Spotted hyena navigation of social-ecological landscapes on a coexistence frontier

Christine E. Wilkinson[1], Wenjing Xu[1], Amalie Luneng Solli[2], Justin S. Brashares[1], Christine Chepkisich[3], Gerald Osuka[4], and Maggi Kelly[1]

[1]University of California Berkeley
[2]University of California Davis
[3]Wildlife Research and Training Institute
[4]Egerton University

October 23, 2023

Abstract

"Coexistence frontiers", or regions where human infrastructure and activity are increasing rapidly or newly appearing, constitute novel environments where wildlife must learn to navigate and coexist with people. It is widely recognized that behaviorally flexible species are more likely to persist in these human-dominated landscapes. Nevertheless, we do not fully understand how these animals navigate landscapes shaped by infrastructure, human activity, and human tolerance. As a widely reviled and behaviorally plastic apex predator, the spotted hyena (Crocuta crocuta) is a model species for understanding how wide-ranging large carnivores navigate social-ecological landscapes in an urbanizing world. Using high-resolution (minimum 5-min fix rates) GPS collar data and supplemental camera trap imagery, we applied resource selection and step selection functions to assess spotted hyena landscape navigation and fine-scale movement decisions in relation to social-ecological features in Lake Nakuru National Park and Soysambu Conservancy, Kenya. Second, we used camera traps and barrier behavior analysis (BaBA) to further examine hyena interactions with barriers. Our results show that environmental covariates—including NDVI, terrain, and proximity to water—were the best predictors of landscape-scale resource selection by hyenas, while human infrastructure and the likelihood of conflict with humans or livestock predicted fine-scale hyena movement decisions. We also found that hyena selection for these characteristics changed seasonally and across land management types. Camera traps documented an exceptionally high number of individual spotted hyenas (234) approaching the national park fence at 16 sites during the study period, and BaBA results suggested that hyenas perceive protected area boundaries' electric fences as risky but may cross them out of necessity. Our results highlight that wildlife adaptability in coexistence frontiers may be expressed differently depending on context and scale. These results also point to the need to incorporate societal factors into multiscale analyses of carnivore movement to effectively plan for human-carnivore coexistence.

Introduction

Human land uses and development are altering landscapes worldwide and restricting the movements of wide-ranging species such as large carnivores (Crooks *et al.* 2011; Ripple *et al.* 2014). One outcome of the expanding human footprint is that carnivores and people are increasingly overlapping with one another. Several tools have been employed in human-dominated landscapes to mitigate carnivore interactions with people, including fencing protected areas or other barriers and policies to separate humans from wildlife (e.g., McInturff *et al.* 2020). Depending on the relative scale and permeability of these physical structures, such efforts often result in new patterns of wildlife movement and navigation (e.g., Wilkinson *et al.* 2021b). On *coexistence frontiers* , where human infrastructure and activity have either recently appeared or are rapidly increasing, carnivores must learn to traverse novel landscapes with novel risks. In such regions, it is critical to identify predictors of landscape navigation for carnivores and determine whether and how these species can adaptively traverse these increasingly human-dominated landscapes (Sanjayan & Crooks 2005).

Understanding carnivore landscape navigation within coexistence frontiers requires social-ecological approaches rather than only considering ecological factors (Lute *et al.* 2020; O'Neal Campbell, 2014). In general, wildlife sharing space with people must navigate three main elements present on the landscape, namely ecological factors, human infrastructure, and human acceptance, that determine *social-ecological landscape permeability* (e.g., Ghoddousi *et al.* 2021). This guiding framework is critical because while certain carnivore species may be able to persist in human-altered habitats (see Athreya *et al.* 2013; Breck *et al.* 2019; Chapron *et al.* 2014; Devens *et al.* 2019), human intolerance may be a strong enough limiting factor that it can override adaptability for carnivore populations or survival of individuals navigating developing landscapes (Moss, Alldredge & Pauli 2016). Thus, human perceptions are likely to be an important factor in determining how carnivores navigate landscapes (Behr *et al.* 2017). On coexistence frontiers, people may not have developed tolerance or acceptance for species which they have not encountered before or which they are now encountering more frequently (e.g., Lute & Carter 2020). In this case, intolerance may serve as a proxy for people employing nonlethal hazing or deterrents or as an indicator for tendencies to conduct illicit persecutory actions toward wildlife (Benson *et al.* 2023; Ditmer *et al.* 2022; Manfredo *et al.* 2021), such as poisoning (see Ogada 2014) or habitat destruction (see Ripple *et al.* 2014). In these social-ecological spaces, people also interact with, respond to, and alter ecological features and processes that influence carnivore movement at different scales, such as vegetation availability (e.g., Bateman & Fleming 2012; Suraci *et al.* 2020) and climatic season (e.g., through changing livestock movements; Schuette *et al.* 2013).

Spatial and ecological scales are important for contextualizing human coexistence with carnivores (Carter & Linnell 2016). For instance, anthropogenic development may have community-level effects by pushing some species into limited remaining natural habitats (Parsons *et al.* 2018), yet at a fine scale, carnivores can exhibit adaptations to anthropogenic development – or even be synanthropic—on an individual level (i.e., Moss *et al.* 2016; Nisi *et al.* 2021; Wang *et al.* 2015; Suraci, Nickel & Wilmers 2020). Through these scale-dependent processes, human-dominated landscapes near protected areas can result in a source-sink dynamic, whereby carnivore populations from protected areas that venture into more densely human-populated regions are more likely to die through anthropogenic causes (Lamb *et al.* 2020). However, individuals may succeed in these spaces by taking advantage of anthropogenic resources at finer scales, depending on human tolerance (i.e., Moss *et al.* 2016). Thus, for large carnivores, which are often highly mobile, social-ecological landscape permeability across scales is essential to maintain populations. Carnivore species living in both human-dominated environments and protected environments may avoid anthropogenic features such as roads and fences (e.g., Baker & Leberg 2018; McInturff *et al.* 2020; Young *et al.* 2019) or change their activity patterns to adjust for human presence (e.g., Gaynor *et al.* 2018). Yet carnivores may also either avoid or be attracted to human infrastructure at different scales (Poessel *et al.* 2014), underpinned by the density of the infrastructure (Morales-Gonzalez *et al.* 2020; Xu *et al* . 2023), the infrastructure's impact on resource availability (i.e., Belton *et al.* 2016), the species involved (Wilkinson *et al.* 2021b), or individual animal characteristics, such as life stage (Thorsen *et al.* 2022).

As a widely reviled (Glickman 1995; Macdonald *et al.* 2022) and behaviorally plastic apex predator (Holekamp & Dloniak 2010), spotted hyenas (*Crocuta crocuta* , hereafter "hyenas") are a model species for understanding the nature of carnivore adaptiveness to human-caused landscape change and negative human perceptions. Hyenas are generally considered one of the most behaviorally flexible carnivore species, yet there have been few empirical conclusions regarding the extent and mechanisms of their adaptiveness to human activities, infrastructure, and tolerance. Green et al. (2018) found that hyena populations in Maasai Mara, Kenya increased in an area of anthropogenic disturbance, possibly linked to increased livestock consumption. In densely populated areas in Ethiopia where native prey is depleted, hyenas have become almost entirely dependent on anthropogenic food (e.g., Yirga *et al.* 2012). However, other studies have found negative, neutral, or nuanced responses to people. In one study in Kenya, hyena activity shifted in response to livestock grazing and other anthropogenic activities (Kolowski *et al.* 2007), while a study in South Africa found that hyena propensity to visit anthropogenic sites varied depending on season, age, or individual (Belton *et al.* 2018). Determining whether a species is surviving or thriving in the presence of humans is complex, as even highly synanthropic species may be exposed to greater levels of stress, toxicants, and disease while living in anthropogenic landscapes (Murray *et al.* 2016; Murray *et al.* 2019). While movement is thus solely the broadest scale at which to assess carnivore survival and wellbeing within coexistence frontiers, understanding how hyenas and other behaviorally plastic mammalian carnivores navigate anthropogenic landscape change is fundamental to forecasting the resilience of movements, food webs, and ecosystems in rapidly developing landscapes.

