Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape

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Abstract. Co-occurrence with humans presents substantial risks for large carnivores, yet human-dominated landscapes are increasingly crucial to carnivore conservation as human land use continues to encroach on wildlife habitat. Flexibility in large carnivore behavior may be a primary factor mediating coexistence with people, allowing carnivores to calibrate their activity and habitat use to the perceived level of human risk. However, our understanding of how large carnivores adjust the timing and location of behaviors in response to variations in human activity across the landscape remains limited, impacting our ability to identify important habitat for populations outside of protected areas. Here we examine whether African lions (*Panthera leo*) modify their behavior and habitat use in response to risk of a human encounter, and whether behavior-specific habitat selection allows lions to access feeding opportunities in a human-dominated landscape in Kenya. We determined fine-scale behavioral states for lions using high-resolution GPS and accelerometer data, and then investigated behavior-specific habitat selection at multiple temporal and spatial scales (ranging from 15 minutes to 12 hours and from approximately 200 meters to several kilometers). We found that lions exhibit substantial differences in habitat selection with respect to humans based on behavioral state and time of day. During the day, when risk of human encounter is highest, lions avoided areas of high human use when resting, meandering, and feeding. However, lions specifically selected for habitat near people when feeding at night. Flexible habitat use by lions thus permits access to prey, which appear to concentrate in areas near humans. The importance of habitat near people for feeding was only apparent when analyses explicitly accounted for lion behavioral state and spatiotemporal scale, highlighting the necessity of incorporating such information when investigating human impacts on large carnivore habitat use. Our results support the contention that behavior-specific habitat selection promotes carnivore persistence in human-dominated landscapes, demonstrating the importance of considering not just whether but how large carnivores use habitat near humans when managing vulnerable populations.

Key words: behavioral state classification; ecology of fear; human–wildlife conflict; large carnivore conservation; movement ecology; Panthera leo; *step selection function.*

Introduction

Many large carnivore populations co-occur with humans over some or all of their range in mixed-used landscapes outside of protected areas (Carter and Linnell 2016). Humans are often a primary source of mortality for these populations (Woodroffe and Frank 2005, Darimont et al. 2015, Oriol-Cotterill et al. 2015*b*), with retaliation for livestock losses, lethal predator control, poaching, and poorly managed trophy hunting all presenting substantial risks to large carnivores (Treves and Karanth 2003, Loveridge et al. 2017), and in many cases resulting in population declines (Woodroffe 2000, Ripple et al. 2014). Yet despite the threat posed by humans, some populations persist and even expand in close proximity to people (Boydston et al. 2003, Chapron et al. 2014), suggesting that large carnivores may employ flexible behavioral strategies to reduce the likelihood of human-caused mortality and thus permit coexistence with people in human-dominated landscapes. The ability

of large carnivores to persist outside of protected areas may be critical to their conservation as human land use continues to expand and encroach on wildlife habitat (Carter and Linnell 2016). Thus, elucidating the behavioral mechanisms that promote coexistence is of considerable conservation importance.

Where human-caused mortality is high, large carnivores exhibit strong fear responses to the perceived presence of people (Smith et al. 2017), as well as changes in activity, movement, and habitat use to avoid interactions with humans (Ordiz et al. 2011, 2012, Valeix et al. 2012, Schuette et al. 2013, Wilmers et al. 2013, Oriol-Cotterill et al. 2015a). Fear of humans may therefore lead to impacts on large carnivore populations beyond those stemming from direct mortality if for instance human presence reduces the amount of habitat (Wilmers et al. 2013) or time (Ordiz et al. 2012, Smith et al. 2015, 2017) available for hunting and feeding. Outright avoidance of valuable foraging habitat may be prohibitively costly, and large carnivores can potentially reduce such costs by using valuable but risky habitats at times when risk of encountering humans is low (Oriol-Cotterill et al. 2015a, b, Gaynor et al. 2018), a strategy known as "temporal partitioning" (Kronfeld-Schor and Dayan 2003). Risk of encountering humans is typically highest during the day when people are most active, and lowest at night. Several studies have correspondingly demonstrated increased nocturnality among large carnivores in areas, or during seasons, characterized by high human presence (Ordiz et al. 2012, Rasmussen and Macdonald 2012, Wang et al. 2015, Wheat and Wilmers 2016, Gaynor et al. 2018).

While restricting the use of habitat near humans to relatively safe times may indeed decrease the likelihood of anthropogenic mortality, temporal partitioning may nonetheless be costly to large carnivores by limiting access to foraging opportunities and/or by promoting behaviors with a negative effect on overall energy budget (e.g., decreased resting, increased duration or intensity of movements). For instance, African lions (*Panthera leo*) use areas of high human presence at night when human activity is low, but individuals tend to move faster and more directly in these areas than they do when farther from humans (Valeix et al. 2012, Oriol-Cotterill et al. 2015a), which may imply limited opportunity for feeding in habitat near people. Similarly, work on brown bears (*Ursus arctos*) shows that these normally diurnal, visual foragers switch to predominantly nocturnal activity when human activity is high, which may impact foraging efficiency (Ordiz et al. 2014, Wheat and Wilmers 2016). A more complete, mechanistic understanding of the costs of coexisting with humans, and the capacity for large carnivores to mitigate those costs through behavioral plasticity, will therefore require an understanding of not just whether, but how individuals use human-dominated landscapes, and whether temporal partitioning indeed permits feeding in areas of high human presence.

