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Spatiotemporal patterns of lion (*Panthera leo*) space use in a human–wildlife system

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Abstract

1. Conserving large carnivores requires protecting landscape spaces that encompass all spatiotemporal scales of their movement. Large carnivores normally roam widely, but habitat loss and fragmentation can constrain their movement in ways that restrict access to resources and increase encounters with humans and potential conflict. Facilitating carnivore population coexistence with humans across landscapes requires conservation plans informed by patterns of carnivore space use, particularly at the human–wildlife interface.
2. We sought to understand lion space use in Laikipia, Kenya. We conducted a path-selection function analysis using GPS collar data from 16 lions to assess patterns of space use across a range of spatial scales (sedentary to home range expanses; 0, 12.5, 25 and 50 km) and temporal scales (day, dusk, night and dawn). Path-selection results were then incorporated into space use maps.
3. We found that most landscape features influenced path-selection at the broadest spatial scale (50 km), representative of home range-wide movement, thereby demonstrating a landscape-wide human impact on lion space use. We also detected sub-diurnal variation in lion path-selection which revealed limited space use during daylight hours and increased space use overnight.
4. Our results highlight that optimal support for human–lion coexistence should be temporally adaptive at sub-diurnal scales. Furthermore, spatial approaches to lion conservation may be better generalized at broad spatial scales so that land management plans can account for home range patterns in lion space use.

KEYWORDS
carnivore, conservation, Kenya, Laikipia, land management, large carnivore, path-selection function, resource selection

1 | INTRODUCTION

The urgency to support human–wildlife coexistence is increasing as human land use and land transformation intensifies worldwide (Ripple et al., 2014). The conservation field is increasingly oriented towards fostering the sharing of landscapes in places where human–wildlife interactions occur, as opposed to exclusionary approaches that fully separate wildlife from humans. To this end, efforts are underway to foster a *coexistence landscapes* approach in human–wildlife systems as a way to lower human–wildlife conflict to tolerable levels of risk for both parties (Carter & Linnell, 2016; Fiasco & Massarella, 2022; Oriol-Cotterill, Valeix, et al., 2015).

Large carnivores pose risks to humans because habitat degradation and fragmentation constrain and channel their long-range movement in ways that often increase proximity to human activity (Ripple et al., 2014). Even when carnivore home ranges are centralized within protected areas, individual animals often move outside of such boundaries and subsequently come into contact with humans (Mills & Harris, 2020; Tumenta et al., 2013; Woodroffe & Ginsberg, 1998). African lions (*Panthera leo*) are an important species to consider when developing human–carnivore coexistence landscapes because of their sensitivity and responses to anthropogenic pressures. Lions persist across most African habitat types, but have declined range-wide for decades (IUCN, 2006a, 2006b). Recent figures suggest that lions occupy as little as 8% of their historic range, having undergone a 43% decline between 1993 and 2014 (Bauer et al., 2017). Continued population decline is anticipated (Bauer et al., 2015), however, uncertainty surrounds past and future estimates of range-wide lion abundance because no systematic survey has ever been conducted across the continent (Gopalaswamy et al., 2022). Lions are thought to be especially vulnerable to anthropogenic pressures because they are less cryptic than other large carnivores (e.g. among the largest in size, social and prefer wild prey whose size overlaps with livestock; Everatt et al., 2019). They are typically the dominant predator within their ecosystem. However, lions succumb to a landscape of fear where they overlap with humans, whereby they alter their spatial and temporal niches to avoid humans (Elliot et al., 2014; Oriol-Cotterill, Macdonald, et al., 2015; Suraci et al., 2019). It is important to simultaneously understand both the spatial and temporal dynamics within a landscape of fear (Palmer et al., 2022)—including lion spatiotemporal trade-offs between anthropogenic risk and space use—in order to inform human–wildlife coexistence strategies.

There have been significant efforts to develop landscape-scale strategies for human–lion coexistence and conflict mitigation (Creel et al., 2013; Packer et al., 2013). Most conservation strategies addressing risks of conflict focus on minimizing localized direct encounters between lions, humans and their livestock, which could otherwise result in preemptive or retaliatory lion killings (Kissui, 2008; Lichtenfeld, 2005; van Eeden et al., 2018). Such approaches increase the likelihood of lion survival in the short term but will not promote long-term survival and coexistence without additionally addressing how landscape-scale patterns of human activity influence lion space use. Understanding space use is key to understanding how lions access resources, such as habitat and prey, and the attendant likelihood of human–lion encounters. Even in the absence of direct contact, the indirect effects of human activity on carnivores include spatiotemporal niche partitioning and less efficient prey consumption stemming from a landscape of fear (Miller & Schmitz, 2019; Oriol-Cotterill, Macdonald, et al., 2015; Smith et al., 2015). This, in turn, can reduce individual fitness and long-term carnivore survival through restricted dispersal and gene flow (Miller et al., 2020; Zollner & Lima, 1999). Effective landscape-scale strategies for lion conservation and coexistence with humans depend upon understanding animal space use in response to both anthropogenic and habitat features within a landscape.

