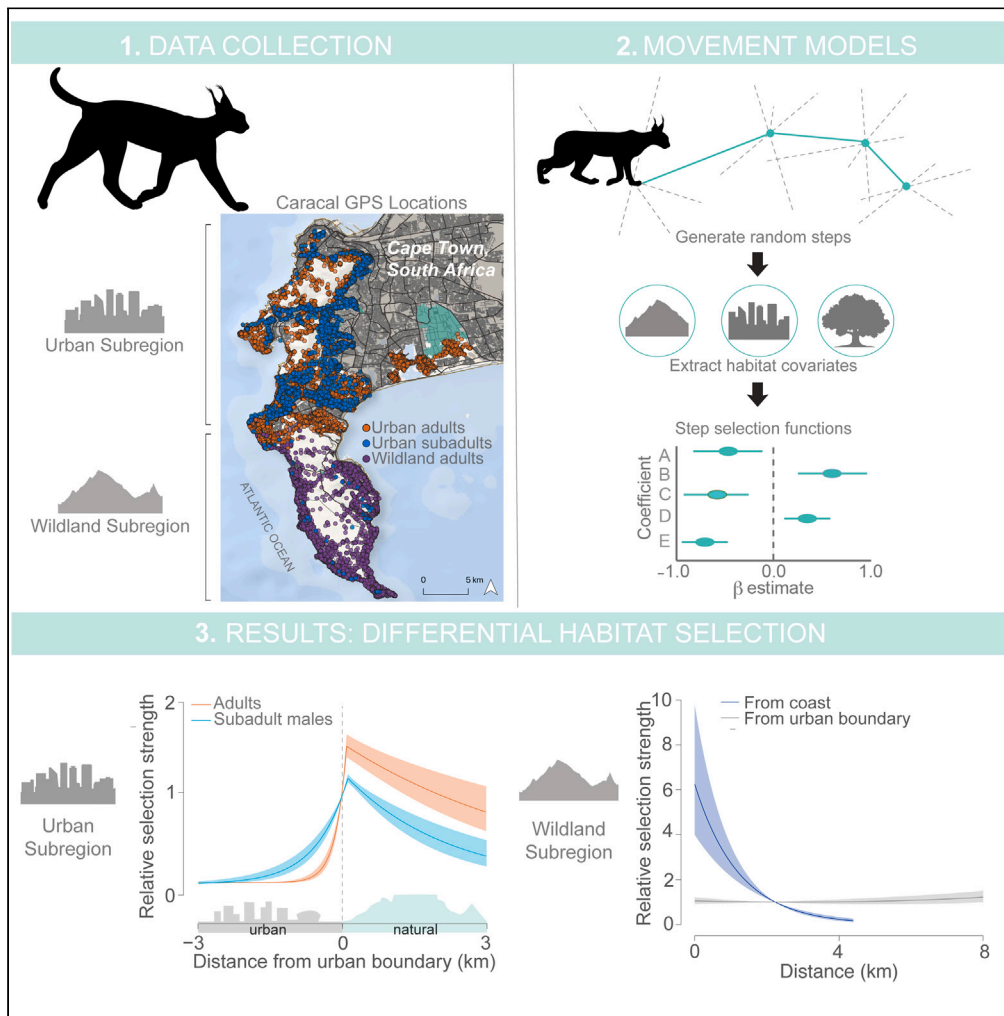


Article

Anthropogenic activities and age class mediate carnivore habitat selection in a human-dominated landscape



Laurel E.K. Serieys, Jacqueline M. Bishop, Matthew S. Rogan, Justine A. Smith, Justin P. Suraci, M. Justin O’Riain, Christopher C. Wilmers

lserieys@panthera.org

Highlights

Urban caracals select to be close to urban areas at night; wildland caracals do not

Subadult caracals select the urban matrix and marginal habitat more than adults

Urban caracals use microhabitat refugia to mitigate risk of human detection

Caracals do not become more nocturnal in urban areas

Serieys et al., iScience 26, 107050
July 21, 2023 © 2023 The Author(s).
<https://doi.org/10.1016/j.isci.2023.107050>



Article

Anthropogenic activities and age class mediate carnivore habitat selection in a human-dominated landscape

Laurel E.K. Serieys,^{1,2,3,4,8,*} Jacqueline M. Bishop,¹ Matthew S. Rogan,^{1,5} Justine A. Smith,⁶ Justin P. Suraci,^{2,7} M. Justin O’Riain,¹ and Christopher C. Wilmers²

SUMMARY

Human activities increasingly challenge wild animal populations by disrupting ecological connectivity and population persistence. Yet, human-modified habitats can provide resources, resulting in selection of disturbed areas by generalist species. To investigate spatial and temporal responses of a generalist carnivore to human disturbance, we investigated habitat selection and diel activity patterns in caracals (*Caracal caracal*). We GPS-collared 25 adults and subadults in urban and wildland-dominated subregions in Cape Town, South Africa. Selection responses for landscape variables were dependent on subregion, animal age class, and diel period. Contrary to expectations, caracals did not become more nocturnal in urban areas. Caracals increased their selection for proximity to urban areas as the proportion of urban area increased. Differences in habitat selection between urban and wildland caracals suggest that individuals of this generalist species exhibit high behavioral flexibility in response to anthropogenic disturbances that emerge as a function of habitat context.

INTRODUCTION

Human activities affect nearly every terrestrial system on earth.¹ Diverse consequences of human activities include habitat loss, altered habitat structure and connectivity,² and shifted ecosystem processes, disturbance regimes,³ and resource availability.⁴ Human infrastructure impedes animal movement,⁵ while human activity can elicit fear in wildlife individuals, causing them to further modify their movement behavior and habitat selection.^{6,7} Wild animal species that live in human-impacted landscapes are also confronted with vehicles, poisons, and pathogens that can increase mortality⁸ and reduce fitness.^{9,10} However, in addition to introducing novel threats, humans also provide resources, such as food, shelter, and refuge from predation.^{11,12} As such, wild animals living in human-dominated landscapes are challenged to take advantage of these benefits while mitigating a suite of anthropogenic threats. Thus, species that can optimize resource-risk tradeoffs near humans may adapt, persist, and even thrive in human-modified landscapes.^{13–15} Understanding the behavioral mechanisms that facilitate species persistence in human-dominated landscapes is critical to informing conservation strategies in our increasingly modified world.¹⁶

An animal’s immediate response to disturbances is typically behavioral (e.g., altered habitat selection, activity, or vigilance);¹⁷ behavioral plasticity is thus central to population persistence in rapidly changing environments.¹⁸ Human activity typically elicits anti-predator behaviors in wild animals equal to or exceeding those caused by non-human predators.^{19,20} Consequent changes in animal behavior have important implications for wild animal communities and ecosystem processes.²¹ Animal movement and space use are behaviors known to be modified in response to human activity and the built environment, particularly in carnivores.^{19,22,23} Resource-specific functional responses (adjustments in selection for a resource or landscape features as a function of changes in their availability)²⁴ can reveal patterns of risk perception, cumulative effects of the human footprint (e.g., spatial response to roads,²⁵ altered predator-prey dynamics²⁶), and changes in species’ distributions.^{27,28} Furthermore, spatial patterns of attraction to or avoidance of human-modified habitats can be mediated by the availability of microhabitats or temporal refuges.^{22,29,30} The complexity of animal movement and space use necessitates evaluation of cross-scale behavioral adaptations that promote coexistence with humans.³¹ Examining movement behavior in heterogeneous

¹Institute for Communities and Wildlife in Africa, University of Cape Town, Cape Town 7701, South Africa

²Environmental Studies Department, University of California, Santa Cruz, Santa Cruz, CA 95064, USA

³Panthera, New York, NY 10018, USA

⁴Cape Leopard Trust, Cape Town 7966, South Africa

⁵Natural State, Nanyuki, Kenya

⁶Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, Davis, CA 95616, USA

⁷Conservation Science Partners, Inc. Truckee, CA 96161, USA

⁸Lead contact

*Correspondence:

lsérieys@panthera.org

<https://doi.org/10.1016/j.isci.2023.107050>



landscapes is, therefore, essential for defining habitat requirements for species; knowledge of the habitat requirements for species can be incorporated into land-use planning.³²

Studies examining wildlife habitat selection, occupancy, and activity in human-dominated landscapes have found that wildlife species may mitigate the risk of humans by spatially or temporally avoiding human activity or structures, or through using microhabitats as refugia.^{22,29,30} By segregating the landscape spatially, animals that are highly sensitive to human disturbance can achieve complete avoidance of anthropogenic stressors.^{33,34} However, animals with higher tolerance of human activities may instead use fine scale refugia to avoid direct spatial overlap with humans or conceal themselves from humans.^{7,35,36} Increasingly, studies demonstrate that the presence of vegetated areas provides microhabitat refugia for wild animals in areas with high human activity, and that the size and spatial arrangement of vegetation patches can facilitate animal movement and use of disturbed landscapes.^{22,30,37} When animals cannot use complete avoidance or refugia to avoid humans spatially, they may instead employ temporal avoidance of humans by becoming more nocturnal.²⁹

We investigated the spatial (i.e., habitat selection) and temporal (i.e., diel activity pattern) responses of a medium-sized generalist carnivore, the caracal (*Caracal caracal*), to the interrelated effects of anthropogenic development and ecological variation in a fragmented landscape isolated by dense urbanization in the City of Cape Town (CoCT), South Africa. We monitored adult and subadult caracals across two subregions that differ in their background level of exposure to human activities and are separated by a major road straddled by dense urban development (Figure 1A, Kommetjie Road): a fragmented urban-dominated subregion in the northern section of the study area and a largely intact, wildland-dominated subregion in the southern section of the study area (Figure 1A). To understand the influence of human activity and land uses on caracal habitat selection and diel activity patterns, we tested three hypotheses, which consider whether caracals avoid anthropogenic environments entirely (hypothesis 1 below) or instead alter their spatial or temporal activity patterns to mitigate risk of encounters with humans while still taking advantage of developed landscapes (hypotheses 2 and 3). The three hypotheses are: (1) *Complete-avoidance hypothesis*, that caracals mitigate the risk of humans by avoiding human activity both temporally and spatially, (2) *Spatial-refuge hypothesis*, whereby caracals mitigate risk of humans by selecting for safe microhabitats within the human-dominated urban interface, and (3) *Temporal-avoidance hypothesis*, that caracals mitigate the risk of humans by increasing their activity during periods of low human activity (e.g., increased nocturnality). To test hypotheses 1 and 2, we examined habitat selection at both coarse (3-hr) and fine (20-min) scales using step-selection functions (SSFs) because habitat selection is a hierarchical process that can generate differing patterns of selection or avoidance depending on the spatiotemporal scales assessed, which can have implications for conservation and management.^{7,38–40} Within this framework, we tested the effects of diel period, subregion, and animal age class on habitat selection behaviors across coarse and fine scales. To test hypothesis 3, we also examined potential differences in diel activity patterns, quantified by variation in movement rates, between subregions. Our work illustrates how a generalist species coexists with humans through intraspecific variation in behavioral responses to anthropogenic disturbances. This study also addresses knowledge gaps to guide local land management and biodiversity conservation objectives.

RESULTS

Sampling movement locations and study area

Individuals were monitored across urban-dominated and wildland-dominated subregions (Figure 1) primarily within Table Mountain National Park (TMNP). The two subregions, located within the Cape Peninsula, are isolated from other Western Cape caracal populations by 2445 km² of CoCT urban matrix (Figure 1). Subregions were defined by degree of fragmentation, extent of urban boundaries, and whether they were located north (urban-dominated subregion) or south (wildland-dominated subregion) of a major road (Figure 1A: Kommetjie Road) straddled by dense urban development (STAR Methods). However, a 630 m section of Kommetjie road was not straddled by urban development and we observed three urban-dominated subregion caracals to cross this road section.