Here we examine behavior-specific habitat selection by lions living in a human-dominated landscape in Laikipia, Kenya. This population occurs outside of any formal protected area on a landscape used by humans for commercial ranching and subsistence pastoralism (Ogada et al. 2003, Frank 2011). Humans are the primary source of mortality for adult lions in Laikipia, with lions killing livestock and being killed in retaliation (Ogada et al. 2003, Woodroffe and Frank 2005). Of 251 documented adult or subadult lion mortalities between 1998 and 2017, 228 (90.8%) were anthropogenic (L. G. Frank, S. Ekwanga, A. Oriol-Cotterill; *unpublished data*). Oriol-Cotterill et al. (2015a) have shown that lions here mostly restrict their use of areas near people to nocturnal hours. However, it remains unknown to what degree nocturnal use of habitat near people involves activities such as feeding, or whether lions are primarily traveling when in these areas (Oriol-Cotterill et al. 2015a). Restricted feeding in areas near people could imply a considerable reduction in overall food availability for lions, as livestock (and thus people) frequently co-occur with wild prey on African rangelands (Allan et al. 2017).

We used a combination of high-resolution GPS telemetry and accelerometry data to determine the location and behavioral state of 14 lions in Laikipia every five minutes for up to five months. This methodology enabled us to quantify where and when lions engage in particular behaviors across a human dominated landscape, and was used to test whether temporal partitioning allows lions to access prey in areas characterized by high human presence. We examined whether lion habitat selection with respect to human land use is dependent on a lion's behavioral state, using behavior-specific step selection function analyses (Thurfjell et al. 2014, Abrahms et al. 2016) conducted at three distinct spatiotemporal scales (Boyce 2006). We ask (1) whether selection for or against habitat near humans changes depending on the interaction between human activity level (and hence risk of a human encounter) and the specific behavior in which the lion is engaged, (2) at what spatiotemporal scale is human activity most relevant to lion habitat use, and (3) whether habitat selection is further influenced by environmental factors (specifically, the presence of protective cover) that may modulate the level of human risk.

Materials and methods

Study area

Laikipia District in northern Kenya is a semiarid region comprised of *Acacia* savannah with occasional open grasslands. Details of the study area are provided by Frank et al. (2011) and Oriol-Cotterill et al. (2015a). The present study took place on commercial ranches, where lion and wild ungulate densities are highest. Ranchers use traditional African livestock management practices involving bomas, livestock corrals

(traditionally built from thorn brush, but increasingly from metal fences) where people and livestock spend the night, and from which livestock are herded out to graze by day. Most bomas locations are moved frequently to track good grazing areas: the median duration a boma remained in place during the present study was 67 d. In this study, we monitored lion movement and behavior (as described in the following two subsections), and human land use (by tracking the position of all bomas) on six commercial ranches comprising a contiguous 1,040-km^2 area (see Appendix S1: Fig. S1).

Lion movement data

Lions were captured at night by drawing individuals to a carcass using audio playbacks and free darting from a vehicle using ketamine and medetomidine, the latter reversed with atipamezole approximately one hour later (Frank et al. 2003). Animal capture was conducted with permission from the Kenya Wildlife Service and each individual ranch under Animal Use Protocols No. 191 from UC Berkeley (issued to L. G. Frank) and WilmC1402 from UC Santa Cruz (issued to C. C. Wilmers).

Fourteen adult lions (nine females and five males) were fitted with species movement, acceleration, and radio tracking (SMART) collars (Williams et al. 2014, Wilmers et al. 2017), which integrate Global Positioning System (GPS) units and tri-axial accelerometers. Collars were provided by Vectronic Aerospace (Berlin, Germany). Collar GPS units were set to sample lion locations every 5 min, and accelerometers sampled continuously at 32 Hz. High resolution location and acceleration data were collected for an average of 77 d (range 30–155 d) between 23 September 2014 and 15 February 2016. High resolution sampling periods were embedded within longer monitoring periods (up to 15 months) for each lion. All simultaneously collared lions were from different prides and were therefore assumed to be moving independently.

Lion behavioral classification

Recordings from tri-axial accelerometers were converted to overall dynamic body acceleration (ODBA) by summing the absolute value of acceleration in all three dimensions (Qasem et al. 2012). We summed ODBA values across 5-min intervals (corresponding to the timing of GPS fixes) as an estimate of lion activity level during the time period immediately preceding each GPS location. We then used a three-step algorithm, similar to that described by Wilmers et al. (2017) for leopards, to classify each 5-min lion location into one of five behavioral states based on ODBA, step length (Euclidean distance between the previous and current locations), and turning angle (relative angle formed by the current location with the previous and succeeding locations). We used Gaussian Mixture Models to first classify all locations for a given lion as "stationary" or "moving," and then to identify finer-scale, activity-linked, behavioral states within each of those broad categories. The behavioral classification algorithm is described in detail in Appendix S2.

Behavior-specific habitat selection

To investigate whether lion habitat selection differs depending on the animal's behavioral state, we carried out a series of step selection function (SSF) analyses (Fortin et al. 2005, Thurfjell et al. 2014). SSFs were formulated using a matched case-control design, wherein locations used by lions were matched with 20 randomly generated available locations. Available locations, representing areas of habitat that lions could have visited instead of used location t, were generated by drawing random vectors from the location immediately preceding t (i.e., location $t - 1$; Thurfjell et al. 2014, Blecha et al. 2018). Vector length was drawn from the distribution of step lengths from all "moving" locations for non-focal lions of the same sex as the focal individual (following Fortin et al. 2005), and vector angles were drawn at random from a uniform distribution between 0 and 2π (Wilmers et al. 2013, Abrahms et al. 2016). Available locations, defined as the end points of these random vectors, were assigned the same behavioral state, date, and time as their matched used location. For analysis, the set of used and available locations for each lion was restricted to those occurring on properties on which bomas were tracked throughout the study period, as well as areas that were within 5 km of the nearest boma. This accounts for 77.5% of the study area and buffers against the influence of bomas on neighboring properties that were not tracked.