We sought to provide insight into spotted hyena abilities to navigate coexistence frontiers by examining the following questions in and around Lake Nakuru National Park and Soysambu Conservancy, Kenya: 1) How do spotted hyenas navigate anthropogenic infrastructure, human activity, tolerance, and ecological factors across scales, seasons, and management types (i.e., fully protected vs. multi-use), and 2) How many spotted hyenas cross through the region's conservation fence, and how does spotted hyena fence navigation manifest at a fine scale? We predicted that (1) hyenas would respond differently to ecological factors than they do to anthropogenic infrastructure and activity, (2) hyena selection for and against landscape characteristics would differ at different scales (i.e., fine-scale and landscape scale), (3) hyenas would exhibit different responses to covariates in the rainy vs. the dry season, (4) hyenas with dens in the fully protected national park would be more avoidant of barriers, less avoidant of roads, and more attracted to verified and perceived livestock predation hotspots outside of the park than would hyenas with dens in the multi-use conservancy, and (5) fence crossing would be limited to a few select individuals and hyenas likely perceive fence navigation to be risky. We employed resource selection functions (RSFs) and step-selection functions (SSFs) to determine hyena space use and landscape navigation at the home range and step scales, respectively (Reinking *et al.* 2019). We then used this information to infer whether and how to consider a suite of social-ecological factors when designing for hyena landscape permeability, and present the implications of these inferences for global human-carnivore coexistence.

Materials and Methods

Study site

Our study was conducted in Nakuru County, in the Rift Valley of southwest Kenya, from June 2018- October 2020. The study area (0°26' S, 36°1' E) includes two major wildlife protected areas: Lake Nakuru National Park (LNNP, 188 km^2), which is one of two fully fenced national parks in Kenya, and Soysambu Conservancy (190 km^2), which is mostly fenced and functions as both a wildlife conservancy and a livestock ranch with over 10,000 cattle, sheep, and goats. Fences used in both protected areas are typically ~2m tall and consist of parallel electrified wires, though some stretches of fence are composed of other materials, are in various states of maintenance, or have an additional component of woven wire mesh to reduce wildlife digging. The two large alkaline lakes in the region, Lake Nakuru and Lake Elementeita, are designated UNESCO World Heritage sites. The region supports many species of large mammals, including large carnivore species such as African lion (*Panthera leo*), spotted hyena, and leopard (*Panthera pardus*), and several mesocarnivore species, such as serval (*Leptailurus serval*) and black-backed jackal (*Lupulella mesomelas*). Many carnivore populations in the region remain stable despite heavy historical persecution (Ogutu *et al.* 2017). The region is characterized by woodland, savanna, and dense brush habitats, as well as two rainy and two dry seasons each year.

Field methods and data

Collar deployment and programming

From February-March 2019, 3 female and 4 male spotted hyenas were collared (Savanna Tracking GPS-GSM FlexTrack), representing 5 clans in LNNP and Soysambu Conservancy. Six of these collars (still representing 5 clans) remained in function for most of the study period. Fixes were taken between 6pm-7am, which are the primary active hours of hyenas in this study area. Hourly fix rates were taken from February-April 2019, after which 5-minute fixes were used until May 2020. After this point, the collars were reprogrammed for 1-hour fixes, 24 hours per day.

Covariates

The following covariates (Table 1) were used in analyses of hyena landscape use and navigation: normalized difference vegetation index (NDVI; 30m, Landsat 8 Surface Reflectance Tier 1, rainy and dry seasonal averages for 2019), slope (30m, Shuttle Radar Topography Mission [STRM]), elevation (30m, STRM), distance to rivers, distance to lakes, distance to boundaries, distance to verified livestock predation locations, distance to regions people perceive as being risky due to hyenas, and distance to participatory mapped livestock predation locations during the study period. The latter two variables were derived using participatory mapping data from communities living within 2 km of the protected area boundaries, while the verified predation dataset was from the local wildlife authority, Kenya Wildlife Service (Wilkinson *et al.* 2021a). Because the killing of or retaliation against wildlife is illegal in Kenya, participatory mapped livestock predation and participatory mapped risks from spotted hyenas can serve as proxies for spatially explicit intolerance or acceptance of spotted hyenas by local communities and are associated with the potential for deterrents and aversive behaviors toward hyenas. Euclidean distance was used for all distance layers, and road layers were derived through Open Street Maps and by hand tracing. Fences assessed in barrier analyses were mapped in person by driving and walking the boundaries of the protected areas. All distance covariates were created as rasters with 30m spatial resolution to match the NDVI, slope, and elevation rasters.

Analyses

Assessing space use and landscape navigation

To determine the individual home ranges of the seven collared hyenas, we used the 'adehabitatHR' package in R (R Core Team, 2018) to assess 50% and 95% kernel utilization distributions (KUD) and calculated overlap among home ranges.

To determine landscape feature selection by spotted hyenas, we derived resource selection functions (RSFs) using the 'lme4' package in R, using only the six collared hyenas (3 male and 3 female) whose collars remained active throughout the study. Random points generated were equal to the number of GPS points used, and we found no evidence of collinearity among our covariates (Dellinger *et al.* 2013). We assessed resource selection using generalized linear mixed-effects models with a logit link. Using the raster package and base R, we scaled the following covariates for use in the RSFs: normalized difference vegetation index (NDVI; 30m, Landsat 8), elevation, slope, distance to rivers, distance to lakes, distance to roads, and distance to protected area boundaries. NDVI in this study site can serve as a proxy for land cover, because areas of higher NDVI are generally brush or forest, whereas lower NDVI areas are typically grasslands. After initial data exploration, we included an interaction term—individual and distance to boundary—as a random effect in our candidate model to control for variation in individual boldness. We assessed a global model (for all hyenas) and compared global seasonal (rainy and dry) models, as well as models for hyenas whose dens were in LNNP (n=3), and for hyenas whose dens were in Soysambu Conservancy (n=3). We also assessed and compared models with the following combinations of variables: ecological variables only, ecological and infrastructure, infrastructure only, infrastructure and human perception/experience, and human perception/experience only. Models were ranked based on their Akaike Information Criterion (AIC; Burnham & Anderson 2002), and models within Δ AIC [?]2 were retained to use when assessing coefficient values.

Assessing fine-scale movement decisions

To understand how hyenas select landscape features at the fine/step scale, we derived step selection functions (SSFs) using the amt package in R (R Core Team, 2018). We prepared the hyena data by creating tracks from the data using the mk_track() package, subset the data to only the 5-minute fix rates, and filtered to assure bursts would have a minimum of 2 points. Five random steps were generated for each step used. Scaled covariates and model comparisons reflected those conducted for the RSF analyses. We fit conditional logistic regressions on the covariates, while also considering hyena ID as a cluster term and log of step length (i.e., speed of movement) as an interaction term with boundaries and roads. We used quasi-likelihood independence model criterion (QIC) to rank models and determine top models. We then used acf.test() on the model that best predicted the data to determine the lag at which autocorrelation is no longer observed, and employed destructive sampling to address autocorrelation, removing 2 points between each individual's clusters. Models were then fit on the destructively sampled data. Last, we created a function in R for individual SSF models and the parameters from the global model to visualize the data.

Barrier interactions

To understand hyena behavior around fences and determine the locations of weak or robust fences on the protected area boundaries, we used the Barrier Behavior Analysis (BaBA) methodology developed by Xu et al. (2020). BaBA examines whether, where, and how often animal movements were altered by linear barriers such as fences by classifying movement trajectories within set buffers around target barriers into normal movement (*quick cross* , average movement), altered movement (*bounce* , *trace* , or *back and forth*), and trapped movement. To assess the appropriate sensitivity for the BaBA results, we used BaBA with 50m, 100m, and 150m fence buffer distances within which GPS locations were classified as fence encounters (Xu *et al.* 2020).