We captured 29 individuals, collared 26 individuals but used data from 25 caracals (STAR Methods) because one individual was opportunistically collared outside the study area. One male was first monitored as a subadult, and later monitored as an adult. Therefore, GPS collar data for 9 adult males, 10 adult females, and 7 subadult males (Figures S1–S3) yielded 17,424 3-hr GPS movement steps and 8,962 20-min

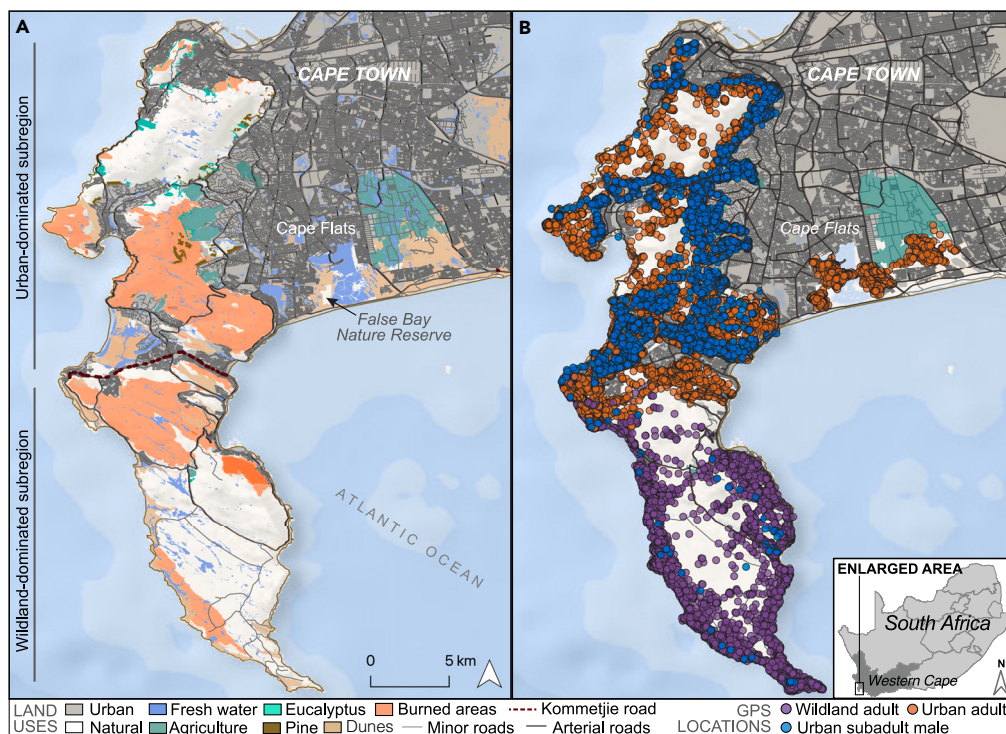


Figure 1. Map of the Cape Peninsula study area in Cape Town, South Africa showing the two subregions (urban and wildland-dominated)

Table Mountain National Park is comprised both the urban and wildland-dominated subregions.

(A) Map of key land uses and extent of burned areas. Kommetjie Road divides the urban-dominated region from the wildland-dominated region although caracals can cross the road on the western side of the peninsula. The agriculture land use primarily comprises vineyards except for crop fields in the Cape Flats.

(B) GPS-collar locations for urban-dominated subregion adults (orange) and subadults (blue), and wildland-dominated subregion adults (purple).

movement steps (STAR Methods) for habitat selection analyses (Figure 1B). Subadults were only detected and monitored in the urban-dominated subregion.

Subgroup and diel period modeling

We divided our dataset into three subgroups based on life history stage (adult vs. subadult) and the subregion of the study area in which individuals were sampled (urban-dominated vs. wildland-dominated). Our three subgroups included: urban-dominated adults ($n = 14$), urban-dominated subadult males ($n = 7$), and wildland-dominated adults ($n = 5$). In the urban subregion, the median distance from the urban boundary was 335.3 m for adults (mean = 458.4, SD = 443.4) and 71.4 m for subadults (mean = 43.7, SD = 552.8); wildland adults were a median distance of 8049.9 m (mean = 8057.5, SD = 5515.9) from the urban boundary (Table S1). These findings suggest the potential for differential habitat selection respective to distance from the urban boundary. SSF models fit to examine habitat selection revealed differences among subgroups at both coarse and fine scales of caracal movement (i.e., the models with the subgroup interaction term performed better than the one without, Table S2; 3-hr data, $\Delta QIC = 395.2$; 20-min data, $\Delta QIC = 52.7$). SSF models fit to examine differences in habitat selection diel period (Table S3) for urban adults performed better than pooled data for both temporal resolutions (3-hr $\Delta QIC = 31.4$, 20-min $\Delta QIC = 69.3$), and for urban subadults using 3-hr data ($\Delta QIC = 14.5$). For wildland adults (using both 3-hr and 20-min data) and urban subadults (using 20-min data only), SSF model fits were not improved by individually modeling diel period data and thus, we used composite day and night datasets for wildland caracal and urban subadult 20-min habitat selection analyses.

We observed that the relative probability of selection for the distance from the urban boundary was best described by a quadratic-transformed distance for wildland caracals, and a segmented linear regression for

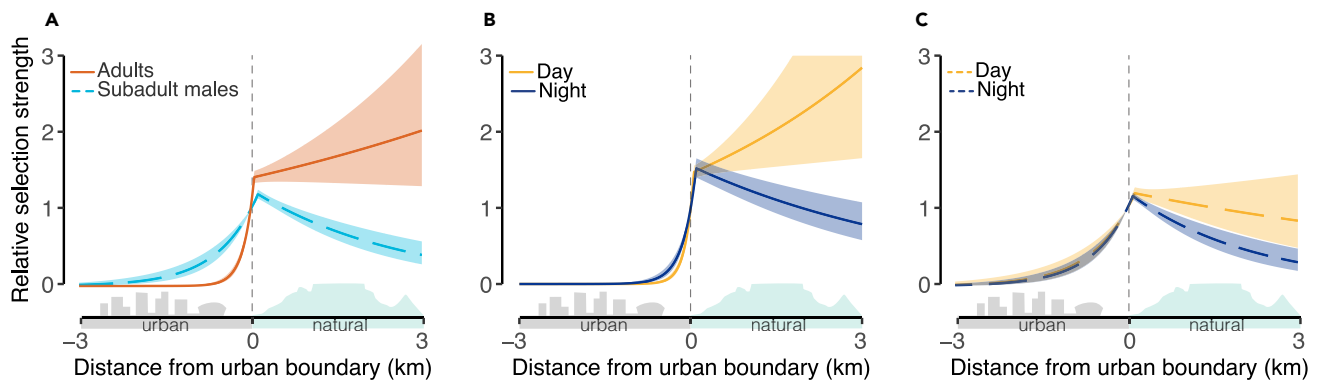


Figure 2. Relative selection for distance from the urban boundary for caracals in the urban-dominated region based on 3-hr datasets Relative strength of selection represented with lines, while shading represents +/- one standard error.

(A) Selection profile based on the composite (day and night) dataset for adults and subadult males.

(B) Selection profile partitioned by diel period for urban adults. The upper standard error for the day portion of the figure extended to five, but was truncated to ease comparison with the other plots.

(C) Selection profile partitioned by diel period for urban subadult males.

both urban caracal subgroups. The segmented regression approach split the distance from the urban boundary into two covariates with different slopes on either side of an optimal breakpoint (e.g., [Figure 2](#)).^{41,42} Breakpoint values ranged between 46 and 144 m from the urban boundary (varying across 3-hr and 20-min datasets; [Table 1](#)). These values indicated that there exists a narrow (natural area) buffer zone around the urban matrix that caracals perceived as equal to the urban matrix itself ([Table 1](#), [Figure 2](#); average subadult width = 118.8 m, average adult width = 74.8 m). We hereafter refer to the urban matrix and the surrounding natural buffer zone as the “urban interface.”

The supported segmented relationship of the effect of distance to the urban interface allowed us to separately analyze habitat selection when urban individuals were within the urban interface or within natural areas (e.g., [Figure 3](#)). We next considered whether the relative probability of selecting for other resources ([Tables S4 and S5](#)) was dependent on whether individuals encountered these features within the urban interface vs. within natural areas; we selected candidate covariates (“split” covariates; pine, burn ratio, cover, elevation, and distance from freshwater and coast; [STAR Methods](#); e.g., [Figure 3](#)). We did not consider a split potential for Normalized Difference Vegetation Index (NDVI), dunes, vineyards, eucalyptus, or roads ([STAR Methods](#)).

Coarse-scale habitat selection varies across age class, region, and diel period

Habitat selection analyses yielded unique trends across subgroups and diel periods ([Figures 2, 3, 4, 5, and 6](#), [Tables S6–S14](#)). Observed model cross-validation scores (r_s , calculated using spearman rank correlations) were high, particularly for urban caracals ([Table 1](#)). Although observed r_s scores for wildland best-fit models were lower (possibly as an artifact of smaller sample size or landscape homogeneity), they still outperformed r_s values expected under random habitat selection.

Across subgroups, selection for sand dunes was universal while selection for greenness (NDVI) was near universal ([Figures 3 and 4](#), [Tables S6–S14](#)). Overall, when comparing across subgroups, a functional response emerged whereby individuals increased their selection for proximity to urban areas as the availability of urban areas increased.

In the wildland-dominated subregion, caracals showed no linear or quadratic response to the urban boundary. However, when dense vegetation (cover) was available, wildland caracals selected for proximity to the urban boundary ([Figure 4](#)). Proximity to the coast was the principal driver of wildland caracal movement ([Figures 4 and 5](#), [Table S6](#)).

Caracals in the urban-dominated subregion exhibited different trends in habitat selection and trends also differed among age classes, diel periods, and microhabitat availability ([Figures 2, 3, and 5](#), [Tables S7–S14](#)). While adults avoided being within the “urban interface” (the urban matrix surrounded by a narrow buffer of natural area; [Figures 2 and 3](#), [Tables S7–S10](#)), they selected to be at the breakpoint

Table 1. Optimal breakpoint values and the results of 5-fold validation values across all modeled datasets and diel periods (when diel period models were warranted)

5-fold Validation					
Demographic	Diel period	Movement dataset	Breakpoint distance	Observed Mean (SD)	Random Mean (SD)
Urban adults	Composite	3-hr	65	0.97 (0.12)	0.001 (0.23)
	Day	3-hr	56	0.95 (0.02)	0.01 (0.22)
	Night	3-hr	96	0.94 (0.03)	-0.03 (0.21)
	Composite	20-min	54	0.88 (0.04)	-0.02 (0.25)
	Day	20-min	46	0.88 (0.05)	-0.04 (0.21)
	Night	20-min	132	0.78 (0.09)	0.01 (0.24)
Urban subadult males	Composite	3-hr	132	0.92 (0.03)	-0.001 (0.22)
	Day	3-hr	144	0.89 (0.02)	0.04 (0.25)
	Night	3-hr	111	0.83 (0.07)	-0.02 (0.23)
	Composite	20-min	88	0.73 (0.09)	-0.02 (0.22)
Wildland adults	Composite	3-hr	NA	0.62 (0.08)	-0.06 (0.25)
	Composite	20-min	NA	0.62 (0.13)	-0.03 (0.21)

Optimal breakpoints values (represented as the distance from the urban boundary) were determined using segmented regressions only for urban-dominated subregion adults and subadults and indicated the functional shift in avoidance-selection trends from the urban interface to natural areas.

between urban and natural areas more so than subadults (Figure 1A). At night, when within natural areas, urban adults selected for proximity to urban areas (Tables S9). Overall, when habitat cover was available they also selected for proximity to urban areas (Figures 3A and 3B). Adults selected for cover during the day, but not at night when human activity decreased. Selection estimates for freshwater and the coast was greater when individuals were located within the urban interface. When situated within the urban interface, adults avoided burned areas, but in natural areas, the relationship was neutral (but see 20-min data models below; Figure 6). Urban adults avoided roads during the day, but not at night when vehicle activity decreased (Figures 3A and 3B). Urban adults also avoided vineyards (Figure 3, Tables S7–S9).

