



Diel patterns of movement activity and habitat use by leopards (*Panthera pardus pardus*) living in a human-dominated landscape in central Kenya

Eric K. Van Cleave^{a,*}, Laura R. Bidner^{b,c}, Adam T. Ford^{c,d}, Damien Caillaud^{a,b}, Chris C. Wilmers^e, Lynne A. Isbell^{a,b,c}

^a Animal Behavior Graduate Group, University of California-Davis, One Shields Ave, Davis, CA 95616, United States of America

^b Department of Anthropology, University of California-Davis, One Shields Ave, Davis, CA 95616, United States of America

^c Mpala Research Centre, Nanyuki 10400, Kenya

^d Department of Biology, University of British Columbia, 1177 Research Road, Kelowna, BC V1V 1V7, Canada

^e Department of Environmental Studies, University of California-Santa Cruz, 1156 High St, Santa Cruz, CA 95064, United States of America

ARTICLE INFO

Keywords:

Leopards
Panthera
Carnivore
Conservation
Human-wildlife conflict
East Africa

ABSTRACT

Large carnivores can exert strong influence on local ecosystems, making them important targets for biodiversity conservation. An important question for conserving large carnivores outside of protected areas is the role of human activity in influencing the behavior of these predators. We used high-resolution animal location tracking and statistical modeling to examine the behavior of seven leopards (*Panthera pardus*) occupying an area that includes a research center and livestock ranch in central Kenya. Our analyses reveal changes in habitat selection around the times of sunrise and sunset, corresponding with changes in human activity at our site. Activity patterns were also variable within and among the leopards in our sample. To explore sources of this variability, we used regression modeling to estimate the relative influence of changing spatial and environmental conditions for leopard ranging behavior. Despite the tendency to be active during the day, we found that leopards strongly avoided areas where they were likely to encounter people during the daytime and showed variable selection for these same areas at night. The use of anthropogenic habitats was also associated with periods of greater ranging activity. We discuss the implications of these results for conservation efforts that attempt to balance the demands of livestock ranching alongside carnivore conservation.

1. Introduction

Large mammalian carnivores are ecologically important because they can regulate primary consumers, thereby having an indirect positive effect on plant biomass and maintaining ecosystem functions (Ford et al., 2014; Ripple et al., 2014). But many populations of large carnivores occur outside of protected areas where they are threatened by declining availability of wild prey, habitat loss, and lethal retaliation from humans over attacks on domesticated animals (Woodroffe et al., 2005; Ripple et al., 2014). As a result, developing strategies to promote the coexistence of people and predators outside of protected areas has been an important goal in carnivore conservation (Treves and Karanth, 2003; Lute et al., 2018).

In East Africa, addressing this issue is especially critical because the region contains some of the greatest diversity of large carnivores in the world. However, many of these species are also threatened, as a result of habitat loss and other conflicts with humans associated with

agricultural and urban developments (Ogutu et al., 2011; Ripple et al., 2014). Livestock production is one of the primary land uses in the region's arid and semi-arid savanna grasslands, and with global demand for livestock production projected to increase into the future, understanding the impact of these changing land use systems for the behavior and ecology of large carnivores is therefore an important question for conservation planning in these increasingly human-dominated landscapes (Ripple et al., 2014).

Advancements in animal tracking technology have now made it possible to gain unprecedented behavioral insights from cryptic carnivore species, leading to renewed interest into the ecological consequences of anthropogenic disturbances that alter predator behavior (Kuijper et al., 2016; Smith et al., 2015). Because carnivores can have disproportionate influence in trophic webs, the effects of human activity and landscape change on carnivore behavior can have cascading consequences for the local ecosystem, even if disturbances are non-lethal (Hebblewhite et al., 2005; Oriol-Cotterill et al., 2015b; Kuijper

* Corresponding author.

E-mail address: evancleave@ucdavis.edu (E.K. Van Cleave).

et al., 2016). Many animals react to non-lethal anthropogenic disturbances by altering their habitat preferences, engaging in evasive movements, increasing their levels of vigilance at the expense of foraging, and decreasing the amount of time spent in productive habitats (Frid and Dill, 2002). Moreover, in many cases anthropogenic influence extends far beyond wild animals' immediate surroundings. Pedestrian and vehicle traffic may cause animals to flee or increase their levels of vigilance even at distances over 0.5 km away (Andersen et al., 1996; Andersen and Aars, 2007). Extensive networks of roads, trails, or other landscape features associated with human movement can also alter how animals assess and use their habitats (Benítez-López et al., 2010), and impact the structure of the local animal community in ways similar to lethal activities (Griffiths and van Schaik, 1993).

Behavioral insights from animal tracking data could help to clarify the impact of livestock ranching and other forms of human activity for carnivores in East Africa. In Laikipia, Kenya, protected areas for the region's diverse and abundant wildlife are almost entirely privately owned, and, in many cases, attempt to remain profitable through a combination of livestock ranching and wildlife tourism (Georgiadis, 2011). This land use strategy creates incentives for property owners and local communities to treat wildlife as valuable resources and adopt policies favorable to their conservation, such as not constructing fences that impede their movements, stocking sustainable densities of livestock to avoid overgrazing, and banning the use of lethal control against carnivores (Georgiadis, 2011).

The livestock husbandry practices used by the region's pastoralists can also modify the environment in ways beneficial for wild and domestic animals. Glades are the sites of abandoned pastoralist settlements where livestock were corralled overnight in fenced structures called *bomas*. Wild herbivores and livestock use these treeless sites because the short, rich grasses provide high quality foods that serve as important resources in nutrient-poor savannas (Augustine et al., 2011) and the greater visibility within glades offers protection from predators (Ford et al., 2014; Riginos, 2015). The intensive use of glades by wild herbivores maintains these key resources for decades or more, where they function as important drivers of the seasonal and spatial distribution of mammalian herbivores (Veblen, 2012). As a result, mixed-use conservancies in Laikipia support a rich abundance and diversity of wild animals, including populations of large carnivores, comparable to those found in areas designated only for tourism (Kinnaird and O'Brien, 2012).

Conservancies and similar land use systems that try to promote livestock ranching alongside wildlife conservation therefore appear promising for preserving biodiversity outside of formal protected areas. Implementing these land use strategies is particularly important in Kenya where an estimated 65% of wildlife occurs outside of protected areas (Western et al., 2009; Ogotu et al., 2011). An important unanswered question for mixed-use conservancies, however, is how the persistent disturbances associated with ranching operations shape the activity patterns and spatial ecology of large carnivores.

We sought to answer this question by studying the movement behavior and activity of seven leopards (*Panthera pardus pardus*) occupying a conservancy and livestock ranch in central Kenya. We use high-resolution animal tracking and fine-scale environmental data to examine how temporal and spatial patterns of habitat use and activity might be shaped by anthropogenic disturbance cues by documenting patterns of leopard movement behavior and habitat selection over the diel period. We find that leopards tended to avoid anthropogenic habitats at all hours of the day, but that patterns of avoidance were strongest during the daytime. We next used exploratory statistical modeling to examine how activity allocation between the day and night was influenced by variation in habitat use and temporally varying environmental factors. Differences in habitat use were generally poor predictors of leopard ranging activity, except for the use of anthropogenic habitats, which were associated with periods of greater movement activity. However, our modeling found that variation in

leopard movement activity was not well explained by diel period. Instead, variation in activity allocation across the day and night was more strongly influenced by the lunar phase.

2. Materials and methods

2.1. Data collection

The data presented here were collected at the Mpala Research Centre (MRC), a 211 km² privately-owned wildlife conservancy and livestock ranch located in Laikipia region of central Kenya (0.29 N, 36.90 E; Fig. 1). MRC is located in a high elevation (1800 m a.s.l.) semi-arid savanna ecosystem dominated by thorny *Vachellia* (*Acacia*) species (especially *V. brevispica* and *V. etbaica*) and grasses from the genera *Cynodon*, *Pennisetum*, *Digitaria*, and *Sporobolus*. Riparian areas along the Ewaso Nyiro River are characterized by fever trees (*V. xanthophloea*) and are an important water source for wildlife and livestock. The site receives approximately 600 mm of rain per year with monthly precipitation following a weakly trimodal seasonal pattern (Young et al., 1995). The site contains a largely intact mammal community.

The activities and living accommodations of livestock ranchers, staff, and researchers are heavily intermixed, and involve movements on foot and by motor vehicle through the landscape. As a result, contrasting predictions for different types of activities could not be made. However, the combined presence of researchers, students, ranch employees, and livestock make MRC comparable to conditions leopards and other animals experience on conservancies in Laikipia. MRC hosts Kenyan and international scientific researchers as well as undergraduate student groups. Livestock graze vegetation throughout the property and the livestock husbandry practices used at MRC closely resemble those traditionally used by the Laikipiak and Maasai pastoralists that inhabited the region prior to European colonization (Young et al., 1995) and which are still practiced on community rangelands (Woodroffe et al., 2005). These include following livestock on foot during the daytime and corraling them in bomas at night to deter thefts and attacks by carnivores.

A field team captured four female and three male leopards using foot-snare trapping methods as described in Frank et al. (2003). Leopards were trapped, and in three instances re-trapped, over two field seasons spanning a total of 14 months. During the first season, leopards were fitted with collars that recorded GPS locations at synchronous 15-min intervals each day starting at midnight. During the second season, we deployed SMART collars (Williams et al., 2014) that sampled locations every 5 min. To make inferences across the diel period, we subsampled the locations collected during the second season to the same 15-min time intervals as the data collected during the first season. Information on the dates and duration of individual leopard movement paths can be found in Appendix A.

We used a base station (e-obs GmbH, Gruenwald, Germany) and a nine-element Yagi antenna (YAGI-869A: Low Power Radio Solutions, Witney, United Kingdom) or an omni-directional marine antenna (cxl 900-3LW: Procom, Frederikssund, Denmark), to download GPS data remotely when within UHF range of each collar throughout the first season. During the second season, GPS data were downloaded each day using Iridium satellite uplink or a handheld UHF base station. Each leopard was tracked for an average of 3.8 months (range: 1.7–7.8 months) before equipment failure or because the collar's lifespan ended.