Finally, to supplement our understanding of hyena interactions with and crossing of the boundary fences, we used images of spotted hyenas from camera traps placed on sixteen key crossing points at the LNNP fence from June 2018 - November 2019 (see Wilkinson *et al.* 2021b for detailed methodology). Spotted hyenas in camera trap images were individually identified using spot patterns and compared to individuals previously listed in both the LNNP and Soysambu Conservancy hyena ID books (see Supporting Information). Hyenas appearing at the fence were first compared to the clan with a range closest to the camera trap site but then expanded to all others in the book if not identified. The hyena was labeled as unknown if we could not definitively identify the individual. These unknown individuals were later added to the Lake Nakuru or Soysambu Conservancy ID Books under a new ID code and used for further identification of images. We assessed the frequency of fence approaches at each site and by specific individuals, as well as the number of different fence crossing sites visited by each individual.

Results

Landscape-scale space use

Spotted hyena 50% and 95% home ranges (Figure 1) comprised between 6.06-27.29 km^2 ((x = 11.6) and 31.38-132.91 km^2 (x = 61), respectively. Dry season 50% and 95% home ranges comprised 5.88-23.73 km^2 (x = 10.99) and 30.71-143.59 km^2 (x = 87.89), respectively. Rainy season 50% and 95% home ranges comprised 6.06-23.85 km^2 (x = 11.46) and 28.53-111.92 km^2(x = 58.08), respectively. The proportion of 95% home range overlap among different clans spanned between 0.108 and 0.317.

For all spatial analyses, all variables were retained for global models after testing for pairwise correlation (maximum correlation was 0.52, while most pairwise correlations were below 0.2). The global model, including all covariates for the RSFs, revealed selection for higher NDVI, roads, lakes, verified livestock predation, and areas of participatory mapped risk from hyenas, and against elevation, steep slopes, rivers, boundaries, and areas of participatory mapped livestock predation (Table 2). Of these, selection for distance to participatory mapped livestock predation (i.e., greater distances away from these regions; $\beta = 0.271$, $p < 0.001$) and selection against distance to verified livestock predation (i.e., closer distances to these regions; $\beta = -0.255$, $p < 0.001$) showed the strongest effects. When comparing models containing combinations of ecological, infrastructure, and human experience/perception covariates, the model that best predicted the data was the model with all covariates, followed by the model containing only ecological and infrastructure covariates.

Seasonal RSFs comparing all covariates across the rainy and dry seasons showed that in the dry season hyenas exhibit an increase in landscape-scale selection for NDVI, boundaries, and areas of participatory mapped livestock predation, and a decrease in selection for elevation, rivers, areas of verified livestock predation, and areas of participatory mapped risk from hyenas (Figure 2a).

When comparing global models across land management types, hyenas with dens in Soysambu showed stronger selection for or against human experience/acceptance covariates than hyenas with dens in LNNP

(Figure 3a). Soysambu hyenas also showed statistically significant selection against boundaries at the landscape scale (β = 0.236, $p < 0.001$), which was not exhibited as strongly by LNNP hyenas (β = 0.122, p = 0.46).

Fine-scale movement decisions

The global model, including all covariates for the SSFs, revealed step selection for higher NDVI, lakes, roads, areas of verified livestock predation, and areas of participatory mapped livestock predation, and selection against rivers, steep slopes, elevation, boundaries, and areas of participatory mapped risk from hyenas (Table 3). Of these, selection against boundaries showed the strongest effect (β = 0.273, $p < 0.01$), yet there was marked individual variation in selection for all covariates (Figure 4). When comparing models containing combinations of ecological, infrastructure, and human experience/perception factors, the two models within Δ AIC [?]2 were the infrastructure-only model and the model containing infrastructure and human experience/perception covariates.

Seasonal SSFs comparing all covariates across the rainy and dry seasons showed that in the dry season hyenas exhibit an increase in fine-scale selection for elevation, lakes, and roads, and selection against boundaries (Figure 2b).

When comparing global models across land management types, Soysambu hyenas differed from LNNP hyenas in that they showed selection for roads (β = -0.19, $p < 0.001$). In contrast, LNNP hyenas differed from Soysambu in that they showed selection for lower NDVI (β = -0.077, $p < 0.001$) and areas of verified livestock predation (β = -0.552, $p < 0.001$) and against boundaries (β = 0.62, $p < 0.001$, Figure 3b). A case study on a single hyena that was known to frequently cross between the two protected areas (Supporting Information) showed selection against boundaries during the dry season (β = 0.186, $p < 0.001$) and for boundaries in the rainy season (β = -0.068, $p < 0.01$), as well as an increase in speed of movement (i.e., log of step length) in relation to boundary selection during the rainy season (β = 0.062, $p < 0.001$) as compared to the dry season (β = 0.035, $p < 0.001$).

Barrier interactions

A 50-meter fence buffer best captured *quick cross* events, or events where hyenas quickly crossed a fence after approaching it. Spotted hyena individuals encountered fences on average 193 (σ=168.5) times during the study period. Overwhelmingly, hyenas encountering fences either exhibited *quick cross* (n=583, or 49% of all fence encounters) or *bounce* (n=507, 42.7%), with *average movement* (n=45, 3.8%), *trace (* 3 times, 0.25%), and *back and forth* (n=7, 0.59%) exhibited occasionally (Figure 5a).*Bounce* is a behavior in which hyenas that encounter the fence immediately walk away from the fence. There was marked individual variation in overall fence encounters, as illustrated by high standard deviations in average fence encounter frequency. *Bounce* behaviors were slightly more prevalent during the dry season (prop. = 0.44 in the dry season, .41 in the wet season), though this result was insignificant (Mann-Whitney p = 0.48 and p = 0.699; Figure 5b). *Quick cross*behaviors remained the same across seasons (prop. = 0.49). Judging by differences in hyena behaviors around different fence segments, some segments may be more permeable than others. The highest concentration of quick cross behaviors appeared to be on the fence lines between the two protected areas, indicating high permeability for those fence segments. Meanwhile, the bounce behaviors had a considerably wider spread along the boundaries (see Supporting Information), indicating regions where hyenas may have attempted to cross but could not due to fence impermeability. Notably, fence behaviors revealed several crossing points connecting LNNP to Soysambu Conservancy.

Camera trap data revealed 234 individual hyenas spanning at least 4 clans and various social ranks approaching the fence across the 16 studied sites, with one site having a minimum of 67 different individuals appearing at the fence (Table 4; Supporting Information). Across all sites, 63 individuals appeared at the fence in more than 10 images during the study period.

Discussion

Spotted hyenas in this rapidly developing landscape appear to be selecting for and against environmental, infrastructural, and human tolerance characteristics at different scales, demonstrating that it is crucial to consider social-ecological landscape permeability on coexistence frontiers and in human-dominated landscapes generally. We found that parallel wire electric fences may be perceived as a risk by hyenas – as indicated by their interactions with the fence largely consisting of either quickly crossing or immediately leaving the area—while simultaneously being highly permeable to this species, which has implications for coexistence and movement for this apex predator. Additionally, the hyenas in this region exhibited several landscape use and navigation propensities that differ from previous studies on this species conducted in landscapes that are on the high or low extremes of anthropogenic influences.

Space use

Hyena ranges were considerably larger than expected given the small size of the two protected areas (Honer *et al.* 2002; Watts & Holekamp 2008), potentially further enabled by the high degree of overlap among home ranges. Other studies have shown that adapting to human-dominated environments may change the fundamental social behaviors of certain carnivore species (e.g., Widdows & Downs 2015). In our study area, hyenas from different clans exhibited consistent range overlap and are known to frequently enter one another's ranges for anthropogenic resources, such as discarded livestock carcasses (C.E. Wilkinson, pers. obs.). This stands in contrast to some other studies (i.e., Barker*et al.* 2022) and runs counter to the known territorial behaviors of spotted hyenas (Boydston *et al.* 2001; Watts & Holekamp 2007), indicating potential resource- or space-driven intraspecific social behavior changes which warrant further research.

