Moon phase and season alter road use by lions

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A R T I C L E   I N F O

A B S T R A C T

Roads within protected areas facilitate management and tourism but can also alter animal movements and foraging opportunities. Animal tracks observed along roads are also used to index species distributions and abundance. We investigated the influence of roads on lion (*Panthera leo*) movements within the Serengeti ecosystem of Tanzania. We used hourly locations from 18 GPS-collared lions to quantify the influence of temporal periodicity (diel, lunar, and seasonal) and land covers on lion road use and road crossing frequency during 2018–2019. Lion road use and crossings did not differ between day and night but varied up to 63% across lunar illumination and 82% between seasons. Greater lion road use and road crossing incidents observed during the dry season and greater lunar illumination can be attributed to reduced foraging because lion prey are less common during the dry season and acquired at a lower success rate during periods of greater lunar illumination. As lion road use varied between seasons and across lunar phases, we recommend consideration of these variations when indexing lion populations using data derived from track surveys that use roads as transects.

1. Introduction

About 80% of large carnivore species populations are declining, and 60% are threatened with extinction (e.g., Ripple et al., 2014; Wolf and Ripple, 2016). Causes for population declines are largely human related and include retaliatory killing (Kissui, 2008), loss of wild prey and land use changes (Wolf and Ripple, 2016). Understanding causes of decline and how they can vary temporally is important to develop techniques that mediate these adverse effects.

Human-made and natural landscape features may influence animal behavior (e.g., movements) spatially and temporary (Bourbonnais et al., 2014; Hill et al., 2021). Roads can influence wild mammals by facilitating movements and providing foraging opportunities (Hill et al., 2021). Roads also can support wildlife conservation actions, including anti-poaching patrols, research, and tourism (Lyamuya et al., 2022). Tourism contributes substantially to the economic growth of sub-Saharan Africa, accounting for up to

10.3% of gross domestic product (GDP) and 11.1% of total employment in Tanzania in 2019 (Kyara et al., 2021). However, roads can also increase mortality (e.g., collisions with vehicles) and present movement barriers to species. Additionally, roads may facilitate illegal activities such as poaching (Haines et al., 2012).

Regarding natural features, greater lion (*Panthera leo*) abundance in Serengeti National Park (SNP), was associated with river confluences due to increased foraging success and access to surface water (Mosser et al., 2009). Similarly, natural and artificial factors can contribute to lion hunting success (Hopcraft et al., 2005). Concealment in the form of vegetation, embankments, and cloud cover can facilitate ambush during lion hunts and improve hunting success (Schaller, 1972; Hopcraft et al., 2005; Davies et al., 2016; Mills et al., 2020).

Lion hunting success can further be influenced by diel (daily), lunar, and seasonal periodicity. Lions are more active and successful hunting during periods of reduced moonlight (Packer et al., 2011; Cozzi et al., 2013; Preston et al., 2019). In response, prey species exhibit a varying anti-predatory behavior across the lunar cycle. For example, wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) avoid foraging near lions, while zebra and buffalo (*Syncerus caffer*) tend to form large herds during the new moon in certain areas like SNP (Palmer et al., 2017). However, in Kruger National Park, nocturnal movements of wildebeest and zebra were largely influenced by their proximity to the lions rather than moon phase (Traill et al., 2016).

Dry and wet seasons in East Africa can create substantial variation in foraging opportunities, consequently influencing lion movements (Sinclair et al., 2000). Within the Greater Serengeti-Mara ecosystem (GSME), about 1.2 million wildebeest and 260 000 zebras (Boone et al., 2006; Sinclair et al., 2015) migrate south during the rainy season and north during the dry season (Sinclair et al., 2015). As predators and scavengers (Mosser et al., 2009), lions in the southern Serengeti ecosystem forage more successfully during the wet season when prey species are more abundant (Hopcraft et al., 2005).