2.2. Temporal movement activity, space use, and habitat selection

To characterize movement behavior from GPS tracks, we calculated the linear displacement and change in heading between successive leopard relocations during each 15-min time window. A multilevel bootstrap procedure was then used to estimate the average distance moved and movement directionality by leopards during each time



Fig. 1. Location of the field site (■) in the Laikipia region of Kenya (shaded).

window. Multilevel bootstrapping allows for the sampling distribution to have a nested structure that more accurately represents the observation process that produced the data. The primary benefit of this approach is that the mean and uncertainty of the bootstrap distribution is less affected by unequal sampling across individuals in the data set. We used circular statistics (Pewsey et al., 2013) to measure the directionality in movement during each time window by calculating the mean vector length of the turn angle distribution. The mean vector length (ρ) is a measure of dispersion of turn angles around the mean where $\rho = 0$ indicates no directionality (i.e., all directions are equally probable) and $\rho = 1$ (complete directionality). In animal tracking studies, a distribution of turn angles with high dispersion around the average direction of travel is usually indicative of short, wandering movements, such as an animal in an exploratory movement state. Circular distributions with little or no directionality, especially coinciding with short observed movement distances, are likely to be the approximately random location observation error about a stationary animal. Statistics were calculated using 500 bootstrap sampling iterations for each 15-min time interval.

A categorical habitat map of our study area was created to investigate the use and selection of habitats by leopards (Fig. 2, Appendix D). Vegetation classes were categorized using a high-resolution (0.6×0.6 m) land cover classification layer (methods in Ford et al., 2014) covering approximately 60% of the spatial extent of leopard movements. The land cover data were then used to derive the proportional coverage of tree canopy, grasses, and bare ground in 30×30 m grid cells. We matched these values with surface reflectance data from Landsat 8 satellite images (bands 2–5), and used these observations to train a support vector machine model to predict vegetation land cover classes outside the extent of the original data set (Appendix B). The study site contains dozens of glades, many of which predate the

establishment of the property by several decades (Young et al., 1995). These and other fine-scale landscape features were manually digitized on the basis of topography or anthropogenic disturbance (Table 1).

To investigate how leopards alter their space use and habitat selection over the diel period, we adopted the methods developed by Byrne et al. (2014) to explore temporal patterns of animal habitat use over fine temporal scales. Here, it is used to measure how leopards alter their use of available habitats during the 15 min observation window between scheduled GPS location fixes. The dynamic Brownian bridge movement model (Kranstauber et al., 2012) was used to estimate utilization distributions (UD) of leopard space use for each time step. The proportional use of habitat $h \in 1, \dots, H$ during each time step was next estimated from the step UD by summing the probability mass over the grid cells g belonging to each habitat category:

$$use_h = \sum_{g \in h} UD(g) \quad \text{and} \quad 1 = \sum_h use_h.$$

For each 15 min time window occurring throughout the day, we then calculated habitat selection ratio statistics (SR) by dividing the average percentage of time an individual leopard used a given habitat by the percent availability of that habitat in the individual's 95% movement-based kernel density home range (i.e., design III in Manly et al., 2002):

$$SR_h = \frac{\frac{1}{n} \sum use_h}{availability_h}$$

where n is the number of observed time steps for which a utilization distribution was generated. We then used the same multilevel bootstrap procedure as above to estimate the mean selection ratio and 95% confidence interval for the selection ratio statistic during every time

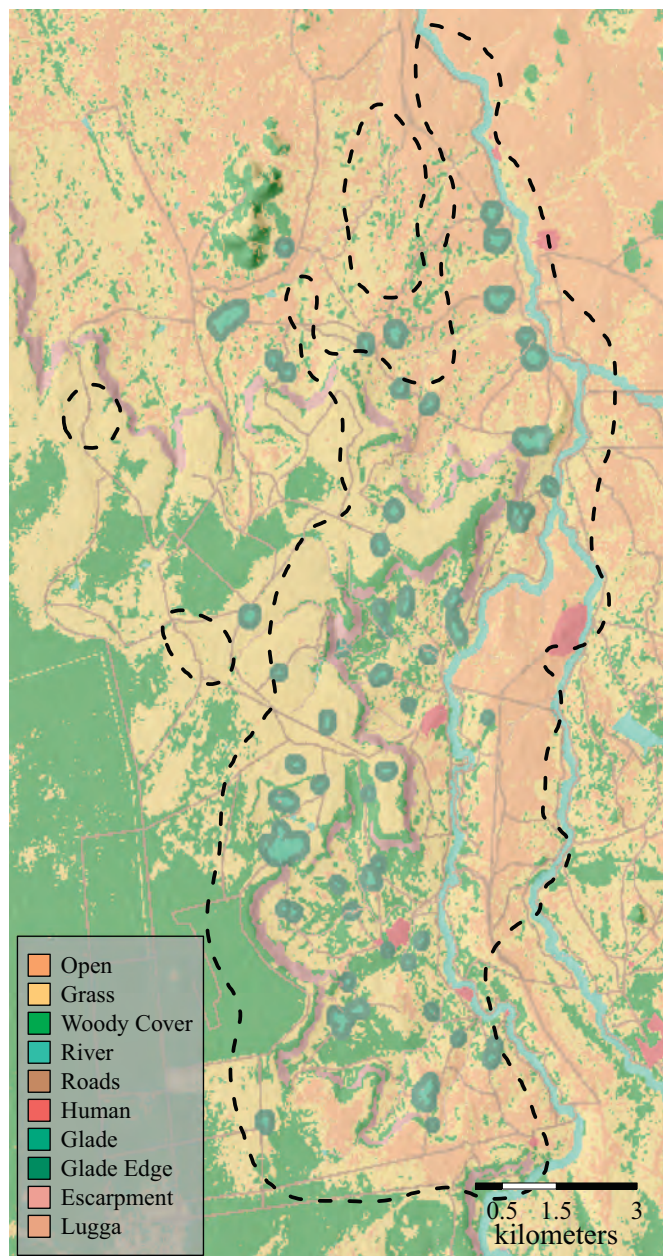


Fig. 2. Categorical habitat map of our study area. The dashed line shows the 95% utilization distribution kernel of leopard movements over the course of the tracking period. In total, ten habitats were classified on the basis of vegetation, topographic, or anthropogenic features. Descriptions of the habitat classes can be found in Table 1.

window. Selection ratio statistics greater than one suggest that an animal uses a given habitat type more than expected given its availability. Conversely, selection ratios less than one suggest animals are avoiding a habitat, using it less than expected.

2.3. Regression models

In addition to understanding temporal variation in habitat selection, we also wanted to clarify the environmental factors affecting allocation of movement activity between the day and night, and whether or not there is evidence that activity allocation is affected by anthropogenic disturbances at our study site. Leopards are known to be active at any time of the day depending on such factors as the activity patterns of their prey and competitors (Martins and Harris, 2013; Carter et al.,

Table 1

Description of the habitats defined at our study site. Each 30 × 30 grid cell is categorized on the basis of vegetation, anthropogenic, and topographic characteristics.

| Habitat | Description |
|-------------|--|
| Open | Majority bare ground |
| Grass | Majority grass cover |
| Woody Cover | > 30% woody canopy cover |
| River | Riverine habitat < approx. 80 m of river edge |
| Roads | Area < approx. 30 m of the unpaved road system |
| Human | Houses, buildings, and fenced spaces |
| Glade | Long-term disturbance; see Materials and methods |
| Glade Edge | The < 150 m band surrounding glades |
| Lugga | Water drainage channels and surrounding area |
| Escarpment | Rugged hilly terrain |

2015; du Preez et al., 2015), the availability of canopy cover for concealment and thermoregulation (Bothma, 1998), and human activity (Athreya et al., 2014). To investigate the relative influence of these and other factors on leopard ranging decisions, we first measured the distance moved by each leopard during day and night time periods, and then fit a set of multilevel regression models containing different combinations of individual, spatial, and temporally varying predictors that we hypothesize will influence the allocation of movement activity across the day and night.

We divided observation periods between continuous night and day movement tracks demarcated by the time the sun reaches an elevation of 0° on the horizon. The equatorial position of our study site means that there was little variation in the duration of night and day over the annual cycle, and the times of sunrise and sunset were approximately 06:00 and 18:00 respectively. The distance moved during each time period was calculated by summing the linear distances between successive pairs of location coordinates. The total distance moved y during time period t served as the dependent variable in the regression analysis. The observed ranging distances had a heavy-tailed distribution so we log-transformed these values and modeled them as a normally distributed random variable.

$$\log(y_t) \sim \text{Normal}(\mu_t, \sigma)$$

A linear model was then used to estimate the change in the average distance moved μ as a function of our model covariates.

$$\mu_t = \alpha_i + \beta X + \gamma_1 \log(y_{t-1}) + \gamma_2 \log(y_{t-2}).$$

where α_i is the random-effect intercept for each individual, β is a vector of slope coefficients, and X is a matrix of independent variables. In order to control for temporal autocorrelation in movement activity and to investigate periodicity in movement behavior, we also included lagged response covariates (γ) in the set of model predictors (Fieberg et al., 2012).

First, we wanted to understand if variation in movement activity could be explained by variation in the amount of time leopards spent among different habitats at our site. To do this, we calculated the total amount of time leopards occupied a habitat during each observation period. Total habitat use was derived by summing together 15-min time step estimates of habitat use described in Section 2.2. Next, to determine how changing local environmental conditions influence leopard activity, we included the total rainfall and mean temperature over of the observation period derived from an automated weather station at our study site. Finally, to examine the influence of the lunar cycle on leopard nocturnal activity, we used the “oce” package for R to calculate the fractional phase $p \in [0,1]$ of the moon during each observation period. In order to include this phasic variable in a linear regression, these values were then transformed using $\sin(2\pi p)$ and $\cos(2\pi p)$ functions before including them as terms in the linear model (Pewsey et al., 2013).