Laikipia, Kenya is considered a particularly important lion conservation area because it is Kenya's second-most wildlife-rich area, located where subsistence and commercial livestock ranching occur alongside wildlife conservation (Frank, 2023; Ogutu et al., 2016). A recent survey estimated 245 lions (PSD = 15.7) within Laikipia (Elliot et al., 2021). This is supported by other estimates calculated between 2003 and 2014 which yielded density estimates of 5.8–6.5 adults and subadults per 100 km^2 and extrapolates to 207–232 lions within the area (Frank, 2023). However, in Laikipia, and Kenya at large, wildlife conservation is challenged by habitat loss and fragmentation from livestock use of rangelands, land conversion and subdivision, and infrastructure development (Ojwang' et al., 2017). Some wildlife populations have experienced declines up to 68% from baseline estimates (Masiga et al., 2016; Ogutu et al., 2016; Western et al., 2009). Approximately 35% of Kenyan wildlife is found on formally protected areas, whereas the remaining majority are reliant on private, communal or local government trust lands for adequate resources (Georgiadis, 2011). Laikipia, in particular, has no national park and, instead, lion conservation is dependent upon sharing the landscape with humans. The Laikipia conservancy model allows individual or communal landowners to designate their land to be wildlife compatible (Crego et al., 2021; KWCA, 2016). For example, area ranches and conservancies are typically managed to support both livestock grazing and wildlife habitat. This land use approach is uniquely promising because Laikipia is a mixed-used landscape. However, human–lion conflict and human-caused lion mortality remains prevalent, particularly among livestock herders and ranchers (Ogada et al., 2003; Oriol-Cotterill, Valeix, et al., 2015; Woodroffe & Frank, 2005). As such, a nuanced understanding of the spatiotemporal dynamics of lion space use is needed to anticipate the prominent risks against, as well as the apparent promises for, human–lion coexistence in the area.

To this end, resource selection functions (RSFs) offer a means to understand how wildlife preferentially utilize space. RSFs assess the probability that an animal uses a resource—for example, a specific habitat type or a landscape feature—relative to its availability within a given area. To calculate RSFs, a resource(s) encountered at an animal's 'used' units (e.g. geospatial point locations) is compared to resources found at randomly 'available' units. Whereas traditional RSFs assume that resource availability is independent of animal locations (Signer et al., 2017), variations of RSFs leverage animal VHF or GPS location data to account for autocorrelation between sequential animal locations (Fortin et al., 2005; Signer et al., 2017). Step-selection functions (SSFs) in particular extend RSFs by assessing resource use and availability along the distance between two consecutive point locations (i.e. *steps*; Fortin et al., 2005, Thurfjell et al., 2014). SSFs compare the mean value of a resource along the 'used' step to the mean value that would otherwise be randomly encountered along 'available' steps (Thurfjell et al., 2014; Zeller et al., 2012). 'Available' steps are taken from the starting point of the 'used' step and distributing the movement across various lengths and angles. PathSFs further extend SSFs by assessing animal movement as a series of steps (i.e. *paths*). 'Available' paths are chosen by randomly rotating directions away from the 'used' path's starting point (Kaszta et al., 2021; Naidoo et al., 2018; Zeller et al., 2012). Both SSFs and PathSFs typically employ conditional logistic regression to account for the temporal dependence between sequential animal locations (Signer et al., 2017; Thurfjell et al., 2014). Furthermore, both SSF and PathSF analyses can be conducted at a range of spatiotemporal scales because of the flexibility in defining the spatiotemporal length of steps or paths. Selection functions ultimately link individual behaviour (e.g. step- or path-selection) to the scale-dependent population-level processes that determine species space use. Selection functions are a popular approach to study species space use and interactions with humans, as well as migration corridors, dispersal behaviour and gene flow (Thurfjell et al., 2014; Zeller et al., 2012). This can inform strategies for species survival and coexistence by informing practitioners about *how* and *when* a species preferentially utilizes a landscape and, subsequently, how to preemptively or actively mitigate conflict with humans across animal preferences for landscape locations (Miller et al., 2015).

Whether the results are meaningful and applicable is dependent upon the spatiotemporal scale(s) of analysis (McGarigal et al., 2016). The identification of the ecologically relevant scale at which animals preferentially utilize space requires systematic examination of the various spatiotemporal scale(s) at which animals respond to different landscape features (Boyce, 2006; McGarigal et al., 2016; Zeller et al., 2016). PathSFs facilitate systematic analyses that determine the optimal scales at which landscape features best explain animal movement (Avgar et al., 2016; Lima & Zollner, 1996), particularly because of their ability to control for spatial autocorrelation and to allow for optimization of selection across a range of scales (Cushman & Lewis, 2010; Zeller et al., 2012, 2016).

We investigated lion space use as a function of landscape features in Laikipia, Kenya by conducting a multi-scale PathSF analysis using high-resolution lion GPS data. Our goal was to understand how different landscape features impact lion space use and to inform practitioners of relevant conservation and human–lion conflict mitigation strategies that can be derived from our results. Previous studies found that lions typically avoid areas of high human presence and anthropogenic risk—including towns, highways and agricultural and livestock areas—over large spatial scales (Elliot et al., 2014; Everatt et al., 2019; Loveridge et al., 2017; Oriol-Cotterill, Macdonald, et al., 2015). However, lions have also exhibited fine-scale temporal partitioning when avoidance of human activity is not possible (Oriol-Cotterill, Macdonald, et al., 2015). As ambush predators, lions are known to spend significant amounts of time in thick bush cover and dense vegetation (Elliot et al., 2014; Oriol-Cotterill, Valeix, et al., 2015; Schuette et al., 2013). Based on these patterns, we expect path-selection to occur at the broadest spatial scale assessed (50 km) given the pervasive presence of humans in the landscape. Temporally, we expect space use to vary sub-diurnally in respect to established patterns of human and lion diurnal behaviour (e.g. human activity peaking during the day, lion activity such as hunting peaking between crepuscular hours; Oriol-Cotterill, Macdonald, et al., 2015). We expect lions to avoid all anthropogenically risky landscape features (e.g. roads, houses, etc.), with the strongest avoidance occurring during daylight hours. On the other hand, we expect lions to select for habitat variables that reflect thicker ground vegetation cover (e.g. grass or shrubland) and avoid more sparse ground habitat (e.g. barren land, tree cover) or energetically taxing locations (e.g. steep slope).

