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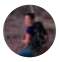

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Effects of tourism on seasonal movements and fine-scale habitat selection of African lions and spotted hyenas in Etosha National Park, Namibia

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ABSTRACT

Understanding the drivers of habitat selection for apex predators, such as African lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), is a vital component of conservation efforts. Large carnivores are especially vulnerable to anthropogenic pressures, which are increasing in areas of Sub-Saharan Africa. As wildlife-based tourism increases human-wildlife interactions, it is crucial to better understand predator habitat selection to inform conservation strategies. In this study, we used GPS collar data from 14 lions and nine hyenas tracked between 2016 and 2024 in Etosha National Park, Namibia to develop step selection functions to determine how roads, waterholes, and vegetation influenced habitat selection during periods of high and low tourism. Our results show that within a protected area popular for tourism, lion and hyena habitat selection is influenced by environmental and anthropogenic factors during both day and night. However, the distribution and availability of habitat and vegetation was a more important driver of habitat selection than anthropogenic factors in our study system. In particular, during both seasons water availability was a main driver of habitat selection for lions. Lions and hyenas selected for areas near roads with less tourism activity, which may indicate they avoid certain areas to minimize interactions with humans. Vegetation density influenced selection by both species, with lions selecting for areas with low vegetation density and hyenas selected for areas with high vegetation density in both seasons. These results contribute to our understanding of lion and hyena habitat selection as human activities continue to increase across the globe.

1. Introduction

Large carnivore populations are declining across the globe due to expansive habitat loss and fragmentation, increased conflicts with humans, and rising global temperatures (Parmesan, 2006; Di Marco et al., 2014; Ripple et al., 2014). In particular, many carnivores are susceptible to anthropogenic conflict due to their vast home ranges, requirements for medium to large prey, and large body sizes (Carbone and Gittleman, 2002). The global decline of carnivores coupled with their vital role in ecosystems has resulted in increased

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conservation efforts to restore dwindling populations, or at the very least, maintain current numbers. While human impacts on animal movement have been studied in some capacities (Doherty et al., 2021), the effects of wildlife-based tourism on predator movement have had less attention.

Apex predators are frequently considered flagship species for conservation and have high appeal for tourism viewing (Van der Meer et al., 2016). Wildlife-based tourism encompasses activities generating income and providing local employment, while increasing tourist education and endorsing conservation for animal species (Moorhouse et al., 2017). Tourism is one of the main economic drivers in some parts of the world, especially in regions of sub-Saharan Africa (Krstic et al., 2016). Despite the economic benefits, it has been shown that tourism can negatively impact wildlife (Broekhuis, 2018; Szott et al., 2019). Some mammals have been shown to increase their movements in response to human presence or disturbance (e.g. tourism; Doherty et al., 2021), which may result in fewer opportunities to acquire energy via foraging or predation (Higginbottom, 2004). While previous studies have focused on the effects of tourism activities on spatial ecology and behavior of several species (Bateman and Fleming, 2017), our understanding of how tourism activities affect charismatic species that tourists seek for viewing opportunities needs to be further developed.

African lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) are two of the most prevalent large carnivores throughout sub-Saharan Africa (Hatton et al., 2015). However, lions and hyenas have experienced range contractions of 94 % and 24 %, respectively since historic times (AD 1500) (Wolf and Ripple, 2017) and are increasingly being restricted to protected areas (Mills and Hofer, 1998; Riggio et al., 2012). These two species play important roles in their ecosystems, by affecting herbivore and mesocarnivore population dynamics and behavior (Ripple et al., 2014) and potentially preventing pathogen spread through both hunting and scavenging activities (Beasley et al., 2015; Moleón et al., 2015; Sonawane et al., 2021). Lions and hyenas also have substantive economic value, as they generate income through tourism (Lindsey et al., 2007; Price, 2017). However, lions have been documented exhibiting stress behaviors (increased breathing rate, sitting up, and moving away) during periods of tourism presence (Hayward and Hayward, 2009). Additionally, lions and hyenas may change their diel activity patterns to avoid human presence (Patterson et al., 2024). Understanding the effects of tourism on lion and hyena movement and habitat selection is pivotal for conservation and management strategies, especially in areas with high tourism, as populations of these species continue to decline across Africa (Wolf and Ripple, 2017).

Water is a vital resource for animals and the availability of surface water can strongly affect species movement, distribution, and range (Western, 1975; Redfern et al., 2003; Chamaillé-Jammes et al., 2013). In resource-limited environments, climatic shifts and weather variability greatly influence vegetation abundance and cover, affecting the distribution and abundance of wildlife. Vegetation abundance is also an important factor for herbivore populations and ranges, which in turn influence carnivore populations and ranges (Sinclair, 2003; Jędrzejewska and Jędrzejewski, 2005). In semi-arid areas with high tourism, waterholes are often man-made and provide wildlife viewing for tourists, whose presence may impact water acquisition by shy or cryptic species (Kamanda et al., 2008; Patterson et al., 2024). Roads are known to aid movements and foraging opportunities for wildlife species (Hill et al., 2021) and support tourism in protected areas (Lyamuya et al., 2021). Though hyenas tend to avoid humans and buildings (Green and Holekamp, 2019) they may use roads to avoid dense vegetation (Kushata et al., 2018), and both lions and hyenas use roads for travel (Hägerling and Ebersole, 2017; Schooler et al., 2022), but our understanding of how roads are used relative to tourism access is minimal. Yet, roads can increase animal mortalities (Moore et al., 2023), fragment landscapes (Andrews, 1990), and prevent movement (Bennett,