Hyena home ranges expanded during the dry season, in contrast to studies in ecologically similar regions that show wildlife tends to disperse more widely in the wet season (Koziarski *et al. 2016*). Previous research has also shown that spotted hyenas have wider ranges in the wet season due to the seasonal movement and presence of their wild ungulate prey (Trinkel *et al.* 2004). Similarly, a study on leopards (*Panthera pardus*) in a mixed-use landscape revealed that they avoided protected areas during the dry season and instead favored tea plantations and forest patches (Naha *et al.* 2021). Our observed counterintuitive increase in hyena range sizes during the dry season rather than the rainy season could thus be due to two factors inherent to this fenced ecosystem. First, due to the electric boundary fences, many ungulate species cannot disperse during the rainy season (Wilkinson *et al.* 2021b), meaning hyenas have little opportunity or need to expand ranges to seasonally track wild prey. Second, the small sizes of the protected areas, coupled with an ongoing rise in lake waters in the national park (James 2022), may be driving seasonal resource limitations for spotted hyenas and causing them to expand their ranges during the dry season.

Social-ecological landscape navigation and fine-scale movement decisions

Hyenas in this region are selecting for different factors at the landscape scale than at a fine scale. Differences in resource selection at different scales were particularly apparent for infrastructure and human experience characteristics, and less apparent for environmental characteristics, selection for which largely remained the same across RSF and SSF results. On a fine scale, hyena navigation appears to be more heavily influenced by roads, fences, and human experiences and acceptance than by environmental characteristics such as NDVI and proximity to water. These scale-dependent affects likely stem from a combination of factors, with fine-scale movements dictated by hyena behavioral flexibility, and landscape scale selection dictated by broader resource availability. While there are changes in the magnitude of effect, at both broad and fine scales hyenas in this region generally select for vegetation greenness, lakes, and roads, and against rivers, boundaries, slopes, and high elevation. In arid environments, spotted hyena hydration is mostly derived from prey rather than water sources (Green *et al.* 1984), and hyenas can also survive for a week or more without water (Holekamp & Dloniak 2010); thus, selection against rivers could reflect the aridity of the region. Additionally, though the two major lakes in the region are highly alkaline, hyenas have been observed hunting flamingos, wallowing, and using the lakesides' heavy vegetation as refuge during the heat of the day (authors' observations). Thus, even undrinkable water sources can serve as critical habitat for hyenas (e.g., Matsumoto-Oda 2021).

At the landscape scale, hyenas are selecting against participatory mapped livestock predation areas and for areas of participatory mapped risk, while the opposite holds true for fine scale selection. The landscape-scale selection for and against these human acceptance covariates may indicate that hyenas are broadly selecting for areas in which they may face hazing or be poisoned (i.e., perceived risks from and low tolerance for hyenas), and against areas that people use for livestock grazing (i.e., participatory mapped livestock predation). People are also likely perceiving the highest risks from hyenas in places that constitute suitable hyena habitat, which supports hyena landscape-scale selection for these areas. In densely populated areas where tolerance is high or there are policies against wildlife killing, carnivore populations may thrive (Athreya *et al.* 2013; Gebresenbet *et al.* 2018), yet in areas where tolerance is low (such as in our study site), carnivore populations can be negatively affected by retaliation and other practices (Ripple *et al.* 2014). Hyenas in this study site may also be avoiding participatory mapped livestock predation areas—which are likely most often used for grazing—as locations with consistent, predictable risks (i.e., through deterrents and higher levels of human activities). This reflects findings from previous studies in regions with less development, in which spotted hyenas reduced their activities in response to livestock grazing (i.e., in the Maasai Mara, Kolowski *et al.* 2007).

Our results also showed seasonal differences in landscape-scale and fine scale hyena selection for environmental and anthropogenic characteristics. At the landscape scale, in the dry season, hyenas exhibited an increase in selection for vegetation greenness, boundaries, and participatory mapped livestock predation. The latter two support our findings that hyenas may be expanding their ranges and traveling outside of the protected areas during the dry season. When resources are scarce, animals living alongside people may be more likely to choose anthropogenic food sources (Johnson *et al.* 2015), and hyena predation on livestock or scavenging of livestock and other anthropogenic food sources may be increasing during dry seasons. The boundary navigation result at the landscape level also supports these hyenas' tendency toward dry season range expansion. Meanwhile, at a fine scale, the dry season showed a minor increase in hyena navigation toward roads, with minimal seasonal differences in selection for environmental and human experience characteristics. While species in other studies have been known to use roads for easier traversal of the landscape (Abrahms *et al.* 2015; Hill *et al.* 2020), hyenas in this study area may also use roads in the dry season for dust bathing and access to artificial water points, particularly in the conservancy.

When looking at variation in movement for hyenas living in different management types across both seasons, at the landscape scale roads were more likely to be avoided by Soysambu hyenas than LNNP hyenas, despite human use of roads being extremely low in the conservancy at night. One reason for this could be that despite being active at night, hyenas in Soysambu associate roads with the abundance of human activities that occur during the day on the roads within the conservancy, while in LNNP, there is only one activity happening on roads: tourism. Vehicle speeds in the national park are also heavily regulated. Hyena avoidance of roads in Soysambu stands in contrast to research that has found that animals may select for human infrastructure at night for resources or ease of movement while avoiding it during the day when humans are more active (e.g., Toverud 2019). However, hyenas are generally more skittish in the conservancy than in the national park, possibly due to historical hyena bounties (K. Combes, pers. comm.) before the conservancy's designation as a wildlife habitat. The anthropogenic activity signature on Soysambu's roads may thus have a strong enough effect on the spotted hyena's human-caused "landscape of fear" (Smith *et al.* 2017; Suraci *et al.* 2019) as to contribute to nighttime avoidance of roads that are devoid of human activity.

SSFs revealed that hyenas with dens in LNNP are also selecting against boundaries to a much stronger degree than hyenas with dens in Soysambu. However, fine scale selection against vegetation greenness and toward verified livestock predation locations outside of the park, as well as known fence-crossing behaviors by LNNP hyenas (Wilkinson *et al.* 2021b), point to a lack of sufficient resources or space in the national park.

Fence behaviors

The abundance of *quick cross* and *bounce* behaviors captured by the barrier behavior analysis, as opposed to walking along the fence or exhibiting average movements near the fence, implies that hyenas may perceive boundaries as risky in this rapidly developing area, and may approach the fence only out of need. When they reach the fence, if they cannot cross, they appear to immediately move away (i.e., *bounce*), and if the fence is permeable, they cross quickly. While McInturff et al. (2020) concluded that fences can create interspecific "ecological winners and losers", the hyena populations in this region may be a combination of both, depending on the individual, season, land management type, or other factors.

Though our study was able to assess movements of hyenas representing 5 clans, the sample size for assessing fence navigation was limited since not every collared hyena approached the fence lines. Our supplementary camera trap analyses of individual hyenas at the fence line revealed hyenas are approaching the fence and possibly crossing in and out of the national park in extraordinary numbers. Previous studies have suggested that social rank, age, and sex influence spotted hyena risk-taking behavior (Belton *et al.* 2018; Green *et al.* 2018) and space use (Boydston *et al.* 2003), yet our analysis shows that individuals spanning different demographics and social ranks may be crossing in and out of the national park. While evidence suggests these behaviors may be caused by resource limitations within this relatively small protected area, further research is needed to assess the ecological factors driving these behaviors.