Our objectives were to determine: (1) whether path-selection was consistent across spatial scales, (2) whether path-selection varied across time, (3) which landscape features were consistently selected or avoided and (4) how results can inform land management and lion conservation. We conducted PathSF analyses across the full suite of spatiotemporal scales at which lion space use occurs. We identified the spatial scale at which path-selection occurs through systematic exploration of varying temporal scales, as well as the directional effects (e.g. selection or avoidance) of these landscape features. We highlight results stemming from each spatiotemporal perspective and reflect upon relevant approaches to lion conservation.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted across the 8700 km^2 semi-arid savannah of Laikipia County, Kenya (Figure 1). Laikipia is a mixed-used landscape comprised of private- and communally owned properties that create a mosaic of farms, conservancies, ranches, pastoral areas and small urban areas (LWF, 2012; Sundaresan & Riginos, 2010). Approximately 38% of the county is explicitly designated as wildlife-compatible

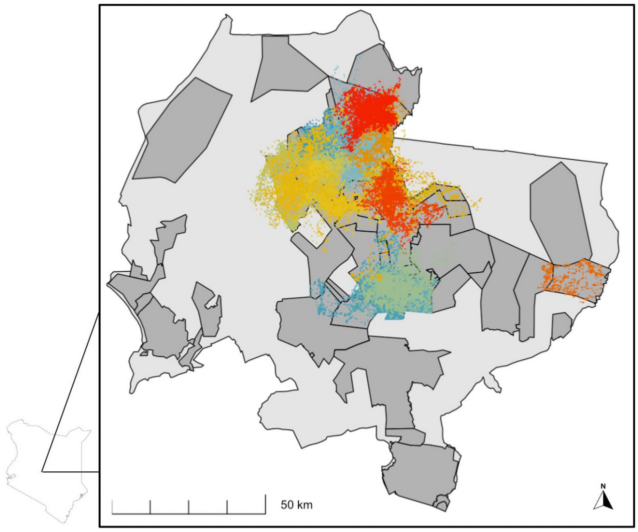

FIGURE 1 The study area of Laikipia County, Kenya. Shaded polygons represent wildlife areas (WAs). Collaring data for 16 lions are overlaid across the study area with a unique colour per lion.

conservancies or ranches (Frank, 2023)—hereafter, referred to as 'wildlife areas' (WAs).

2.2 | Lion data

Between 2014 and 2016, 16 adult lions (11 females, 5 males) were fitted with GPS-enabled SMART collars (Williams et al., 2014; Wilmers et al., 2017) provided by Vectronic Aerospace (Berlin, Germany). Capturing and collaring protocols and permits for these lions are detailed in Oriol-Cotterill, Macdonald, et al. (2015). Collars recorded a GPS location every 30 min and averaged 234 days of data (range 38–613 days). Lions were selected based upon ease of collaring. Consequently, our sample frame was limited to lions whose home ranges are centralized within WAs, although non-WAs should be within an accessible distance from these locations. Lions live in fission–fusion groups ('prides') in which females are philopatric and subadult males either disperse into vacant areas or challenge resident adult males for territory (Packer et al., 1990; Pusey & Packer, 1987). Each collared lion was a member of a different pride for the duration of the study. We assume that each lion had the same capability of moving across the landscape and that each lion moved independently within their home range. We also assume that the number of prides and their respective home range boundaries did not change during the study. The majority of GPS points (97%, $n = 163{,}537/168{,}650$) were located inside WAs, although most lions (88%, $n = 14/16$) were observed in non-WAs at least once during the study period.

2.3 | Environmental data

We applied PathSFs to shed light on the functional relationship between lions and landscape features, thereby providing estimates of space use. We limited the scope of our study to assess the relationship between lion path-selection and physical, static landscape features. Specifically, we focused on anthropogenic infrastructure (e.g. roads, buildings, dams) as well as land cover and composition (e.g. agricultural locations, proportions/indices of vegetation types, slope). We included human density and livestock density because these are major components of human–lion conflict in the area (Frank, 2023). We grouped variables, a priori, into three categories known to affect lion habitat preferences and human–lion interactions (Elliot et al., 2014; Kingdon, 1997; Pettorelli et al., 2010):

1. *Anthropogenic*: human-built features (e.g. built infrastructure, human settlements, land conversion, human population, etc.).
2. *Land use*: locations which host varying types of human activity (e.g. agro-pastoral activities on cropland, WAs, dams, etc.).
3. *Habitat*: natural landscape characteristics (e.g. land cover types, vegetative indices, slope, natural water, etc.).

We used open-source geographic information system (GIS) layers for variables or otherwise created our own. Some variables were transformed into multiple layers to identify the most ecologically relevant predictor for path-selection (e.g. comparing distance from WA edges vs. WA centres as the predictor variable). Additionally, some GIS layers that represented similar landscape features were grouped together to determine which best predicted path-selection (e.g. varying vegetative indices). This provided a total of 37 GIS layers to be initially assessed (Table S1). Layers were resampled to 92 m to standardize to the finest original resolution among layers using the nearest neighbour method for categorical variables and bilinear interpolation method for continuous variables in R (Hijmans & van Etten, 2012). When appropriate, continuous raster layers were standardized to the same extent and values were re-scaled from 0 to 1.

Due to the scope of our study, we did not examine the effect of prey accessibility on path-selection. Prey accessibility—not mere presence—can influence predator path-selection (Trainor & Schmitz, 2014). Prey presence is ubiquitous across Laikipia, but recent studies suggest there are higher rates of prey occupancy (a potential proxy for accessibility) within central Laikipia (the WAs; Crego et al., 2020, 2021). However, the location and strength of prey accessibility is influenced by the landscape features that we investigated in the study.