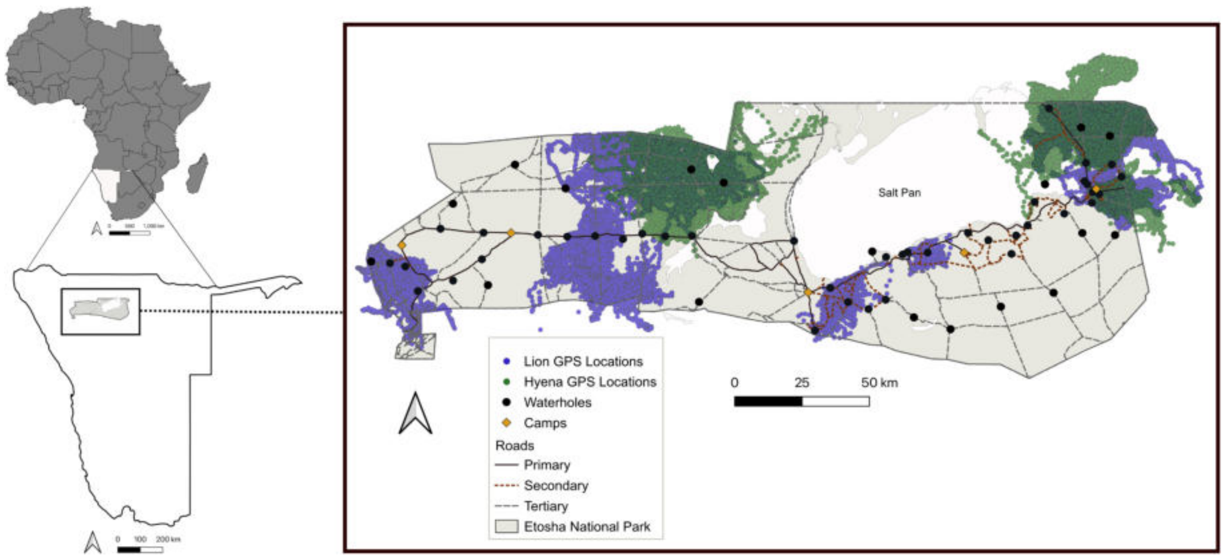

Fig. 1. Study site and GPS locations (1-h interval) for collared African lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) habitat selection in etosha national park, Namibia between 2016 and 2024. Camps, waterholes, and tourism-related covariates are indicated on the map – primary road with high tourist traffic (primary), less-trafficked (secondary) roads branching from the primary road, and smaller (tertiary) roads only accessible by park staff.

2017). Understanding how imperiled carnivores, such as lions and hyenas, are affected by roads, waterholes, and associated tourism activity can inform conservation and management strategies. This can provide insight into minor changes that can be made in the tourism industry to reduce behavioral changes by wildlife species due to human presence.

In this study, we used Global Positioning System (GPS)-collar data from lions and hyenas in Etosha National Park, Namibia, to determine the effects of environmental and anthropogenic variables on their habitat selection. Specifically, we investigated how roads that are accessed by tourists, waterholes, and vegetation type, affected lion and hyena habitat selection in different seasons and times of the day. We predicted that both species would have a strong selection for areas near water since it is a limited resource where prey species congregate. We expected that this effect would be stronger during the dry season relative to the wet season, given that prey often disperse across the landscape during the rainy season. We also predicted that due to differences in hunting techniques, lions would select for areas with high vegetation cover providing increased ambush opportunities (Schaller, 1972) while hyenas would select for areas with less vegetation cover (Mills, 1990; Holekamp and Dloniak, 2010; Barker et al., 2023). Finally, we expected that both species would select areas close to roads for ease of navigation and movement during foraging and hunting but would avoid heavily trafficked roads during the day, especially hyenas due to their tendency for human avoidance (Boydston et al., 2003; Pangle and Holekamp, 2010).

2. Materials and methods

2.1. Study area

This study was conducted in Etosha National Park ("Etosha") in north-central Namibia (Fig. 1). Etosha is a 22,900 km^2 fenced area in the semi-arid weather zone, with an average annual rainfall of 380 mm (De Beer et al., 2006). The main vegetation types in the park are grasslands; steppe, dominated by dwarf shrubs; shrubland; Mopane (*Colophospermum mopane*) tree savanna; and mixed tree savanna (Le Roux et al., 1988). Water is available to wildlife throughout the year at a limited but varying number of natural springs and 59 artificial waterholes spread across the park (Etosha Ecological Institute, unpublished data). During the dry season (May-October) these sources represent the only available surface water. During the wet season (November-April), rainfall provides additional water sources for animals in natural depressions across the landscape (Engert, 1997; Berezin et al., 2023).

Etosha is one of the main tourist destinations in Namibia, with over 200,000 visitors annually (Ministry of Environment, Forestry, and Tourism, n.d.), and the peak tourism season typically occurs during the dry season. Etosha encompasses six tourist camps, four of which have large waterholes with artificial lighting to improve wildlife viewing at night, one camp has a waterhole without any light, and one camp has no waterhole. The remaining 59 waterholes are not lit. Between sunset and sunrise, no tourist vehicles are permitted to drive throughout the park. There is one main (primary) road that runs through the central region of Etosha along the 19 °S longitude and is heavily trafficked by tourists as it is connected directly to the gated entrances. Less-trafficked (secondary) roads branching from the main road are also accessible to tourists. Additionally, there are smaller (tertiary) roads only accessible by park staff where the traffic volume is low (Fig. 1). The primary, secondary, and tertiary roads are 565 km, 467 km, and 2562 km in total length, respectively.