Habitat selection analyses are known to be highly sensitive to the spatiotemporal scale at which available habitat is defined, and mismatches between the scale chosen by researchers and the scale actually relevant to animal decision making could potentially lead to erroneous results (Boyce 2006, Kittle et al. 2008, Wilmers et al. 2013, Thurfjell et al. 2014). The definition of available habitat under the case-control sampling design used here is dependent on the distribution of step lengths in the data set since an animal could only have moved to locations within the maximum step length (Thurfjell et al. 2014). We therefore conducted SSF analyses at three spatiotemporal scales by subsampling our five-minute lion location data at progressively longer time intervals (corresponding to progressively larger average step lengths). This procedure allowed us to asses not only whether but at what scale(s) anthropogenic activity is relevant to lion habitat use. In our study system, the majority of available habitat is more than a kilometer from the nearest active boma (mean distance to nearest boma for all available points $\pm$ SD = 2.47 $\pm$ 1.18 km), and bomas may therefore have relatively limited influence on fine-scale habitat selection. We subsampled lion relocation data at (1) fifteen-minute (corresponding to

mean ± SD step length of 292 ± 297 m), (2) four-hour (1.24 ± 1.42 km), and (3) twelve-hour (2.15 ± 2.02 km) intervals to capture habitat selection at fine, intermediate, and relatively large spatiotemporal scales. We then conducted SSF analyses at all three scales. Because we were interested in lion behavior at the specific point in space (and thus specific habitat type) associated with each subsampled location, the behavior assigned to each 15-min, 4-h, or 12-h step was that determined for the 5-min location corresponding to the endpoint of each step. Thus, we do not consider the range of behaviors in which the individual may have engaged across the full time interval (up to 12 h) between subsampled locations. For all three data sets, when considering "stationary" locations (i.e., those involving little or no displacement, see Appendix S2 for details), we further subsampled the data to more accurately reflect separate habitat use decisions made by lions. If, for instance, a lion rested in the same area for longer than the sampling interval, this would generate multiple resting locations in the data set that do not reflect separate decisions on where to rest. We therefore only included locations classified as a given "stationary" behavior (e.g., resting, feeding) if they were separated by at least 200 m and 12 h from any location of the same behavioral state already included in the data set. All "moving" locations were considered to represent separate habitat use decisions and were included in the data set.

For each used and available location, we estimated the distance to the nearest active boma, as well as the slope (from a digital elevation model with 90-m resolution; World Resources Institute; SLOPE) and distance to the nearest river (RIVER), as covariates with potential influence on lion habitat selection (data *available online*).[8] Preliminary analyses indicated a nonlinear relationship between lion habitat selection and distance to the nearest boma, with selection for or against bomas being strongest at relatively short distances (i.e., within approximately 1.5 km). We therefore natural log-transformed distance to nearest boma (hereafter, BOMA) in the analyses presented here. (Note that analyses run using untransformed boma distances yielded very similar results.) We also estimated the level of concealment provided by habitat cover (COVER), as previous studies indicate that large carnivores increase their use of high cover areas in human-dominated landscapes (Boydston et al. 2003, Ordiz et al. 2011). COVER was based on a GIS raster layer (Centre for Training and Integrated Research in ASAL Development) containing eight habitat classes, which were subsequently collapsed into three levels describing the amount of concealment provided for lions (data *available online*).[9] Open habitats (e.g., grasslands) were assigned *low concealment*, grassland with some tree or shrub cover was assigned *medium concealment*, and classes consisting predominantly of tree or shrub cover, or which included

large rocky outcroppings were assigned *high concealment*. We further noted whether each used and available location occurred diurnally (i.e., between 08:00 and 18:00 local time) or nocturnally, corresponding to times of relatively high and low risk of human encounter, respectively (Oriol-Cotterill et al. 2015a).

Our approach for fitting SSF models is described in detail in Appendix S3 and was identical for all three spatiotemporal data sets. Briefly, we divided our data into diel period (i.e., diurnal or nocturnal) and behavior-specific subsets and analyzed separate SSFs for (1) all data (i.e., all behaviors across both diel periods) and (2) each behavior type and diel period individually. We did not fit separate models for males and females, as preliminary analyses suggested minimal variation between individuals in habitat selection with respect to human land use (see Appendix S3). We estimated SSF coefficients using conditional logistic regression (CLR) via the coxph function in the *survival* package in R (Therneau 2018), and calculated robust standard errors for all model coefficients using generalized estimating equations (GEE; Koper and Manseau 2009, Prima et al. 2017). For GEE analysis, we created independent data clusters (two for each lion, 28 clusters total; see Appendix S3) using destructive sampling as described by Forester et al. (2009) and Prima et al. (2017). Prior to model fitting, all continuous covariates (BOMA, SLOPE, and RIVER) were standardized to mean = 0 and standard deviation = 1, and the single categorical variable (COVER) was converted to centered, binary indicator variables for each COVER level (with *low concealment* set as the reference condition). Pairwise Pearson correlations between all covariates were examined to confirm that no two covariates were strongly collinear (all $|r| \leq 0.21$).

For each time- and behavior-specific data subset, we modeled the relative probability of a lion selecting a particular location as function of BOMA, RIVER, SLOPE, COVER, and a BOMA × COVER interaction. For each subset, we fit models consisting of every combination of these terms (20 models total), and compared all models for a given behavior and time period using the quasi-likelihood under independence criterion (QIC), as suggested by Craiu et al. (2008) for GEE-based analyses. Below, we report the results of the top model as determined by QIC selection. Following Manly et al. (2002), we obtained values for the relative probability of selection w for habitat covariate x by substituting the parameter estimates β (derived from the top CLR model) into the exponential model

$$w(\boldsymbol{x}) = \exp(\beta_1 x_1 + \ldots + \beta_n x_n). \qquad (1)$$

For ease of interpretation, we provide parameter estimates and 95% confidence intervals (derived from robust standard errors) on the logit scale, as estimated by CLR, and plot $w(\boldsymbol{x})$ values for all graphical interpretations of changes in selection across a gradient of distances to the nearest boma.