Implications for landscape permeability

At broad scales, hyenas in this developing region appear to be selecting for ecological characteristics that reflect their resource selection in other, less developed systems. In contrast, movement choices at a fine scale are more nuanced and influenced by anthropogenic factors. Hyena clan sizes in this region are relatively large (with more than 50 animals per group for clans assessed thus far) despite the small size of the protected areas, which could be influencing the apparent movement of hyenas toward people and likely toward anthropogenic resource subsidies. Other studies in similar environments have estimated hyena carrying capacity to be orders of magnitudes lower than the populations seen in our study site (e.g., Holekamp & Smale 1995; Yirga *et al.* 2014).

Despite this suspected significant reliance on anthropogenic resources, hyenas showed a general aversion to roads, with different selection strengths depending on scale and land management type, which is contrary to what we expected. Fences also present a semi-permeable barrier for spotted hyenas, which appear to cross them as quickly as possible rather than lingering. Other studies have found that keeping development and subdivision below a certain threshold may allow for sustained carnivore navigation of the landscape between core habitat areas (Smith *et al.* 2019; Xu *et al.* 2023). This may also prove true for the spotted hyenas, which appear to have complex relationships with infrastructure within and surrounding the two protected areas. Yet, hyena relationships with fences can also provide information that is helpful for management efforts. We can use fence behavior analyses to determine existing permeable fence segments (Xu *et al* . 2020) and make ecologically-informed decisions about where carnivore (and other wildlife) corridors in and out of fenced regions will be the most useful, practical, and cost-effective.

Overall, our results imply that anthropogenic factors may influence fine scale decision making differently than landscape-scale selection. Hyenas may be adaptable enough to switch to anthropogenic food sources in regions of depleted natural prey or limited resources, yet their ability to rely on anthropogenic food may be linked to regional tolerance of hyenas (e.g., Yirga *et al.* 2012). Spatially explicit human acceptance and experience have the potential to predict where wildlife corridors are likely to succeed for certain species or taxa, while also providing insight into how wildlife may be using anthropogenic resources (Behr *et al.* 2017; Ghoddousi *et al.* 2021). Coupled with hyena context-specific selection for and against infrastructure characteristics, these results demonstrate that a multiscale and multidisciplinary understanding of social-ecological landscape use and navigation can help to determine where and when this species may thrive in human-dominated landscapes. This approach is essential for a species that is key for removing carcasses and diseases from the environment (Sonawane *et al.* 2021), and in a location that is becoming increasingly fenced, but the social-ecological approaches used here can also be applied to movements and reintroductions of other controversial wildlife species in other settings (see Ditmer *et al.* 2022; Manfredo *et al* . 2021; Vasudev *et al.* 2023; Williamson *et al.* 2023; Williamson & Sage 2020). Future research on social-ecological landscape permeability for wildlife should include the incorporation of detailed land cover covariates, in-depth quantification of tolerance and experience as spatial proxies for behaviors, and testing of GPS collar data across RSF- and SSF-informed social-ecological least cost corridor models.

Conclusion

Spotted hyenas are one of the most behaviorally flexible large carnivores. Yet, their reputation for adaptiveness has previously discouraged studies on whether and to what extent people impact their movements and behaviors. As a widespread species across Africa, spotted hyenas provide us with a litmus test for understanding carnivore abilities to live alongside people and navigate landscapes on coexistence frontiers. Yet, we also know that coexistence requires adaptation by both people and carnivores to succeed (Chapron *et al.* 2014). This study has demonstrated that integrating spatial and contextual information on ecology, infrastructure, and human tolerance can help us to better examine how carnivores may adapt to proliferating human disturbances and learn to navigate human-dominated landscapes at different scales. By gaining these holistic understandings of the effects of ongoing global urbanization on behaviorally flexible, ecologically critical species, we may be able to design and redesign anthropogenic landscapes that prioritize ecological resilience and environmental justice.

Data availability statement : Data will be made public upon acceptance of this manuscript (https://doi.org/10.5061/dryad.0vtb8h52).

References

Abrahms, B., Jordan, N.B., Golabek, K.A., McNutt, J.W., Wilson, A.M., & Brashares, J.S. (2015). 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

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., & Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* ,**8** ,e57872.https://doi.org/10.1371/journal.pone.0057872

Baker, A.D., & Leberg, P.L. (2018). Impacts of human recreation on carnivores in protected areas. *PloS ONE* ,**13** ,e0195436.

Bateman, P.W., & Fleming, P.A. (2012). Big city life: carnivores in urban environments. *J Zool* ,**287** , 1-23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

Behr, D.M., Ozgul, A., & Cozzi, G. (2017). Combining human acceptance and habitat suitability in a unified socio-ecological suitability model: A case study of the wolf in Switzerland. *J Appl. Ecol.* ,**54** ,1919-1929.https://doi.org/10.1111/1365-2664.12880

Belton, L.E., Cameron, E.Z., & Dalerum, F. (2018). Spotted hyaena visitation at anthropogenic sites in the Kruger National Park, South Africa. *African Zoology,* **53** ,113–118.https://doi.org/10.1080/15627020.2018.1518728

Belton, L.E., Cameron, E.Z., Dalerum, F. (2016). Spotted hyaena space use in relation to human infrastructure inside a protected area.*PeerJ* ,**4** ,e2596.

Benson, J.F., Dougherty, K.D., Beier, P., Boyce, W.M., Cristescu, B., Gammons, D.J., . . . Dellinger, J.A. (2023). The ecology of human-caused mortality for a protected large carnivore.*PNAS* ,**120** ,e2220030120. https://doi.org/10.1073/pnas.2220030120

Boydston, E.E., Kapheim, K.M., Szykman, M., Holekamp, K.E. (2003). Individual variation in space use by female spotted hyenas. *J Mammal.,* **84** ,1006-1018.

Boydston, E.E., Morelli, T.L., Holekamp, K.E. (2001). Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, Crocuta crocuta). *Ethology* ,**107** ,369-385. https://doi.org/10.1046/j.1439-0310.2001.00672.x

Breck, S.W., Poessel, S.A., Mahoney, P., & Young, J.K. (2019). The intrepid urban coyote: a comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Nature Scientific Reports*

,**9** ,2104.https://doi.org/10.1038/s41598-019-38543-5

Burnham, K.P., & Anderson, D.R. (2002). *Model selection and inference: A practical information-theoretic approach* , 2nd Ed. Springer.

Carter, N.H., & Linnell, J.D.C. (2016). Co-adaptation is key to coexisting with large carnivores. *TREE* ,**31** ,575-578.https://doi.org/10.1016/j.tree.2016.05.006

Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andren, H., ... Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* ,**346** ,6216.https://doi.org/10.1126/science.1257553

Crooks, K.R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* ,**16** ,488-502.https://doi.org/10.1046/j.1523-1739.2002.00386.x

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Phil. Trans. B.,* **366** ,2642-2651.https://doi.org/10.1098%2Frstb.2011.0120

Cushman, S.A., McRae, B., Adriaensen, F., Beier, P., Shirley, M., & Zeller, K. (2013). Biological corridors and connectivity. In Macdonald DW, Willis, K.J. (eds) *Key topics in conservation biology 2* . Wiley-Blackwell, Hoboken, pp. 384-404.https://doi.org/10.1002/9781118520178.ch21

Devens, C.H., Hayward, M.W., Tshabalala, T., Dickman, A., McManus, J.S., Smuts, B., & Somers, M.J. (2019). Estimating leopard density across the highly modified human-dominated landscape of the Western Cape, South Africa. *Oryx* ,**55** ,34-45.https://doi.org/10.1017/S0030605318001473

Ditmer, M.A., Wittemyer, G., Breck, S.W., & Crooks, K.R. (2022). Defining ecological and socially suitable habitat for the reintroduction of an apex predator. *Global Ecology and Conservation* ,**38** ,e02192.https://doi.org/10.1016/j.gecco.2022.e02192

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., & Mao, J.S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* ,**86** ,1320-1330.https://doi.org/10.1890/04-0953