2.2. Carnivore GPS data

Between 2016 and 2024, we recorded locations from GPS-satellite collars (Vectronic Aerospace Vertex Plus Iridium) deployed on lions and hyenas in Etosha at a fix rate between 15 min and 24 h. During chemical immobilization, each individual was fitted with a GPS collar. Collaring protocol included vehicular darting with baits (zebras [*Equus quagga*], springbok [*Antidorcas marsupialis*]) and calls to lure animals in Smuts et al. (1977), using a combination of dart-administered Zoletil and Medetomidine for immobilization, and Atipamezole and Yohimbine as reversal agents, with dosages determined by the veterinarian based on species and individual body size. Typically, this included 40 mg Zoletil and 5 mg Medetomidine reversed with 20–30 mg Atipamezole and 12 mg Yohimbine for hyenas, 80–110 mg Zoletil and 10 mg Medetomidine reversed with 40–50 mg Atipamezole and 20–50 mg Yohimbine for male lions, 60–80 mg Zoletil and 8–10 mg Medetomidine reversed with 40–50 mg Atipamezole and 20–30 mg Yohimbine for female lions. In this study, we only included individuals with collars recording locations every hour or less that were not in the same prides or clans, which resulted in the inclusion of 14 adult lions (eight females and six males) and nine adult hyenas (six females and three males) (Fig. 1). All immobilizations and collaring procedures were performed by veterinarians registered with the Namibian Veterinary Council and the Ministry of Environment, Forestry, and Tourism and were approved by the Namibian Ministry of Environment, Forestry, and Tourism (permit #AN202101004) as well as the University of Georgia Institutional Animal Care And Use Committee under protocols A2024 05-009-06 and A2021 04-013-Y3-A11.

2.3. Environmental and anthropogenic variables

We quantified both environmental and anthropogenic variables to determine the drivers of lion and hyena habitat selection. For environmental variables, we used vegetation and habitat covariates comprising distance to waterholes (m) (Etosha Ecological Institute, unpublished data), shrub biomass (metric tons), tree density (trees/ha), and grass cover (% in 1 m cell). We chose these vegetation covariates to account for habitat selection being influenced for thermoregulation and ambush hunting (shrubs and trees) purposes (Schaller, 1972; Swanson, 2016), and to account for prey preference of grazers (grass) or browsers (trees) (Hayward and Kerley, 2005; Trinkel, 2010). All vegetation data were collected in 2011 and 2012 by Tsalyuk et al. (2017) at a spatial resolution of 231 by 231 m. Each GPS location was assigned a season (wet or dry) and a time of day (day or night) based on sunset and sunrise times in Etosha determined using the 'suncalc' package in R (Thieurmel et al., 2019). To determine how tourism affected lion and hyena habitat selection, we defined the following anthropogenic covariates: distance to road (m), road type (primary [19°S longitude road],