Habitat selection differed among urban adults and subadults (Figures 2-3 and 5, Tables S11–S14). Subadults avoided the urban interface itself, but that avoidance was 3.9 times lower than that of adults and there were 4.7 times as many subadult locations within the urban matrix itself compared with adults (subadults = 30.7%, adults = 6.5% of locations). While located in natural areas, subadults selected for proximity to the urban interface, particularly at night (Figures 2 and 3, Tables S11 and S14). Within the urban interface where human activity is highest, subadults selected for cover and avoided burned areas (Figure 3). In contrast with adults in both subregions, subadults avoided the coast (Figures 3 and 5). Subadults generally selected for low elevations irrespective of where they were on the landscape. However, when the use of high elevation areas brought subadults closer to the urban interface, they used higher elevations (Figures 3A and 3C). Unlike adults, subadults selected for vineyards (Figure 3, Tables S11 and S14).

Fine-scale habitat selection

Median step length across all individuals during 20-min movement intervals was 136.8 m, indicating that fine-scale decision-making about habitat use is observable on the scale of < 150 m. In some cases, the avoidance of anthropogenic features tended to relax relative to coarse-scale analyses, while selection for natural features tended to increase (Figure 6, Tables S6–S12). The most intriguing result of the fine-scale habitat selection analyses in both regions was selection of burned areas. Wildland adults uniformly selected burned areas (Figure 6; Table S6). In contrast, urban adults selected for burned areas when they were in natural areas but avoided burned areas when they were within the urban interface (Figure 6; Tables S7 and S10). Urban subadults avoided burned areas when within the urban interface but were indifferent to burned areas in natural areas (Figure 6, Tables S11 and S12).

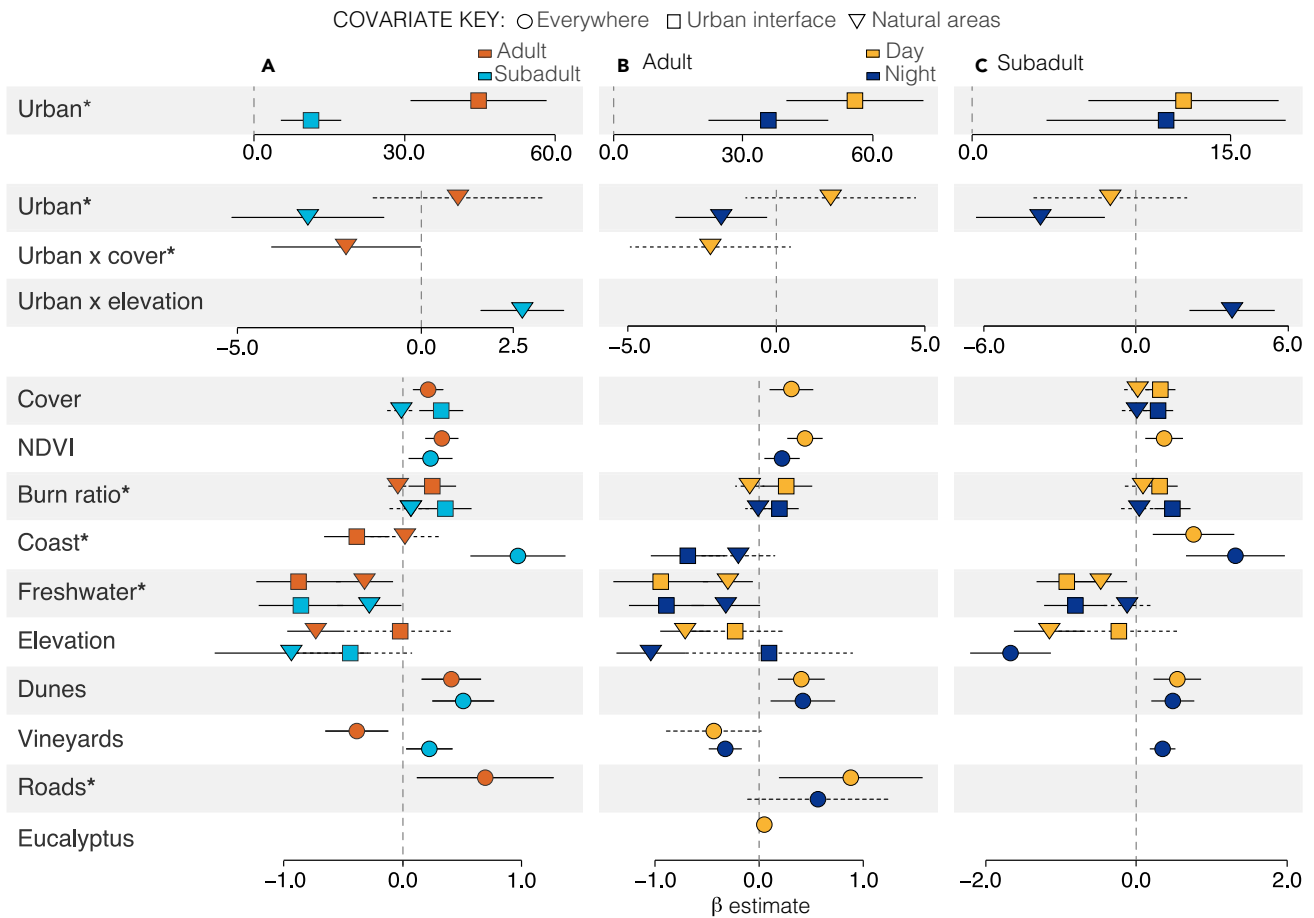


Figure 3. Selection estimates and 95% confidence intervals for the urban-dominated subregion segmented regression models based on the 3-hr datasets (A) composite (day and night), (B) adults, and (C) subadult males

Segmented models resulted in cases where β coefficients were generated separately for split covariates depending on whether individuals were situated within the urban interface (squares) or natural areas (triangles). When covariates were static, the β coefficients (circles) applied throughout the landscape irrespective of where individuals were located on the landscape. The distance from the urban boundary (urban) covariate was always split, resulting in two β coefficients with substantially different values, thus plotted on separate axes. * indicates distance covariates where positive β values indicate a negative association, and negative β values indicate a positive association. Where 95% confidence intervals are represented by a dashed line, the β estimate is not significant at $\alpha \leq 0.05$.

Wildland adults selected for gentler slopes at the fine temporal scale, although a topographic covariate was not included in the best-fit coarse temporal scale model (Table S6). For urban adults, the interaction between distance from the urban interface and cover was particularly pronounced (Tables S7, S8, and S10). For urban subadults, primary differences included that neither cover nor NDVI were in the best-fit model (Tables S11 and S12).

Activity

We tested whether caracals in any subgroup increased nocturnality, defined as the proportion of active locations (movements ≥ 50 m within 20-min intervals;⁴³), to avoid exposure to human activities. Activity patterns were calculated from 20-min fix interval data that we subsampled to 1-h intervals to reduce autocorrelation.⁴⁴ Our dataset comprised 8,582 hourly locations collected from 22 individuals (4 wildland adults, 12 urban adults, 6 urban subadults) for which we had 20-min data. We found no significant differences in nocturnality among subgroups. Specifically, the variance-variance weighted mean log risk ratio among the 1,000 bootstrap replications was -0.005 (equivalent to 0.5% greater nocturnality among wildland-dominated caracals), with 48.6% of replicates indicating greater nocturnality among caracals in the urban-dominated region (bootstrap confidence interval: -0.18 – 0.18 ; Table S15). Overall, caracals from all subgroups had crepuscular activity patterns (Figure S4).

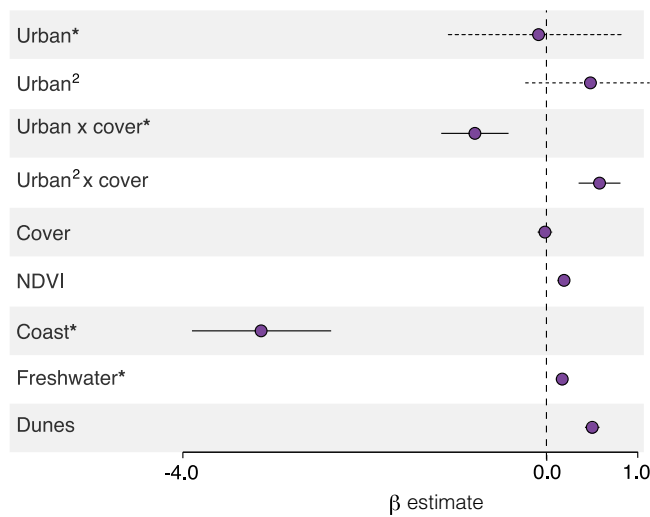


Figure 4. Selection estimates and 95% confidence intervals for day and night best-fit models for adults in the wildland-dominated subregion based on the 3-hr datasets

*indicates distance covariates where positive β values indicate a negative association, and negative β values indicate a positive association. Where 95% confidence intervals are represented by a dashed line, the β estimate is not significant at $\alpha \leq 0.05$.

DISCUSSION

We compared habitat selection and activity patterns of caracals in a fragmented urban-dominated setting to those utilizing a contiguous, wildland-dominated setting, and among demographic classes at two spatiotemporal scales. We tested three hypotheses centered on spatiotemporal avoidance of human activities. We found the strongest evidence for hypothesis 2 (the *spatial-refuge hypothesis*), some support for hypothesis 1 (the *complete-avoidance hypothesis*), and little support for hypothesis 3 (the *temporal-avoidance hypothesis*). Caracals in landscapes exposed to high human activity appear to mitigate the risk of humans by selecting for safe microhabitats within the human-dominated urban interface. This pattern was mediated by diel period, whereby use of spatial refugia was higher during times of greater human activity.

Despite a smaller sample size in the wildland subregion (habitat selection analyses, $n = 5$; activity patterns, $n = 4$), we conclude that the habitat selection of caracals in the wildland-dominated subregion represents caracal baseline habitat selection trends for the broader Cape Town region. In cases where the habitat selection of urban adults deviated from that of wildland adults, we posit these differences represent behavioral adaptations to frequent exposure to anthropogenic activities or landscape modification.

Although, we did not observe changes in temporal activity patterns as a function of urban exposure, caracals mediated risks and rewards across the diel period by changing their habitat selection. Urban adults avoided vineyards with considerable human traffic and avoided roads during the day when vehicle traffic is heaviest. Both urban adult and subadult avoidance of the urban matrix increased during the day, and they selected for the urban boundary at night. Wolves (*Canis lupus*), brown bears (*Ursus arctos*) and African lions (*Panthera leo*) similarly avoided anthropogenic disturbances more strongly during the day than night.^{7,45} Thus, particularly during the day when human activity is higher, the availability of spatial refugia may aid the persistence of carnivores in human-dominated landscapes. The availability of resources may have also played a role in temporal patterns being observed in habitat selection but not activity. Preferred caracal prey are largely diurnal and are more available at the urban edge during the day,^{43,46} restricting the ability for caracals to modify their activity patterns in response to people.