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[8] www.wri.org/resources/data-sets/kenya-gis-data
[9] www.cetrad.org

As discussed in detail in the Results, we found evidence of selection for habitat near bomas when lions were feeding at night. To help clarify whether this pattern results from selection for bomas themselves, or selection for habitat with which bomas are sometimes associated (e.g., good quality grazing areas where wild prey may also congregate), we took advantage of the fact that the majority of bomas only remain in a single location for a relatively short period of time (67 d on average; Appendix S1: Fig. S1). We tested whether lions selected for locations where bomas were currently absent but where they were known to occur at some point during the study. This analysis was formulated in two ways. We first tested for selection of locations where bomas are currently absent, but where they occurred at any other point in the study by measuring, for each used and available lion location, the distance to the nearest point at which a boma occurred at any other time (i.e., either before or after the date of the current used/available location) but which was boma-free on the date of the current location (hereafter referred to as the "non-boma analysis"). This approach addresses selection for general habitat features that are associated with boma locations but are independent of bomas themselves. Second, we tested for selection of locations where bomas are currently absent, but where a boma will be established in the near future (i.e., within four weeks of the current lion location), again measuring the distance to the nearest such point for each used and available lion location (hereafter referred to as the "pre-boma analysis"). The logic behind the pre-boma analysis is that, if bomas are tracking good grazing habitat, which likely changes through time, wild ungulates may arrive at such habitat patches before the bomas do, which may then attract lions prior to the presence of the boma. Both the non-boma and pre-boma analyses were run exactly as described above (SSF estimated by CLR, QIC model selection), but with terms for (natural log-transformed) distance to the nearest boma-free location replacing BOMA. These analyses were conducted for nocturnal feeding at the four-hour timescale, as the results of the previously described SSF analyses indicated that this was the timescale most relevant to lion habitat selection with respect to bomas (see Results).

Time allocation to feeding

To corroborate behavior-specific habitat selection patterns revealed by SSF analyses, we calculated the proportion of time lions allocate to nocturnal feeding across a gradient of distances to the nearest boma. For each night of an individual lion's collaring period, we determined the proportion of all nocturnal 5-min GPS locations classified as feeding, as well as the average distance to the nearest boma experienced by the individual on that night. We then grouped these average nightly distance-to-boma values into 500-m bins ranging from 0 to 5 km, and calculated the mean proportion of time spent

feeding by an individual lion across all nights for each 500-m distance to boma bin. To capture the observed non-linear relationship between distance to nearest boma and proportion of time spent feeding, these data were fit with a generalized additive mixed effects model (GAMM), using a smoothing term for average distance to boma (fit via thin plate regression spline, with number of knots determined by generalized cross validation [Wood 2006]). Individual lion ID was included as a random effect. The GAMM was estimated using the mgcv package in R (Wood 2006).

RESULTS

Behavior classification and feeding locations

Our three-step behavioral classification algorithm identified five distinct behavioral states exhibited by all lions (Fig. 1, Appendix S2: Table S1). We identified three stationary behaviors: "feeding" (average ± SD percent of total locations for a given lion = $7.0\% \pm 1.9\%$), characterized by high and sporadic acceleration, indicative of intensive head movements; "active resting" ($53.3\% \pm 13.7\%$ of locations), characterized by overall low activity interspersed with short bursts of higher activity; and "inactive resting" ($16.9\% \pm 15.4\%$ of locations), characterized by consistent periods of very low activity, presumably indicative of sleeping. We also identified two "moving" behaviors exhibited by all lions: "traveling" ($11.5\% \pm 2.1\%$ of locations), characterized by long, relatively straight movements and consistent, high acceleration; and "meandering" ($11.3\% \pm 2.2\%$ of locations), characterized by shorter steps, greater turning angles, and interrupted burst of high acceleration (Fig. 1, Appendix S2: Table S1).

Oriol-Cotterill et al. (2015a) determined that areas within 1.5 km of a boma represent high risk for human encounter. We detected a total of 131 independent feeding events (i.e., those separated by at least 200 m and 12 h from any other feeding event) occurring within 1.5 km of the nearest boma. This corresponds to an average across lions of 0.84 feeding events per week (range 0–2.5) within 1.5 km of a boma. As addessed in the Discussion, these feeding events may consist of either hunting or scavenging.