Table 2

Summary of the environmental covariates used to model ranging distance over the diel period. Models are ranked in ascending order by their WAIC scores (lower values indicate greater support). To investigate the impact of human activity on leopard movement behavior, we included in the “Spatial × Diel” and “Anthro × Diel” models an interaction term between the amount of time spent in a given habitat and the diel period. These interactions are indicated with a “d” in the above table.

| | Covariates | Anthro × Diel | Additive + | Spatial × Diel | No Temporal | Additive | No Anthro |
|---------------|--------------------------|---------------|------------|----------------|-------------|----------|-----------|
| Spatial | Open | x | x | x,d | x | x | x |
| | Grass | x | x | x,d | x | x | x |
| | Woody Cover | x | x | x,d | x | x | x |
| | River | x | x | x,d | x | x | x |
| | Escarpment | x | x | x,d | x | x | x |
| Anthropogenic | Lugga | x | x | x,d | x | x | x |
| | Roads | x,d | x | x,d | x | x | |
| | Human | x,d | x | x,d | x | x | |
| | Glade | x,d | x | x,d | x | x | |
| | Glade Edge | x,d | x | x,d | x | x | |
| Temporal | Lunar Phase ^a | x,d | x,d | x,d | | x | x,d |
| | Diel Period ^b | x | x | x | | x | x |
| | Mean Temperature | x | x | x | | x | x |
| Individual | Rainfall (mm) | x | x | x | | x | x |
| | Sex | x | x | x | | x | x |
| | WAIC | 1869.7 | 1870.1 | 1871.7 | 1873.6 | 1873.7 | 1894.0 |

^a Sine and cosine transformations of the fractional lunar phase.

^b Binary variable with a level for day and night.

All models were written in the Stan language for Bayesian statistics (Carpenter et al., 2017). Each model was updated for 3000 iterations, discarding the first 2000 iterations as the warm-up, and sampling every tenth position of the Markov chain (i.e., the thin rate). We ran three chains and used diagnostic plots to assess problems with convergence of parameter estimates. The relative fit of the set of candidate models was assessed using the widely applicable information criterion (WAIC).

To avoid bias in movement distance calculations resulting from missed location observations, only those time periods with > 90% location fix success rates were included in the regression analysis. Furthermore, because we use lagged response covariates to control for temporal autocorrelation, we eliminated from our data set those time periods with missing observations from either of the two preceding time periods. Using these criteria resulted in 455 nighttime (mean: 65 paths/leopard, range: 11–182) and 404 daytime (mean: 57.7 paths/leopard, range: 4–175) movement paths across $n = 7$ leopards. All analyses were carried out using R v3.4 (R Core Team, 2017).

3. Results

3.1. Diel movement behavior and habitat selection

Leopard movement activity was variable over the diel period, (Fig. 3). Averaging across all individuals, the linear displacements between location fixes were greatest in the minutes following sunrise (mean_{06:30} ± 1.96 × SD = 94 ± 43 m/15 min) and sunset (mean_{19:00} ± 1.96 × SD = 132 ± 40 m/15 min), and were generally low throughout the day, with the minimum movement rate occurring around mid-day

(mean_{12:45} ± 1.96 × SD = 38 ± 13 m/15 min). In addition to the rate of movement, there was some variation in directional persistence over the course of a day. Directional persistence was also greatest just after sunset ($\rho_{12:45} \pm 1.96 \times SD = 0.34 \pm 0.12$), concurrent with the observed increase in movement speed. Interestingly, with the exception of a single individual, this increase in directional persistence does not occur in the minutes following sunrise ($\rho_{06:30} \pm 1.96 \times SD = 0.087 \pm 0.076$), where there is a similar concerted increase in average movement speed. Instead, the bootstrap analysis reveals a second, smaller change in movement directionality in the hours before sunrise ($\rho_{04:15} \pm 1.96 \times SD = 0.18 \pm 0.11$).

The bootstrap analysis of selection ratios over the diel period also shows that the changes in movement patterns detected around sunrise and sunset also coincided with marked shifts in habitat preferences (Fig. 4). We found consistent between-individual selection patterns for habitats classified on the basis of vegetation characteristics. Areas lacking in overstory cover were avoided by leopards during the day and night, although avoidance was stronger for areas without vegetation cover (“Open”) than those dominated primarily by grasses (“Grass”). Instead, the leopards in our sample strongly preferred areas that provided concealment. The “Woody Cover”, “Luggas”, and “Escarpment” habitats are each characterized by tree cover and rugged topography. Leopards spent a disproportionate amount of their time in these habitat types, and this preference was most pronounced during the daylight hours.

Landscape disturbances associated with the research and ranching operations at our study site were also avoided by leopards. Roads and other areas where encounters with people are likely to occur were

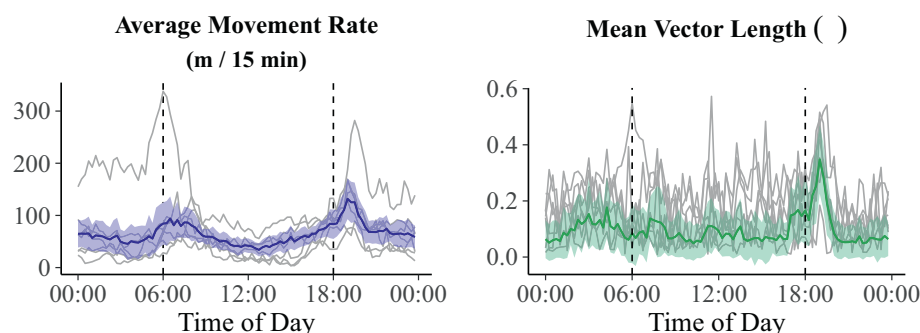


Fig. 3. Average distance moved (top) and directionality in movement (bottom) over the diel period across $n = 7$ leopards. Lower mean vector length values indicate more tortuous travel. Gray lines are individual-level averages. Colored lines are the mean and 95% confidence interval of each statistic from the multilevel bootstrap distribution. The vertical dashed lines indicate the approximate times of sunrise and sunset at our study site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

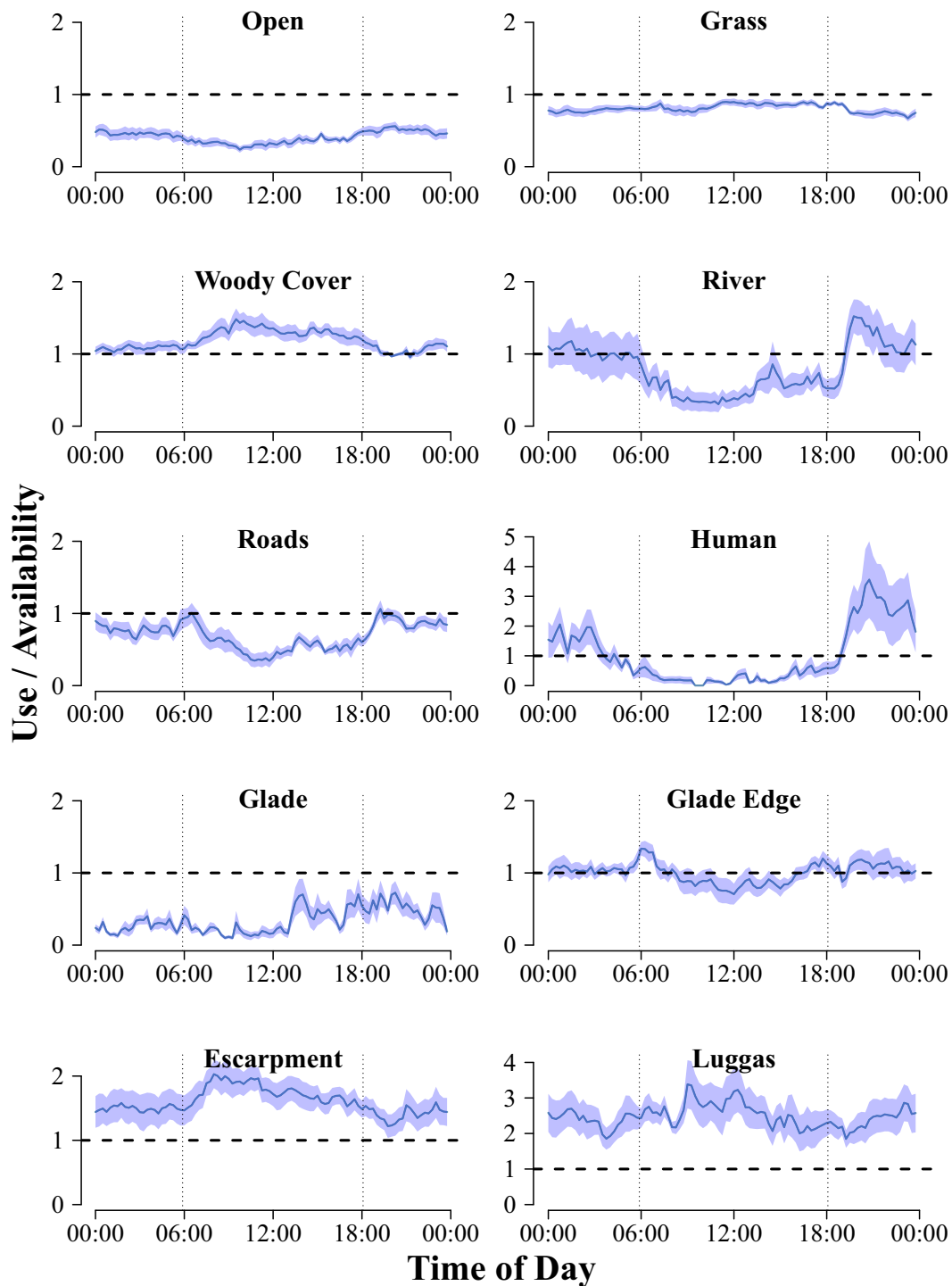


Fig. 4. Temporal patterns of habitat selection by habitat category. Trend lines and shading display the mean selection ratio and 95% confidence interval at each regularly scheduled 15-min time interval. Vertical lines are the approximate times of sunrise and sunset. Ratios < 1 indicate avoidance while ratios > 1 indicate preference.

regularly avoided from sunrise to shortly before sunset. In contrast to the stark patterns of avoidance observed during the day, we detected greater individual variation in the use of these landscape features at night, particularly the use of fenced areas and buildings. These areas were disproportionately utilized by some of the leopards in our sample and avoided outright by others, resulting in the greater uncertainty of the selection ratio statistic during nighttime hours. Selection for areas disturbed by roads exhibited this same trend, although leopards showed mild aversion rather than a preference for these areas at night. Glades

were avoided at all times of day much in the same way that leopards avoided other areas devoid of canopy cover. However this avoidance did not mean that glades were unimportant for the spatial ecology of leopards at our site. We found a moderate preference for the band of regenerating vegetation surrounding during the night, but especially so in the minutes around sunrise and sunset. Otherwise leopards showed a mild aversion to glade edges during the daytime.