Despite clear demonstration of variation in lion movements and numerous studies using roads as sampling units to estimate lion abundance (e.g., track surveys; Stander, 1998; Funston et al., 2010; Winterbach et al., 2016), potential temporal variation in lion road use and how this could influence population estimates has not been considered. We used global positioning system (GPS) collars to investigate lion movements in relation to roads and investigated whether road use was influenced by land cover or temporal cyclic events (i.e., diel, lunar, and seasonal). We predicted that lion use of roads would be greater at night, during periods of reduced lunar illumination, and during the wet season. Because seasonal cycles substantially influence prey distributions in our study system and lion foraging success can be negatively associated with lunar illumination. As roads facilitate lion movements, road embankments can
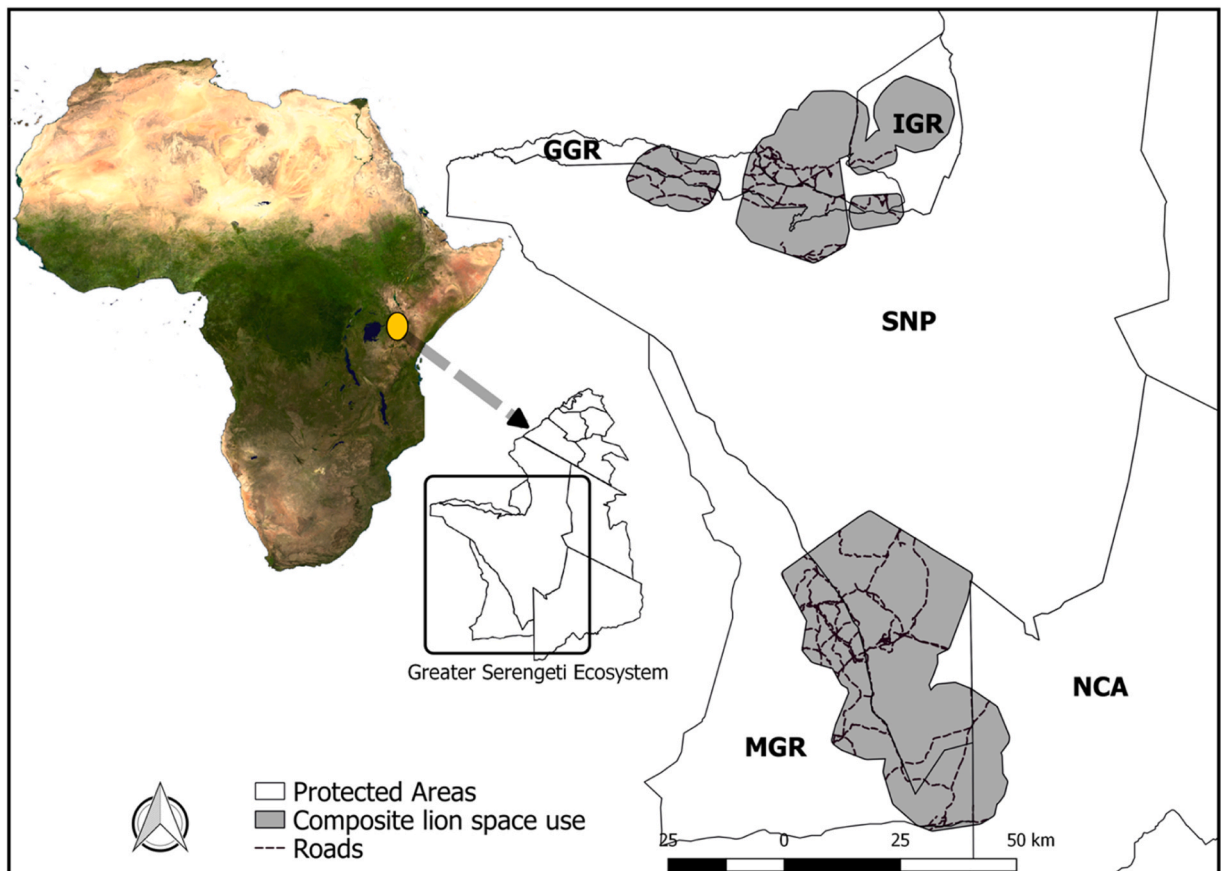

Fig. 1. Composite space use of GPS-collared lions and roads, Serengeti ecosystem, Tanzania, 2018–2019.

facilitate their approach toward prey when hunting (Hopcraft et al., 2005), we predicted lions would use roads more frequently and cross them more often during moon illumination and dry season, periods of reduced foraging opportunities.