Complex vegetation offers the best cover for ambush predators to stalk prey,⁴⁷ and it offers concealment from humans.^{7,37} In our study system, this resource (cover) appears to play an important role in promoting urban caracal use of areas in proximity to the urban edge. Previous studies have observed that other carnivore species, such as spotted hyenas (*Crocuta crocuta*),⁴⁸ brown bears,⁴⁹ lions,⁷ and pumas (*Puma concolor*)⁴⁰ increase their use of protective vegetation when in proximity to humans. Caracals are known to

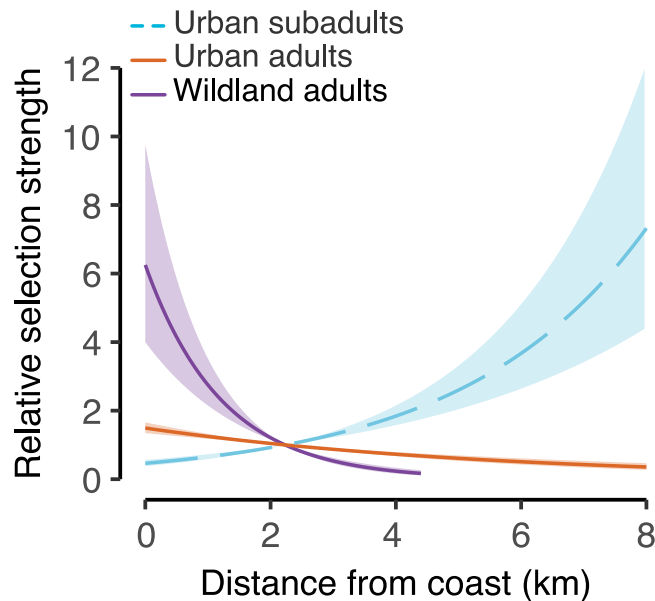


Figure 5. The relative selection for the coast for adults in the wildland and urban-dominated subregions, and subadult males in the urban-dominated subregion based on 3-hr datasets

Relative strength of selection represented with lines, while shading represents +/- one standard error.

Wildland adults were a maximum distance of approximately 4.4 km from the coast. Their selection profile is plotted accordingly.

occupy more open habitats than other similarly sized wild cats⁵⁰ and thus that wildland adults utilizing areas with substantially less human activity were indifferent to cover was not surprising. In contrast, urban adults that were more exposed to human activity selected for cover during the day when human activity was high, but not at night when human activity decreased. Subadult response to cover was even more nuanced; when within the urban interface where human activity is highest, they selected for cover, but when in natural areas further from human activity their relationship with cover was neutral. Our findings suggest that in areas with high human activity, caracals will use complex vegetation as microhabitat refugia to conceal themselves from humans.

Caracals in the wildland-dominated subregion used areas an average of 16-fold further from urban areas than caracals in the urban-dominated subregion, despite having access to urban areas. This may support the contention that animals with less exposure to human development are more likely to use a *complete-avoidance* strategy, in contrast to the *spatial-refuge* strategy observed in animals in the more developed subregion. In contrast to wildland adults, the distance of urban subadult locations were an average of 44 m from the urban edge; adult locations were on average 458 m from the urban edge. Because the generation of available points sufficiently constrains their location such that any observed effect cannot be an artifact of landscape composition, but rather reflects areas within caracal home ranges, our habitat selection results demonstrate selection for proximity to urban areas by urban caracals. A similar trend of differential selection of anthropogenic landscapes by individuals with varying exposure to anthropogenic activities was observed for pumas inhabiting rural and wilderness areas in Canada; rural individuals reduced their avoidance of oil and gas pipelines and well sites as those features became more common on the landscape.⁵¹ In a foraging-explicit habitat selection study of the same caracal population, wildland caracals avoided the urban edge whereas urban caracals selected for the urban edge while foraging.⁴⁶ Our findings, combined with the results from Leighton et al.,⁴⁶ illustrate the ability of individuals exposed to varying degrees of human activity to modify their habitat selection strategies depending on the landscape in which they find themselves.

Additionally, we observed that urban adult and subadult selection for freshwater, and adult selection for the coast, increased when the caracals encountered those features within the urban interface. These findings, combined with selection for the urban edge while moving (observed in this study) and foraging,⁴⁶ suggest that valuable resources lie within the urban edge. Other studies have likewise found selection for developed areas possibly to access valuable foraging opportunities in bobcats (*Lynx rufus*)⁵² and pumas.⁵³

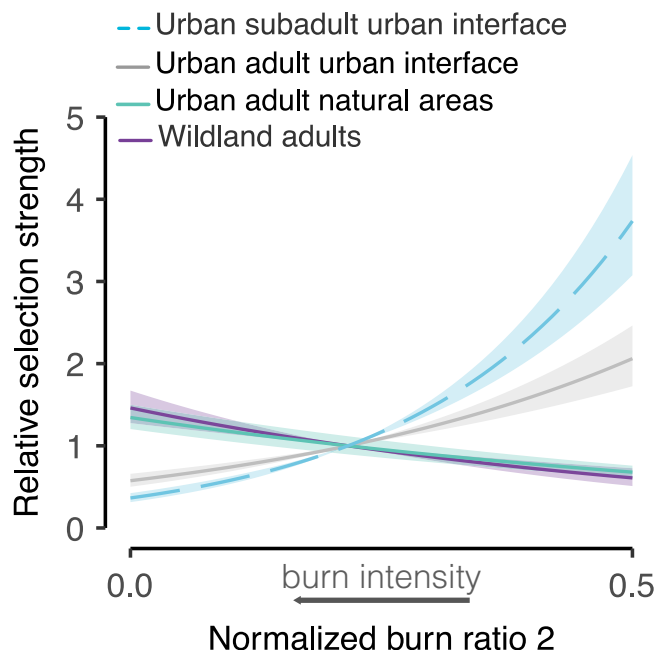


Figure 6. Avoidance and selection of burned areas (measured as the vegetation index normalized burn ratio 2 [NBR2]) depended on region, age class, and for adults and subadults in the urban-dominated region, where on the landscape individuals were situated (e.g., within urban interface or natural areas)

Relative strength of selection represented with lines, while shading represents +/- one standard error.

Figure based on night 20-min dataset for each group. More severe fire damage is represented by lower NBR2 values.

Anthropogenic disturbances can provide novel foraging opportunities for a variety of wild animal species because of greater ease of hunting, decreased search effort, or increased capture success,⁵⁴ making inhabiting areas near and within urban areas attractive for a variety of carnivore species.⁵⁵ Our results are consistent with these trends, particularly for caracals in areas with greater access to urban spaces.

However, the ability of urban caracals to take advantage of anthropogenic resources may come at a cost. The near constant exposure of caracals to human activities in the urban-dominated subregion could habituate them to human disturbance,⁵⁶ or lead to reduced anti-predator behavior with increasing exposure to high-risk situations (risk-allocation hypothesis).⁵⁷ Life on the edge comes with severe fitness-reducing costs; they are vulnerable to mortality due to vehicle collision, poaching and lethal management, and domestic dog attacks (> 82% of mortalities, Serieys et al. unpubl.data), in addition to exposure to noxious chemicals, such as rat poisons⁵⁸ and persistent organic pollutants.⁵⁹

Young carnivores (particularly males) disperse from their natal range.⁶⁰ Thus, habitat selection for this cohort is essential to understand landscape features that promote connectivity.⁶¹ Subadult males selected locations in or close to the urban interface more so than urban adults. We anticipate that these subadult space use patterns may be explained by use of marginal habitat to avoid intraspecific competition and high relative tolerance for risk. In addition to using habitats, such as the urban matrix and vineyards that adults avoided, subadults avoided coastal areas that adults preferred (Figure 5). Similar use of marginal habitat by subadults has been documented in numerous other carnivore species that inhabit human-dominated landscapes,^{61,62} including other medium-sized felids such as bobcats⁶³ and Iberian lynx (*Lynx pardinus*).⁶⁴ The costs of competing with adults may be substantial for younger individuals attempting to establish home ranges in this type of system. At least two subadult caracals have been killed by older adult males (Serieys et al., unpubl.data). Future investigations could focus on the dynamic interactions⁶⁵ between adults and subadults or explore the latency after visitation by pairs of adults and subadults,⁶⁶ to explicitly examine the influence of adult movement on subadult movement.

Selection patterns varied between scales of temporal data resolution. At fine scales (20-min locations), in some cases, selection for natural landscape features (e.g., burned areas, NDVI, selection for the coast) was stronger

than avoidance of risky landscape features such as the urban matrix and vineyards (e.g., urban adults night, [Table S9](#)), as has been observed in other carnivore studies.^{7,40} The fine-scale analyses (20-min data) indicated that wildland caracals avoid steep slopes, which are energetically costly to movement^{40,67,68} and have been observed to drive habitat selection at fine, but not coarse, temporal scales in other carnivores.⁴⁰ The fine-scale models also provided important insights into nuanced selection and avoidance patterns of burned areas ([Figure 6](#), [Tables S6](#), [S7](#), and [S10](#)). For example, wildland caracals, and urban adult caracals when in natural areas, selected burned areas at fine scales, possibly because seeds from fynbos vegetation that are released post-fire can be a valuable resource for small mammals.⁶⁹ With reduced protective cover because of fire, however, those small mammals may be more easily detected and preyed upon. Urban caracals avoided burned areas when within the urban interface, possibly because they were more exposed to humans, which may be an example of sacrificing optimal foraging to avoid risky areas.

Many studies have examined carnivore spatial or temporal strategies for living in a human-dominated landscape.^{7,21,22,29,30,63} However, recent research has indicated that risk-reward tradeoffs are inherently spatiotemporal in nature as the two processes interact.⁷⁰ This should be especially true for animal responses to humans, which are complex and dynamic. Our study indicates that landscape context drives spatiotemporal avoidance behaviors in a generalist carnivore, but that more fine-scale avoidance behaviors emerge in individuals that experience greater levels of human exposure. Exploring such complexity is necessary to understand dynamics of human-carnivore coexistence and the ecology of carnivores in shared landscapes.

Local city and national park land managers have expressed interest in using the movement data of caracals to promote biodiversity conservation within the CoCT. Caracals, especially reproductive adults, avoid the urban matrix. Yet the CoCT is a rapidly urbanizing landscape⁷¹ and this caracal population is effectively isolated and restricted to habitat fragments within TMNP. Despite being fragmented and isolated, TMNP is one of the most important biodiversity hotspots on Earth.⁷² Maintaining this rich biodiversity and the ecological processes that underpin it require dedicated, adaptive interventions to conserve populations and habitats. Our findings point to four critical interventions needed to sustain the Cape Peninsula's caracal population. The first is to maintain as many coastal areas and wetlands as possible for wild animals; based on our analyses, these are resource-rich areas on the peninsula. Second, our monitoring efforts demonstrate that small reserves (< 3 km²) within the heavily impacted Cape Flats ([Figure 1](#)) can support caracals. The purchase (by the CoCT) of even relatively small tracts of land, particularly dune systems (selected for by caracals), within the Cape Flats ([Figure 1](#)) can increase the amount of viable habitat and possibly new avenues of connectivity. Third, our fine-scale analyses reveal that to restore impacted areas, areas close to urban development (< 200 m) should be prioritized for restoration of vegetation. Fourth, areas such as pine plantations (that were avoided) should be restored by South Africa National Parks (SANParks) to native fynbos vegetation. We encourage the CoCT, SANParks, and their partners to take the steps needed to ensure that key habitats utilized by wildlife are protected and maintained. Achieving this goal, and conserving fauna globally throughout the rapidly expanding urban-wildland interface, requires data-informed conservation strategies and initiatives that better accommodate many challenges wild animals face living in human-dominated landscapes.

Limitations of the study

We experienced two primary limitations of this study. Our trapping permits in the wildland-dominated subregion constrained us to a few hundred meters from the coast, which potentially contributed to an inability to sample subadults (that avoided the coast in the urban-dominated region) in the wildland subregion. Additionally, we did not have explicit data on human activity, so we were unable to disentangle the influence of human infrastructure from various human activities on the behavioral parameters we assessed.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- [KEY RESOURCES TABLE](#)
- [RESOURCE AVAILABILITY](#)
 - Lead contact
 - Materials availability
 - Data and code availability
- [EXPERIMENTAL MODEL AND SUBJECT DETAILS](#)
- [METHOD DETAILS](#)

- Study area
- Capture, GPS-collaring, and subgroup classification
- Landscape covariates
- **QUANTIFICATION AND STATISTICAL ANALYSIS**
 - Step selection functions
 - Testing model complexity: Subgroups
 - Testing model complexity: Diel period
 - Modeling approach for each subgroup
 - Cross validation
 - Activity

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.107050>.