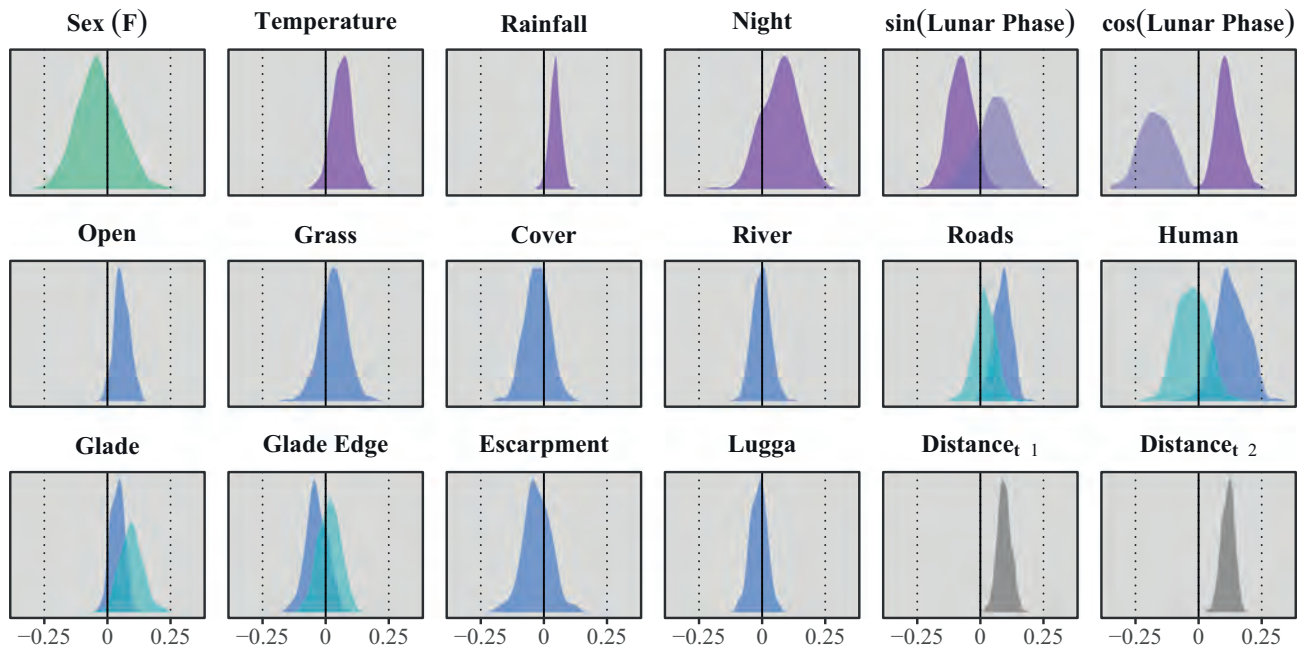


Fig. 5. Posterior distributions of the model slope coefficients from the best fit regression model (Anthro \times Diel) for predicting leopard ranging distances. Units on the horizontal axes are standard deviations. Prior to model estimation, predictor variables were centered to a mean of zero and scaled to unit variance to assist comparisons of coefficient effect sizes. Sex was the only individual level fixed effect and is shown in green, covariates for temporal predictors are purple (interactions are light purple), and spatial covariates are blue (interactions are light blue). The lagged response covariates are shown in gray. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Regression models of leopard ranging behavior

We first fit a model containing a complete additive set of our predictor variables (“Additive”) and examined the magnitude of the estimated covariate effect sizes. We noted that the effect of lunar phase on leopard ranging activity was strong relative to other predictors and that this effect applied to both day and nighttime ranging activity. We therefore fit an additional model with an interaction term between the lunar phase and diel period (“Additive +”) in order to determine if the influence of lunar phase depended on the diel period. Adding this interaction term lowered the WAIC score ($\Delta\text{WAIC} = -3.6$) and was included in later models.

The habitats at our study site are defined on the basis of vegetation cover, topography, and anthropogenic impact. The physical characteristics of the substrate and vegetation cover directly influence animal movement behavior, and therefore observed movement rate, by requiring individuals to alter their gait and travel route (Shepard et al., 2013). In contrast, those habitats defined on the basis of anthropogenic influence are relatively scarce on the landscape and whose influence on leopard ranging patterns may be likely to be the result of behavioral responses to disturbance cues. Therefore we fit two regression models in order to examine the relative influence of anthropogenic landscape features on observed ranging patterns. The “No Anthro” model removes anthropogenic spatial covariates, representing a case where leopard movement activity is unaffected by the amount of time spent in habitat types defined on the basis of human influence, regardless of the time of day. The “Anthro \times Diel” model includes interaction terms between the anthropogenic spatial covariates such that the specified relationship between time spent in these habitats and leopard movement activity depends on the time of day. Despite the greater model complexity, adding these interaction terms to the set of model predictors improved the fit relative to the “Additive” model ($\Delta\text{WAIC} = -4.0$), but removing them entirely substantially increased the WAIC score ($\Delta\text{WAIC} = 20.3$).

Our multilevel bootstrap analysis revealed numerous changes in habitat selection and features of movement behavior coinciding with sunrise and sunset. These correlated changes in activity and space use

led us to fit an additional model where the influence of habitat structure varied depending on the time of day that it was used (“Spatial \times Diel”). Including these terms marginally worsened the fit when compared to the model containing only additive predictors ($\Delta\text{WAIC} = 1.9$).

While we can be certain much of the observed variation in ranging patterns can be accounted for by spatial covariates that directly influence the manner by which leopards move across the landscape, the relative importance of temporally varying environmental factors is less obvious. We examined the influence of these variables by fitting a model where we removed the subset of temporal predictors (“No Temporal”). Removing these covariates marginally reduced model performance ($\Delta\text{WAIC} = 0.2$).

The posterior distribution from the best-fit regression model was used to make inferences about the relative effect sizes of the set of linear predictor variables on leopard ranging distances (Fig. 5; Appendix C). There was considerable variation in the distance traveled by leopards over each 12 h time period, though much of the variation in ranging distances occurred within rather than among individuals (Table 3). While individuals showed variability in their ranging patterns, the results of our regression model indicate that much of the observed variation in ranging distances is not easily explained by simple individual differences. The intraclass correlation coefficient (ICC) reports the proportion of the total variance in the model explained by the between-individual variation captured by the random effect parameters. In our model the ICC was 0.26 (95% highest posterior density interval; HPDI [0.10, 0.41]), indicating that little of the unstructured variability in ranging distances, after accounting for fixed effects, could be attributed to individual-level variation.

The sex of the leopards was a poor predictor of ranging behavior during each 12 h time period. Female leopards had a tendency to move shorter distances than males although this effect had a wide posterior distribution that overlapped extensively with zero ($\beta_{\text{sex}} = -0.03[-0.19, 0.14]$). A more consistent individual-level factor that explained ranging patterns was the periodicity in ranging patterns detected by the lagged-response covariates. The distances moved over the preceding 24 h were strong and consistent predictors of future

Table 3

Summary of individual ranging distances included in the regression analysis. All measures are in units of kilometers. The coefficient of variation (CV) is $100 \times (\text{SD}/\text{Mean})$ and has no units.

| Leopard ID | Sex | Mean (day) | Mean (night) | Range (day) | Range (night) | CV (day) | CV (night) |
|------------|-----|------------|--------------|-------------|---------------|----------|------------|
| CH | F | 4.23 | 3.51 | 0.83–8.99 | 0.82–6.94 | 48.5 | 42.6 |
| EW | F | 2.37 | 1.74 | 0.19–6.93 | 0.16–8.42 | 58.2 | 72.6 |
| HA | F | 2.61 | 2.86 | 0.50–6.37 | 0.41–5.05 | 68.8 | 59.9 |
| KO | F | 2.53 | 3.92 | 0.39–7.76 | 0.25–12.70 | 58.1 | 55.9 |
| LM | F | 1.91 | 1.44 | 0.29–5.68 | 0.15–2.77 | 71.9 | 70.5 |
| MZ | F | 2.76 | 8.90 | 0.82–7.74 | 3.61–14.53 | 69.7 | 50.2 |
| TA | F | 3.04 | 2.60 | 0.41–7.89 | 0.30–7.05 | 58.2 | 57.1 |

ranging activity, and including these lagged-response terms in the model proved to be important for accounting for the variation in ranging distances explained by autocorrelation in movement activity. The estimates from these coefficients reveal that the distance moved by leopards during the 12–24 h window prior had a greater predicted effect on future ranging behavior ($\gamma_{t-2} = 0.11[0.06, 0.16]$) than did the distance moved during the 12 hours just before ($\gamma_{t-1} = 0.09[0.04, 0.15]$).