Spatiotemporal scale of habitat selection

Step selection function analyses revealed that bomas had the strongest (i.e., parameter estimates farthest from zero) and most pervasive (i.e., affecting the greatest number of behaviors) effect on habitat selection at the 4-h timescale (Fig. 2) relative to both the fifteen-minute (Appendix S1: Fig. S2) and twelve-hour (Appendix S1: Fig. S3) timescales. Top model results and QIC model selection tables for habitat selection analyses on all behavioral subsets at all timescales are presented in Appendices S4 and S5, respectively. QIC model selection
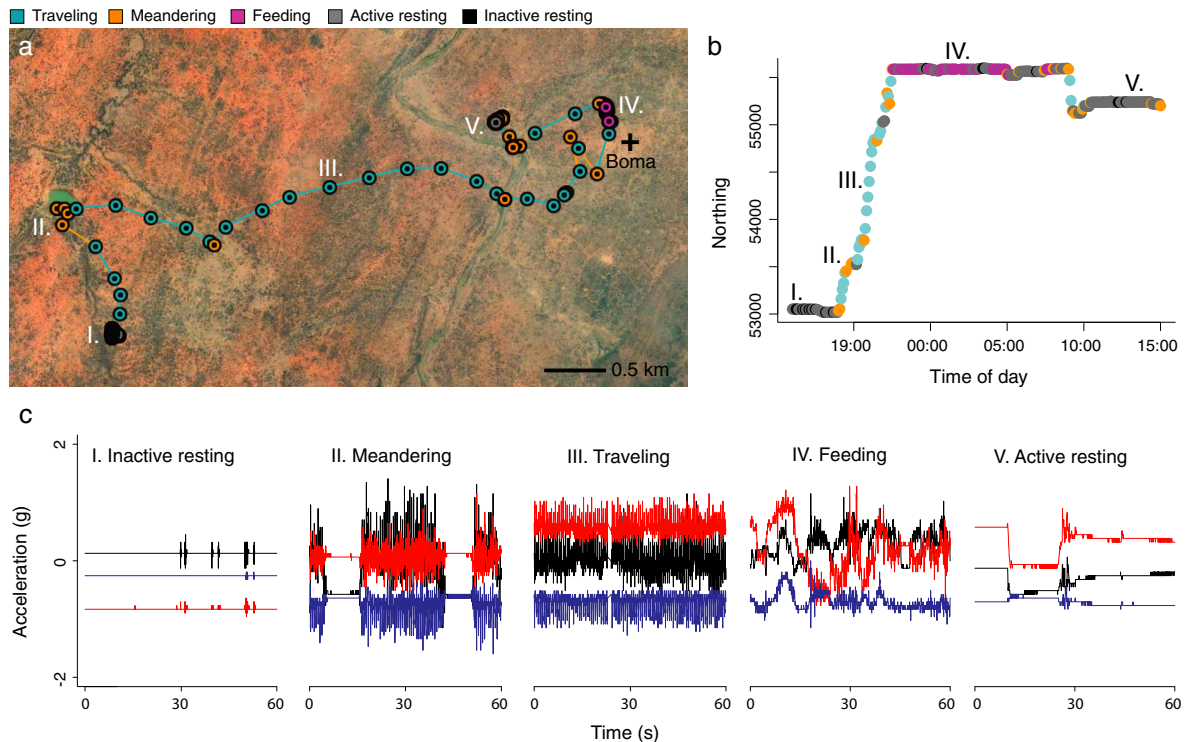
FIG. 1. Characterizing lion behavior across the landscape. (a) An example 24-h movement path from a single lion. Five-minute GPS locations (points) are colored based on the lion's behavioral state, as determined by the behavior classification procedure described in Appendix S2. The location of an active boma (black cross) is shown. (b) The same 24-h movement path is plotted against time of day, highlighting the interspersion of different "stationary" behavioral states. (c) Example accelerometry traces illustrating characteristic acceleration patterns for each of the five behavioral states, and corresponding to 1-min portions of the 5 min used to characterize each example location. Acceleration along the x (red), y (black), and z (blue) axes are shown. The lion engages in (I) inactive resting and (II) meandering at a distance of approximately 3.3 km from the boma. The animal then (III) travels to within 300 m of the boma, where it (IV) feeds intermittently throughout the night (~11.5 h), before moving off to a distance of approximately 800 m from the boma to engage in (V) active resting.

indicated that, at the 4-h timescale, bomas affected diurnal and/or nocturnal habitat selection during all behavioral states except traveling (Fig. 2). By contrast fewer behaviors were affected by bomas at the 15-min and 12-h timescales (Appendix S1: Figs. S2,S3), and parameter estimates for affected behaviors tended to be less extreme than at 4 h. The influence of BOMA was also more likely to interact with that of COVER at the 4-h timescale (compare Fig. 2 to Appendix S1: Figs. S2, S3). For these reasons, all SSF results presented below are from analyses at the four-hour timescale.

Behavior-specific habitat selection

When considering all locations (i.e., across all behaviors and both diel periods) at the 4-h timescale, lions showed no habitat selection with respect to bomas, the term for distance to nearest boma being excluded from the top model (Appendix S4: Table S4). However, considering all data together masks strong diel period- and behavior-specific differences in habitat selection. During the day, when the risk of human encounter is high, lions showed general (i.e., across all behaviors) avoidance of

habitat near bomas (Appendix S4: Table S6), instead selecting for areas >2 km from the nearest boma (Fig. 3a). Lions similarly selected against habitat near bomas during the day when engaged in behaviors associated with low to moderate levels of movement. Lions tended to avoid bomas when engaged in diurnal active resting, inactive resting, meandering, and feeding (Figs. 2, 3b,c); instead selecting for relatively safe areas >2 km from the nearest boma. Behavior-specific habitat selection was markedly different at night (Appendix S4: Table S5), with lions exhibiting selection *for* habitat near bomas when engaged in nocturnal feeding (Figs. 2, 3c).