2. Methods

2.1. Study area

We conducted this study in four protected areas within two areas of the Greater Serengeti-Mara ecosystem (GSME), Tanzania (Fig. 1). The northern area (3 500 km^2) included GrumetiGame Reserve (GGR), Ikona Wildlife Management Area (IWMA), Ikorongo Game Reserve (IGR), northern Serengeti National Park (SNP) and nearby villages. The southern area (3 300 km^2) included Maswa Game Reserve (MGR), parts of southern SNP, and Ngorongoro Conservation Area (NCA). The Serengeti ecosystem has an extensive network of roads to facilitate movements of people within and among protected areas. Lion or other wildlife movements were not restricted by anthropogenic barriers, with the exception of a 30-km fence along part of the northern border of IGR (Grumeti Funds, 2020). Legal hunting of lions occurs annually only in MGR during 1 July–31 December (Veldhuis et al., 2019); however no lions have been hunted for this purpose since 2015 (L. Masinde, personal communication).

Abbreviations: GGR, Grumeti Game Reserve; IGR, Ikorongo Game Reserve; MGR, Maswa Game Reserve; NCA, Ngorongoro Conservation Area; SNP, Serengeti National Park.

Annual rainfall increases along a gradient from southeast (500 mm) to northwest (1100 mm), with rains typically occurring from November to mid-May (Ogutu and Dublin, 1998). Grassland is the dominant land cover within GSME (Reed et al., 2009); other land covers include wooded grassland and patches of dense woodland (McNaughton, 1983; Veldhuis et al., 2019; Buchhorn et al., 2020). The GSME also supports the seasonal migration of approximately 1.2 million wildebeests and 260 000 zebras (Boone et al., 2006; Sinclair et al., 2015), which influence lion movements and distributions within the ecosystem (Packer et al., 2005). During December–April, most wildebeest occupy the southern GSME and then travel through the western-Serengeti corridor before migrating to the northern portion of the GSME during May–July (Boone et al., 2006).

2.2. Data collection

We captured 18 lions (14 females, 4 males) from 11 prides during 2018–2019. Pride sizes were 5–25 individuals. For prides with more than ten individuals, we collared up to two females. Among study prides we only collared resident males, selecting one male per
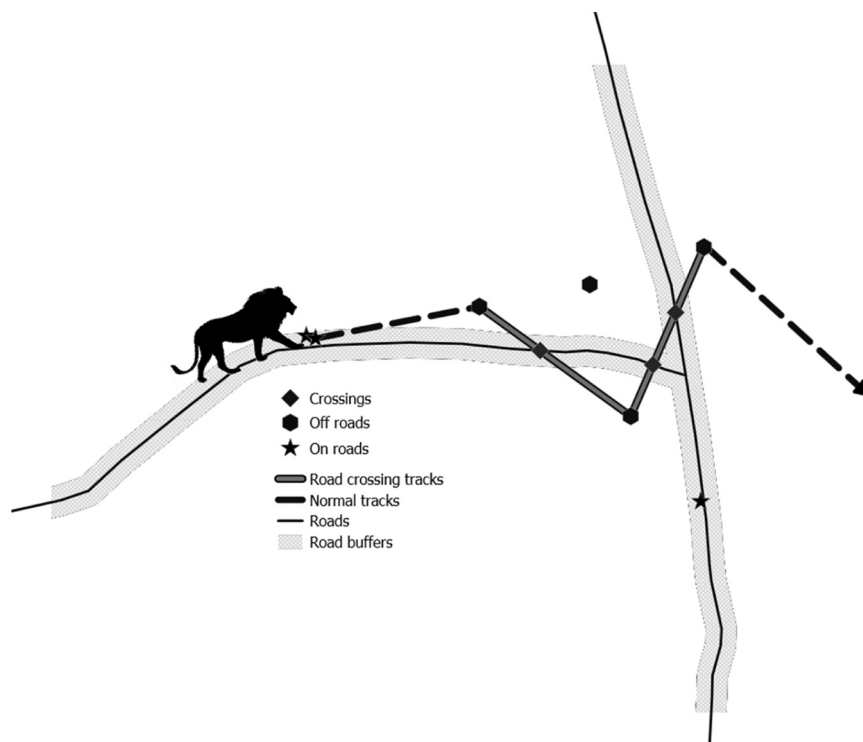