There was a tendency for leopards to move greater distances at night, although this effect had high uncertainty ($\beta_{\text{Night}} = 0.07[-0.6, 0.21]$). Instead, total movement activity over a 24 h period and the relative allocation of activity between the day and night were more strongly associated with the lunar cycle ($\beta_{\sin(\text{LunarPhase})} = -0.08[-0.17, 0.01]$; $\beta_{\cos(\text{LunarPhase})} = 0.11[0.02, 0.20]$). Importantly, our model selection procedures and the posterior distribution of model covariates also show that the effect of lunar phase was different for day and nighttime movement activity ($\beta_{\sin(\text{LunarPhase}) \times \text{Night}} = 0.6[-0.05, 0.19]$; $\beta_{\cos(\text{LunarPhase}) \times \text{Night}} = -0.17[-0.32, -0.06]$). Overall, total daily ranging activity was greatest towards the end of the lunar cycle, just prior to the new moon (Fig. 6). During these periods, leopards tended to allocate a greater proportion of their ranging activity to the daytime while simultaneously reducing nighttime movement activity. Leopards were least active just before the full moon, and altered their activity patterns by reducing daytime ranging activity and moving slightly more at night.

Environmental variability from changing temperature and rainfall during each movement period also had modest effects on leopard ranging behavior. After controlling for diel period, our model predicted that leopards would travel greater distances with rising average temperatures ($\beta_{\text{Temp.}} = 0.11[0.06, 0.16]$) and greater amounts of total rainfall ($\beta_{\text{Rain}} = 0.04[0.00, 0.09]$) during each movement period.

Generally, variation in ranging distances was not associated with

changes in the use of naturally occurring habitat types. Notably, however, greater ranging activity was associated with greater use of roads ($\beta_{\text{Roads}} = 0.08[0.01, 0.14]$), buildings ($\beta_{\text{Human}} = 0.13[0.01, 0.23]$), and glades ($\beta_{\text{Glade}} = 0.04[-0.01, 0.09]$). The association between glade use and increased movement was also stronger for nighttime ranging activity than during the day ($\beta_{\text{Glade} \times \text{Night}} = 0.10[0.02, 0.19]$). Interaction terms of diel period and use of roads ($\beta_{\text{Roads} \times \text{Night}} = 0.02[-0.07, 0.10]$), buildings ($\beta_{\text{Humans} \times \text{Night}} = -0.03[-0.14, 0.09]$), and glade edge ($\beta_{\text{GladeEdge} \times \text{Night}} = 0.01[-0.07, 0.10]$) habitats did not show this same effect, but including these additional terms marginally improved the fit of the model.

4. Discussion

Our study combined exploratory statistical modeling, animal location tracking, and quantitative computational methods from the field of movement ecology to uncover the environmental and behavioral impetus of leopard movement activity in a human-dominated landscape. We found changes in leopard movement speed and directional persistence around the times of sunrise and sunset. Changing light regimes were also associated with shifts in habitat preferences. During the daytime, leopards increased their use of areas that provide concealment, avoided areas devoid of cover, and generally avoided anthropogenic landscape modifications. At night, use of anthropogenic habitats became more variable with some leopards in our sample exhibiting a moderate to strong preference for roads and the areas surrounding dwellings and other structures.

These insights were then used in a regression model comparison framework to examine the relative influence of space use and temporally varying environmental variables in shaping leopard movement activity over the diel period. In particular, we were interested in testing if allocation of movement activity between night and day was influenced by anthropogenic landscape modifications at MRC, and whether or not the influence of anthropogenic habitats depended also on the diel period, which corresponds with human activity at our study site. The results of our model rankings and interpretation of model covariates support this conclusion. Use of anthropogenic habitats, but not naturally occurring ones, was associated with longer ranging forays, and the strength of this association was influenced by the time of day these habitats were used. The allocation of movement activity between the day and night was also influenced by the lunar phase, which had independent effects for night and daytime ranging activity. During darker phases of the moon, leopards moved greater distances overall, but tended to allocate a greater portion of their ranging activity to the daytime. When the moon was at its brightest in the night sky, leopards tended to reduce their overall ranging distances while allocating a greater proportion of their movement activity to the nighttime.

4.1. Environmental influence on leopard activity patterns

Leopards' widespread geographical distribution, behavioral flexibility, and varied diet has led them to be labeled habitat generalists, but vegetation and terrain features that provide concealment are known

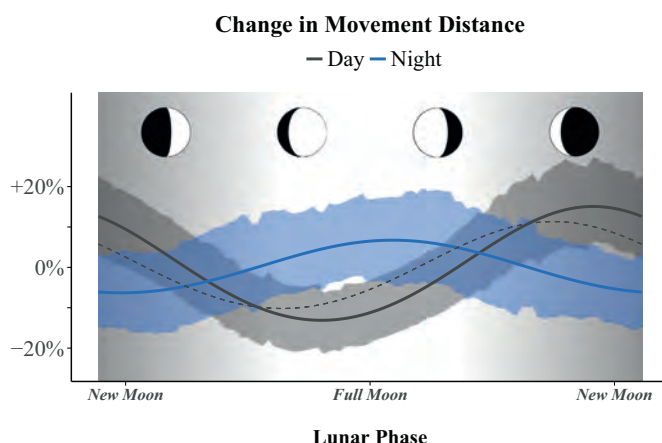


Fig. 6. Predicted changes in night (blue) and day (gray) ranging distances over the lunar cycle (mean and 95% highest posterior density interval). The dashed line shows the average net change in total (24 h) movement distance. Estimates are derived from the posterior probability distribution of the “Anthro \times Diel” regression model (see Table 2).

to be important fine-scale resources that can act as important determinants of leopard space use, particularly in arid landscapes with patchy distribution of forest cover (Bothma, 1998; du Preez et al., 2015). As ambush predators, leopards' success in hunting is primarily determined by their ability to stalk prey undetected and attack from a nearby concealed position (Sunquist and Sunquist, 1989). Leopards may also exploit the concealment offered by terrain and vegetation features to cache recent kills in order to prevent theft by scavengers or competitors (Ford et al., 2014; du Preez et al., 2015). Furthermore, species adapted for stealth should be expected to employ these same traits in order to avoid detection in response to threats (Caro, 2005). It seems plausible, although it remains to be demonstrated in this species, that greater use of habitats providing concealment indicates leopards are using these areas to avoid predation by other large carnivores such as hyenas, lions, or other leopards, which are an important source of mortality for adult leopards and their cubs (Balme et al., 2013). These and other benefits provided by concealment likely explain the strong preference for low-visibility habitats at our site, particularly during the daytime when they are more likely to be detected by prey or competitors (Sunquist and Sunquist, 1989; Bothma, 1998).

The importance of concealment may also underlie the strong effect of lunar phase on leopard ranging behavior. Moonlight is known to be an important factor shaping rates of interactions in predator-prey systems. For example, avoidance of moonlight was important in shaping the trade-off among predation risk, foraging efficiency, and energetic state in gerbils (*Gerbillus andersoni allenbyi*; Kotler et al., 2010). During brighter lunar phases, gerbils increased rates of vigilance and sooner abandoned experimental food patches compared to darker nights. Following the full moon, however, as the period of threat grew longer, gerbils had to reduce antipredator effort in order to compensate for their lower energetic state (Kotler et al., 2010). If greater levels of moonlight increase perception of environmental risk, then similar dynamics could explain why our regression model predicts that the average overall ranging distances would be lowest at the onset of a pulse of risk, just prior to the full moon, and greatest immediately following it.

Variation in hunting success driven by shifting environmental conditions could also explain the effect of lunar phase on predicted ranging distances. One study tracking the movements of leopards in South Africa found that they were primarily nocturnal and had greater hunting success during darker phases of the lunar cycle, although they reportedly hunted diurnal species, which might be particularly vulnerable to predation on darker nights (Martins and Harris, 2013). In that study, poorer hunting success was also associated with longer ranging distances as leopards needed to travel further in order to locate prey. Lions in Tanzania were also more successful at capturing prey during darker lunar phases (Packer et al., 2011). However, we found that travel distances were generally shorter during brighter phases of the lunar cycle, suggesting perhaps that hunting success would be greater on moonlit rather than darker nights. This pattern of hunting success is similar to cycles of predation risk for snowshoe hares (*Lepus americanus*) by Canada lynx (*Lynx canadensis*; Griffin et al., 2005). Snowshoe hares experienced higher predation rates on nights surrounding the full moon than during other phases of the lunar cycle. In that study, moonlight was thought to allow lynx to locate and track their prey more effectively under snowy winter conditions (Griffin et al., 2005).

Using more advanced techniques to document behavioral responses of wild animals could help clarify how lunar phase might shape the trade-off between foraging rate (hunting success and movement efficiency) and environmental risk. Accelerometer-based behavioral monitoring and other biologging instruments are now more commonly used to estimate detailed activity budgets of wild animals, allowing for accurate reconstructions of time and energy allocation for cryptic and wide-ranging species (Brown et al., 2013; Wilmers et al., 2017). Such devices can be used to directly test if leopard foraging effort and

hunting success varies over the lunar cycle by identifying signatures of predation events (Wilmers et al., 2017). The behavioral inferences generated from these approaches could be used to test whether leopards alter their behavior in response to proposed threats in ways consistent with predictions from behavioral ecology (Brown and Kotler, 2004). Following from the risk allocation hypothesis, if leopards avoid moonlight because of greater environmental risk, we should expect that the strength of their individual behavioral responses will be greatest during the second quarter lunar phase. During this period, individuals should be most risk averse, and respond to the onset of threat by reducing energy expenditure, changing activity patterns, and altering space use in order to reduce exposure to risky areas. Reductions in energetic state resulting from avoidance should then cause leopards to increase their foraging effort relative to other activities (e.g., rest) in order to avoid starvation. At these times, we predict that leopards will be less risk averse and therefore more likely to visit exposed or disturbed habitats that would otherwise be avoided.