ACKNOWLEDGMENTS

We are grateful for the logistical support of SANParks, the CoCT, and the SPCA. We thank D.Winterton, L.Mossop, J.Broadfield, and numerous volunteer interns for field assistance. Essential veterinarians were B.Stevens, A.Knight, E.Jordan, T.Hepburn. We thank the Claude Leon Foundation, the University of Cape Town Research Council, Botanica Wines, Stellenbosch University, the National Research Foundation, Wildlife ACT, CoCT, Experiment, Big Cat Rescue, and numerous private donors for funding. We would like to thank four anonymous reviewers for their thoughtful reviews.

AUTHOR CONTRIBUTIONS

L.E.K.S., J.M.B., M.J.O., and C.C.W. conceptualized the study. L.E.K.S. collected, analyzed, and interpreted data, and wrote the manuscript. M.S.R. analyzed data and contributed writing the manuscript. J.A.S., J.P.S., M.S.R., and C.C.W. interpreted data. All authors read, edited, and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We worked to ensure sex balance in the selection of non-human subjects. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. We avoided “helicopter science” practices by including the participating local contributors from the region where we conducted the research as authors on the paper.

Received: April 28, 2022

Revised: April 23, 2023

Accepted: June 1, 2023

Published: June 7, 2023

REFERENCES

1. Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., et al. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7, 12558. <https://doi.org/10.1038/ncomms12558>.
2. Kareiva, P., Watts, S., McDonald, R., and Boucher, T. (2007). Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* 316, 1866–1869. <https://doi.org/10.1126/science.1140170>.
3. Alberti, M., Correa, C., Marzluff, J.M., Hendry, A.P., Palkovacs, E.P., Gotanda, K.M., Hunt, V.M., Apgar, T.M., and Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proc. Natl. Acad. Sci. USA* 114, 8951–8956. <https://doi.org/10.1073/pnas.1606034114>.
4. Rebele, F. (1994). Urban ecology and special features of urban ecosystems. *Global Ecol. Biogeogr.* 4, 173–187.
5. Tucker, M.A., Böhning-Gaese, K., Avgar, T., et al. Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., et al. (2018). Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359, 466–469. <https://doi.org/10.1126/science.aam9712>.
6. Frid, A., and Dill, L.M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11. <https://doi.org/10.5751/es-00404-060111>.
7. Suraci, J.P., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M., and Wilmers, C.C. (2019). Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology* 100, e02644.
8. Collins, C., and Kays, R. (2011). Causes of mortality in North American populations of large and medium-sized mammals. *Anim. Conserv.* 14, 474–483. <https://doi.org/10.1111/j.1469-1795.2011.00458.x>.

9. Flesch, A.D. (2017). Influence of local and landscape factors on distributional dynamics: a species-centred, fitness-based approach. *Proc. Biol. Sci.* 284, 20171001. <https://doi.org/10.1098/rspb.2017.1001>.
10. Johnson, H.E., Lewis, D.L., and Breck, S.W. (2020). Individual and population fitness consequences associated with large carnivore use of residential development. *Ecosphere* 11, e03098. <https://doi.org/10.1002/ecs2.3098>.
11. Gámez, S., and Harris, N.C. (2021). Living in the concrete jungle: carnivore spatial ecology in urban parks. *Ecol. Appl.* 31, e02393. <https://doi.org/10.1002/eap.2393>.
12. Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., and Dickman, C.R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecol. Biogeogr.* 24, 1–11. <https://doi.org/10.1111/geb.12236>.
13. Lowry, H., Lill, A., and Wong, B.B.M. (2013). Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549. <https://doi.org/10.1111/brv.12012>.
14. Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L.M., Forrester, T., Green, A.M., et al. (2021). Disturbance type and species life history predict mammal responses to humans. *Global Change Biol.* 27, 3718–3731. <https://doi.org/10.1111/gcb.15650>.
15. Rodewald, A., and Gehrt, S. (2014). Wildlife population dynamics in urban landscapes. In *Urban wildlife conservation: Theory and practice*, R. McCleery, C. Moorman, and M. Peterson, eds. (Springer), pp. 117–148. <https://doi.org/10.1007/978-1-4899-7500-3>.
16. Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., Sullam, K.E., Bird, K.C., Thomas, M.K., Hanley, T.C., and Turner, C.B. (2011). Toward an integration of evolutionary biology and ecosystem science. *Ecol. Lett.* 14, 690–701. <https://doi.org/10.1111/j.1461-0248.2011.01627.x>.
17. Tuomainen, U., and Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biol. Rev.* 86, 640–657. <https://doi.org/10.1111/j.1469-185x.2010.00164.x>.
18. Wong, B.B.M., and Candolin, U. (2015). Behavioral responses to changing environments. *Behav. Ecol.* 26, 665–673. <https://doi.org/10.1093/beheco/aru183>.
19. Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., and Boyce, M.S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS One* 7, e50611. <https://doi.org/10.1371/journal.pone.0050611>.
20. Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., and Macdonald, D.W. (2016). Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. *Behav. Ecol.* 27, arw117–1832. <https://doi.org/10.1093/beheco/arw117>.
21. Suraci, J.P., Clinchy, M., Zanette, L.Y., and Wilmers, C.C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.* 22, 1578–1586. <https://doi.org/10.1111/ele.13344>.
22. Nickel, B.A., Suraci, J.P., Allen, M.L., and Wilmers, C.C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biol. Conserv.* 241, 108383. <https://doi.org/10.1016/j.biocon.2019.108383>.
23. Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V., and Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS One* 8, e60590.
24. Mysterud, A., and Ims, R.A. (1998). Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79, 1435–1441.
25. Mumma, M.A., Gillingham, M.P., Johnson, C.J., and Parker, K.L. (2019). Functional responses to anthropogenic linear features in a complex predator-multi-prey system. *Landscape Ecol.* 34, 2575–2597. <https://doi.org/10.1007/s10980-019-00905-9>.
26. Pigeon, K.E., MacNearnay, D., Hebblewhite, M., Musiani, M., Neufeld, L., Cranston, J., Stenhouse, G., Schmiegelow, F., and Finnegan, L. (2020). The density of anthropogenic features explains seasonal and behaviour-based functional responses in selection of linear features by a social predator. *Sci. Rep.* 10, 11437. <https://doi.org/10.1038/s41598-020-68151-7>.
27. Duparc, A., Garel, M., Marchand, P., Dubray, D., Maillard, D., and Loison, A. (2019). Revisiting the functional response in habitat selection for large herbivores: a matter of spatial variation in resource distribution? *Behav. Ecol.* 30, 1725–1733. <https://doi.org/10.1093/beheco/arz141>.
28. Mason, T.H.E., and Fortin, D. (2017). Functional responses in animal movement explain spatial heterogeneity in animal-habitat relationships. *J. Anim. Ecol.* 86, 960–971. <https://doi.org/10.1111/1365-2656.12682>.
29. Gaynor, K.M., Hohnowski, C.E., Carter, N.H., and Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235. <https://doi.org/10.1126/science.aar7121>.
30. Grilo, C., Lucas, P.M., Fernández-Gil, A., Seara, M., Costa, G., Roque, S., Rio-Maior, H., Nakamura, M., Álvares, F., Petrucci-Fonseca, F., and Revilla, E. (2019). Refuge as major habitat driver for wolf presence in human-modified landscapes. *Anim. Conserv.* 22, 59–71. <https://doi.org/10.1111/acv.12435>.
31. Reilly, C.M., Suraci, J.P., Smith, J.A., Wang, Y., and Wilmers, C.C. (2022). Mesopredators retain their fear of humans across a development gradient. *Behav. Ecol.* 33, 428–435. <https://doi.org/10.1093/beheco/ab150>.
32. Wittemyer, G., Northrup, J.M., and Bastille-Rousseau, G. (2019). Behavioural valuation of landscapes using movement data. *Philos. Trans. R. Soc. B* 374, 20180046.
33. Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., and Swenson, J.E. (2010). Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Can. J. Zool.* 88, 875–883. <https://doi.org/10.1139/z10-053>.
34. Lesmerises, F., Déry, F., Johnson, C.J., and St-Laurent, M.-H. (2018). Spatiotemporal response of mountain caribou to the intensity of backcountry skiing. *Biol. Conserv.* 217, 149–156. <https://doi.org/10.1016/j.biocon.2017.10.030>.
35. Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L., and Musiani, M. (2011). Human activity helps prey win the predator-prey space race. *PLoS One* 6, e17050. <https://doi.org/10.1371/journal.pone.0017050>.
36. Schuette, P., Creel, S., and Christianson, D. (2013). Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. *Biol. Conserv.* 157, 148–154. <https://doi.org/10.1016/j.biocon.2012.09.011>.
37. Suraci, J.P., Nickel, B.A., and Wilmers, C.C. (2020). Fine-scale movement decisions by a large carnivore inform conservation planning in human-dominated landscapes. *Landscape Ecol.* 35, 1635–1649. <https://doi.org/10.1007/s10980-020-01052-2>.
38. Rettie, W.J., and Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23, 466–478. <https://doi.org/10.1111/j.1600-0587.2000.tb00303.x>.
39. Bastille-Rousseau, G., Murray, D.L., Schaefer, J.A., Lewis, M.A., Mahoney, S.P., and Potts, J.R. (2018). Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling. *Ecography* 41, 437–443. <https://doi.org/10.1111/ecog.02655>.
40. Nisi, A.C., Suraci, J.P., Ranc, N., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M., and Wilmers, C.C. (2022). Temporal scale of habitat selection for large carnivores: balancing energetics, risk and finding prey. *J. Anim. Ecol.* 91, 182–195. <https://doi.org/10.1111/1365-2656.13613>.
41. Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P.J., Smith, D.W., and MacNulty, D.R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* 88, 638–652. <https://doi.org/10.1002/ecm.1313>.
42. Smith, J.A., Duane, T.P., and Wilmers, C.C. (2019). Moving through the matrix: promoting permeability for large carnivores in a human-dominated landscape. *Landscape Urban Plan.* 183, 50–58. <https://doi.org/10.1016/j.landurbplan.2018.11.003>.