Selection for or against habitat near bomas was further mediated by the availability of protective habitat cover when lions were meandering or feeding. When meandering during the day, lions tended to avoid areas of low concealment cover overall, and strongly increased their selection for areas far from bomas as cover increased (Fig. 3d). When engaged in diurnal feeding, lions avoided areas near bomas at all levels of cover, but sharply increased their selection for areas of high (and to a lesser extent, medium) cover as distance to boma increased (Fig. 3e). At night, lions largely avoided low
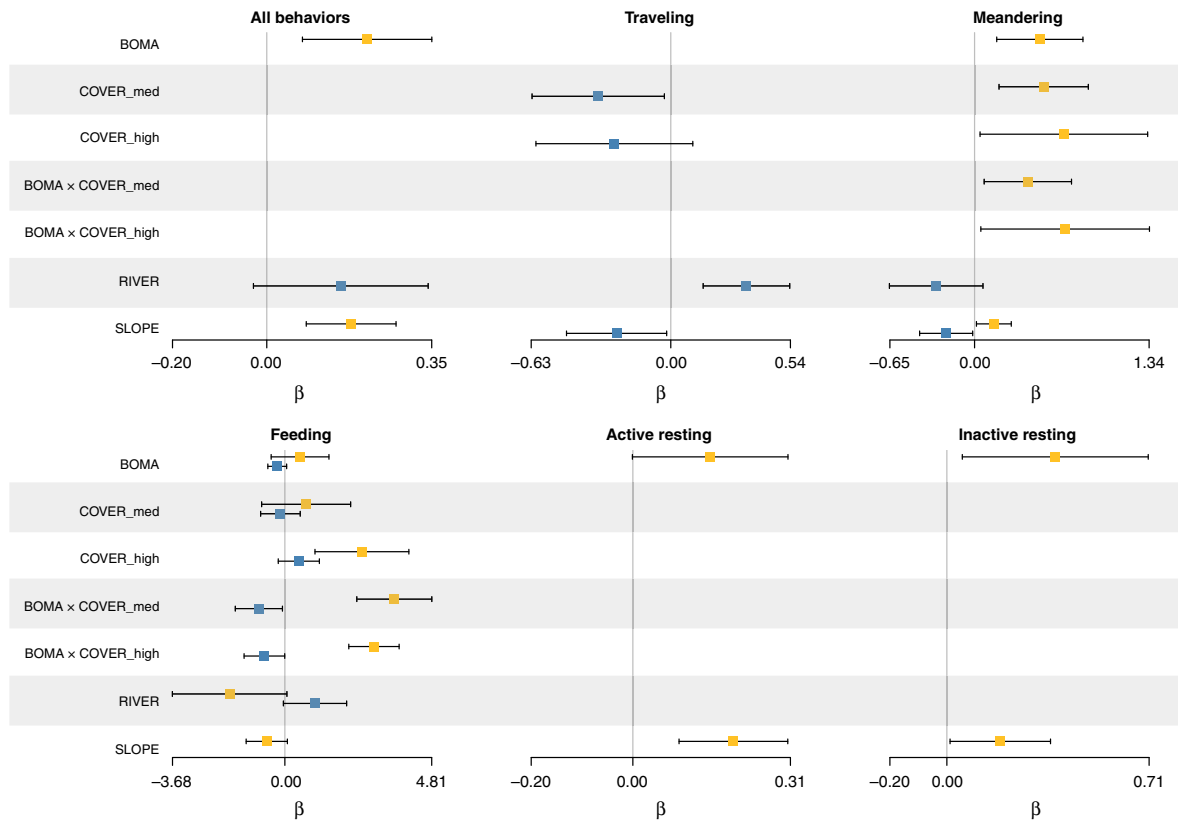
FIG. 2. Parameter estimates (β) and 95% confidence intervals (derived from robust standard errors) for step-selection function analyses conducted at the 4-h timescale. Results of analyses conducted on different behavioral subsets (or all behaviors combined) are shown in separate panels. For each behavioral subset, estimates are shown for those parameters included in the top nocturnal (blue) and diurnal (yellow) models (as determined by QIC model selection). For clarity, parameter estimates and CI are shown on the logit scale (as estimated by conditional logistic regression), with values farther from zero indicating a greater influence on lion habitat selection. Note that BOMA terms denote the effect of increasing distance to the nearest boma (on the log scale), such that negative values indicate selection for habitat closer to bomas. x-axes differ between plots. Values for βs and 95% CIs are provided in Appendix S4: Tables S5, S6.

cover areas when feeding (particularly near bomas) but exhibited a strong preference for medium and high cover habitats within approximately 1.5 to 2 km of the nearest boma (Fig. 3f).

The "non-boma" and "pre-boma" analyses both indicated that distance to the nearest location at which a boma was currently absent but present at some point during the study had no effect on habitat selection while lions were engaged in nocturnal feeding (neither of the top models included terms for currently absent boma locations; Appendix S4: Table S10; Appendix S5: Table S4). Thus, lion selection for habitat near bomas when feeding at night appears dependent on the presence of the boma itself.

Time allocation to feeding

The average proportion of time that lions spent feeding on a given night was strongly related to the average distance to boma experienced on that night (GAMM smoothing term for distance to boma: *P* < 0.001). Lions

spent on average between 18% and 22% of their time feeding on nights when the average distance to boma was ≤1 km, but proportion feeding time declined quickly and remained low at all greater boma distances (Fig. 4).