4.2. Implications for conservation in mixed-use landscapes

The geographic ranges of leopard subspecies are in decline, and much of the remaining extant range occurs outside of protected areas (Jacobson et al., 2016). Although recent studies have shown that leopard populations are capable of persisting in human-dominated landscapes (Athreya et al., 2013), conflicts with humans remain a challenge for conserving this species in mixed-use landscapes (Inskip and Zimmermann, 2009; Athreya et al., 2014). While lethal predator control and other direct negative interactions with leopards are reportedly rare on pro-wildlife ranches on the Laikipia plateau (Romañach et al., 2007), and are not practiced at MRC, the results of our exploratory analyses and regression modeling suggest that anthropogenic landscape modifications and human activity remain important drivers of leopard space use.

Despite the tendency for leopards to be active at all times of the day, they avoided roads and other areas where encounters with people during the daytime. Elsewhere, leopards have been reported to exhibit similar behavioral responses when inhabiting areas disturbed by human activity. Leopards in the Kaeng Krachan National Park, Thailand showed significantly less diurnal activity in areas near human traffic, and roads inside of the park were barriers for leopard movements during the day (Ngoprasert et al., 2007). Carter et al. (2015) compared the activity patterns of leopards in a protected area to those adjacent forests where resource extraction by local people was common. Leopards outside the park showed greater temporal displacement to human activity than did leopards inside the park where human disturbance was confined to select trails. We also detected avoidance of the riverine habitat during the day time, despite our impression that this habitat contained a relatively high density of potential prey species. The river at our site runs parallel to a heavily-used road and the river itself is an important source of water for wild animals and livestock. Similar avoidance patterns have been documented in spotted hyenas (*Crocuta crocuta*) on a wildlife reserve in Kenya (Boydston et al., 2003). Hyenas responded to short-term influxes of livestock grazing by avoiding recently grazed areas despite their greater density of wild and domestic prey (Boydston et al., 2003). As in other instances, these activities may present a barrier to leopard movements.

The diel cycle of human activity on conservancies and similar land uses might also contribute to conflicts with humans as leopards were most likely to be active around roads and buildings around sunrise and sunset, overlapping with periods of human activity. Studies from pumas (*Puma concolor*) occupying recreation areas have reported similar findings, showing that individuals often adjusted to the daily influx of visitors by avoiding trails and other impacted areas during the daytime; however, this also created the opportunity for conflict as the pumas were also most active around trails and buildings in the evening, when there was a low expectation of encounters (Morrison et al., 2014;

Sweaner et al., 2008). In Laikipia, attitudes of subsistence livestock herders towards carnivores are strongly influenced by the dangers posed by predators to human safety and livelihoods (Romañach et al., 2007). Direct encounters with predators and other signs of their presence on community rangelands can increase negative attitudes towards predators, thwarting tolerance for wildlife conservation and leading to lethal control in anticipation of depredation events (Romañach et al., 2007, 2011). Furthermore, the results of our regression modeling showed that use of anthropogenic habitats, but not naturally occurring ones, were strongly associated with periods of greater ranging activity. This might indicate that use of these habitats is associated with more conspicuous movement states, driven by underlying environmental factors that influence the trade-off between risk from humans and foraging efficiency (Oriol-Cotterill et al., 2015a; Valeix et al., 2012). Given the importance of direct and indirect interactions in shaping human perceptions of predators, future research should focus on uncovering the ecological and behavioral correlates of individual leopard movement decisions in human-dominated landscapes.

This study is among the first to examine in detail leopards' use of glades, which are the legacy of the pastoral practices endemic to the region. Many of these practices, including corralling livestock at night in bomas, are still used on conservancies and community rangelands in Kenya to protect livestock from theft and attacks by carnivores (Ogada et al., 2003). In recent years, development and social change in formerly rural areas has led to community rangelands being divided into smaller, family-owned units that reduce herders' mobility, and lead to an increased density of glades on the landscape. At the same time, intensification of agricultural production has also seen many open grasslands converted to commercial ranching operations that forgo these husbandry practices that can beneficially modify ecosystems (Ogutu et al., 2011; Vuorio et al., 2014). Given the cultural origins of glades, and their importance to the ecology of East African savanna-woodlands, understanding the role of leopards and other carnivores in the dynamics of these unique landscape features remains an important direction of research for conservation efforts in this region.

As expected, leopards avoided entering glades at all times of the day, likely either because these open habitats are used by prey as high-visibility refuges (Ford et al., 2014; Riginos, 2015) or are occasionally used by herders to graze livestock during the daytime. Nonetheless, the leopards in our sample used glade edge habitat, more often at night and around the times of sunrise and sunset. This pattern may reflect the use

and activity patterns of leopard prey species that use these landscape features (Augustine, 2004). These results also suggest that the influence of glades for the distribution of leopards might be better understood at broader spatial scales. The leopards in our study ranged over a relatively small area with a well-enforced conservation management strategy. Further studies might compare the population densities of leopards to the presence or absence of glades across different land use systems in Laikipia in order to clarify the relative influence of glades on leopard movement decisions in this matrix of varying land use systems.

Given the importance of wild herbivores in maintaining glades, and the threat of predation in driving intensive use of these high visibility refuges, resource selection studies could also consider other qualities of glades when assessing their importance in driving the spatial distribution of ungulates and their predators. For example, the edges of adjacent glades have greater tree cover density for concealment than do isolated glades, but they also contain a lower abundance of unique grass and ungulate species (Porensky, 2011). Other factors such as aridity, the amount of time since a boma was abandoned, and seasonal variation in rainfall can affect the nutrient quality of glades relative to the background landscape (Augustine, 2003, 2004). Considerations of these and other factors in shaping the use of glades by leopards and other carnivores could further illuminate the role of predators in the dynamics of these nutrient hotspots.

Conflicts of interest

The authors have no conflicts of interest to declare.

Acknowledgments

Mark N. Grote, the Crofoot/Caillaud labs at UC Davis, and two anonymous reviewers provided helpful feedback that greatly improved the original manuscript. This work was supported by NSF Grant DBI-1255913 (C.C.W.); NSF Grants BCS 99-03949 and BCS 1266389, the L.S.B. Leakey Foundation, and the University of California, Davis, Committee on Research (L.A.I); and the Wenner-Gren Foundation (grant no. 8386) to L.R.B. The research was conducted under University of California, Davis IACUC protocol #17477 and Kenya Government NACOSTI permit No. P/15/5820/4650. We thank the Kenya Wildlife Service, D. Simpson, S. Ekwanga, M. Mutinda, G. Omondi, W. Longor for their assistance with field research.

Appendix A

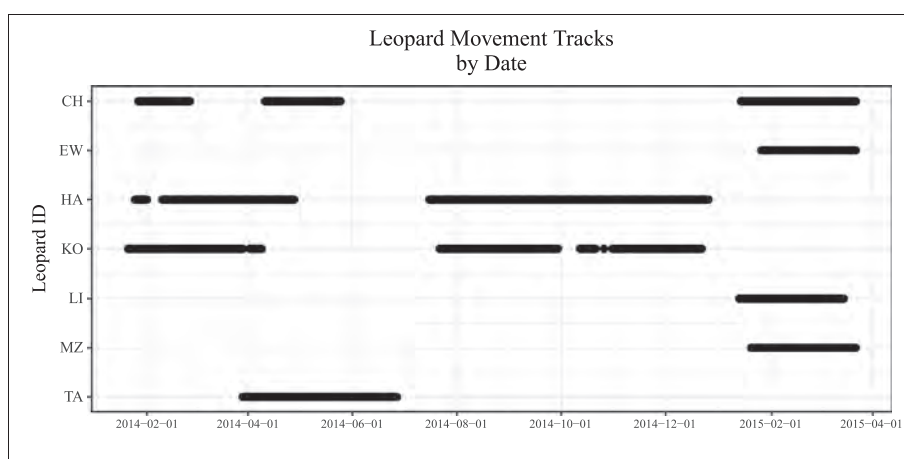


Fig. A1. Timing and duration of individual leopard movement tracks.

Appendix B

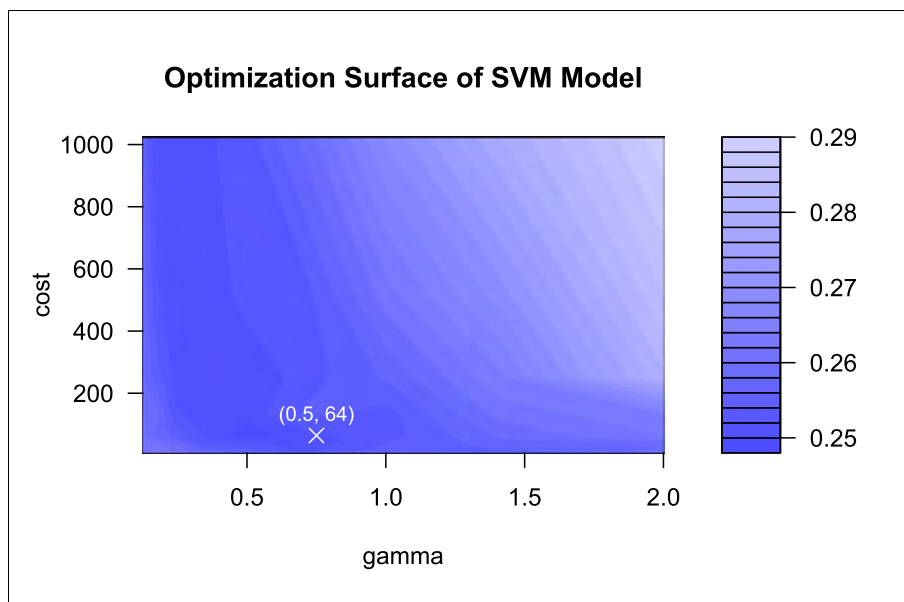


Fig. B1. Optimization surface for the support vector machine model (SVM) that was used to predict vegetation cover land classes for the habitat map. The model uses two parameters, “cost” and “gamma”, to generate the best fit model. Grid approximation was used to find the optimum parameter values (labeled) based on a goodness-of-fit statistic.