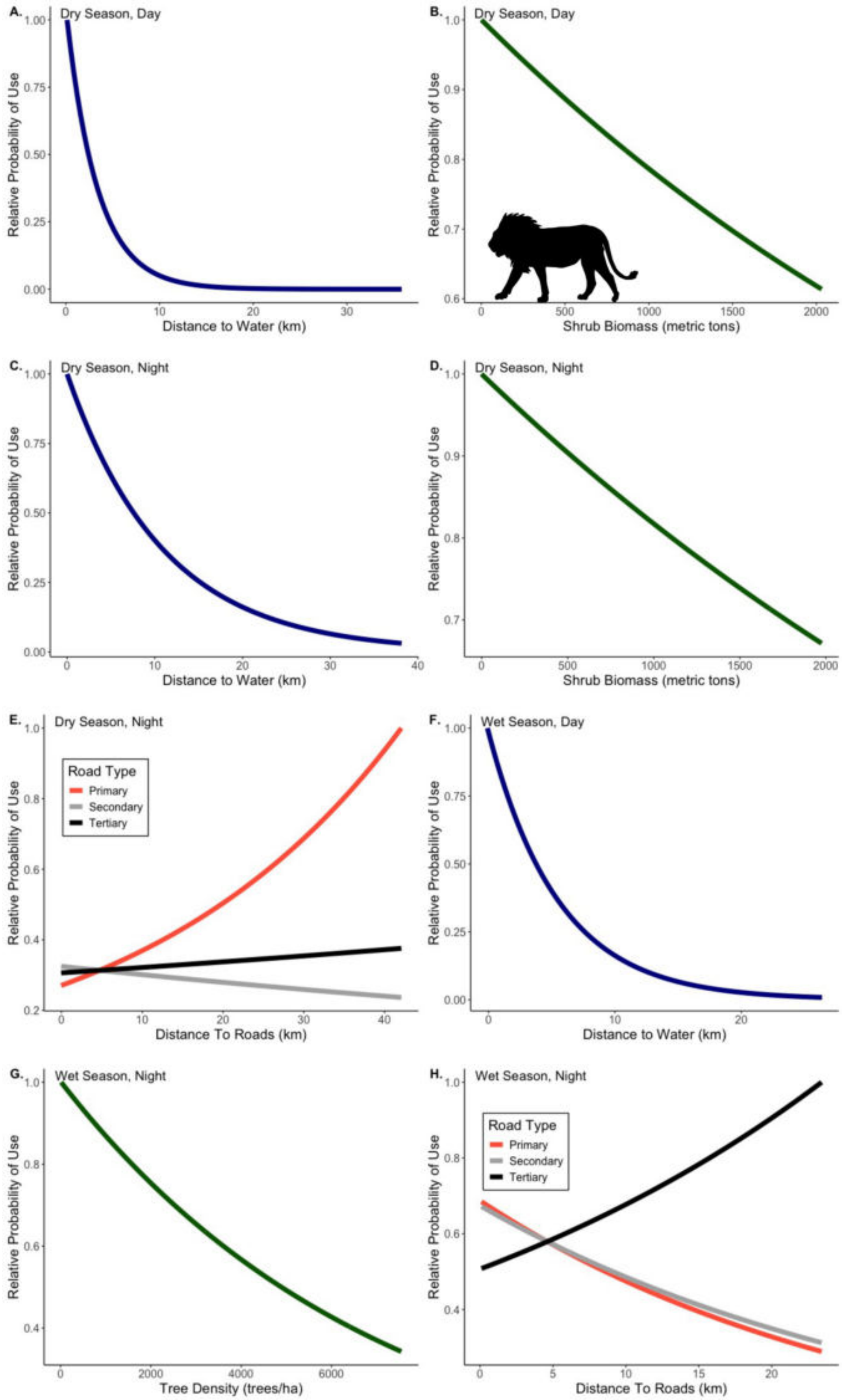

Fig. 2. Relative probability of habitat selection for African lions (*Panthera leo*) during the dry season (May–October) and wet season (November-April) in etosha national park, Namibia, 2016–2024.

secondary [connect to primary and accessible by tourists], and tertiary [only accessible by management staff]) and distance to waterholes (m). Distances to roads and waterholes were measured using the "distance to nearest hub" tool in QGIS-LTR 3.34 (QGIS Development Team, 2022).

2.4. Data analyses

After cleaning the data to remove any duplicate points or those outside of deployment times, we used 213,186 and 128,470 data points for 14 lions and 9 hyenas, respectively. We subset the data into the wet (November – April) and dry (May – October) seasons during both day and night. This resulted in 177,273 data points for lions in the dry season (females = 116,039, males = 61,234) and 35,913 in the wet season (females = 22,905, males = 13,008), and 100,340 data points for hyenas in the dry season (females = 84,088, males = 16,252) and 28,130 in the wet season (females = 24,940, males = 3190) (Table S1).

We then applied a step-selection function (SSF) to location data from their GPS collars, which can associate parameters of movement rules with landscape features (Thurfjell et al., 2014) and mitigate statistical problems posed by autocorrelation (Alston et al., 2023). For individuals with GPS locations recorded more frequently than one per hour, we sub-sampled their track at a 1-h fix rate with a 10-min tolerance (Signer et al., 2019; Hofmann et al., 2024). To generate step lengths, turn angles, and random steps, we used the 'amt' package in R (Signer et al., 2019). Observed step lengths and turn angles were calculated for each individual's trajectory using all true steps pooled together across all individuals of each species. These values were then used to fit probability distributions, with step lengths modeled using a gamma distribution and turn angles using a von Mises distribution (Signer et al., 2019). For each observed step, nine random steps were generated (Signer et al., 2019) by sampling step lengths and turn angles from these fitted distributions. This resulted in a dataset of 1,344,803 and 736,455 used and available steps for lions and hyenas, respectively. For the end point of each used or available step, we extracted the value for each environmental and anthropogenic covariate and standardized the continuous variables to help in model convergence. Because waterholes were located at most tourist camps, to determine if waterholes at camps should be included in our water distance covariate, we tested the effects of distance to waterholes including camps and without camps on species presence/absence. We compared Poisson models by Akaike's Information Criterion (AICc) (Burnham and Anderson, 2004) for each season and time of day combination for both species. We found that for lions, the best models included tourist camps in the distance to waterhole predictor (ΔAICc < 2) (Table S2), and for hyenas, the best models excluded camp waterholes as a predictor (dry season, day and night ΔAICc $= 6$, wet season ΔAICc < 2). To test if we should include year in the models, we ran

Table 1
Generalized linear mixed model results for habitat selection from a step-selection function based on season (wet and dry) and time of day (day and night) for African lions (*Panthera leo*) in Etosha national park, Namibia. Estimates, standard errors (SE), z-values (z), p-values (P), and upper and lower confidence intervals (2.5–97.5 %) (CI) are shown for each covariate.