Gebresenbet, F., Baraki, B., Yirga, G., Sillero-Zubiri, C., & Bauer, H. (2018). A culture of tolerance: coexisting with large carnivores in the Kafa Highlands, Ethiopia. *Oryx* ,**52** ,751-760.https://doi.org/10.1017/S0030605316001356

Ghoddousi, A., Buchholtz, E.K., Dietsch, A.M., Williamson, M.A., Sharma, S., Balkenhol, N., ... Dutta, T. (2021). Anthropogenic resistance: accounting for human behavior in wildlife connectivity planning. *One Earth* ,**4** ,39-48.https://doi.org/10.1016/j.oneear.2020.12.003

Glickman, S. (1995). The spotted hyena from Aristotle to the Lion King: Reputation is everything. *Social Research* ,**62** ,501-537.https://www.jstor.org/stable/40971108

Green, D.S., Johnson-Ulrich, L., Couraud, H.E., & Holekamp, K.E. (2018). Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodivers. Cons* ,**27** ,871-889.https://doi.org/10.1007/s10531-017-1469-7

Green, B., Anderson, J., & Whateley, T. (1984). Water and sodium turnover and estimated food consumption in free-living lions (Panthera leo) and spotted hyenas (Crocuta crocuta). *J. Mammal.* ,**65** ,593-599.https://doi.org/10.2307/1380842

Hill, J.E., Devault, T.L., & Belant, J.L. (2020). A review of ecological factors promoting road use by mammals. *Mammal Review* ,**51** ,214-227.https://doi.org/10.1111/mam.12222

Holekamp, K.E., & Dloniak, S.M. (2010). Chapter 6- Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Adv. Study Behav.* ,**42** ,189-229.https://doi.org/10.1016/S0065-3454(10)42006-9

Holekamp, K.E., & Smale, L. (1995). Rapid change in offspring sex ratios after clan fission in the spotted hyena. *Amer. Nat.* ,**145** ,261-278.https://doi.org/10.1086/285739

Honer, O.P., Wachter, B., East, M.L., & Hofer, H. (2002). The response of spotted hyenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *J. Animal Ecol.* ,**71** ,236-246.https://doi.org/10.1046/j.1365-2656.2002.00596.x

James, M.M. (2022). Establishing the relationship between LULC changes, temperature, precipitation, and water level rise: Case study of Lake Nakuru Basin, Kenya. Thesis, University of Nairobi.

Johnson, H.E., Breck, S.W., Baruch-Mordo, S., Lewis, D.L., Lackey, C.W., Wilson, K.R., ... Beckmann, J.P. (2015). Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. *Biological Conservation* ,**187** ,164-172.https://doi.org/10.1016/j.biocon.2015.04.014

Kolowski, J.M., Katan, D., Theis, K.R., & Holekamp, K.E. (2007). Daily patterns of activity in the spotted hyena. *J. Mammal.,* **88** ,1017-1028.https://doi.org/10.1644/06-MAMM-A-143R.1

Koziarski, A., Kissui, B., & Kiffner, C. (2016). Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. *Biological Conservation* ,**199** ,41-50.https://doi.org/10.1016/j.biocon.2016.04.029

Lamb, C.T., Ford, A.T., McLellan, B.N., Proctor, M.F., Mowat, G., Ciarniello, L., ... Boutin, S. (2020). The ecology of human-carnivore coexistence.*PNAS* ,**117** ,17876-17883.https://doi.org/10.1073/pnas.1922097117

Lute, M.L., & Carter, N.H. (2020). Are we coexisting with carnivores in the American West? *Front. Ecol. Evol.* ,**8** ,48.https://doi.org/10.3389/fevo.2020.00048

Lute, M.L., Serenari, C., Drake, M.D., Peterson, M.N., Jensen, J., Belyea, C., ... White, M. (2020). Modeling urban socio-ecological drivers of human-carnivore coexistence. *J. Urban Ecol.* ,**6** ,juaa022.https://doi.org/10.1093/jue/juaa022

Macdonald, D.W., Johnson, P.J., Burnham, D., Dickman, A., Hinks, A., Sillero-Zubiri, C., & Macdonald, E.A. (2022). Understanding nuanced preferences for carnivore conservation: To know them is not always to love them. *Global Ecol. Cons.* ,**37** ,e02150.https://doi.org/10.1016/j.gecco.2022.e02150

Manfredo, M.J., Berl, R.E. W., Teel, T.L., & Bruskotter, J.T. (2021). Bringing social values to wildlife conservation decisions. *Front. Ecol. Environ.* ,**19** ,355-362.https://doi.org/10.1002/fee.2356

Matsumoto-Oda, A. (2021). Bathing behaviour in spotted hyenas (Crocuta crocuta) in Laikipia, Kenya: Two observational cases. *J. East Afr Nat. Hist.* ,**110** ,87-92.https://doi.org/10.2982/028.110.0202

McClure, M., Dickson, B.G., & Nicholson, K.L. (2017). Modeling connectivity to identify current and future anthropogenic barriers to movement of large carnivores: A case study in the American southwest.*Ecol. Evol.* ,**7** ,3762-3772.https://doi.org/10.1002/ece3.2939

McInturff, A., Xu, W., Wilkinson, C.E., Dejid, N., & Brashares, J.S. (2020). Fence ecology: Frameworks for understanding the ecological effects of fences.*BioScience* ,**70** ,971-985.https://doi.org/10.1093/biosci/biaa103

Morales-Gonzalez, A., Ruiz-Villar, H., Ordiz, A., Penteriani, V. (2020). Large carnivores living alongside humans: Brown bears in human-modified landscapes. *Global Ecology and Conservation* ,**22** ,e00937.

Moss, W.E., Alldredge, M.W., & Pauli, J.N. (2016). Quantifying risk and resource use for a large carnivore in an expanding urban-wildland interface. *J. Appl. Ecol.,* **53** ,371-378.https://doi.org/10.1111/1365-2664.12563

Murray, M.H., Sanchez, C.A., Becker, D.J., Byers, K.A., Worsley-Tonks, K.E.L., & Craft, M.E. (2019). City sicker? A meta-analysis of wildlife health and urbanization. *Front. Ecol. Environ.* ,**17** ,575-583.https://doi.org/10.1002/fee.2126

Murray, M.H., Hill, J., Whyte, P., & Cassady St. Clair, C. (2016). Urban compost attracts coyotes, contains toxins, and may promote disease in urban-adapted wildlife.*EcoHealth* ,**13** ,285-292.doi:10.1007/s10393-016-1105-0

Naha, D., Dash, K.S., Kupferman, C., Beasley, J.C., & Sathyakumar, S. (2021). Movement behavior of a solitary large carnivore within a hotspot of human-wildlife conflicts in India. *Nature Scientific Reports* ,**11** ,3862.https://doi.org/10.1038/s41598-021-83262-5

Nisi, A.C., Suraci, J.P., Ranc, N., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S, *et al* . (2021). Temporal scale of habitat selection for large carnivores: Balancing energetics, risk and finding prey.*J. Animal Ecol.* ,**91** ,182-195.