2.4 | Spatiotemporal path-selection and scaling

We used PathSFs to predict lion space use as a function of landscape features at varying spatiotemporal scales (sensu Cushman et al., 2016; Elliot et al., 2014). To reduce the effects of non-stationarity, we defined 'used paths' by dividing sequential GPS data into temporal windows (Cushman et al., 2005). We established four temporal scales to assess variation in space use over time using R package hms (Müller, 2021). The four temporal scales are as follows: daytime (07:00–17:00 h), dusk (17:00–19:00 h), nighttime (19:00–05:00 h) and dawn (05:00–07:00 h). They were selected to detect variation in space use sub-diurnally, based on known fluctuations of human and lion activity. Each temporal scale was treated as an independent PathSF analysis. Although seasonality can be an important driving force in wildlife movement, there is no major seasonal wildlife migration which would prompt broadscale spatiotemporal variation in lion movement in Laikipia. Additionally, livestock grazing is integrated across the landscape. Therefore, there is no significant spatial stratification of seasonal vegetation regrowth that we would expect in order to similarly induce broadscale wildlife movements. We discuss potential ways to address seasonality in the system below but focus our study on categorizing sub-diurnal path-selection patterns more generally.

The ecological processes driving animal space use can be influenced at multiple spatial scales. It is therefore important to determine the scale at which a species responds to a particular landscape feature (Galpern et al., 2012; Sawyer et al., 2011; Wiens, 1989). For each temporal analysis, we assessed the relationship between lion space use and landscape features across four spatial scales: 0, 12.5, 25 and 50 km. The four spatial scales represent the bounds of anticipated lion movement, from sedentary (0 km) to maximum-daily, home range-wide movement (50 km). We created nine available paths for every used path. Autocorrelation was avoided by creating available paths of identical length and topology for each corresponding used path. Available paths were randomly rotated 0°–360° from the used path's starting location, and randomly shifted a distance in *x* and *y* coordinates (Cushman, 2010; Cushman & Lewis, 2010). The four spatial scales were represented in the random shift distance: 0 km (no shift), 0–12.5, 0–25 and 0–50 km (Elliot et al., 2014). This was done for each PathSF analysis using R packages raster and sp (Hijmans, 2021; Pebesma & Bivand, 2005). This resulted in 36 available paths (nine per spatial scale) for each used path.

2.5 | Conditional logistic regression analyses

We used a conditional logistic regression approach (Elliot et al., 2014; Kaszta et al., 2021) to compare landscape variables encountered along used versus available paths (no intercept estimated). Conditional logistic regression provides a robust way to rank alternative spatiotemporal models using Akaike information criterion corrected for small sample size (AICc; Anderson & Burnham, 2002; Compton et al., 2002; Cushman & Lewis, 2010; Hegel et al., 2010). Consistent with Coulon et al. (2008), we used Cox models and performed all statistical analysis in R 4.1.1 (R Core Team, 2021) using package coxme v.2.2-16 (Therneau, 2012). Predictor variables were derived in R by calculating the mean value of a GIS layer for all pixels that fell along used and available paths using the package raster (Hijmans, 2021). Lion ID was a random effect in all models.

We employed conditional logistic regression in a series of analytical steps: First, we performed a univariate scaling analysis to determine the spatial scale at which path-selection occurred for each variable (McGarigal et al., 2016; Thompson & McGarigal, 2002). We used model selection to identify the spatial scale (0, 12.5, 25 and 50 km) at which a variable impacted path-selection based on AICc (Anderson & Burnham, 2002). The scale with the lowest AICc ranking was retained. Next, model selection was performed to retain the strongest predictor among correlated variables (≥|0.7| based on Pearson's correlation) and/or between different metrics of the same variable (Dormann et al., 2013). Again, only the variable with the lowest AICc was retained. This yielded uncorrelated variables at their best-performing metric and spatial scale. Lastly, remaining variables were incorporated into multivariate model selection to determine the most appropriate *anthropogenic*, *land use* and *habitat* model for each temporal scale (Elliot et al., 2014). Candidate models were progressively more complex, starting with the univariate model and finishing with the maximal model that included all variables in the group (e.g. Elliot et al., 2014; Zeller et al., 2016). We again used model selection to identify the best supported model (Tables S2–S4).

2.6 | Space use maps

We used results from multivariate model selection to create empirically optimized space use maps (Cushman et al., 2016; Elliot et al., 2014). Each multivariate PathSF provides quantitative insight on animal selection or avoidance of landscape features. This information was subsequently used to parametrize lion space use maps with the equation $z = b_1 v_1 + b_2 v_2 + \ldots + b_n v_n$, where b_i is the coefficient for variable v_i (Table 1, Figure 2).

3 | RESULTS

3.1 | Univariate scaling analysis

Univariate scaling analyses revealed that lions most frequently selected or avoided landscape features at the 50 km spatial scale (Tables S2–S4). This remained consistent across temporal scales, with the 50 km scale being selected in 86% ($n = 131/148$) of all scaling analyses of variables. It was selected in 91% of anthropogenic ($n = 58/64$), 96% of land use ($n = 27/28$) and 82% of habitat ($n = 46/56$) scaling analyses. Habitat variables comprised the majority of the 0, 12.5 and 25 km selected spatial scales (59%; $n = 10/17$; Table S4).

3.2 | Multivariate analysis

Results are reported in Table 1 and Tables S5–S8.

3.2.1 | Anthropogenic

Lions selected for proximity to fences and WA roads in every sub-diurnal model. Fences were most strongly selected at dawn (more than twice that of daytime) followed by dusk and night, with the

TABLE 1 Parameter estimates—coefficients (Coeff.) and standard errors (S.E.)—of multivariate conditional logistic regression models.