Model	Covariate	Estimate	SE	z	P	CI
Lion: Dry, Day	Intercept	− 21.9	1.01	− 21.7	**< 0.001**	− 23.8 to − 19.9
	Water Distance	− 1.96	0.45	− 4.31	**< 0.001**	− 2.85 to − 1.07
	Tree Density	− 0.01	0.01	− 0.77	0.44	− 0.03 to 0.01
	Grass Cover	0.01	0.01	1.67	0.09	0.002– 0.02
	Shrub Biomass	− 0.08	0.01	− 7.39	**< 0.001**	− 0.10 to − 0.06
	Road Distance	0.02	0.05	0.31	0.75	− 0.09 to 0.12
	Road Distance: Road Type-Secondary	− 0.09	0.06	− 1.54	0.12	− 0.21 to 0.02
	Road Distance: Road Type-Tertiary	0.01	0.06	0.16	0.89	− 0.10 to 0.12
Lion: Dry, Night	Intercept	− 22.0	0.96	− 22.8	**< 0.001**	− 23.9 to − 20.1
	Water Distance	− 0.60	0.18	− 3.26	**0.001**	− 0.95 to − 0.24
	Tree Density	− 0.01	0.01	− 0.70	0.49	− 0.02 to 0.01
	Grass Cover	0.001	0.01	0.30	0.77	− 0.01 to 0.01
	Shrub Biomass	− 0.06	0.01	− 6.34	**< 0.001**	− 0.08 to − 0.04
	Road Distance	0.10	0.05	2.11	**0.03**	0.01–0.20
	Road Distance: Road Type-Secondary	− 0.13	0.05	− 2.42	**0.02**	− 0.23 to − 0.02
	Road Distance: Road Type-Tertiary	− 0.09	0.05	− 1.65	0.10	− 0.19 to 0.02
Lion: Wet, Day	Intercept	− 22.3	2.08	− 10.8	**< 0.001**	− 26.4 to − 18.2
	Water Distance	− 1.03	0.14	− 7.33	**< 0.001**	− 1.3 to − 0.75
	Tree Density	− 1.01	0.64	− 1.57	0.12	− 2.27 to 0.25
	Grass Cover	0.01	0.01	0.95	0.34	− 0.01 to 0.04
	Shrub Biomass	− 0.02	0.02	− 1.06	0.29	− 0.07 to 0.02
	Road Distance	− 0.15	0.10	− 1.59	0.11	− 0.34 to 0.04
	Road Distance: Road Type-Secondary	− 0.09	0.10	− 0.84	0.40	− 0.29 to 0.11
	Road Distance: Road Type-Tertiary	0.16	0.10	1.61	0.11	− 0.04 to 0.36
Lion: Wet, Night	Intercept	− 22.0	2.26	− 9.76	**< 0.001**	− 26.5 to − 17.6
	Water Distance	− 2.21	1.78	− 1.24	0.21	− 5.69 to 1.27
	Tree Density	− 0.07	0.03	− 2.59	**0.01**	− 0.12 to − 0.02
	Grass Cover	− 0.01	0.01	− 0.73	0.46	− 0.04 to 0.02
	Shrub Biomass	0.03	0.02	1.47	0.14	− 0.01–0.08
	Road Distance	− 0.12	0.10	− 1.22	0.22	− 0.31 to 0.07
	Road Distance: Road Type-Secondary	0.01	0.10	0.13	0.90	− 0.18 to 0.21
	Road Distance: Road Type-Tertiary	0.21	0.11	1.97	**0.04**	0.01–0.42

each global model without year, with year as a fixed effect, and with year as a random effect, then compared the models by AICc for each season and time of day combination for both species. We found for both species in all combinations of day and time, the best model did not include year (ΔAICc < 2) (Table S3). To fit the SSFs, we used the 'glmmTMB' function from the R package 'glmmTMB' to run a generalized linear mixed model with a Poisson distribution (Magnusson et al., 2017). We assessed model diagnostics and quality (normality of residuals, normality of random effects, linear relationship, homogeneity of variance, multicollinearity) using the 'check_model' function in the 'performance' package in R (Lüdecke et al., 2021).

Our goal was to determine which of the environmental or anthropogenic covariates had the strongest influence on lion and hyena habitat selection. Therefore, we created one global model for each species, which we ran for both seasons and times of day (day and night), totaling four models per species. Prior to fitting the models, we assessed collinearity (Pearson's correlation) among predictors for each season and time of day combination using the 'cor' function in the R package 'stats' (R Core Team, 2024) and for all model results, we used a threshold of $p < 0.05$ for determining significance for predictors. The model structure included location type (used versus random) as a binary response variable, while predictor variables were distance to waterholes, distance to roads, shrub biomass, tree density, and grass cover. We included interaction terms between distance to road and road type, including random intercepts for each stratum (one used step and its set of matched available steps) (Muff et al., 2020) and a random slope for individuals. We found no collinearity using Pearson's correlation among predictors ($r < 0.6$) (Fig. S1) for any combination of season and time of day for either species, thus all predictors were retained in the analyses (Baniya et al., 2025).