Ogada, D.L. (2014). The power of poison: pesticide poisoning of Africa's wildlife. *Ann NY Acad Sci,* **1322** ,1–20.https://doi.org/10.1111/nyas.12405

O'Neal Campbell, M. (2014). Urban planning for cougar presence in North America: Practices, challenges, and benefits. In *Urban Planning: Practices, Challenges, and Benefits* . Amado, M.P. (Ed). Nova Science Publishers

Parsons, A.W., Rota, C.T., Forrester, C.T., Baker-Whatton, M.C., McShea, W.J., Schuttler, S., . . . Kays, R. (2018). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *J. Appl. Ecol.* ,**56** ,1894-1904.https://doi.org/10.1111/1365-2664.13385

Poessel, S.A., Burdett, C.L., Boydston, E.E., Lyren, L.M., Alonso, R.S., Fisher, R.N., & Crooks, K.R. (2014). Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. *Biological Conservation,* **180** ,224-232.https://doi.org/10.1016/j.biocon.2014.10.010

Reinking, A.K., Smith, K.T., Mong, T.W., Read, M.J., & Beck, J.L. (2019). Across scales, pronghorn select sagebrush, avoid fences, and show negative responses to anthropogenic features in winter.*Ecosphere* ,**10** ,e02722.https://doi.org/10.1002/ecs2.2722

Ripple W.J., Estes J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., . . . Wirsing, A.J. (2014). Status and ecological effects of the world's largest carnivores.*Science* ,**343** ,1241484.https://doi.org/10.1126/science.1241484

Sanjayan, M.A., & Crooks, K.R. (2005). 11. Maintaining connectivity in urbanizing landscapes. In *Nature in Fragments: The Legacy of Sprawl* . Eds Elizabeth A. Johnson and Michael W. Klemens, New York Chichester, West Sussex: Columbia University Press. pp.239-262.https://doi.org/10.7312/john12778-014

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proc Roy. Soc. B.* ,**284** , 20170433.https://doi.org/10.1098/rspb.2017.0433

Sonawane, C., Yirga, G., Carter, N.H. (2021). Public health and economic benefits of spotted hyenas Crocuta crocuta in a peri-urban system.*J. Appl. Ecol.* ,**58** ,2892-2902.

Suraci, J.P., Nickel, B.A., Wilmers, C.C. (2020). Fine-scale movement decisions by a large carnivore inform conservation planning in human-dominated landscapes. *Landscape Ecology* ,**35** ,1635-1649.

Suraci, J.P., Clinchy, M., Zanette, L.Y., Wilmers, C.C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* ,**22** ,1578-1586.https://doi.org/10.1111/ele.13344

Thorsen, N.H., Hansen, J.E., Stoen, O.-G., Kindberg, J., Zedrosser, A., Frank, S.C. (2022). Movement and habitat selection of a large carnivore in response to human infrastructure differs by life stage.*Movement*

Ecology, **52.**

Toverud, F.S.K. (2019). Linking high frequency GPS data with multiscale habitat selection; A study of an adaptable carnivore in a fragmented landscape. *Masters thesis,* Norwegian University of Life Sciences.

Trinkel, M., Fleischmann, P.H., Steindorfer, A.F., & Kastberger, G. (2004). Spotted hyenas (Crocuta crocuta) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia. *J. Zool.* ,**264** ,125-133.Doi:10.1017/S0952836904005588

Vasudev, D., Fletcher Jr., R.J., Srinivas, N., Goswami, V.R. (2023). Mapping the connectivity-conflict interface to inform conservation.*PNAS* ,**120** ,e2211482119.

Wang, Y., Allen, M.L., Wilmers, C.C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation* ,**190** ,23-33.

Watts, H.E., & Holekamp, K.E. (2008). Interspecific competition influences reproduction in spotted hyenas. *J. Zool.* ,**276** ,402-410.https://doi.org/10.1111/j.1469-7998.2008.00506.x

Watts, H.E., & Holekamp, K.E. (2007). Hyena societies. *Current Biology* , **17** .

Wilkinson, C.E., Brashares, J.S., Bett, A.C., & Kelly, M. (2021a). Examining drivers of divergence in recorded and perceived human-carnivore conflict hotspots by integrating participatory and ecological data. *Front. Cons. Sci.,* **2** ,681769. https://doi.org/10.3389/fcosc.2021.681769

Wilkinson, C.E., McInturff, A., Kelly, M., & Brashares, J.S. (2021b). Quantifying wildlife responses to conservation fencing in East Africa.*Biological Conservation,* **256** ,109071.https://doi.org/10.1016/j.biocon.2021.109071

Williamson, M.A., Parrot, L. Carter, N.H., Ford, A.T. (2023). Implementation resistance and the human dimensions of connectivity planning. *People and Nature* .https://doi.org/10.1002/pan3.10525

Williamson, M.A., & Sage, A. (2020). Integrated spatial analysis for human-wildlife coexistence in the American West. *Environmental Research Letters* ,**15** ,021001-1- 021001-7.

Xu, W., Gigliotti, L.C., Royaute, R., Sawyer, H., Middleton, A.D. 2023. Fencing amplifies individual differences in movement with implications on survival for two migratory ungulates. *J. Animal Ecol.* ,**92** ,677-689.

Xu, W., Dejid, N., Herrmann, V., Sawyer, H., Middleton, A.D. (2020). Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. *J. Appl. Ecol.,* **58** ,690-698.https://doi.org/10.1111/1365-2664.13806

Yirga, G., Gebresenbet, F., Deckers, J., & Bauer, H. (2014). Status of lion (Panthera leo) and spotted hyena (Crocuta crocuta) in Nechisar National Park, Ethiopia. *Momona Ethiopian J. Science* ,**6** ,127-137.https://doi.org/10.4314/mejs.v6i2.109714

Young, J.K., Golla, J., Draper, J.P., Broman, D., Blankenship, T., Heilbrun, R. (2019). Space use and movement of urban bobcats.*Animals* ,**9** ,275.https://doi.org/10.3390/ani9050275

Zeller, K.A., McGarigal, K., Cushman, S.A., Beier, P., Vickers, W., & Boyce, W.M. (2016). Using step and path selection functions for estimating resistance to movement: pumas as a case study.*Landscape Ecology* ,**31** ,1319-1335.doi:10.1007/s10980-015-0301-6

Figures and Tables

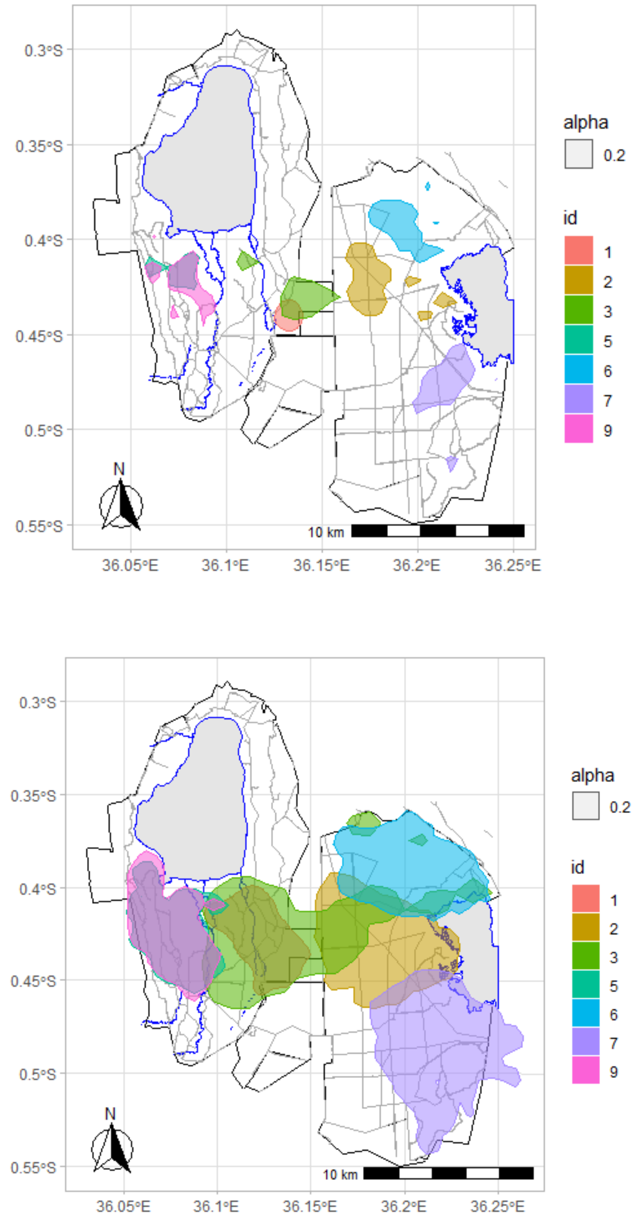

Figure 1. 50% (left panel) and 95% (right panel) kernel utilization distribution home ranges based on GPS collar data for 7 spotted hyenas representing 5 clans in Lake Nakuru National Park (western side of maps) and Soysambu Conservancy (eastern side of maps), Kenya. Hyenas 1 and 3 are in the same clan and hyenas 5 and 9 are in the same clan.

