/cox080

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. https://doi.org/10.1016/j.ecolind.2017.08.039

Jones, K. R., Venter, O., Fuller, R. A., Allan, J. R., Maxwell, S. L., Negret, P. J., & Watson, J. E. (2018). One-third of global protected land is under intense human pressure. *Science*, *360*(6390), 788–791.

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*, 51–59.

Ministério da Terra, Ambiente e Desenvolvimento. (2016). Aprova o plano de maneio do Parque Nacional da Gorongosa para o período de 2016 a 2020. *Boletim Da República*, *1*, 527–568.

Moss, C. J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of the Zoological Society of London*, *255*, 145–156. https://doi.org/10.1017/S0952836901001212

Ndaimani, H., Murwira, A., & Kativu, S. (2014). Predicting the spatial distribution of hunted and non-hunted Sable antelope (Hippotragus niger niger) using remotely sensed woody cover in a Southern African savanna. *Geocarto International*, *29*(2), 198–210. https://doi.org/10.1080/10106049.2012.754499

Oriol-Cotterill, A., Macdonald, D. W., Valeix, M., Ekwanga, S., & Frank, L. G. (2015). Spatiotemporal patterns of lion space use in a human-dominated landscape. *Animal Behaviour*, *101*, 27–39. https://doi.org/10.1016/j.anbehav.2014.11.020

Pangle, W. M., & Holekamp, K. E. (2010). Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve. *Journal of Mammalogy*, *91*(1), 154–164. https://doi.org/10.1644/08-MAMM-A-359R.1

Parker, G. E., Osborn, F. V., Hoare, R. E., & Niskanen, L. S. (2007). Human-elephant conflict mitigation: A training course for community-based approaches in Africa trainer's manual (pp. 1–39).

Poole, J. H., & Granli, P. (2017). ElephantVoices 2016 report to the Gorongosa Restoration Project (pp. 1–21).

Poole, J. H., & Granli, P. (2018). ElephantVoices 2017 report to the Gorongosa. Restoration Project.

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*, 455–456. https://doi.org/10.1038/434455a

Pringle, R. M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, *89*(1), 26–33. https://doi.org/10.1890/07-0776.1

Rasmussen, G. S. A., & Macdonald, D. W. (2011). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, *286*(3), 232–242. https://doi.org/10.1111/j.1469-7998.2011.00874.x

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. https://doi.org/10.1198/jabes.2009.08038

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., … Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*(4), e1400103–e1400103. https://doi.org/10.1126/sciadv.1400103

Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L., & Strickland, D. (2017). Mule deer and energy development—Long-term trends of habituation and abundance. *Global Change Biology*, *121*, 3–9. https://doi.org/10.1111/gcb.13711

Scholssberg, S., Chase, M. J., & Griffin, C. R. (2018). Poaching and human encroachment reverse recovery of African savannah elephants in south-east Angola despite 14 years of peace. *PLoS ONE*, *13*(3), e0193469. https://doi.org/10.1371/journal.pone.0193469

Setsaas, T. H., Holmern, T., Mwakalebe, G., Stokke, S., & Roskaft, E. (2007). How does human exploitation affect impala populations in protected and partially protected areas? - A case study from the Serengeti Ecosystem, Tanzania. *Biological Conservation*, *136*, 563–570. https://doi.org/10.1016/j.biocon.2007.01.001

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. https://doi.org/10.1046/j.1365-2664.2003.00828.x

Songhurst, A., McCullouch, G., & Coulson, T. (2016). Finding pathways to human–elephant coexistence: A risky business. *Oryx*, *50*(4), 713–720. https://doi.org/10.1017/S0030605315000344

Stalmans, M., & Peel, M. (2016). Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2016 (pp. 1–31).

Stalmans, M., & Beilfuss, R. (2008). Landscapes of the Gorongosa National Park (pp. 1–103).

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, *141*, 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J. A., Fisher, J. T., Burton, A. C., … Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, *15*(1), 26–34. https://doi.org/10.1002/fee.1448

Tinley, K. L. (1977). Framework of the Gorongosa Ecosystem.

Treves, A. (2009). The human dimensions of conflicts with wildlife around protected areas. In M. J. Manfredo, J. J. Vaske, P. Brown, D. J. Decker, & E. A. Duke (Eds.), *Wildlife and society: The science of human dimensions* (pp. 214–228). Washington, DC: Island Press.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466–469.

Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, *90*(1), 23–30. https://doi.org/10.1890/08-0606.1

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., … Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*, 1–11. https://doi.org/10.1038/ncomms12558

Vines, A. (1991). *Renamo: Terrorism in Mozambique*. Bloomington, IN: Indiana University Press.

VonGerhardt, K., VanNiekerk, A., Kidd, M., Samways, M., & Hanks, J. (2014). The role of elephant *Loxodonta africana* pathways as a spatial variable in crop-raiding location. *Oryx*, *48*(3), 436–444. https://doi.org/10.1017/S003060531200138X

Wasser, S. K. (2015). Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science*, *349*(6243), 84–87.

Wittemyer, G., Elsen, P., Bean, W. T., Burton, A. C. O., & Brashares, J. S. (2008). Accelerated human population growth at protected area edges. *Science*, *321*(5885), 123–126.

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 of the United States of America*, *111*(36), 13117–13121. https://doi.org/10.1073/pnas.1403984111

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