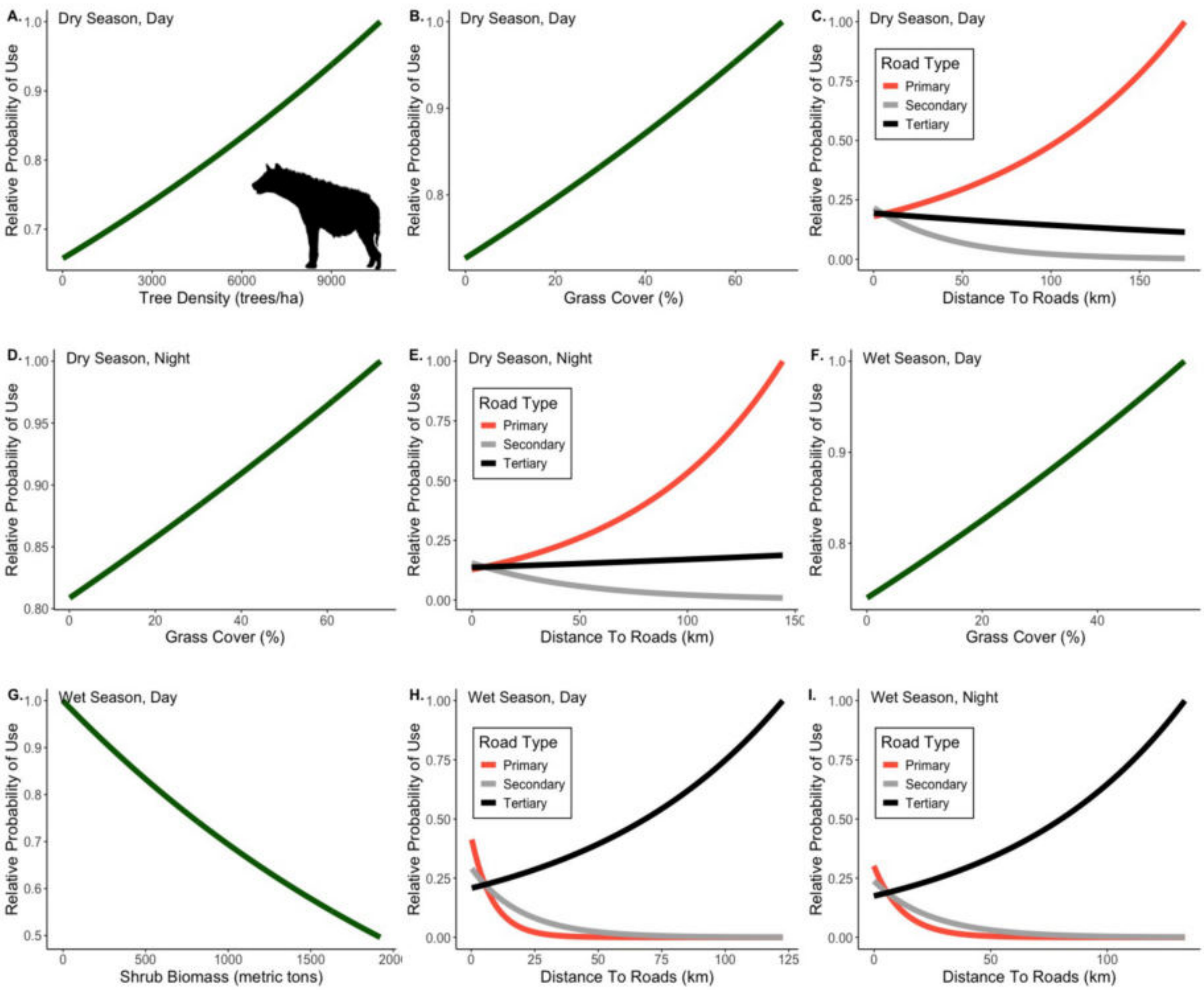

Fig. 3. Relative probability of habitat selection for spotted hyenas (*Crocuta crocuta*) during the dry season (May–October) and wet season (November–April) in etosha national park, Namibia, 2016–2024.

3. Results

3.1. Lion habitat selection

During the dry season, lions selected for areas near water (Fig. 2A, C) and with low shrub biomass (Fig. 2B, D) during both day and night (Table 1). During the night only, lions selected for areas away from primary roads, near secondary roads, and with no preference for tertiary roads (Fig. 2E). During the wet season, lions selected for areas near water during the day (Fig. 2F). At night, they selected for areas with low tree density (Fig. 2G), near primary and secondary roads, and away from tertiary roads (Fig. 2H).

3.2. Hyena habitat selection

During the dry season, hyenas selected for areas with high tree density during the day (Fig. 3A). During the day and night, they selected for areas with high grass cover (Fig. 3B, D), away from primary roads, and close to secondary roads (Fig. 3C, E) (Table 2). During the wet season during the day, hyenas selected for areas with high grass cover (Fig. 3F) and low shrub biomass (Fig. 3G). During the day and night of the wet season, they selected for areas near primary and secondary roads and away from tertiary roads (Fig. 3H, I).

4. Discussion

Understanding the factors influencing carnivore spatial ecology is crucial to optimizing conservation and management strategies, especially in protected areas with high wildlife-based tourism representing the main source of income. Our results indicate that in large, protected areas frequented by tourists, the movement of apex predators is influenced by both anthropogenic and environmental factors, although the distribution and availability of habitat was a more important driver of habitat selection than the intensity of tourist presence in our study system. Most notably, distance to water was a main driver of habitat selection during the wet and dry seasons for lions, which was expected given that water is a key limiting factor in northwestern Namibia (Wanke et al., 2014). However, water was not a main driver of habitat selection for hyenas. Furthermore, abundance and composition of vegetation influenced habitat selection for both species, which was modulated by season and time of day, supporting our prediction that vegetation is a major driver of predator habitat selection likely due to concealment from prey and tourists, hunting, and for thermoregulation. Although

Table 2
Generalized linear mixed model results for habitat selection from a step-selection function based on season (wet and dry) and time of day (day and night) for spotted hyenas (*Crocuta crocuta*) in Etosha national park, Namibia. Estimates, standard errors (SE), z-values (z), p-values (P), and upper and lower confidence intervals (2.5–97.5 %) (CI) are shown for each covariate.