DISCUSSION

Temporal partitioning of habitat is hypothesized to be a primary mechanism promoting coexistence between large carnivores and people in human-dominated landscapes, with carnivores expected to use otherwise risky habitat at times when the likelihood of encountering people is low. The potential for large carnivores to not just move through risky habitat, but access the resources therein, is a fundamental, but largely overlooked component of successful coexistence. Here we show that, not only do lions feed in areas of high perceived risk within 1.5 km of bomas (as frequently as twice a week for some individuals), but that lions actively select these areas when feeding at night, using areas near bomas more (in proportion to their availability) than anywhere else on
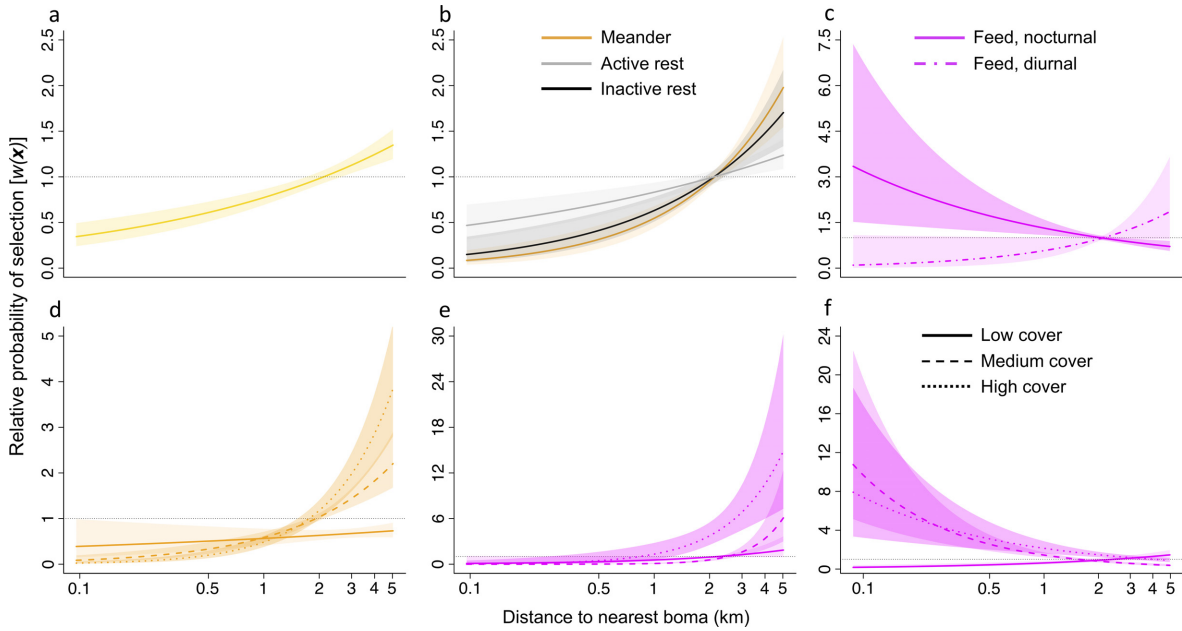
FIG. 3. Relative probability of a lion selecting habitat given distance to the nearest boma, (a–c) overall and (d–f) at the three levels of habitat cover. The overall effect of distance to nearest boma on habitat selection is shown (a) during the day when all behaviors are considered; (b) during the day when lions are meandering (orange), active resting (gray), or inactive resting (black); and (c) when lions are feeding at night (solid line) or during the day (dot-dashed line). The interaction between distance to nearest boma and amount of cover in their effect on habitat selection is shown for (d) diurnal meandering, (e) diurnal feeding, and (f) nocturnal feeding at low (solid lines), medium (dashed lines), and high (dotted lines) levels of habitat cover. The effect of distance to boma is only shown for those behaviors and diel periods for which this covariate was included in the top model (see Fig. 2). In all panels, plotted lines represent the relative probability of selection, $w(x)$ (derived from Eq. 1), and shaded areas are ±SE. The thin horizontal line in each panel denotes a relative selection probability of one. Values above one indicate selection for and values below one indicate selection against habitat at the specified distance to nearest boma. Note that y-axes differ between plots and x-axes are on the log scale. Results represent habitat selection at the four-hour time scale.
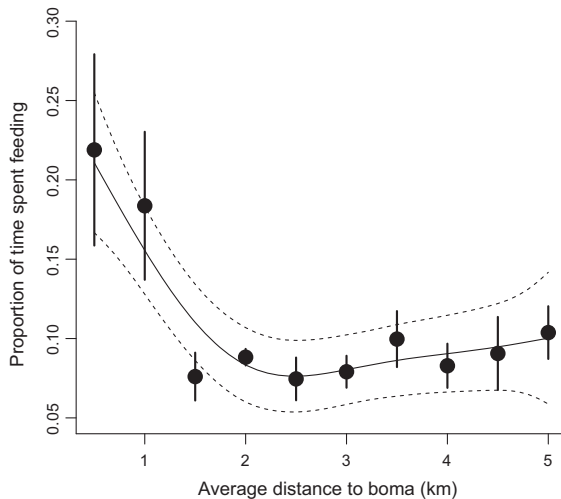

FIG. 4. Proportion of time spent feeding is influenced by distance to the nearest boma. Points (and error bars) are the population-level averages ± SE of the mean nightly proportion of nocturnal GPS locations classified as feeding for an individual lion at a given distance to the nearest boma. The fit of a Generalized Additive Mixed Effects Model (GAMM) with a smoothing term for distance to the nearest boma is shown (solid line) along with 95% confidence intervals (dashed lines).

the landscape (Fig. 3c), particularly when protective cover is available (Fig. 3f). This selection for areas near bomas when feeding is further borne out by lion time allocation, with individuals spending the greatest proportion of their time feeding when near bomas (Fig. 4).

Our data reveal a remarkable degree of flexibility in lion habitat use with respect to human presence, with lions apparently adjusting where and when they engage in particular behaviors based on predictable differences in the risk of human encounter. When engaged in behaviors associated with relatively low movement, large amounts of time spent in a single area, and thus high risk of detection by people (i.e., active and inactive resting, meandering, and feeding), lions exhibited marked avoidance of habitat near bomas during the day, when human activity around bomas is high (Fig. 3b). Notably, however, our SSF results indicate that lions are largely indifferent to the presence of bomas when traveling (both during the day and night), a behavior associated with high movement, high alertness, little time spent in a single area, and thus limited risk of human encounter. When the risk of human encounter is low (i.e., at night), lions shift to selecting for habitat near bomas when feeding (Fig. 3c).

Lion use of habitat near bomas was further mediated by the availability of protective cover, with lions showing

a sharp increase in selection for habitat near bomas during nocturnal feeding when medium or high concealment habitat was available (Fig. 3f). Indeed, feeding near bomas was apparently dependent on the availability of cover, as low cover habitat near bomas was avoided by lions feeding at night (Fig. 3f). Previous studies have similarly found that large carnivore species (e.g., hyenas [Boydston et al. 2003], brown bears [Ordiz et al. 2011]), increase their use of protective cover when near humans. Our results suggest that such use of cover may be particularly important during feeding events, which can last up to several hours and may therefore be associated with especially high risk of detection by people. Thus, cover availability may mediate carnivore ability to access feeding opportunities in human-dominated landscapes.