Fig. 2. Example of lion movement with a road crossing pathway. Solid black lines represent roads, and adjacent gray areas are 25-m road buffers. Stars represent on-road locations, hexagons represent off-road locations, and diamonds represent road crossing events. Dashed lines indicate nonroad-crossing pathways, and solid gray lines indicate road crossing pathways.

coalition. We attracted individuals using broadcasted vocalizations (Belant et al., 2016; Belant et al., 2017) and rifle-fired (Palmer CapChur SS cartridge-fired rifle; Cap-Chur Equipment, Powder Springs, Georgia, USA) darts (Pneudart Type U Remote Delivery Devices; Pneudart Inc., Williamsport, PA, USA) from vehicles (Fyumagwa et al., 2012). We fitted lions with GPS collars (Model IR-SAT, African Wildlife Tracking, South Africa). We programmed collars to collect hourly locations. Lion capture and handling protocols were approved by Mississippi State University (17−122) and State University of New York, College of Environmental Science and Forestry (180502), Institutional Animal Care and Use Committees.

We obtained 2017 road feature and land cover data (each 30-m resolution) from the Serengeti-Mara database (https://serengetidata.weebly.com/). Because data on traffic volume and road substrate were unavailable, we combined gravel and ungraveled roads into one category and used ArcGIS (ESRI, Redlands, California, USA) to create a 25-m buffer around each (Kautz et al., 2021). We created these 25-m buffers to account for lion ecology and GPS error (Kautz et al., 2021). We classified lion locations within these buffers as road use locations. We used the 'suncalc' package (Thieurmel et al., 2019) in R ver. 4.1.3 (R Development Core Team, 2022) to quantify the amount of lunar illumination as a fraction of visible moon, a numeric variable which ranged from 0.0 (new moon) to 1.0 (full moon) (Stolzenberg et al., 2017; Thieurmel et al., 2019). Similarly, we used suncalc package to categorize diel cycle into day and night, we defined night as darkness level suitable for astronomical observations (Thieurmel et al., 2019). We did not incorporate the effect of nightly cloud cover in our model, due to its consistency across lunar phases and seasons (Traill et al., 2016). We categorized seasons as follows: dry, mid-May–October, and wet, November–mid-May (Cusack et al., 2015).

For each lion location, we determined land cover using a reclassification of the initial 24 land cover types (Reed et al., 2009) into four categories: woodland, forest, grassland, and shrubland (Cusack et al., 2015). For each lion, we identified road crossings by first generating steps using the 'amt' package (Signer et al., 2019) in R ver. 4.1.3 (R Development Core Team, 2022). We then used ArcGIS (Arc Map 10.8.2) to create a path for each individual. We used the start and end locations of each step as start and end points of the path. We extracted road crossings as the intersection between movement paths and road centerlines (Laurian et al., 2008, Fig. 2; Baigas et al., 2017).

2.3. Statistical analyses

We examined the influence of temporal cycles and land cover on lion road crossings and road uses. We developed eight models (Table 1) to investigate these relationships. Four models focused on the impact of temporal cycles and land cover on the lion road use, while the remaining four assessed the influence of these factors on lion road crossing events. Road-use models considered land cover types (forest, grassland, shrubland and woodland), temporal cycles (diel, lunar, season), global (land covers and temporal cycles), and a null model. Similar models were used for road crossing analysis.

We employed a binomial linear mixed-effects model without interaction, to investigate factors potentially affecting lion road crossing and road use. In our initial analysis, we found that including pride as a random variable resulted in global models with higher Akaike Information Criteria adjusted for small samples (AICc) values, indicating poor model fit (Anderson and Burnham, 2002). Therefore, we accounted for pseudo-replication, by using only individual IDs as random variables. We considered temporal cycle and land cover models to examine the influential covariates (Table 2), which were determined from the most parsimonious model(s) (ΔAICc < 2).