43. Leighton, G.R.M., Bishop, J.M., O'Riain, M.J., Broadfield, J., Meröndun, J., Avery, G., Avery, D.M., and Serieys, L.E.K. (2020). An integrated dietary assessment increases feeding event detection in an urban carnivore. *Urban Ecosyst.* 23, 569–583. <https://doi.org/10.1007/s11252-020-00946-y>.
44. Hertel, A.G., Swenson, J.E., and Bischof, R. (2017). A case for considering individual variation in diel activity patterns. *Behav. Ecol.* 28, 1524–1531. <https://doi.org/10.1093/beheco/arn122>.
45. Whittington, J., Hebblewhite, M., Baron, R.W., Ford, A.T., and Paczkowski, J. (2022). Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. *Mov. Ecol.* 10, 17. <https://doi.org/10.1186/s40462-022-00318-5>.
46. Leighton, G.R.M., Bishop, J.M., Meröndun, J., Winterton, D.J., O'Riain, M.J., and Serieys, L.E.K. (2021). Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. *Anim. Conserv.* 25, 244–258. <https://doi.org/10.1111/acv.12732>.
47. Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J., Bidder, O.R., and Middleton, A.D. (2019). Habitat complexity mediates the predator–prey space race. *Ecology* 100, e02724.
48. Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M., and Holekamp, K.E. (2003). Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv.* 6, 207–219. <https://doi.org/10.1017/s1367943003003263>.
49. Ordiz, A., Støen, O.G., Delibes, M., and Swenson, J.E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166, 59–67. <https://doi.org/10.1007/s00442-011-1920-5>.
50. Hunter, L. (2015). *Wild Cats of the World* (Bloomsbury Publishing Plc).
51. Knopff, A.A., Knopff, K.H., Boyce, M.S., and St Clair, C.C. (2014). Flexible habitat selection by cougars in response to anthropogenic development. *Biol. Conserv.* 178, 136–145. <https://doi.org/10.1016/j.biocon.2014.07.017>.
52. Dunagan, S.P., Karels, T.J., Moriarty, J.G., Brown, J.L., and Riley, S.P.D. (2019). Bobcat and rabbit habitat use in an urban landscape. *J. Mammal.* 100, 401–409. <https://doi.org/10.1093/jmammal/gyz062>.
53. Benson, J.F., Sikich, J.A., and Riley, S.P.D. (2016). Individual and population level resource selection patterns of mountain lions preying on mule deer along an urban-wildland gradient. *PLoS One* 11, e0158006. <https://doi.org/10.1371/journal.pone.0158006>.
54. Fleming, P.A., and Bateman, P.W. (2018). Novel predation opportunities in anthropogenic landscapes. *Anim. Behav.* 138, 145–155. <https://doi.org/10.1016/j.anbehav.2018.02.011>.
55. Bateman, P.W., and Fleming, P.A. (2012). Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23. <https://doi.org/10.1111/j.1469-7998.2011.00887.x>.
56. Rodríguez-Prieto, I., Fernández-Juricic, E., Martín, J., and Regis, Y. (2009). Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* 20, 371–377. <https://doi.org/10.1093/beheco/arn151>.
57. Lima, S.L., and Bednekoff, P.A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649–659. <https://doi.org/10.1086/303202>.
58. Serieys, L.E.K., Bishop, J., Okes, N., Broadfield, J., Winterton, D.J., Poppenga, R.H., Viljoen, S., Wayne, R.K., and O'Riain, M.J. (2019). Widespread anticoagulant poison exposure in predators in a rapidly growing South African city. *Sci. Total Environ.* 666, 581–590. <https://doi.org/10.1016/j.scitotenv.2019.02.122>.
59. Leighton, G.R.M., Bishop, J.M., Camarero, P.R., Mateo, R., O'Riain, M.J., and Serieys, L.E.K. (2022). Poisoned chalice: use of transformed landscapes associated with increased persistent organic pollutant concentrations and potential immune effects for an adaptable carnivore. *Sci. Total Environ.* 822, 153581. <https://doi.org/10.1016/j.scitotenv.2022.153581>.
60. Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28, 1140–1162. [https://doi.org/10.1016/s0003-3472\(80\)80103-5](https://doi.org/10.1016/s0003-3472(80)80103-5).
61. O'Neill, H.M.K., Durant, S.M., and Woodroffe, R. (2020). What wild dogs want: habitat selection differs across life stages and orders of selection in a wide-ranging carnivore. *BMC Zool.* 5, 1. <https://doi.org/10.1186/s40850-019-0050-0>.
62. Hinton, J.W., Proctor, C., Kelly, M.J., van Manen, F.T., Vaughan, M.R., and Chamberlain, M.J. (2016). Space use and habitat selection by resident and transient red wolves (*Canis rufus*). *PLoS One* 11, e0167603. <https://doi.org/10.1371/journal.pone.0167603>.
63. Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., and Wayne, R.K. (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in Southern California. *Conserv. Biol.* 17, 566–576. <https://doi.org/10.1046/j.1523-1739.2003.01458.x>.
64. Palomares, F., Delibes, M., Ferreras, P., Fedriani, J.M., Calzada, J., and Revilla, E. (2000). Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. *Conserv. Biol.* 14, 809–818.
65. Doncaster, C.P. (1990). Non-parametric estimates of interaction from radio-tracking data. *J. Theor. Biol.* 143, 431–443. [https://doi.org/10.1016/s0022-5193\(05\)80020-7](https://doi.org/10.1016/s0022-5193(05)80020-7).
66. Martinig, A.R., Riaz, M., and St Clair, C.C. (2020). Temporal clustering of prey in wildlife passages provides no evidence of a prey-trap. *Sci. Rep.* 10, 11489. <https://doi.org/10.1038/s41598-020-67340-8>.
67. Dunford, C.E., Marks, N.J., Wilmers, C.C., Bryce, C.M., Nickel, B., Wolfe, L.L., Scantlebury, D.M., and Williams, T.M. (2020). Surviving in steep terrain: a lab-to-field assessment of locomotor costs for wild mountain lions (*Puma concolor*). *Mov. Ecol.* 8, 34. <https://doi.org/10.1186/s40462-020-00215-9>.
68. Nickel, B.A., Suraci, J.P., Nisi, A.C., and Wilmers, C.C. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. *Proc. Natl. Acad. Sci. USA* 118, e2004592118. <https://doi.org/10.1073/pnas.2004592118>.
69. Bond, W., and Breytenbach, G. (1985). *Ants, rodents and seed predation in Proteaceae*. *S. Afr. J. Zool.* 20, 150–154.
70. Smith, J.A., Donadio, E., Bidder, O.R., Pauli, J.N., Sheriff, M.J., Perrig, P.L., and Middleton, A.D. (2020). Where and when to hunt? Decomposing predation success of an ambush carnivore. *Ecology* 101, e03172. <https://doi.org/10.1002/ecy.3172>.
71. Holmes, P.M., Rebelo, A.G., Dorse, C., and Wood, J. (2012). Can Cape Town's unique biodiversity be saved? Balancing conservation imperatives and development needs. *Ecol. Soc.* 17, 28. <https://doi.org/10.5751/es-04552-170228>.
72. Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. <https://doi.org/10.1038/35002501>.
73. Sunquist, M., and Sunquist, F. (2002). *Wild Cats of the World* (The University of Chicago Press).
74. Schroeder, M.A., Robb, L.A., and Braun, C. (2005). *Criteria for Gender and Age* (The Wildlife Society).
75. Furstenburg, D. (2010). *Focus on the caracal (Caracal caracal)*. *SA Hunter* 10045, 34–38.
76. Bernard, R., and Stuart, C. (1987). *Reproduction of the caracal Felis caracal from the Cape province of South Africa*. *S. Afr. J. Zool.* 22, 177–182.
77. Storey, E.A., Stow, D.A., and O'Leary, J.F. (2016). Assessing postfire recovery of chamise chaparral using multi-temporal spectral vegetation index trajectories derived from Landsat imagery. *Remote Sens. Environ.* 183, 53–64. <https://doi.org/10.1016/j.rse.2016.05.018>.
78. Gelmen, A., and Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Heirarchical Models* (Cambridge University Press).
79. Zuur, A.F., Ieno, E.N., and Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210x.2009.00001.x>.

80. Thurfjell, H., Ciuti, S., and Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. *Mov. Ecol.* 2, 4.
81. Boyce, M.S. (2006). Scale for resource selection functions. *Divers. Distrib.* 12, 269–276. <https://doi.org/10.1111/j.1366-9516.2006.00243.x>.
82. Kays, R., Crofoot, M.C., Jetz, W., and Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science* 348, aaa2478–1. <https://doi.org/10.1126/science.aaa2478>.
83. LaPoint, S., Gallery, P., Wikelski, M., and Kays, R. (2013). Animal behavior, cost-based corridor models, and real corridors. *Landsc. Ecol.* 28, 1615–1630. <https://doi.org/10.1007/s10980-013-9910-0>.
84. Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., and Mao, J.S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330.
85. Forester, J.D., Im, H.K., and Rathouz, P.J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* 90, 3554–3565. <https://doi.org/10.1890/08-0874.1>.
86. Duchesne, T., Fortin, D., and Courbin, N. (2010). Mixed conditional logistic regression for habitat selection studies. *J. Anim. Ecol.* 79, 548–555. <https://doi.org/10.1111/j.1365-2656.2010.01670.x>.
87. Nicosia, A., Duchesne, T., Rivest, L.P., and Fortin, D. (2017). A multi-state conditional logistic regression model for the analysis of animal movement. *Ann. Appl. Stat.* 11, 1537–1560. <https://doi.org/10.1307/aos/1507168839>.
88. Therneau, T.M. (2018). Survival: Survival Analysis. R Package Version 2.46-6. <https://CRAN.R-project.org/package=survival>.
89. R Core Team (2022). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing).
90. Koper, N., and Manseau, M. (2009). Generalized estimating equations and generalized linear mixed effects models for modelling resource selection. *J. Appl. Ecol.* 46, 590–599. <https://doi.org/10.1111/j.1365-2664.2009.01642.x>.
91. Prima, M.C., Duchesne, T., and Fortin, D. (2017). Robust inference from conditional logistic regression applied to movement and habitat selection analysis. *PLoS One* 12, e0169779. <https://doi.org/10.1371/journal.pone.0169779>.
92. Manly, B., McDonald, L., Thomas, D., McDonald, T., and Erickson, W. (2002). *Resource Selection by Animals* (Springer). <https://doi.org/10.1007/0-306-48151-0>.
93. Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology* 90, 2480–2490. <https://doi.org/10.1890/08-0345.1>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Caracal GPS collar dataset	Movebank	https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1832666571
Dataset used for step selection functions	Mendeley Data	https://doi.org/10.17632/n7c4ntkz7f.1
Dataset used for activity analyses	Mendeley Data	https://doi.org/10.17632/n7c4ntkz7f.1
Other		
GIS layer denoting urban boundary	City of Cape Town	Urban edge
GIS layer denoting roads	City of Cape Town	Roads
GIS layer for sand dunes	City of Cape Town	Dunes
GIS layer for wetlands and freshwater	City of Cape Town	Freshwater
GIS layer for vegetative cover	DEA National Landcover 2018 (sanbi.org)	Cover
GIS layer denoting location of pine plantations	South African National Parks	Pine plantations
GIS layer denoting vineyards and other agriculture	City of Cape Town	Vineyard
Normalized burn ratio 2	Landsat 8 (USGS 2018, usgs.org)	Burn.index
Eucalyptus	Hand-drawn in QGIS	Eucalyptus
Normalized difference vegetation index (NDVI)	Landsat 8 (USGS 2018, usgs.org)	NDVI
GIS layer with 10 m elevation resolution	City of Cape Town	Elevation

RESOURCE AVAILABILITY

Lead contact

Further information and requests for materials should be directed to Dr. Laurel Serieys (Lserieys@panthera.org).

Materials availability

This study did not generate new unique materials.

Data and code availability

- All data are publicly available. Tracking data are available through the Movebank: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1832666571. Data used for analyses are available through Mendeley Data: <https://doi.org/10.17632/n7c4ntkz7f.1>
- Code is available from the [lead contact](#) upon request.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Animal handling was approved by the University of Cape Town Animal Ethics Committee (2014/V20/LS), Cape Nature (AAA007-0147-0056), and SANParks (2014/CRC/2014-017, 2015/CRC/2014-017, 2016/CRC/2014-017, 2017/CRC/2014-017).

METHOD DETAILS

Study area

We assessed habitat selection and activity of free-ranging caracals on the Cape Peninsula ([Figure 1](#)) and within a small nature reserve (False Bay Nature Reserve, [Figure 1A](#)), both of which are isolated from other

caracal populations by 2445 km² of dense urban matrix (encompassing residential, commercial, and industrial areas) of the City of Cape Town. Within the Cape Peninsula, we primarily monitored individuals in TMNP, which encompassed approximately 320 km² of fragmented, natural habitat, which we split into the 'urban-dominated subregion' and the 'wildland-dominated subregion' (Figure 1). The urban and wildland-dominated subregions of the Cape Peninsula were separated by a major road (Kommetjie Road, Figure 1A) with dense urban development on both sides of the road except for one 630 m section where caracals were able to move between the two subregions of the study area. While we did observe urban caracals to use the northern boundary of the wildland-dominated subregion, we did not observe wildland caracals to utilize the urban-dominated subregion of the study area. We monitored two additional individuals in an urban-dominated region within the small fragmented False Bay Nature Reserve (comprising <3 km²) surrounded by an extremely densely populated region of Cape Town (Cape Flats human population densities: 9,000–17,000 people/km²).