Table B1

A confusion matrix showing the predictive accuracy of the support vector machine model. A balanced data set with 1000 reference observations from each habitat class (columns) was used here to assess model performance. This table was created using the “caret” packages for R.

| | Open | Grass | Cover |
|----------------------|------|-------|-------|
| Sensitivity | 0.83 | 0.61 | 0.81 |
| Specificity | 0.91 | 0.83 | 0.89 |
| Pos pred value | 0.82 | 0.64 | 0.78 |
| Neg pred value | 0.91 | 0.81 | 0.90 |
| Precision | 0.82 | 0.64 | 0.78 |
| Recall | 0.83 | 0.61 | 0.81 |
| F1 | 0.83 | 0.63 | 0.80 |
| Prevalence | 0.33 | 0.33 | 0.33 |
| Detection rate | 0.28 | 0.20 | 0.27 |
| Detection prevalence | 0.34 | 0.32 | 0.35 |
| Balanced accuracy | 0.87 | 0.72 | 0.85 |

```

#install.packages("e1071")
library(e1071)
#load land cover classification layer
landCover = raster("landcover.tif")
#load Landsat data
lsatFiles = list.files("Landsat_LC81680602014178LGN00/",
                      pattern = ".TIF", full.names=TRUE)
#stack Landsat 8 bands (QA, 5, 4, 3, and 2)
lsatData = stack(lsatFiles)
#see https://landsat.usgs.gov/qualityband for QA band code definitions.
dataCells = 1:ncell(cover)[which(getValues(lsatData["QA"])==20480)]
train_cells = sample(dataCells, 1e3, replace=FALSE)
#get reflectance values
trainData = data.frame(raster::extract(lsatData, train_cells))
names(trainData) = c("B2","B3","B4","B5","QA")
#get proportion cover data
trainData$cover = raster::extract(cover, train_cells)
#estimate support vector machine model
svmTune = tune(svm, cover ~ B2 + B3 + B4 + B5,
              data=trainData, #training data set
              #search for optimum parameter values using a grid search
              ranges = list(gamma = 2^seq(0.5, 3, by = 0.5),
                           cost = 2^seq(3, 6, by = 1)
              )
plot(svmTune) #examine fit
print(svmTune) #output summary

#calculate confusion matrix
#install.packages("caret")
library(caret)
#get known land cover values
predict_cells = sample(1:ncell(cover)[which(getValues(lsatData["QA"])==20480)
                      & which(
                        getValues
                        (!is.
                        na(
                        cover
                        )))],
                      1e3, replace=FALSE)
#get predicted land cover class from tuned SVM model.
preds = predict(best.tune(svmTune), predict_cells)
cM = confusionMatrix(preds, reference = trainData)
print(cM)

```

Fig. B2. R code for fitting the support vector machine model and calculating the confusion matrix.

Appendix C

Table C1

Summary of the "Anthro × Diel" model posterior. The \hat{R} statistic reported here was used to assess convergence of the Markov chains. α_i are individual random effect parameters, and $\bar{\alpha}$ is the model intercept.

| | Mean | 2.5% | 25% | 50% | 75% | 97.5% | \hat{R} |
|--------------------------|-------|-------|-------|-------|-------|-------|-----------|
| Distance _{t-1} | 0.09 | 0.04 | 0.07 | 0.09 | 0.11 | 0.15 | 0.99 |
| Distance _{t-2} | 0.11 | 0.06 | 0.09 | 0.11 | 0.13 | 0.16 | 1.00 |
| SexF | -0.03 | -0.19 | -0.09 | -0.03 | 0.03 | 0.14 | 1.00 |
| Night | 0.07 | -0.06 | 0.02 | 0.08 | 0.12 | 0.21 | 0.99 |
| Temperature | 0.11 | 0.06 | 0.09 | 0.11 | 0.13 | 0.16 | 1.00 |
| Rainfall | 0.04 | 0.00 | 0.03 | 0.05 | 0.06 | 0.09 | 1.01 |
| sin(Lunar Phase) | -0.08 | -0.17 | -0.12 | -0.08 | -0.05 | 0.01 | 1.01 |
| cos(Lunar Phase) | 0.11 | 0.02 | 0.08 | 0.11 | 0.14 | 0.20 | 0.99 |
| sin(Lunar Phase) × Night | 0.06 | -0.05 | 0.02 | 0.06 | 0.11 | 0.19 | 0.99 |
| cos(Lunar Phase) × Night | -0.17 | -0.32 | -0.22 | -0.17 | -0.13 | -0.06 | 1.00 |
| Open | 0.06 | 0.00 | 0.04 | 0.06 | 0.08 | 0.12 | 1.00 |
| Grass | 0.03 | -0.07 | -0.00 | 0.03 | 0.07 | 0.13 | 0.99 |
| Cover | -0.03 | -0.12 | -0.06 | -0.03 | 0.01 | 0.07 | 1.00 |
| River | -0.00 | -0.07 | -0.03 | -0.00 | 0.02 | 0.07 | 0.99 |
| Roads | 0.08 | 0.01 | 0.06 | 0.09 | 0.11 | 0.14 | 0.99 |
| Humans | 0.13 | 0.01 | 0.09 | 0.12 | 0.17 | 0.23 | 1.00 |
| Glades | 0.04 | -0.01 | 0.02 | 0.04 | 0.06 | 0.09 | 0.99 |
| Glade Edge | -0.04 | -0.12 | -0.06 | -0.04 | -0.00 | 0.05 | 1.01 |
| Escarpment | -0.03 | -0.14 | -0.06 | -0.03 | 0.01 | 0.09 | 1.00 |
| Luggas | -0.02 | -0.08 | -0.04 | -0.01 | 0.01 | 0.04 | 1.00 |

(continued on next page)

Table C1 (continued)

| | Mean | 2.5% | 25% | 50% | 75% | 97.5% | \hat{R} |
|--------------------|-------|-------|-------|-------|------|-------|-----------|
| Roads × Night | 0.02 | −0.07 | −0.01 | 0.02 | 0.04 | 0.10 | 1.00 |
| Humans × Night | −0.03 | −0.14 | −0.07 | −0.03 | 0.02 | 0.09 | 1.00 |
| Glades × Night | 0.10 | 0.02 | 0.07 | 0.09 | 0.12 | 0.19 | 1.00 |
| Glade Edge × Night | 0.01 | −0.07 | −0.02 | 0.01 | 0.05 | 0.10 | 0.99 |
| σ | 0.70 | 0.67 | 0.69 | 0.70 | 0.72 | 0.73 | 1.00 |
| α_1 | 7.97 | 7.77 | 7.89 | 7.97 | 8.04 | 8.17 | 1.00 |
| α_2 | 7.67 | 7.39 | 7.58 | 7.68 | 7.76 | 7.99 | 1.00 |
| α_3 | 7.77 | 7.67 | 7.74 | 7.77 | 7.80 | 7.86 | 0.99 |
| α_4 | 7.47 | 7.38 | 7.44 | 7.47 | 7.51 | 7.59 | 1.00 |
| α_5 | 7.45 | 7.14 | 7.36 | 7.45 | 7.56 | 7.71 | 1.01 |
| α_6 | 7.71 | 7.39 | 7.61 | 7.71 | 7.82 | 8.01 | 1.00 |
| α_7 | 7.60 | 7.39 | 7.53 | 7.59 | 7.67 | 7.81 | 1.00 |
| $\bar{\alpha}$ | 7.64 | 7.48 | 7.59 | 7.63 | 7.69 | 7.78 | 1.00 |
| σ_{α} | 0.25 | 0.11 | 0.17 | 0.23 | 0.31 | 0.52 | 1.00 |

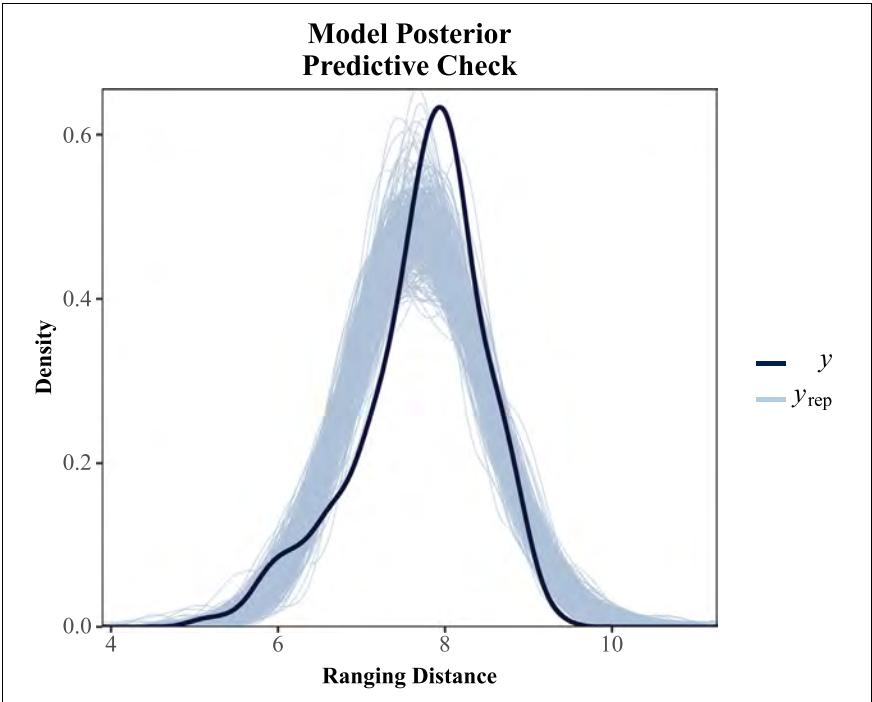


Fig. C1. Posterior predictive checks for the best-fit regression model. Predicted ranging distances from the model posterior distribution (y_{rep} ; $n = 100$) are compared against observed ranging distances (y). Values are on the log scale.