Our comparison of habitat selection at multiple spatiotemporal scales suggests that the relevance of bomas to lion habitat use decisions depends on the scale considered. As noted in *Methods*, at fine temporal scales (e.g., 15 min; Appendix S1: Fig. S2) lions are only selecting among habitat options within at most a few hundred meters of their current location, meaning that, in many cases, the difference between used and available locations in their proximity to the nearest boma will be negligible, particularly during the day, when lions spend most of their time >2 km from the nearest boma. Our results suggest that bomas have a greater influence on lion habitat use at the intermediate, 4-h (Fig. 2) scale (and to a lesser extent the twelve-hour scale, Appendix S1: Fig. S3), when lions are selecting among habitat options at distances of more than 1 km from their current location (average step length at the 4-h scale = 1.24 km, with 12% of steps > 3 km). This intermediate scale may better represent the spatial scale at which decisions to move between safe and risky habitat are made. Choice of the appropriate spatiotemporal scale is well known to have a major influence on habitat selection studies (Boyce 2006, Kittle et al. 2008, Wilmers et al. 2013, Thurfjell et al. 2014), and the potential pitfall of selecting a movement scale that is too fine to detect selection/avoidance of some habitat features has previously been discussed (Thurfjell et al. 2014). While our comparison of three timescales could have overlooked the most relevant scale at which bomas influence lion habitat use, our results support the conclusion that lion habitat selection relative to bomas occurs on the timescale of several hours rather than several minutes, as lions make relatively long distance (i.e., one to several km) movements between safe habitat during the day and areas near humans at night (Fig. 3).

That lions not only feed in areas of high human activity, but actively select these areas when doing so may seem counterintuitive, given that feeding far from bomas would incur less risk of detection by people. Selection for habitat near bomas when feeding could arise because bomas are a potential source of food themselves (i.e., livestock; Woodroffe and Frank 2005, Frank 2011), or because they co-occur with wild prey. Substantial dietary

overlap between livestock and native ungulates, along with the patchiness of nutrient-rich forage and water sources in Laikipia (Augustine et al. 2011), means that "habitat selection" by ranch managers when deciding where to place bomas may overlap substantially with habitat used by wild prey. Preliminary data on lion kills indicate that wild prey, rather than livestock, account for the large majority (87%) of prey at investigated kill sites in close proximity (<1.5 km) to bomas (*unpublished data*; see also Frank 2011), supporting the notion that lions use areas near bomas because of access to wild prey. However, both the "non-boma" and "pre-boma" analyses show that lion selection for these areas of habitat when feeding is dependent on the presence of the boma (i.e., lions show no selection for these areas when bomas are absent), indicating that habitat (and associated prey) at boma locations is not a major attractant to lions independently of the bomas themselves. Alternatively, wild prey may cluster around bomas at night, driving nocturnal use of these areas by lions. Nighttime is the riskiest time for lion prey (76.8% of independent lion feeding events were at night), and it is possible that wild prey avoid humans and cattle during the day, but move closer to bomas at night in an attempt to take advantage of a "human shield" (Berger 2007) against lions. Assessing whether wild prey are distributed nonrandomly with respect to boma locations, and whether this changes between day and night, will be an important topic for future research.

The data on feeding events presented here does not allow us to distinguish between hunting and scavenging. Lions in some areas derive a substantial proportion of their diet from scavenging (e.g., from kleptoparasitized hyena kills), and any increase in scavenging opportunities near bomas could also contribute to lion selection for these areas, though this hypothesis has not been tested.

This work highlights the value of considering fine-scale behavioral states in studies of wildlife habitat use. When all lion location data were pooled, SSF analysis indicated that lions were indifferent to the presence of bomas, and even separating nocturnal and diurnal locations failed to reveal the importance of habitat near bomas for feeding. Habitat selection studies have frequently taken advantage of relatively coarse-scale differences in animal behavior (e.g., between day and night or across seasons [Valeix et al. 2012, Cristescu et al. 2013, Oriol-Cotterill et al. 2015a]), and a growing number of studies are incorporating fine-scale information on wildlife behavioral states (including studies on coyotes *Canis latrans* [Wilson et al. 2012], pumas *Puma concolor* [Wilmers et al. 2013], African wild dogs *Lycaon pictus* [Abrahms et al. 2016], and African elephants *Loxodonta africana* [Roever et al. 2014]). Several such studies have similarly found that habitat use is highly dependent on behavioral state, with selection for certain habitat types only apparent when behavior is accounted for (e.g., Roever et al. 2014, Abrahms et al. 2016). With the

proliferation of bio-logging technology (reviewed in Wilmers et al. 2015) and analytical methods to extract both behavioral and spatial information from bio-logger data (e.g., Williams et al. 2014, Wilmers et al. 2017), incorporating fine-scale behavioral data into habitat selection studies should become increasingly feasible, improving our understanding of how wildlife populations use their environment, and thus our ability to manage and conserve them.

Our study builds on previous work documenting temporal habitat partitioning between humans and large carnivores (e.g., Ordiz et al. 2012, Rasmussen and Macdonald 2012, Valeix et al. 2012, Oriol-Cotterill et al. 2015*a*) by demonstrating that, for lions, this flexible behavioral strategy permits access to valuable feeding habitat. Indeed, the finding that lion time allocation to feeding is greatest when near bomas (Fig. 4) indicates that access to food may be the primary motivation for the use of areas with high human presence by our study population. The Laikipia lions represent one of the only stable lion populations outside of a protected area (Frank 2011), and the only one in Kenya. We suggest that the flexible behavioral strategy employed by these lions to access resources in a human-dominated landscape may play a major role in promoting their persistence. Wilmers et al. (2017) recently proposed a conceptual framework linking large carnivore energy budget to fitness-enhancing behaviors (including territorial defense and parental care), which suggests that decreased access to food could shift individuals from a reproductive to a non-reproductive state, potentially leading to population decline even where adult mortality is low. Recognizing where and when human-dominated landscapes can serve as feeding habitat may therefore be critical to the management of sustainable large carnivore populations as the extent of land area converted for human use continues to grow.

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Supporting Information

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