The northern 'urban-dominated subregion' of the study area comprised six habitat patches that encompassed 190 km² (northern half, Figures 1A), 78.7% of which was bordered by urban development and 21.3% of which was bordered by ocean. The southern 'wildland-dominated subregion' (Figure 1A) encompassed 133 km² of contiguous protected national park area, 46.2% of which was bordered by urban development and 53.8% of which was bordered by ocean. In both subregions, land uses included low to high density urban development, light industrial and commercial areas, golf courses, vineyards (only 3.9% of land area in the wildland-dominated subregion), eucalyptus stands, and pine plantations (urban-dominated subregion only). The fynbos biome that comprised low-growing, dense shrubland with a fire-dependent ecology dominated the natural areas of both the urban- and wildland-dominated subregions. Across the study period, 35.2% of the available wildlife habitat intensively burned while caracals were monitored. Extensive coastal sand dune fields were also common natural features (Figure 1A).

Capture, GPS-collaring, and subgroup classification

The caracal occurs throughout much of Africa except for the Sahara and Namib deserts, and the dense equatorial forests of central and west Africa. They also occur in parts of Turkey and the Middle East, and in south-west Asia.⁷³ They are found in a variety of habitats including coastal scrub, woodland savannas, dry forest, grasslands, and arid semi-desert regions.⁵⁰ Although their ecology is poorly studied, they are considered solitary and territorial.^{50,73}

We sampled a previously unstudied population occupying approximately 320 km² of natural habitat with severely limited connectivity to neighboring populations. Between November 2014 and September 2016, during approximately 3500 trap nights, we captured 29 caracals, and collared 26, using custom-built box traps (length: 125 cm, width: 36 cm, height: 55 cm). Trapping locations were distributed across all major habitat fragments and collared individuals used almost the entirety of available habitat (Figures 1B and S1–S3). Three captured individuals were kittens that were too young to collar. One individual was opportunistically collared outside of the study area and thus data from only 25 collared individuals were included in our analyses. Collared animals weighed a minimum of 6.5 kg and the collars (215 g) weighed no more than 3.5% of the animal's body weight. Individuals were chemically immobilized using a mixture of ketamine HCl (7 mg/kg) and medetomidine (0.08 mg/kg). Once immobilized, we recorded age class, sex, weight, and morphological measurements. Individuals were classified as subadults or adults based on body size, weight, tooth wear and eruption, and reproductive status.⁷⁴ Males were considered adult if their estimated age was >2 years, because this is the approximate age at which they typically establish home ranges and reproduce.⁷⁵ Females were considered adult if their estimated age was >1 year because they sexually mature between 7 to 12 months of age.⁷⁶ Individuals were fitted with Tellus 1C collars (FollowIt™, Lindesberg, Sweden) that were programmed to record GPS locations at three-hour intervals throughout the 24 hr cycle. To assess fine-scale movement patterns and the use of potential movement corridors through urban areas, we increased the GPS-sample rate to 20-minute intervals every 10th day for 24–36 consecutive hours (resulting in a target of 72–96 consecutive locations). Collar data were downloaded via that FollowIt™ GEO web interface or obtained directly from collars after units dropped-off. Collars were equipped with both a drop-off mechanism and a rot-off cotton spacer to ensure eventual drop-off. The drop-off mechanism functioned in three ways: 1) a drop-off date was pre-programmed, 2) the drop-off could be activated through the FollowIt™ GEO web interface, or 3) the drop-off could be activated using FollowIt's portable terminal ground unit (RCD-04) that allowed us to send a signal to the collar. We primarily used method 3 because method 2 often did not function and collars often lost battery power before the pre-programmed drop

date. In every case but one, we successfully retrieved dropped collars. We were not able to locate the collar of the animal opportunistically collared outside of the study area, although even if the drop-off mechanism failed, the cotton spacer would have rotted such that the collar dropped-off eventually. Individuals were collared for an average of 123.0 days (SD = 49.6, median = 132.0).

Individuals were monitored throughout the two subregions in the Cape Peninsula. One urban individual was initially collared as a subadult, and subsequently recollared as an adult. His GPS data were classified according to his respective age class. In total, 19 unique individuals (but data for 7 adult males, 7 subadults males, 6 adult females) were GPS-collared in the urban-dominated subregion. In the wildland-dominated subregion, six individuals (2 adult males, 4 adult females) were captured. However, one wildland female presented a unique case. After being initially detected preying on endangered African penguins (*Spheniscus demersus*), the City of Cape Town and SANParks decided to capture, GPS-collar, and relocate her (on the day of capture) 21 km north to the urban-dominated region. We reclassified her as an urban individual but excluded the first 23 days (during which time her movements stabilized) of her data. We included her subsequent locations in habitat selection and activity analyses.

Landscape covariates

Caracals primarily used undeveloped habitat patches with intact shrubland vegetation (hereafter 'natural areas'), and secondarily, areas within the fully transformed urban matrix (consisting of commercial, residential, altered open areas, etc.). To capture the influence of the urban matrix on caracal habitat selection, we used distance measure (urban) that fell along a continuum of negative to positive values, where 0 indicated the line (in our GIS layer, Table S4) demarcating the urban matrix-natural area boundary (hereafter 'urban boundary'). Negative values were measured as the distance inside the urban matrix from the urban boundary; positive values represented the distance into natural areas.

To control for the relative influences of natural and anthropogenic landscape features on caracal habitat selection, we tested the influence of natural features including topography (slope, elevation), distance from freshwater (freshwater) and coastline (coast), and whether individuals were located in sand dune fields (dunes). We used three different measures of vegetation: i) cover (cover; binary), ii) NDVI (continuous), and iii) habitat burn intensity (burn ratio, normalized burn ratio 2 [NBR2], continuous). Vegetative cover information was extracted from the 2018 South African National Landcover dataset (Department of Environmental Affairs, www.sanbi.org) which described 72 vegetation classes using Landsat Spectral Indices 8 imagery (usgs.gov). Among these 72 vegetation classes, we characterized whether each class offered caracals: i) low cover (e.g., bare ground, beaches, manicured grass lawns), or ii) high cover (e.g., intact fynbos, well-vegetated ornamental urban gardens, vineyard vines). We also tested the interaction between cover and the distance from the urban boundary (cover x urban).

We included an indication of burn intensity because the landscape is fire prone. The NBR2 provides a useful metric of habitat burn intensity and post-fire recovery in Mediterranean ecosystems.⁷⁷ Because of frequent wildfires, we attempted to sample NDVI and the burn ratio covariates within a two-week period of each GPS location (matching the frequency of Landsat Spectral 8 updates). However, daily cloud cover frequently interfered with the satellite imagery and consequently confounded our ability to evaluate all locations within our preferred two-week interval. Therefore, where NDVI and NBR2 information was unavailable for a particular time point and location within an individual stratum (the collection of used and available points used for SSFs, see 'Step selection functions' below for more information), we substituted extraction for all locations within that stratum to the next closest time point that vegetation information was available for that location that was seasonally consistent (maximum 94 days). The median time difference between location date and vegetation index date was seven days for 3-hour fix intervals and six days for 20-min fix intervals.

Anthropogenic features included pine plantations (pine), eucalyptus stands (eucalyptus), vineyards (vineyards), and distance from arterial roads (roads, high traffic primary and secondary arterial roads where vehicle speeds > 55 kmph). Each categorical variable was converted to indicator covariates (vineyard, eucalyptus, pine, dunes, cover).

All covariates were standardized (across all individuals in a single dataset) to have a mean = 0 and a standard deviation = 2.⁷⁸ However, for the urban-dominated subregion caracals, instead of centering the urban

covariate, we simply standardized by two standard deviations because the urban distribution for available locations was disproportionately skewed towards negative values. Importantly, this method of standardizing urban did not change the selection coefficients or standard errors that resulted from urban-dominated subregion models; rather this standardization approach aided our ability to create representative plots of the relative probability of selection for the distance from the urban boundary (e.g., [Figure 2](#)).

We calculated variance inflation factors (VIF) to ensure that no two covariates were strongly colinear (VIF <3.0).⁷⁹ In the wildland-dominated region, distance from roads and the distance from the urban boundary were highly colinear (VIF >20), although they were not colinear in the urban-dominated subregion. Thus, for wildland-dominated region, we used only the distance from the urban boundary in model-fitting.

Further details for covariates are reported in [Tables S4](#) and [S5](#).

QUANTIFICATION AND STATISTICAL ANALYSIS

Step selection functions

We analyzed habitat selection using step-selection functions which assess habitat selection while animals are moving across the landscape (SSFs).⁸⁰ To ensure we used only movement relocations, we removed locations associated with feeding and resting sites (where animals are stationary and not making continuous habitat selection decisions). We filtered consecutive GPS-locations to have ≥ 50 -meter step lengths because, for both fix intervals, a 50-meter step length was the validated criteria for detecting caracal foraging and resting sites in our study area⁴³ and follows Hertel et al.⁴⁴

We assessed both fine-scale (20-min) and coarse-scale (3-hr) habitat selection because habitat selection is a hierarchical process and step selection analyses are sensitive to both the spatial and temporal scale at which available habitat is defined.^{23,80,81} Analyses at two different scales can provide unique insights into differing factors influencing movement on the landscape.^{39,40,80} Indeed, it has been recommended that analyzing movement over multiple spatial scales yields models more representative of animal movement-making decisions.³⁹ At fine scales, movement choices reflect options within several hundred meters^{7,80} and thus can elucidate landscape features that connect habitats⁸² and inform conservation planning.^{37,83} In contrast, using intermediate fix intervals (e.g., 3-hour) for habitat selection analyses best captures the response to risky anthropogenic landscape features relative to natural landscape features.^{7,40}

We performed SSFs on both 3-hour and 20-min interval data separately using a 1:20 match-case control empirical design. Strata were created where each individual's end 'used' location (t) was paired with 20 'available' locations.⁸⁴ 'Available' locations were created using random vectors originating from the location immediately preceding 'used' location t (i.e., location $t-1$). Random vectors were drawn based on the empirical distribution of turn angles and step lengths between consecutive locations derived from data on all individuals that were the same sex and age group as the focal individual but excluding the focal individual to avoid circularity.⁸⁴

For both fix intervals, three resource-independent movement parameters (step length, log-transformed step length, and directional persistence) were calculated for all steps within each stratum to control for inherent biases in animal movement that influence habitat use.^{7,85-87} Step length (calculated between t and $t-1$) and log-transformed step length control for the habitat selection biases arising from the ability of individuals to travel to available locations. Directional persistence controlled for the inherent tendency of individuals to move in a constant direction and was calculated between t , $t-1$, and $t-2$ ^{7,86,87} as ([Equation 1](#)):

$$\cos(\theta_t - \theta_{t-1}) \quad (\text{Equation 1})$$

where θ_t is the absolute (angle relative to North) of the vector resulting in the current step t , and θ_{t-1} is the absolute angle of the preceding vector resulting in step $t-1$. For the fine scale 20-min interval data subset, we additionally calculated terms to control for potential tendency for movement along the same topographical gradient. Elevation persistence and slope persistence were calculated as the difference in elevation or slope between consecutive locations (t and $t-1$). We tested the performance of each term in fine-scale habitat selection models and found that controlling for slope persistence substantially improved model performance.

To assess whether habitat selection varied with differing degrees of exposure to human activities, we divided our data into diel period based on local sunset and sunrise times. Caracals, as with other carnivores,^{7,22,37,63} may perceive less risk from humans at night when human activity is lower, potentially resulting in differing habitat selection trends across diel periods.