Before performing models we tested continuous variables for correlation and found that they were not strongly correlated (|r| < 0.57). Typically, parameters are considered highly correlated when pairwise correlation (|r|) exceed 0.7 (Dormann et al., 2013). We addressed the high frequency of non-road-crossing and non-road-use events by fitting zero-inflation models using the 'glmmTMB' package (Brooks et al., 2017) in R ver. 4.1.3 (R Development Core Team, 2022). We used lion location on versus off the road as a response variable for road use and road crossing versus non-crossing events as response variable for road crossing incidents. We accounted for non-independence within individuals by adding collar identity as random factors. We used AICc to select the most

Table 1
Model comparison between temporal cycles and land cover parameters for lion road use and road crossing events, Serengeti ecosystem, Tanzania, 2018–2019. K = number of parameters, ΔAIC = difference in Akaike Information Criterion score between best supported model and competing models, LL = −2 log likelihood, and w = Akaike weight.

	Model[a]	K	ΔAICc	LL	w
Road crossing	Temporal cycle	5	0.00	-2280.54	0.93
	Global	9	5.21	-2279.13	0.07
	Null	2	34.53	-2300.81	0.00
	Land cover	6	38.44	-2298.76	0.00
Road use	Global	9	0.00	-853.28	0.64
	Temporal cycle	5	1.14	-857.86	0.36
	Land cover	6	10.35	-861.47	0.00
	Null	2	13.44	-857.86	0.00

[a] Models include:

Global = season + lunar + diel + shrubland + grassland + w/grassland + woodland + (1|ID)

Temporal cycle = season + lunar + diel + (1|ID)

Land cover = shrubland + grassland + w/grassland + woodland + (1|ID)

Null = 1 + (1|ID).

Table 2

Generalized linear mixed effects (family binomial) models assessing the influence of covariates on lion road use (on or <25 m of a road) and road crossings, Serengeti ecosystem, Tanzania, 2018–2019. Estimates are reported with 95% confidence intervals (CI); significant covariates (p < 0.05) are in bold font. Seasons = wet versus dry, Lunar = new moon (0.0) to full moon (1.0), Diel = day versus night; reference levels are dry season and day.

Effects	Covariate	Estimate	p-value	95% CI	
				Lower	Upper
Road crossing	**Intercept**	**-1.172**	**0.007**	**-1.600**	**-0.745**
	Season	**-0.698**	**< 0.001**	**-0.844**	**-0.546**
	Lunar	**0.414**	**< 0.001**	**0.305**	**0.524**
	Diel	-0.128	0.080	-0.221	-0.060
Road use	**Intercept**	**-5.171**	**< 0.001**	**-5.589**	**-4.753**
	Season	**-0.481**	**< 0.001**	**-0.567**	**-0.395**
	Lunar	**0.453**	**< 0.001**	**0.391**	**0.515**
	Diel	0.0426	0.30	0.001	0.084

parsimonious model as that with the lowest AICc score or with an AICc score < 2 of the most supported model whose parameters were contained within this model (Anderson and Burnham, 2002). We estimated overdispersion of the global model by calculating c-hat. Overdispersion occurs when the c-hat value is > 1, perfect model fit occurs when c-hat equals 1, and underdispersion occurs when c-hat < 1. We considered parameters with $p < 0.05$ as significant.

3. Results

We identified 1 133 road crossing and 3 397 non-crossing events. The temporal cycle model was most supported for lion road crossings (c-hat = 1.0), followed by the global model (Table 1). Lion road crossings were more frequent during the dry season and periods of greater lunar illumination. Our model predicted about an 82% increase in road crossing frequency between wet (0.143 [95% CI: 0.073, 0.282]) and dry (0.260 [95% CI: 0.133, 0.447]) seasons (Table 2; Fig. 3). Additionally, road crossing frequency increased with lunar illumination, with predicted road crossing frequency during greatest illumination (i.e., full moon; 0.201 [95% CI: 0.105, 0.372]) was 35% greater than estimated road crossing frequency during least illumination (i.e., new moon; 0.149 [95% CI: 0.072, 0.282]). Diel cycle did not influence lion road crossing events, but as we predicted, lunar and seasonal cycles did and were more influential to lion road crossing compared to landscape features.