		Day		Dusk		Night		Dawn	
Category	**Variable**	**Coeff.**	**S.E.**	**Coeff.**	**S.E.**	**Coeff.**	**S.E.**	**Coeff.**	**S.E.**
Anthropogenic	Built settlements	−0.288	0.207	0.501	0.100	−0.344	0.207	0.523	0.121
	Fences	−0.733	0.396	−1.941	0.320	−0.998	0.498	−2.023	0.375
	Human population	−26.338	4.132	−28.212	11.562	−19.419	3.446	−44.675	21.460
	Infrastructure	0.800	0.635	−0.329	0.296	0.552	0.596	−0.455	0.530
	Land conversion	−1.363	0.449	–	–	−4.615	1.566	−17.614	0.000
	Roads (all)	1.163	0.726	–	–	0.044	1.228	–	–
	Roads (non-WAs)	0.369	0.200	−0.338	0.313	−0.889	0.351	0.451	0.421
	Roads (WAs)	−6.290	1.163	−4.874	1.317	−7.079	1.851	−4.527	0.880
Land use	Cropland	−1.665	0.687	−4.137	4.302	−1.167	0.037	−1.207	1.356
	Cultivated land	−0.329	0.270	−1.158	0.635	−0.206	8.669	−1.255	0.721
	Dams	−1.062	0.441	−0.367	0.285	–	–	−0.456	0.234
	Livestock	−3.056	0.695	−1.383	0.200	−2.079	1214.529	−1.522	0.273
	WAs	−1.564	0.309	–	–	–	–	–	–
Habitat	Barren land	−1.113	1.546	–	–	–	–	–	–
	Deciduous cover	−7.650	0.920	−2453.803	0.000	−10.534	4838	−764.822	0.000
	EVI	–	–	−0.508	0.345	–	–	0.041	0.397
	Habitat heterogeneity	–	–	−0.040	0.465	–	–	−0.406	0.433
	Herbaceous cover	–	–	2.081	0.989	–	–	1.953	0.969
	Shrubland	–	–	−1.961	3.550	−0.085	467.800	−1.036	2.778
	Slope	−0.513	18.908	−1.801	0.383	−1.137	120,300	−0.648	0.256
	VCF NTV	–	–	–	–	1.506	0.051	–	–
	Water	−0.348	0.022	−0.250	0.147	−0.722	4.829	–	–

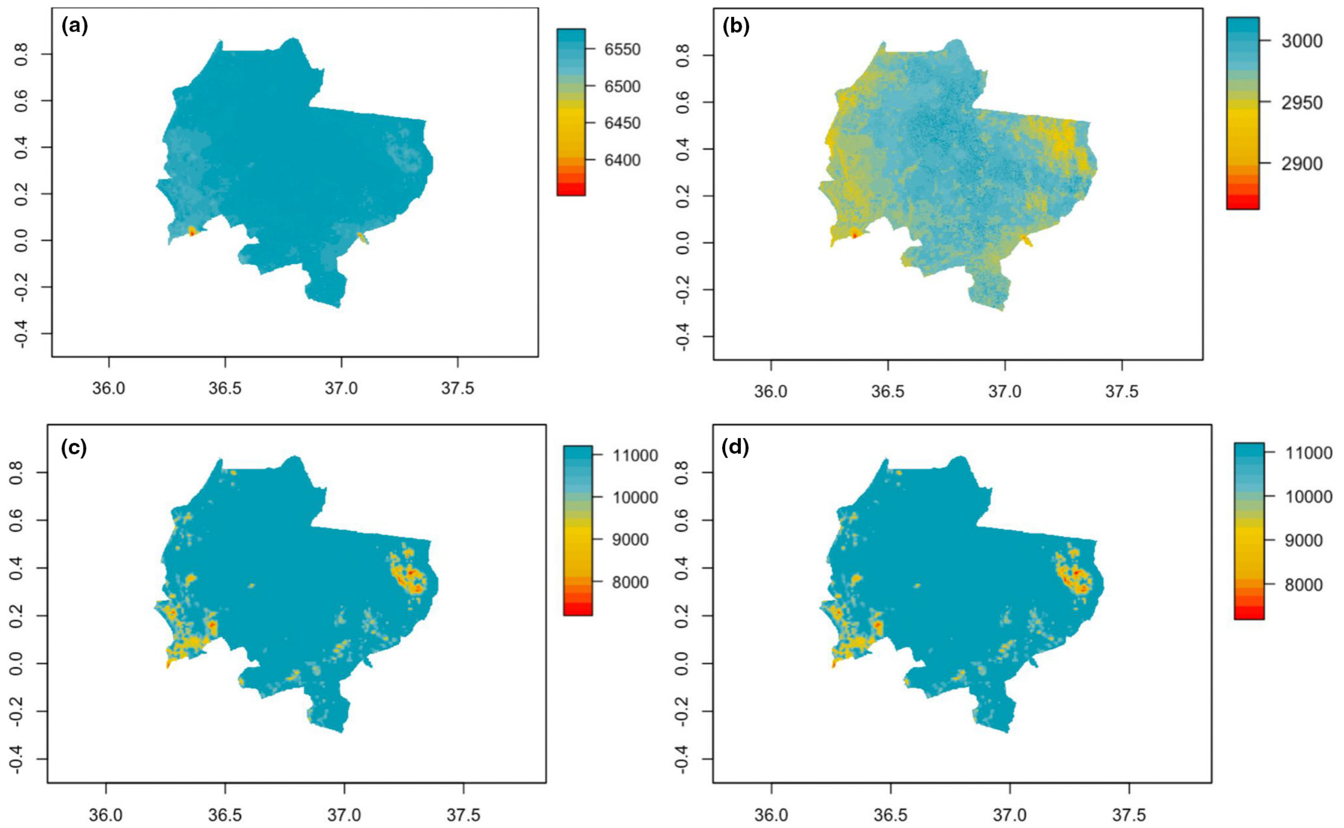

FIGURE 2 Space use maps for Laikipia, Kenya parameterized across (a) daytime, (b) dusk, (c) nighttime and (d) dawn temporal scales; larger values indicate greater space habitat use.