Model	Covariate	Estimate	SE	z	P	CI
Hyena: Dry, Day	Intercept	− 22.6	1.41	− 16.0	**< 0.001**	− 25.3 to − 19.8
	Water Distance	− 0.35	− 0.57	− 0.60	0.55	− 1.47 to 0.78
	Tree Density	0.05	0.01	3.65	**0.02**	0.02–0.07
	Grass Cover	0.04	0.01	4.33	**0.02**	0.02–0.05
	Shrub Biomass	0.02	0.01	1.48	0.14	− 0.01 to 0.04
	Road Distance	0.05	0.07	0.70	0.48	− 0.08 to 0.18
	Road Distance: Road Type-Secondary	− 0.16	0.07	− 2.14	**0.03**	− 0.30 to − 0.01
	Road Distance: Road Type-Tertiary	− 0.06	0.07	− 0.87	0.39	− 0.20 to 0.08
Hyena: Dry, Night	Intercept	− 22.6	1.37	− 16.5	**< 0.001**	− 25.3 to − 19.9
	Water Distance	− 0.42	0.28	− 1.49	0.14	− 0.98 to 0.13
	Tree Density	0.02	0.01	1.46	0.14	− 0.01 to 0.04
	Grass Cover	0.02	0.01	2.74	**0.01**	0.01–0.04
	Shrub Biomass	− 0.01	0.01	− 0.91	0.37	− 0.04 to 0.01
	Road Distance	0.07	0.06	1.16	0.25	− 0.05 to 0.20
	Road Distance: Road Type-Secondary	− 0.17	0.07	− 2.50	**0.01**	− 0.31 to − 0.04
	Road Distance: Road Type-Tertiary	− 0.06	0.07	− 0.93	0.35	− 0.19 to 0.07
Hyena: Wet, Day	Intercept	− 22.1	2.67	− 8.27	**< 0.001**	− 27.3 to − 16.9
	Water Distance	0.01	0.05	0.25	0.80	− 0.09 to 0.12
	Tree Density	− 0.14	0.15	− 0.97	0.33	0.01– 0.11
	Grass Cover	0.05	0.02	2.91	**0.003**	0.02–0.08
	Shrub Biomass	− 0.15	0.03	− 5.68	**< 0.001**	− 0.50 to − 0.08
	Road Distance	− 0.54	0.11	− 4.87	**< 0.001**	− 0.71 to − 0.27
	Road Distance: Road Type-Secondary	0.31	0.13	2.32	**0.02**	0.01–0.53
	Road Distance: Road Type-Tertiary	0.60	0.12	4.92	**< 0.001**	0.32–0.79
Hyena: Wet, Night	Intercept	− 22.6	2.64	− 8.55	**< 0.001**	− 27.7 to − 17.4
	Water Distance	0.02	0.05	0.32	0.75	− 0.08 to 0.12
	Tree Density	0.01	0.03	0.50	0.62	− 0.04 to 0.06
	Grass Cover	0.002	0.02	0.18	0.86	− 0.03 to 0.03
	Shrub Biomass	− 0.04	0.03	− 1.35	0.18	− 0.09 to 0.02
	Road Distance	− 0.41	0.10	− 3.93	**< 0.001**	− 0.61 to − 0.20
	Road Distance: Road Type-Secondary	0.21	0.13	1.60	0.11	− 0.05 to 0.46
	Road Distance: Road Type-Tertiary	0.47	0.11	4.17	**< 0.001**	0.25–0.70

environmental attributes appeared to be the main driver of habitat selection among our study species, roads with concentrated tourist activity appeared to exert some influence over habitat selection patterns. Our results suggest lions and hyenas use roads for moving throughout the landscape, but that they may be avoiding roads that are more frequented by tourists.

Lions selected for areas close to water during both seasons, except during the wet season at night, while water did not influence hyena habitat selection. Etosha is a semi-arid ecosystem with limited water availability, especially during the dry season. As such, we expected that water would drive habitat selection for lions and hyenas, with variation in strength of selection based on species, season, and waterhole type. Access to water typically defines spatiotemporal use of a semi-arid landscape for most herbivore species (Smit et al., 2007; Ogutu et al., 2014) and their predators who are attracted to these prey hotspots and frequently hunt in their vicinity. For example, lions adjust their behavior to reduce time spent away from waterholes to increase their chances of prey acquisition (Valeix et al., 2010; Davidson et al., 2012). Additionally, lions may be more water dependent than hyenas who are generally more dispersed across the landscape and highly adaptable (Mills, 1990; Barker et al., 2023). Thus, the strong selection of waterholes by lions likely reflects their need to access water both as a vital resource and for increased hunting opportunities, while hyenas may be less reliant on water or acquire more water from consuming prey (Green et al., 1984; Holekamp and Dloniak, 2010; Jones et al., 2021).