Parameters are season (wet or dry), lunar (new moon =0.0 to full moon = 1.0), diel (day or night), land cover (shrubland, grassland, wooded grassland, and woodland) and ID are the collared individuals (lions).

We identified 2 391 on-road and 93 204 off-road locations. The global (c-hat value = 1) and temporal cycle models were most supported (ΔAICc < 2; Table 1), and using AIC criteria selected the temporal cycle model for further analyses. The proportion of lion road use was 56% greater during the dry season (0.014 [95% CI: 0.006, 0.031]) than during the wet season (0.009 [95% CI: 0.004, 0.020], [Fig. 3]). Similarly, the proportion of lion road use increased with lunar illumination; we predicted about a 63% increase in road use between the new moon (0.008 [95% CI: 0.004, 0.018]) and full moon (0.013 [95% CI: 0.006, 0.028]). While the diel period did not impact lion road use, our findings support the hypothesis that seasonal and lunar cycles influence lion road use, aligning with our predictions regarding temporal cyclicity.

4. Discussion

We found no variation between day and night in lion road use but an increase in road use frequency with lunar illumination. Additionally, lions used roads more during the dry season. One likely reason for greater lion road use incidences during the dry season
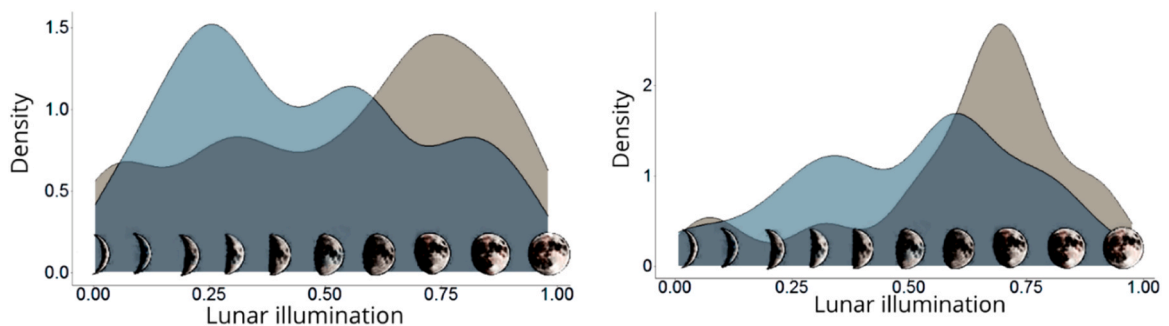

Fig. 3. Kernel density estimate indicating changes in lion road crossing (left panel) and road use (right panel) between seasons (wet and dry) and with lunar illumination, Serengeti Ecosystem, Tanzania, 2018–2019. Wet season estimates are in blue and dry season estimates in gray.

and periods of greater lunar illumination is that lions' increase search effort during these periods, which are associated with reduced foraging opportunities. In our study area prey density is low during the dry season, and lion hunts are less successful during moonlit nights (Orsdol, 1984; Packer et al., 2011; Preston et al., 2019). Moonlit nights and dry seasons coincided with limited foraging opportunities including hunting and scavenging, which are consequently successful only with greater search effort (Packer et al., 2011). Travel on roads during these periods however could also facilitate movements between foraging locations. Greater usage of roads during moonlit nights and dry season is likely attributable to improved traveling efficiency when foraging during food-scarce periods.

Similar to road use, we found no variation in road crossing within the diel cycle, but lion road crossing frequency was greater during the dry season and increased with lunar illumination. Most roads within our study system were developed for game viewing tourism, including observations of lions, which is higher during the dry season. Consequently, more roads occur near known lion resting areas, especially along rivers and near rock outcrops (kopjes). To reach other resources or engage in other activities including territorial marking and patrols (Schaller, 1972), lions must frequently cross roads. Lion road use and road crossing incidents did not differ between day and night, likely due to lions using roads not only for foraging, but also for accessing other resources during the day.

Crossing frequencies are likely to be greater during periods of prey scarcity (e.g., dry season and during moonlit nights) because territoriality of lions in our study area is more pronounced during these periods (Mosser et al., 2009). Additionally, we observed that road features changed between seasons; overall roads are more heavily vegetated due to low traffic during the wet season (Okello and Yerian, 2009). Further, roads could be covered with mud or standing water, conditions likely undesirable to lions which probably contribute to reduced road crossings or use during these periods.