weakest selection during the day. There was strong selection for WA roads across time, with the strongest selection occurring during the night. Lions avoided locations of high human population in every model, with avoidance peaking during daylight hours (dusk–dawn) and nighttime exhibiting the weakest avoidance. Lions avoided areas of high land conversion in most models, with the strongest avoidance at dawn, followed by night and day. Selection or avoidance of built settlements and infrastructure followed no discernible pattern: Built settlements were avoided at dusk and dawn, but selected during the day and night whereas infrastructure was selected at dusk and dawn but avoided during the day and night. Coefficient values for selection and avoidance of these variables remained relatively weak overtime. Non-WA roads were selected at night but avoided during daylight hours.

3.2.2 | Land use

Lions avoided livestock, cultivated land and cropland in every sub-diurnal model, but the extent to which they did varied as evidenced by the coefficients. Avoidance of livestock peaked during the daytime and was weakest at dusk and dawn. Avoidance of cropland peaked at dusk and remained relatively constant during all other times of day. Similarly, avoidance of cultivated land peaked at dusk and dawn and remained relatively constant during the day and night. Lions selected for proximity to dams in most models, with the strongest selection during daytime hours. Lions only selected for proximity to WAs in the daytime model.

3.2.3 | Habitat

Lions avoided steep slopes and deciduous cover across all scales. Lions also avoided shrubland, except during the day. Lions selected for proximity to water in most models. Lions avoided areas of high habitat heterogeneity at dusk and dawn, but selected for high herbaceous cover during these periods. Lions selected for EVI at dawn, but avoided EVI at dusk and selected for VCF NTV (non-tree vegetation) at night. Lastly, barren land was avoided during the day.

3.3 | Space use maps

Table 1 summarizes variable coefficients incorporated into space use maps. All sub-diurnal maps revealed higher space use in central Laikipia where WAs are concentrated and limited lion space use in the more urban southwest (Nyahururu town) and northwest (Nanyuki town) corners of the county (Figure 2). Additional constraints to space use were detected near pastoral grazing areas in the north-east part of the county at night (Figure 2c). General estimates of lion space use increased at night and dawn (Figure 2c,d) and decreased during the day towards dusk (Figure 2a,b).

4 | DISCUSSION

Univariate scaling analyses overwhelmingly demonstrated that landscape features were most frequently selected or avoided at the 50 km spatial scale. The broad-scale impact of anthropogenic and land use variables was expected given the pervasive effects of human land use, activity and presence that has been demonstrated on wildlife populations worldwide (Tucker et al., 2018). The selection of all variable types, including habitat variables, at the 50 km scale is likely reflective of the broad homogeneity of the study area landscape. Laikipia is comprised of varying anthropogenic, ecological and climatic features, however, on average, their spatial juxtaposition creates an apparent uniform pattern across the landscape (Pringle et al., 2010; Schmitz, 2010). This does not imply that path selection is not determined by features at finer scales. But such an assessment would require relating lion use of a landscape's fine-scale nuances in terms of the behavioural and/or energetic basis of animal movement between features such as vegetation cover types and water availability, something that is currently precluded by the nature of our data.

Whereas landscape features impacted path-selection at a uniform spatial scale, multivariate model selection and subsequent space use maps demonstrated temporal variation in lion path-selection and space use. The variation that we observed in sub-diurnal space use reveals decreased space use during daylight hours, as demonstrated by lower variation in space use values (Figure 2a,b). Such findings are supported by established lion ecology: lions typically rest during daylight hours when energetic demands are heightened by temperature and when anthropogenic risk is heightened by increased human activity (Elliot et al., 2014; Suraci et al., 2019). However, even at night when space use estimates increase, there is still limited space use in the more urban southwest corner and the community livestock grazing areas of northeast Laikipia (Figure 2c,d). These results support the presence of a human–lion landscape of fear in which anthropogenic risk is predictable in both space and time, and subsequently lions minimize such risk by using spatiotemporal refuges (Palmer et al., 2022). Previous studies demonstrate that lions resort to spatiotemporal niche partitioning in human-dominated landscapes, rather than complete avoidance of humans (Elliot et al., 2014; Oriol-Cotterill, Macdonald, et al., 2015). The sub-diurnal variation in lion space use in Laikipia suggests some level of spatiotemporal adaptability to human presence, despite continued avoidance of some anthropogenically risky locations.