Lion selection for low shrub biomass and tree density was unexpected, as they are primarily nocturnal hunters (Cozzi et al., 2012; Mugerwa et al., 2017) and ambush predators (Schaller, 1972) that use vegetation to hide while they stalk prey. Further, lions are known to use waterholes as hunting grounds, ambushing prey from nearby vegetation (Valeix et al., 2009; Kittle et al., 2022). As such, we expected lions would select for areas with high vegetation density close to water for optimal hunting opportunities at night. However, although vegetation structure has been identified as important for lion hunting success, other environmental variables (e.g., prey species, wind orientation, grass height) have been found to be more influential (Funston et al., 2001), possibly indicating that lions in Etosha may not rely heavily on dense vegetation. Furthermore, prey may perceive increased danger in areas with dense vegetation (Sinclair, 1985; Sinclair and Arcese, 1995) therefore they may avoid these areas, causing lions to hunt in more open areas. For example, several studies (Hay et al., 2008; Smit and Prins, 2015; Soto-Shoender et al., 2018) have documented prey species having an increased perceived predation risk associated with high shrub cover. Likewise, dense vegetation can also deter lion hunting success (Davies et al., 2016) and females are known to hunt in sparse vegetation (Loarie et al., 2013) which may explain why the lions in our study were selecting for areas with lower vegetation density, especially shrub biomass.

Selection for high tree density, especially during the day, may be an indicator that hyenas are seeking refuge from the sun for thermoregulation purposes (Swanson et al., 2016; Périquet et al., 2017) and access to prey browsers. As cursorial predators, hyenas tend to hunt in more open areas (Mills, 1990; Holekamp and Dloniak, 2010; Barker et al., 2023), which may explain the selection for areas with low shrub biomass in the wet season. Nonetheless, we did find that hyenas consistently selected for areas with high grass cover. Springbok (*Antidorcas marsupialis*), one of the preferred prey species for Etosha hyenas (Trinkel, 2010), are primarily grazers in Etosha and tend to select for areas with increased grass height (Burger et al., 2000), which may explain the consistent and strong selection for areas with high grass cover.

While traffic intensity did not appear to largely affect lion and hyena habitat selection, both species avoided primary roads during the dry season when tourism is highest, while hyenas utilized tourism roads during the wet season as predicted. Previous studies (Vitale et al., 2020; Mwampeta et al., 2023; Wilkinson et al., 2024) have shown that lions and hyenas in other protected areas frequently use roads, especially when water is located along those roads. However, we suspect inconsistent usage of roads, especially by lions in the wet season, was driven by prey dispersion across the landscape rather than tourism. During the wet season, rain allows prey species to disperse away from waterholes as surface water becomes more widely distributed across the landscape and the vegetation becomes greener (Huang et al., 2023). However, during the dry season, both prey and predator species congregate around predictable waterhole locations, which are primarily situated along the primary and secondary roads for tourism viewing. Fewer waterholes are sparsely located along the tertiary roads, which may explain the lack of tertiary road usage for both species. Thus, we hypothesize that during the dry season, lions and hyenas largely avoided primary roads due to increased tourism activity, while continuing to use secondary roads to access waterholes and prey. In contrast, during the wet season, when tourist presence and road traffic were reduced, hyenas made greater use of primary and secondary roads.

Some use of tourism areas was expected, especially for lions who tend to be less elusive in Etosha. However, these results were surprising given that we predicted hyenas would avoid tourism areas due to their aversion to human presence and competition with lions (Barker et al., 2023; Zanette et al., 2023; Patterson et al., 2024). Given the strong influence of vegetation type for hyena habitat selection in this study, and their tendency to select for dense vegetation for safety and shade (Kushata et al., 2018; Mwampeta et al., 2021), the vegetation types around the waterholes along tourist roads, and accessibility along roads, may be the driver of their selection for areas near secondary roads during the dry season. Moreover, wildlife are protected inside Etosha which receives approximately 200,000 visitors annually, likely resulting in some animal habituation to people. In fact, habituation has been documented in Etosha across various studies, for black-faced impalas (*Aepyceros melampus petersi*) (Matson et al., 2005), hyenas and their prey species (Trinkel, 2010), and African elephants (*Loxodonta* Africana) (Ringstad, 2015). These findings align with other studies where carnivores were habituated to tourism presence in (Lasky, 2022) or near (Wentzel et al., 2021) Kruger National Park, which has 1.2 million visitors annually (Ferreira and Harmse, 2014).

4.1. Conclusions

Collectively, our results show that lions and hyenas exhibit considerable spatio-temporal variation in their habitat selection based on season and time of day, highlighting the complexity of large carnivore habitat selection and management. Nonetheless, water was a main driver of habitat selection for lions, indicating the importance of artificial water sources in sustaining wildlife populations in semi-arid landscapes where natural water is sparce. Further, the selection for areas near less trafficked roads for both species may indicate their use of roads for navigating the bush and accessing water. Nonetheless, the use of secondary tourist roads and waterholes accessible by tourists by both species supports prior studies that have documented habituation of apex predators to humans in large, protected areas (Chizzola et al., 2018; Gunther et al., 2018). While habituation by apex predators to human activities can improve tourist experiences, it increases the likelihood of conflicts with humans at the interface of protected areas and the surrounding landscape, which is often dominated by anthropogenic land uses (Bailey et al., 2016). Thus, further studies are needed to better elucidate the movement behavior of apex predators and other species around protected area boundaries to facilitate conservation initiatives while mitigating human-wildlife conflicts.

CRediT authorship contribution statement

Jessica R. Patterson: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **James C. Beasley:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Stéphanie Périquet-Pearce:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Claudine Cloete:** Writing – review & editing, Resources. **Dipanjan Naha:** Writing – review & editing, Data curation. **Brennan PetersonWood:** Writing – review & editing, Data curation. **Madeline H. Melton:** Writing – review & editing, Data curation.

Ethics statement

Not applicable: This manuscript does not include human or animal research.

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03681.

Data availability

The data that has been used is confidential.

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