We demonstrated that temporal factors, especially lunar and seasonal cycles have a stronger impact on road use than does land cover types. One reason is that the Serengeti ecosystem has greater variation in prey abundance between seasons than across vegetation covers. For instance, during the wet season, over 1.2 million ungulates migrate to the southern part of this ecosystem, a major portion of our study area, and then move north during the dry season (Sinclair et al., 2015). These migratory species provide numerous scavenging opportunities and abundant prey for lions and other carnivores (Schaller, 1972; Packer et al., 2005). Consequently, lower effort is required to obtain forage during the wet season and new moon periods which may have resulted in reduced road use by lions. Indeed, most migratory wildebeests and zebras provide a substantial proportion to lion diets during the wet season (Hopcraft et al., 2005).

Roads traversing protected areas serves as a transportation routes for goods and services. Additionally, roads facilitate movements of anti-poaching patrol crews, tourists, and management personnel (Lyamuya et al., 2022). Though roads can facilitate movements and foraging opportunities for wildlife species (Hill et. al, 2021), roads also can have negative effects on species including vehicle collisions, habitat fragmentation, littering and facilitate illegal harvests (Haines et al., 2012; Krief et al., 2020). While roads in protected areas offer valuable advantages, it is important to be aware of their negative effects and practices to mitigate these effects.

Our data indicates that lions increase road use and crossings during the dry season and full moon, potentially increasing their risk of vehicle collisions. These findings highlight the needs of wildlife authorities to regulate vehicle movements during these critical periods. Additionally, we suggest that similar data can be collected for other species, especially those more vulnerable to vehicle collisions to better understand their road use patterns and implement measures to protect them from traffic-related incidents.

Lion population size is frequently estimated using track counts (Stander, 1998; Wilson and Delahay, 2001; Belant et al., 2019). Advantages of track surveys include low cost and large spatial coverage within short time periods (Belant et al., 2019). Our study revealed a potential interdependence between lion movements and lunar illumination, which can ultimately influence track deposition rates, a metric important to estimating lion abundance using track surveys (Funston et al., 2010; Winterbach et al., 2016). Using roads as sampling units during track surveys, investigators could increase track detection rates by conducting surveys during dry seasons and periods of greater lunar illumination, preferably during early mornings when tracks are more visible and before tracks are obliterated by vehicles (Funston et al., 2010; Belant et al., 2016; Belant et al., 2019).

5. Conclusion

Though roads may facilitate illegal activities (e.g., poaching), roads also have several advantages for wildlife conservation and management (e.g., population estimation). However, an increase in road use by species of interest must be considered in development of survey designs. We have demonstrated temporal increases in lion road use and road crossing frequency influenced by lunar illumination and season. Variation in lunar illumination undoubtedly contributed to observed imprecision derived from track-based population estimates for lions (Belant et al., 2019). We suggest that studies using track count surveys to estimate abundance or occurrence of lions consider the potential effects of seasonal and lunar periodicity. Track counts are commonly used for abundance estimates of lions and other large carnivores including tigers (*P. tigris*; Panwar, 1979), cougars (*Puma concolor*; Smallwood and Fitzhugh, 1995), and spotted hyenas (*Crocuta crocuta*; Mills, 1992; Bauer et al., 2016). We suggest that in addition to lions, road use of other large carnivore species may also vary due to seasons or lunar illumination. We encourage consideration of temporal cycles and other factors that may influence animal movements before conducting surveys and explicitly account for these sources of variation in model development. Further, we suggest that population estimates of lions and other large carnivores that have not considered these sources of errors to be interpreted with caution.

CRediT authorship contribution statement

SM performed the analyses and summarized the results. **SM** and **JB** were the primary authors of the manuscript. **LM**, and **RF** participated in lion collaring and collection of lion location data. **JB**, **ER** and **RF** designed the study and secured resources. All authors

edited and improved later drafts of the manuscript.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request. Data used in this manuscript are available from the corresponding author upon reasonable request.

Acknowledgments

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