Appendix D. Supplementary data

Supplementary data associated with this article can be found in the online version at <https://doi.org/10.1016/j.biocon.2018.08.003>. These data include the Google map of the most important areas described in this article.

References

Andersen, M., Aars, J., 2007. Short-term behavioural response of polar bears (*Ursus maritimus*) to snowmobile disturbance. *Polar Biol.* 31, 501–507.

Andersen, R., Linnell, J.D.C., Langvatn, R., 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biol. Conserv.* 77, 169–176.

Athreya, V., Odden, M., Linnell, J., Krishnaswamy, J., Karanth, U., 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* 8, 1–8. <https://doi.org/10.1371/journal.pone.0057872>.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, K.U., 2014. A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* 1–7.

Augustine, D.J., 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *J. Appl. Ecol.* 40, 137–149.

Augustine, D.J., 2004. Influence of cattle management on habitat selection by Impala on central Kenyan rangeland. *J. Wildl. Manag.* 68, 916–923.

Augustine, D.J., Veblen, K.E., Goheen, J.R., Riginos, C., Young, T.P., 2011. Pathways for positive cattle-wildlife interactions in semiarid rangelands. In: Georgiadis, N.J. (Ed.), *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem*. Smithsonian Institution Press vol. 632 of I, Washington, D.C..

Balme, G.A., Batchelor, A., de Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D.W., Hunter, L.T.B., 2013. Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Rev.* 43, 221–237.

Benítez-López, A., Alkemade, R., Verweij, P., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* 143, 1307–1316.

Bothma, J.D.P., 1998. *Carnivore Ecology in Arid Lands*. Springer-Verlag, New York.

Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M., Holekamp, K.E., 2003. Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv.* 6, 207–219.

- Brown, D.D., Kays, R., Wikelski, M., Wilson, R., Klimley, A.P., 2013. Observing the unwatchable through acceleration logging of animal behavior. *Anim. Biotelem.* 1, 1–20.
- Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7, 999–1014.
- Byrne, M.E., Clint, M.J., Hinton, J.W., Chamberlain, M.J., Collier, B.A., 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. *J. Anim. Ecol.* 83, 1234–1243.
- Caro, T.M., 2005. Antipredator defenses in birds and mammals. In: *Interspecific interactions*. University of Chicago Press, Chicago.
- Carpenter, B., Lee, D., Brubaker, M., Riddell, A., Gelman, A., Goodrich, B., Guo, J., Hoffman, M., Betancourt, M., Li, P., 2017. Stan: A Probabilistic Programming Language.
- Carter, N., Jasny, M., Gurung, B., Liu, J., 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Glob. Ecol. Conserv.* 3, 149–162.
- du Preez, B., Hart, T., Loveridge, A.J., Macdonald, D.W., 2015. Impact of risk on animal behaviour and habitat transition probabilities. *Anim. Behav.* 100, 22–37. <https://doi.org/10.1016/j.anbehav.2014.10.025>.
- Fieberg, J., Dittmer, M., Freckleton, R., 2012. Understanding the causes and consequences of animal movement: a cautionary note on fitting and interpreting regression models with time-dependent covariates. *Methods Ecol. Evol.* 3, 983–991.
- Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M., Ward, D., Woodroffe, R., Pringle, R.M., 2014. Large carnivores make savanna tree communities less thorny. *Science* 346, 346–349.
- Frank, L., Simpson, D., Woodroffe, R., 2003, 03. Foot snares: an effective method for capturing African lions. *Wildl. Soc. Bull.* 31, 309–314.
- Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11.
- Georgiadis, N.J., 2011. Introduction: conserving wildlife in Kenya's Ewaso Landscape. In: *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem*. Smithsonian Contributions to Zoology, vol. 632. Smithsonian Institution Scholarly Press, Washington, D.C., pp. 1–10.
- Griffin, P.C., Griffin, S.C., Waroquiers, C., Mills, L.S., 2005. Mortality by moonlight: predation risk and the snowshoe hare. *Behav. Ecol.* 16, 938–944.
- Griffiths, M., van Schaik, C.P., 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conserv. Biol.* 7, 623–626.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144.
- Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43, 18.
- Jacobson, A.P., Gerngross, P., Lemeris Jr., J.R., Schoonover, R.F., Anco, C., Breitenmoser-Würsten, C., Durant, S.M., Farhadinia, M.S., Henschel, P., Kamler, J.F., Laguardia, A., Rostro-García, S., Stein, A.B., Dollar, L., 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 4, e1974. <https://doi.org/10.7717/peerj.1974>.
- Kinnaird, M.F., O'Brien, T.G., 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. *Conserv. Biol.* 26, 1026–1039.
- Kotler, B.P., Brown, J., Mukherjee, S., Berger-Tal, O., Bouskila, A., 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc. R. Soc. Lond. B Biol. Sci.* 277, 1469–1474.
- Kranstauber, B., Kays, R., Lapoint, S.D., Wikelski, M., Safi, K., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *J. Anim. Ecol.* 81, 738–746.
- Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., Cromsigt, J.P.G.M., 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. Lond. B Biol. Sci.* 283, 20161625.
- Lute, M.L., Carter, N.H., López-Bao, J.V., Linnell, J.D.C., 2018. Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. *Biol. Conserv.* 218, 223–232. <https://doi.org/10.1016/j.biocon.2017.12.035>.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals*, second. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Martins, Q., Harris, S., 2013. Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *Afr. J. Ecol.* 51, 571–579.
- Morrison, C.D., Boyce, M.S., Nielsen, S.E., Bacon, M.M., 2014. Habitat selection of a re-colonized cougar population in response to seasonal fluctuations of human activity. *J. Wildl. Manag.* 78, 1394–1403.
- Ngoprasert, D., Lynam, A.J., Gale, G.A., 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx* 41.
- Ogata, M.O., Woodroffe, R., Ogue, N.O., Frank, L.G., 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conserv. Biol.* 17, 1521–1530.
- Ogutu, J.O., Owen-Smith, N., Piepho, H.P., Said, M.Y., 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. *J. Zool.* 285, 99–109.
- Oriol-Cotterill, A., Macdonald, D., Valeix, M., Ekwanga, S., Frank, L., 2015a. Spatiotemporal patterns of lion space use in a human-dominated landscape. *Anim. Behav.* 101, 27–39.
- Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015b. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* 124, 1263–1273. <https://doi.org/10.1111/oik.02224>.
- Packer, C., Swanson, A., Ikanda, D., Kushnir, H., 2011. Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLoS One* 6, 1–4. <https://doi.org/10.1371/journal.pone.0022285>.
- Pewsey, A., Neuhauser, M., Ruxton, G., 2013. *Circular Statistics in R*, first. Oxford University Press, Oxford; New York.
- Porensky, L.M., 2011. When edges meet: interacting edge effects in an African savanna. *J. Ecol.* 99, 923–934.
- Core Team, R., 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Riginos, C., 2015. Climate and the landscape of fear in an African savanna. *J. Anim. Ecol.* 84, 124–133.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484.
- Romañach, S.S., Lindsey, P.A., Woodroffe, R., 2007. Attitudes toward predators and options for their conservation in the Ewaso ecosystem. *Oryx* 41, 185.
- Romañach, S.S., Lindsey, P.A., Woodroffe, R., 2011. Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. In: Georgiadis, N.J. (Ed.), *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem*. Smithsonian Institution Press vol. 632 of I, Washington, D.C..
- Shepard, E.L., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., Vosper, S.B., 2013. Energy landscapes shape animal movement ecology. *Am. Nat.* 182, 298–312.
- Smith, J.A., Wang, Y., Wilmers, C.C., 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc. Biol. Sci.* 282.
- Sunquist, M.E., Sunquist, F., 1989. Ecological constraints on predation by large felids. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Ithaca, New York.
- Sweaner, L.L., Logan, K.A., Bauer, J.W., Millsap, B., Boyce, W.M., 2008. Puma and human spatial and temporal use of a popular California State Park. *J. Wildl. Manag.* 72, 1076–1084.
- Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* 17, 1491–1499.
- Valeix, M., Hemson, G., Loveridge, A.J., Mills, G., Macdonald, D.W., 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *J. Appl. Ecol.* 49, 73–81. <https://doi.org/10.1111/j.1365-2664.2011.02099.x>.
- Veblen, K.E., 2012. Savanna glade hotspots: plant community development and synergy with large herbivores. *J. Arid Environ.* 78, 119–127.
- Vuorio, V., Muchiru, A.N., Reid, R.S., Ogutu, J.O., 2014. How pastoralism changes savanna vegetation: impact of old pastoral settlements on plant diversity and abundance in south-western Kenya. *Biodivers. Conserv.* 23, 3219–3240.
- Western, D., Russell, S., Cuthill, I., 2009. The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS One* 4, e6140.
- Williams, T.M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G.H., Wilmers, C.C., 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* 346, 81–85. <https://doi.org/10.1126/science.1254885>.
- Wilmers, C.C., Isbell, L.A., Suraci, J.P., Williams, T.M., 2017. Energetics-informed behavioural states reveal the drive to kill in African leopards. *Ecosphere* 8, 1–12.
- Woodroffe, R., Thirgood, S.J., Rabinowitz, R., 2005. The impact of human-wildlife conflict on natural systems. In: Woodroffe, R., Thirgood, S.J., Rabinowitz, R. (Eds.), *People and wildlife: conflict or coexistence?* University of Cambridge, Cambridge, pp. 1–12.
- Young, T.P., Partridge, N., Macrae, A., 1995. Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. *Ecol. Appl.* 5, 97–108.