Notably, although our maps visualized relatively high estimates of lion space use in Laikipia (Figure 2), lions are utilizing seemingly suitable areas very little. This is evidenced by an overwhelming selection for WAs, most of which are condensed in central Laikipia (e.g. 97% of GPS points vs. 38% of land area). There are no physically impermeable barriers confining lions to WAs (Dupuis-Désormeaux et al., 2016; Evans & Adams, 2016), and non-WAs lie within lion home ranges. Other studies have similarly found carnivore preference for WAs (Klaassen & Broekhuis, 2018). WA selection may be driven by a landscape of fear in which lions avoid perceived anthropogenic risk by erecting behavioural barriers in lieu of physical barriers (Gaynor et al., 2019; Oriol-Cotterill, Macdonald, et al., 2015; Oriol-Cotterill, Valeix, et al., 2015). The generally high estimates of space use may be due to the fact that risk variation decreases when a species accesses spatial and temporal refuges within a landscape of fear (Palmer et al., 2022). Studies demonstrate that human–wildlife conflict and anthropogenic mortality risk can concentrate along WA edges and immediately outside of WAs (Schiess-Meier et al., 2007). In Laikipia, some WAs border community-run livestock grazing areas, and unauthorized livestock grazing also frequently occurs along WA boundaries. Lion spatiotemporal avoidance of livestock grazing areas has been well documented (Everatt et al., 2023; Loveridge et al., 2017; Valeix et al., 2012). WA preference is also reflected in our results by the selection for WA roads and daytime avoidance of binary non-WA roads. Large carnivores are known to utilize low-trafficked dirt roads—commonly WA roads—for ease of movement and hunting but avoid high-trafficked and noisy paved roads—commonly non-WA roads—which are a significant mortality risk (Caro et al., 2014; Kelly et al., 2012; Wynn-Grant et al., 2018; Yiu et al., 2019). Additionally, prey accessibility within the WAs (Crego et al., 2020, 2021) can influence predator space use. Follow-up studies are required to discern whether selection for WAs is an artefact of our non-random sampling *or* is derived from the presence of non-collared lions in surrounding areas, a landscape of fear and/or prey accessibility. We encourage future studies to synchronize predator–prey GPS collaring events such that complementary fix-rates of GPS data provide the sub-diurnal spatiotemporal variation needed to study predator–prey interactions. This could support a foraging study that compares selection of prey, and livestock, across land use types that vary in anthropogenic risk.

Multivariate model selection also revealed that anthropogenic and land use variables—landscape features that can pose anthropogenic mortality risk—do not always impact path-selection in the same manner across temporal scales. Indeed, some variables were universally avoided: Lions avoided locations of high human population, livestock presence and cropland across all scales ($n = 4/4$), as well as areas of high land conversion in most sub-diurnal models ($n = 3/4$). This avoidance is likely indicative of the inherent anthropogenic risk at such locations. For example, avoidance of humans was highest during daylight hours (dusk, day and dawn) when human activity is highest. Similarly, avoidance of livestock was highest during the day when livestock is grazed. However, some anthropogenic and land use variables were universally *selected* across temporal scales: Lions selected for proximity to fences ($n = 4/4$), likely indicative of their use of fence lines in movement and hunting strategy. Lions have been observed using fences 'like a net [to] drive prey up against them' (Alayne Oriol-Cotterill, pers. comm., 2022). Lions also selected for proximity to dams ($n = 3/4$), and it was surprising that selection was strongest during the day when livestock is most frequently brought to dams to drink water. This is likely reflective of a trade-off in which anthropogenic risk at dams is outweighed by the selection for a specific resource (e.g. water, or accessible livestock and/or prey). Lions selected for proximity to WAs during the day, which was expected because WAs act as wildlife-friendly refuges from anthropogenic mortality risk during hours of peak human activity. Lastly, path-selection for some anthropogenic and land use variables—infrastructure, built settlements, cultivated land, non-WA roads and WAs—fluctuated between selection and avoidance across temporal scales. This was surprising because we expected the anthropogenic risk inherent in the variables to be reflected in the same directional effect (avoidance) across scales. Avoidance of non-WA roads during the day, but selection at night, is likely because of the higher and lower rates of road usage and subsequent anthropogenic risk during these times. Overall, multivariate model selection for anthropogenic and land use variables demonstrates that, although some variables have uniform impact on path-selection overtime, others are more nuanced and may depend on their interaction with other variables included in model selection.

Multivariate model selection for habitat variables revealed similar contextual nuances. Lions selected for proximity to natural water (e.g. streams, rivers), potentially a reflection of prey presence at these locations. As expected, lions avoided steep slopes because of lower energetic demands in movement (Nisi et al., 2022). Lions also avoided barren land and selected for shrubland during the daytime when exposure to anthropogenic risk is greatest. Building off this, lion path-selection for other vegetative variables was mixed. General avoidance of deciduous cover may be because this vegetation type is limited in the landscape and because deciduous trees typically do not offer significant understorey to camouflage lions. Selection for herbaceous cover and high VCF NTV reflects lion preference for thicker vegetation cover, particular at night while hunting (Elliot et al., 2014; Oriol-Cotterill, Valeix, et al., 2015; Schuette et al., 2013). However, selection and avoidance of EVI did not follow a discernible pattern. As a metric of general greenness, this may reflect nuances between locations that are similarly 'green' but vary in anthropogenic activity or risk (e.g. conservancy grassland vs. livestock grazing areas).

4.1 | Synthesis and applications

Selection functions can be instrumental in informing the design of coexistence landscapes (Everatt et al., 2023). Our results demonstrate that strategies for lion conservation and human–lion coexistence should recognize how spatiotemporal context drives variation in the impact of landscape features on lion space use.

The 50 km spatial scale at which path-selection was detected is conducive to the broad scale at which land management strategies are designed and executed. As such, we suggest that land management focus on this home range-scale spatial approach when designing, implementing and/or adaptively managing strategies to support free-ranging lions and long-term human–lion coexistence. This could include the construction or removal of fencing, road design and regulations (e.g. size and speed limitations of carriageways), and location of wildlife crossings or corridors. Some level of lion adaptability within the landscape is demonstrated by path-selection which does not completely avoid anthropogenic and land use variables. In turn, scenario modelling that incorporates the quantified *direction* (selection or avoidance) and *strength* of a variable's impact on lion path-selection can help to predict whether a specific conservation goal (e.g. avoidance of a high-conflict area, enhanced lion connectivity) would be achieved within various land management options. However, assessment of scenario modelling will need to carefully consider lions' limited use of seemingly accessible land, particularly if the lesser-utilized northeastern corner of Laikipia is to continue to be considered a connectivity corridor into the neighbouring Samburu ecosystem and lion population (Elliot et al., 2021; Frank, 2011, 2023). A home range-scale approach will spatially cross private properties (e.g. ranches, conservancies, private properties, etc.) and land use types (e.g. WAs, non-WAs), thereby requiring conservation programs that are community engaged, if not community driven. This will require negotiated relationships with landowners and other stakeholders (Sachedina & Nelson, 2010). Land management strategies this human–wildlife system must account for individual and collective decision-making, as well as stakeholder tolerance, that support wildlife-friendly properties. This propels a continued need to reconcile co-occurring, and sometimes opposing, landscape activities (e.g. lion–livestock conflict on wildlife-compatible livestock ranches; Frank, 2011; Suraci et al., 2019).