We estimated selection (β) coefficients using the *coxph* function in the *survival* package⁸⁸ for R statistics software.⁸⁹ To account for autocorrelation we calculated robust standard errors for selection coefficients using generalized estimating equations (GEE)^{90,91} by specifying intra-group ('cluster') correlation.⁹¹ GEEs are only appropriate for datasets in which individual variation is low. Thus, we first calculated the slope of individual-based random effects using the *coxme* function in the *survival* package.⁸⁸ We detected little variation across individual subgroups (urban adult variance = 0.001, SD = 0.036, subadult variance = 0.0002, SD = 0.014, wildland adult variance = 0.0006, SD = 0.024), indicating that our downstream model results represent generalized trends across individuals.

To specify clusters, we used a destructive sampling approach⁹¹ which required that we first estimate the time lag past which temporal autocorrelation between successive caracal locations is no longer significant ($\alpha = 0.05$). We fit an intercept-only mixed-effects model⁸⁵ and plotted the autocorrelation function of the model (Figure S5). Autocorrelation decayed after a lag of 54 h. We collected data during 31 collaring events from 25 unique individuals and it is recommended to use a minimum of 20 clusters per analysis group.⁹¹ Thus, we destructively sampled our data (by removing 54 hours) of data between successive clusters resulting in 1–6 clusters per collaring event (urban-dominated subregion: 31 adult and 27 subadult male clusters, wildland-dominated subregion: 24 adult clusters; range: 13–92 days/cluster). Because 20-min data collection occurred every 9th–10th day, we assigned clusters according to the individual ID and consecutive period of collection ($n = 277$ clusters).

To assess model performance, we compared quasi-likelihood under independence criterion (QIC) scores of each model and selected that with the lowest QIC.⁹⁰ We fit models consisting of every combination of terms and compared the QIC of all resulting models. In cases where >1 best-fit model was identified with a Δ QIC <2 , we selected the most parsimonious model. In cases where there were ≥ 2 models with the same number of terms and Δ QIC <2 , we report that with the lowest QIC in figures and results, and report all best-fit models in the Supplemental Tables. We report the selection coefficient β , and 95% confidence intervals calculated using the robust standard errors (Tables S6–S14).

Testing model complexity: Subgroups

We identified three putative subgroups based on sampling subregion and demographics (urban adults, urban subadults, wildland adults). We predicted selection differences between urban adults and subadults because subadult carnivores are previously documented to utilize more human land uses compared with adults in human-dominated landscapes.^{62–64} We also predicted that selection for human land use covariates would differ between caracals in the wildland and urban-dominated subregions because exposure to anthropogenic activities may increase the caracal tolerance to human activity.^{46,51} We expected that caracals in different subregions would experience differential tolerance to human activities because: 1) the median distance of individuals captured in the urban subregion from the urban boundary was 335.3 m for adults and 71.4 m for subadults, while wildland adult median distance from the urban boundary was 8049.9 m (see results, Table S1); and 2) individuals captured in the wildland-dominated subregion were not recorded in the urban-dominated subregion, while only three adult males (Figure S1) captured in the urban-dominated subregion utilized only the northern edge of the wildland-dominated subregion abutting urban development (Figure 1B). While situated in the wildland-dominated subregion, the median distance of the two adult urban male locations was 85.9 m (mean = 217.4, SD = 383.5) from the urban boundary, indicating that most of their locations, while situated in the wildland-dominated region, were <100 m from the urban boundary.

We used a model-selection process to test the validity of these subgroupings. To approach the model selection, we made hypotheses (Table S2) and predictions about differing selection trends for select covariates that included distances from the urban boundary, freshwater, and coast, and vineyard. We ran two

models where we calculated the relative probability of selection w for landscape covariate x using coefficients β via the standard exponential model²²(Equation 2):

$$w(x) = \exp(\beta_1 x_1 + \dots \beta_n x_n) \quad (\text{Equation 2})$$

The first model was a global model with all individuals and all covariates (without a subgroup interaction term; see list of all covariates in [Tables S4](#) and [S5](#)). In contrast, the second global model included all individuals and all covariates, but with a subgroup interaction term on distances from the urban boundary, freshwater, and coast, and vineyard (see [Table S2](#) for hypotheses surrounding each covariate interaction term). We found the subgroup models were best-supported, and thus for all downstream modeling, we modeled each subgroup separately.

Testing model complexity: Diel period

We expected potential varying diel period habitat selection for each group.^{7,37} Therefore, we used a similar approach as described above to determine whether running separate models according to diel period was warranted for each subgroup's datasets. We performed the model selection process for each subgroup individually and individually for each subgroups' 20-min and 3-hr datasets. Thus, for each subgroup's datasets, we ran two models: 1) a model that included all covariates, and 2) a model that included all covariates but with a diel period interaction on select covariates that included distances from the urban boundary and roads, and vineyards, NDVI, and cover (see hypotheses concerning these covariate interactions in [Table S3](#)).

Modeling approach for each subgroup

A primary objective was to evaluate the relationship between proximity to the urban matrix and habitat selection. Thus, we built our SSF modeling framework around the urban covariate, which captures additional impacts of urban areas such as heightened human activity (e.g., pedestrian and vehicle traffic). For each life history and regional subgroup, we used a model selection procedure within the SSF framework to evaluate the functional form of the relationship between proximity to the urban matrix and habitat selection. We hypothesized that different subgroups would not only show differential selection for urban areas, but also that the functional form of that selection may differ. We therefore tested whether the relative probability of selection for the distance from the urban boundary was best described by a linear, quadratic-transformed, log-transformed, or a segmented linear regression approach. Using the model selection process, we determined that a model with a quadratic-transformed distance from the urban boundary covariate performed best for wildland caracals. The segmented linear regression performed best for both caracal subgroups in the urban-dominated subregion.

The segmented linear regression used for urban caracals split the distance from the urban boundary into two (or three) covariates with different slopes on either side of a breakpoint.^{41,42} The value of the segmented approach is that it identifies breakpoints in selection response which in the context of our study, provides valuable information on how animals perceive the urban edge and the influence of human activity beyond the immediate footprint of urban development. We tested candidate breakpoint values at one-meter intervals ranging between the minimum and maximum distances from the urban boundary. We selected the optimal breakpoint using a grid search approach by comparing QIC scores of candidate segmented models ([Figure S6](#)). At the scale of one-meter intervals, multiple well-supported breakpoints were identified ($\Delta\text{QIC} < 2$) but the difference in distances among the well-supported breakpoints was trivial ($< 10\text{m}$). Thus, we averaged well-supported candidate breakpoint values to obtain a single value. Next, for urban caracals, we split their data according to diel period when warranted and performed the same grid search.

For caracals in the urban-dominated subregion, we next considered that the relative probability of selecting certain landscape features was dependent on where individuals encountered this feature (urban interface vs. natural area). Candidate covariates included pine burn ratio, cover, elevation, and distance from freshwater and coast ('split' covariates). We predicted the potential for split pine, burn ratio, and cover because these features are indicative of available vegetative concealment that may be more strongly selected (i.e., cover) or avoided (i.e., pine, burn ratio) within the urban interface where concealment would mitigate detection risk. Within the urban interface, we predicted that the relative importance of elevation would diminish substantially. Freshwater within the urban interface may be linked with increased opportunity to find urban-associated prey.^{43,46} We predicted that caracals would avoid coastline closely bordered

by residential or commercial development. We did not consider a split potential for NDVI, dunes, vineyard, eucalyptus, or roads, because with rare exception, roads, eucalyptus stands, and vineyards were primarily located within, in proximity to, or adjacent to the urban interface. We could not think of a biological reason why selection for dunes or NDVI would differ with proximity to the urban boundary.

To incorporate split covariates in urban-dominated subregion models, we created an indicator variable l , where $l = 1$ when an individual was within natural areas, and $l = 0$ when individuals were within the urban interface. This allowed us to model parameters α_n representing the selection estimate when individuals were within the urban interface, and $\alpha_n + \beta_n$ representing the selection estimate when individuals were within natural areas. For caracals in the urban-dominated subregion, we calculated the relative probability of selection w for landscape covariates x as follows (Equation 3):

$$w(x) = \exp(\beta_1 x_1 + (\alpha_2 + \beta_2 l) x_2 \dots \beta_n x_n + (\alpha_n + \beta_n l) x_n) \quad (\text{Equation 3})$$

In contrast, for wildland-dominated subregion caracals, we calculated the relative probability of selection w for landscape covariate x using coefficients β via the standard exponential model⁹² described above (Equation 2).

For each of the three caracal subgroups, diel period, and fix interval-specific data subset, we modeled the relative probability of a caracal selecting a particular location as a function of landscape covariates. For caracals in the urban-dominated subregion, we tested an additional interaction urban \times elevation to assess whether caracals select for proximity to urban areas because urban areas are generally at lower elevations in this region.

Cross validation

To evaluate the robustness of all top (best-fit) models we used 5-fold cross validation following.^{37,93} We built case-control SSFs using covariates retained in the top model fit to 80% of randomly selected strata. We used this model to predict $w(x)$ scores for used and available locations from the 20% of withheld strata. For each stratum comprising used ($n = 1$) and available ($n = 20$) movement locations, we calculated the $w(x)$ score which was then used to assign each location a rank of 1–21 (lowest to highest). We next used Spearman rank correlations to compare the frequency with which the withheld used locations received each of the 21 possible rankings. We iterated this process 100 times for each top model. We report the mean and standard deviation values of Spearman correlation coefficients (r_s) across all iterations (Table 1). Models with strong predictive power exhibit mean r_s values close to 1. We also report mean r_s values expected under random habitat selection (i.e., if models have no predictive power).⁹³

Activity

We assessed relative activity patterns to test whether caracals in the urban-dominated region changed activity patterns mitigate risk of detection in areas with high human activity.²⁹ We additionally assessed whether subadults in the urban-dominated region alter activity patterns to avoid interactions with adults. We defined risk as a function of whether: i) individuals utilized the urban-dominated subregion (as opposed to the low-risk wildland-dominated subregion), and ii) individuals were of the subadult male demographic. For risk scenario (i), we compared the activity data of four adults from the wildland-dominated subregion, and 12 adults from the urban-dominated region (for which we had 20-min data). For risk scenario (ii), we compared the activity data of 12 adults to the data of six subadult males in the urban-dominated region. We assessed effect size using log risk ratios (“RR”)²⁹ calculated from 20-min fix interval data that we subsampled to one-hour intervals to reduce autocorrelation.^{44,49} RR is a ratio of the mean nocturnality at sites of high human disturbance to the mean nocturnality at sites of low human disturbance. We defined each caracal observation as “active” if individuals moved ≥ 50 meters in the 20-minutes preceding each one-hour observation (otherwise, the time point was classified as “inactive”). This selected movement threshold is consistent with the threshold described above to isolate movement locations from the larger GPS dataset, and follows the approach previously described for classifying active periods based on GPS-movement data.⁴⁴

Our dataset was skewed towards more daytime than nighttime locations because 20-min data were collected for an interval of 36-hours beginning at 02:00. We thus used bootstrap resampling to control for individual effects and maintain even sampling among individuals. We sampled without replacement 24 daytime observations and 24 nighttime observations for each caracal for 1000 replications. For each

replicate, we calculated the log proportion of active observations that occurred during the night for populations in both the urban and wildland-dominated subregions. We report a weighted mean log RR with weights assigned according to the inverse variance of each replicate, the proportion of replicates for which nocturnality was greater in the population in the urban-dominated subregion, and the 95% bootstrap confidence interval based on the 25th and 95th greatest RRs. To interpret our results of these analyses, we back-transformed mean effect sizes and converted to unlogged risk ratios to assess percent shift towards nocturnality in areas of high risk. We assessed significance using confidence intervals— those that overlapped zero were not significant.