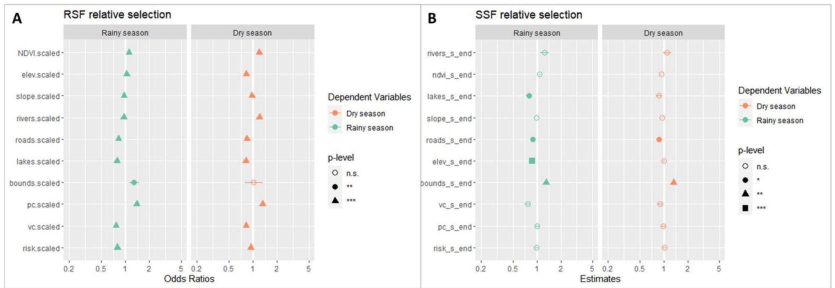

Figure 2. Seasonal results using a) resource selection functions and b) step selection functions for spotted hyena. Bounds = protected area boundaries, VC= verified livestock predation, PC = participatory mapped livestock predation, and risk = participatory mapped risk from spotted hyenas.

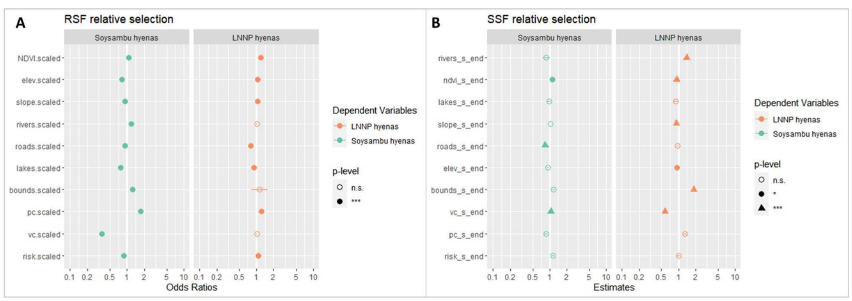

Figure 3. A) Resource selection and b) step selection function model outputs across land management types (LNNP: fully protected, or Soysambu: multi-use) for spotted hyena. Bounds = protected area boundaries, VC= verified livestock predation, PC = participatory mapped livestock predation, and risk = participatory mapped risk from spotted hyenas. "N.S." indicates not significant.

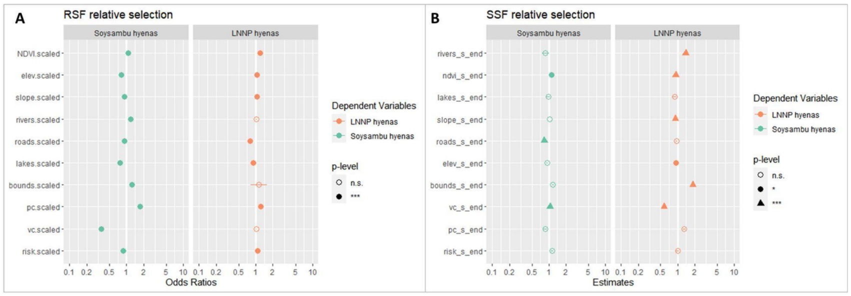

Figure 4. Relative covariate selection strength by individual collared spotted hyenas living in and near Lake Nakuru National Park and Soysambu Conservancy, Kenya, revealed through step selection functions using conditional logistic regression. Only the six hyenas whose data were retained for the movement analyses are included.

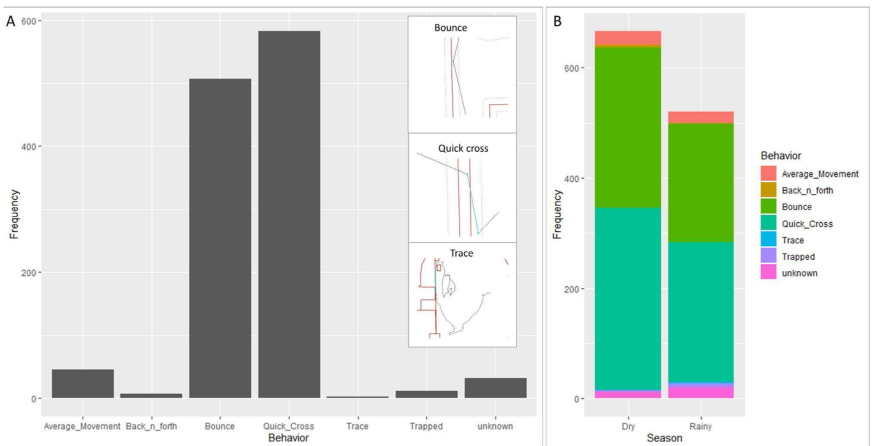

Figure 5. A) Total frequency of fence behaviors revealed through Barrier Behavior Analysis (BaBA) using a buffer distance of 50, and b) seasonal frequency of fence behaviors for spotted hyenas living in and near Lake Nakuru National Park and Soysambu Conservancy, Kenya.

Table 1. Covariates analyzed for resource selection and step selection functions. All rasters were resampled to 30m^2 spatial resolution.

Covariate Type	**Covariate**	**Source**
Ecological	Normalized difference vegetation index (NDVI); rainy season average for 2019	Landsat 8 S
	NDVI; dry season average for 2019	Landsat 8 S
	Slope	Shuttle Rad
	Elevation	Shuttle Rad
	Distance to rivers	Derived fro

	Distance to lakes	Derived fro
Anthropogenic infrastructure	Distance to roads	Open Stree
	Distance to boundaries	Derived fro
Human tolerance	Distance to verified livestock predation locations	Derived fro
	Distance to participatory mapped livestock predation locations	Derived fro
	Distance to regions perceived as risky due to hyenas	Derived fro

Table 2. Results from global resource selection function model (generalized linear model with a logit link) for spotted hyenas.

Variable	*coeff*	*se*	*z-value*	*p-value*
NDVI	0.142	0.003	42.738	<0.001
Elevation	-0.151	0.004	-36.702	<0.001
Slope	-0.031	0.003	-11.448	<0.001
Distance to rivers	0.111	0.007	16.684	<0.001
Distance to roads	-0.172	0.003	-59.327	<0.001
Distance to lakes	-0.207	0.003	-60.249	<0.001
Distance to boundaries	0.148	0.0923	1.609	0.108
Distance to perceived livestock predation locations	0.271	0.006	47.135	<0.001
Distance to verified livestock predation locations	-0.255	0.004	-63.387	<0.001
Distance to locations perceived as risky due to hyenas	-0.16	0.005	-35.14	<0.001

Table 3. Results from global step selection function model for spotted hyenas.

Variable	**coeff**	**se**	**z-value**	**p-value**
Distance to rivers	0.179	0.047	0.862	0.389
NDVI	0.026	0.004	0.458	0.647
lakes_s_end	-0.193	0.028	-2.303	<0.05
slope_s_end	-0.027	0.003	-0.835	0.404
roads_s_end	-0.121	0.007	-2.160	<0.05
elev_s_end	-0.08	0.012	-3.346	<0.001
bounds_s_end	0.273	0.017	2.791	<0.01
vc_s_end	-0.163	0.029	-1.193	0.233
pc_s_end	-0.002	0.028	-0.015	0.988
risk_s_end	0.013	0.017	0.163	0.87

Table 4. Number of spotted hyena individuals appearing on camera at the Lake Nakuru National Park fence line across 8 sites.

Site	**# Individuals**
C1	24
C2	56
C3	37
C4	22
C6	3
C7	1
C8	47
C17	67
Total # Individuals on Camera*: 234 **some individuals appeared at more than one site*	**Total # Individuals on C**