We suggest that human–lion conflict mitigation strategies be sub-diurnally adaptive. Our results highlight fine-scale temporal variance in lion path-selection and space use, suggesting that some ecologically informed conservation approaches must be enacted sub-diurnally, rather than seasonal or annual agendas, or pre/post-landscape change (Cushman et al., 2011; Kaszta et al., 2021; Zeller et al., 2018). Community-based conservation organizations already practice sub-diurnal conflict mitigation strategies, such as enhanced livestock guarding between dusk and dawn when lions move closer to agro-pastoral areas (Oriol-Cotterill, Macdonald, et al., 2015). These practices could be expanded to increase the availability of vegetative patches that act as spatiotemporal refuge within a landscape of fear (Palmer et al., 2022), thereby reprieving lions from daytime anthropogenic risk (sensu Oeser et al., 2023; Schuette et al., 2013). Increased vegetative cover could also bolster lion hunting success, potentially enhancing prey accessibility at night and lessening the need to consume livestock.

Seasonality is becoming increasingly irregular across Kenya, evidenced by prolonged droughts and intermittent rains. Seasons have typically been designated based on months of the year, but this is now unreliable and often inaccurate. Annual rainfall in Laikipia is patchy and can vary dramatically between properties (e.g. 400–1200 mm; Butynski & Jong, 2014), thus the impact of seasonality on wildlife distribution is most acutely observed within property with wildlife moving between natural and artificial water sources (e.g. rivers and dams). We encourage future assessments of wildlife resource selection in Laikipia to focus on climatic analyses at a sub-property scale, rather than the traditional county level. The collection of such data (rainfall, water availability and temperature; e.g. Funk et al., 2014) will be critical to appropriately designate seasons or, at least, accurately describe temporal climatic conditions. This could bolster ecological knowledge by quantifying the effect of climate on wildlife resource selection.

We recommend that future research more intricately assess landscape suitability versus usage for lions, and other species. Understanding how landscape features affect species behaviour, path-selection and space use will contribute to understanding other aspects of species viability (e.g. dispersal and gene flow). Future research should parse out the behavioural patterns behind lion *selection for* or *avoidance of* specific landscape features and, in turn, how this affects frequency of space use. For example, research on food-web interactions and foraging ecology may shed light on whether lions' preferential selection of WAs is correlated with livestock and/or prey accessibility. If lions select for prey irrespective of livestock presence (i.e. irrespective of a landscape of fear), then conflict mitigation strategies could focus on enhancing prey availability (Bauer et al., 2010; Everatt et al., 2019, 2023). If livestock are being selected where there is equally accessible prey, then lion accessibility to livestock will need to be reduced (e.g. enhanced landscape barriers, stronger livestock corrals, reduced retaliatory lion killings; Hazzah et al., 2014; Loveridge et al., 2017). Or, if lion path- and prey-selection stems from a landscape of fear, then conflict mitigation strategies could include livestock grazing which is centralized near landscape features that lions are known to avoid (Everatt et al., 2023).

Finally, our study is based upon data from pride lions—known to be the most risk-averse lion demographic. We encourage future research to pursue similar analyses on dispersing males—known to be less risk-averse and subsequently more prone to human conflict (Elliot et al., 2014)—to quantify space use for the entire species, provide information on suitable habitat for breeding populations, and more comprehensively address human–lion conflict. The persistence of large carnivores like lions will continue to depend on adequate space use, minimized conflict events and human tolerance (Kissui, 2008; Lichtenfeld, 2005). Understanding the spatiotemporal scales at which large carnivores navigate human–wildlife systems will offer insight into continued strategies for species resilience under continued landscape change.

AUTHOR CONTRIBUTIONS

Mary K. Burak and Alayne Oriol-Cotterill were involved in conceptualization. Alayne Oriol-Cotterill, Steven Ekwanga, Laurence Frank, Terrie M. Williams and Christopher C. Wilmers were involved in critical fieldwork and data collection. Mary K. Burak, Alayne Oriol-Cotterill and Christopher C. Wilmers were involved in data management and cleaning. Mary K. Burak, Femke Broekhuis and Nicholas Elliot were involved in data analysis conceptualization and coding. Mary K. Burak was involved in data analysis, interpretation of results, writing and data visualizations. Oswald Schmitz, Femke Broekhuis, Amy Dickman and Alayne Oriol-Cotterill were involved in feedback and edits.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

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DATA AVAILABILITY STATEMENT

Data used in this paper are available from the Figshare data repository: https://doi.org/10.6084/m9.figshare.24021474 (Burak, 2023).

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SUPPORTING INFORMATION

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

Table S1. The 25 variables transformed into 37 total unique GIS layers (variables) for univariate scaling analysis.

Table S3. A summary of land use univariate scaling results.

Table S4. A summary of habitat univariate scaling results.

Table S5. Multivariate model selection results for the *day* temporal scale.

Table S6. Multivariate model selection results for the *dusk* temporal scale.

Table S7. Multivariate model selection results for the *night* temporal scale.

Table S8. Multivariate model selection results for the *dawn* temporal scale.

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