


Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge

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Abstract

As natural habitat is progressively transformed, effective wildlife conservation relies on understanding the phenotypic traits that allow select species to persist outside of protected areas. Through behavioural flexibility such species may trade off abundant resources with risks, both real and perceived. As highly adaptable meso-carnivores, caracals (*Caracal caracal*) provide an opportunity to examine development of successful foraging strategies in high-risk developed areas. Here we investigated caracal resource selection of both anthropogenic and environmental factors relative to availability at varying levels of urbanization in and around the city of Cape Town, South Africa, using GPS cluster-located feeding events ($n = 326$ prey remains, $n = 384$ scat). We also examined spatial and temporal risk mitigation strategies by assessing behaviours at feeding clusters. We find that, within home ranges, caracals living in the urban-dominated region ($n = 14$; 548 feeding events) select for the urban edge, while caracals in the wildland-dominated region ($n = 3$; 162 feeding events) avoid it. Adults selected more strongly for foraging at the urban edge than juveniles and may competitively exclude them from resources. By including back-traced scat feeding event locations, we were able to improve model resolution. We argue that caracals foraging on the edge of a large metropole mitigate risk of detection by remaining cryptic, prolonging handling time, and maintaining high feeding site fidelity where cover was available. Along with the strong functional response to the urban edge, this strategy suggests that carnivores are being drawn into, and stay longer in, areas with potentially increased prey availability despite higher risk. While behavioural plasticity clearly enables carnivore coexistence with humans in urban ecosystems, it can also be maladaptive if it reduces fitness and leads the population into an ecological trap. We provide mitigative recommendations to promote the conservation of this predator in a spatially isolated and rapidly urbanizing landscape.

Introduction

In today's rapidly expanding cities, wildlife winners and losers are determined by their behavioural responses to the interplay of risk and reward within and adjacent to urban areas. Cities are highly challenging environments; they are noisy (Shannon *et al.*, 2016), polluted (Serieys *et al.*, 2015), fragmented by roads and other barriers (Crooks, 2002), and support novel diseases (Bradley & Altizer, 2007). Despite these challenges many urban areas sustain permanent wildlife communities (Shochat *et al.*, 2006). As urban ecosystems expand, behaviourally flexible species must balance the

possible advantage of increased foraging opportunities while developing behavioural strategies to mitigate anthropogenic risks (Lowry *et al.*, 2013; Nattrass & Lusseau, 2016; Fleming & Bateman, 2018).

Urban-adapted species respond behaviourally to both direct risks, such as persecution due to human-wildlife conflict (Inskip & Zimmermann, 2009), poaching (Kaltenborn & Brainerd, 2016) and vehicle collisions (Seiler & Helldin, 2006; Hill *et al.*, 2020), and to perceived risks. For species that persist in human-dominated landscapes, fear of the 'human apex predator' may elicit responses (Darimont *et al.*, 2015; Smith *et al.*, 2017) that can exceed that of even

natural top predators (Clinchy *et al.*, 2016). In doing so, fear responses, even to nonlethal activities, can cause a shift in behaviours to reduce exposure to human activities, with individuals seeking temporal or spatial refugia (Gaynor *et al.*, 2018, 2020; Smith *et al.*, 2019; Nickel *et al.*, 2020). For example, brown bears (*Ursus arctos*) avoid disturbed areas, especially during the day when human activity is high (Ordiz *et al.*, 2014), while African lions (*Panthera leo*) hunt closer to human structures only at night (Suraci *et al.*, 2019b), and bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) increase their nocturnality to avoid human activity (Murray & St. Clair, 2015; Wang *et al.* 2015). Even the recorded sound of human voices can lead to shifts in behaviour across trophic levels, causing carnivores to behave more cautiously and elusively (Suraci *et al.*, 2019a). Numerous species also reduce movement rates (Tucker *et al.*, 2018; Nickel *et al.*, 2021) or increase vigilance (Benítez-López, 2018) in human-dominated landscapes.

Avoidance strategies that mitigate direct and perceived risks can be costly, particularly if animals shift their behaviour while foraging (McNamara & Houston, 1990; Houston *et al.*, 1993). To avoid spatial overlap with human activity, large carnivores will abandon kills altogether, thereby decreasing prey consumption time and reducing net caloric gain (Kerley *et al.*, 2002; Smith *et al.*, 2017). Temporal avoidance may also require increased bursts of rapid movement and less resting (Oriol-Cotterill *et al.*, 2015; Fehlmann *et al.*, 2017). Together these behavioural changes may have adverse implications for foraging activity, reproduction, and animal condition in species living in proximity to humans (Ditchkoff *et al.*, 2006; Strasser & Heath, 2013).

As urbanization intensifies globally (Seto *et al.*, 2012), understanding the behavioural strategies of species that persist in these landscapes is important for conserving urban biodiversity (Sol *et al.*, 2013). Relative adaptability to human disturbance varies widely across species and populations. At the species level, habitat and dietary generalists demonstrate greater success in persisting in human-modified landscapes (Bateman & Fleming, 2012). Across populations, differences may depend on the level of exposure to disturbance (Benson *et al.*, 2016), while within populations individual personalities and demographic factors may play important roles (Wat *et al.*, 2020). For example, female bobcats are more sensitive to urbanisation than males, while subordinate juveniles without defined home ranges are pushed into marginal habitats by adults (Riley *et al.*, 2003). Where populations inhabit areas with high heterogeneity in landscape disturbance, individuals may adjust their resource selection as a function of changes in local resource availability (Myerud & Ims, 1998). This 'functional response' can reveal both associated benefits and risks of a given habitat, and provide insight into the ecological effects of landscape change on wildlife (Matthiopoulos *et al.*, 2011).

In this study, we explore behaviourally explicit resource selection by caracals (*Caracal caracal*) occurring within a national park surrounded by a mosaic of land-uses in the city of Cape Town, South Africa. In this rapidly urbanizing landscape (Turok & Borel-Saladin, 2014), we test whether individuals adjust their foraging behaviour in response to

modified landscape cover, thereby accommodating urban development as it becomes more prevalent in their foraging range. Caracals are elusive, medium-sized felids with a diverse prey base across their geographic range (Avenant & Nel, 2002; Drouilly *et al.*, 2019). In Cape Town, they are the largest remaining indigenous predator and hunt largely within 200 m of urban areas, where human-associated prey (i.e., exotic and synanthropic species) forms almost half of consumed prey biomass (Leighton *et al.*, 2020), suggesting that caracals may selectively forage at the resource-rich urban edge, despite associated risks (Serieys *et al.*, 2019) and high mortality. The primary lethal threats to caracals in this system include vehicle collisions, poaching and lethal management, and domestic dog attacks (>82% of mortalities, $n = 90$; Serieys *et al.*, unpubl. data), demonstrating that risk associated with human activities is real. Here we first use resource selection models to determine the effect of anthropogenic and natural landscape features on caracal foraging behaviour relative to their local established environments (primarily urban or wildland areas). We then test whether caracals mitigate risk of detection when foraging in urban areas by exploiting temporal or spatial refugia, including adjusting timing of foraging and prey handling. We discuss our findings within the framework of how flexible behavioural strategies may influence species persistence in ostensibly sub-optimal urban habitats and the possible consequences of foraging at the urban edge.

Materials and methods

Study area

We investigated foraging habitat selection across the Cape Peninsula (hereafter 'Peninsula'), a fragmented mosaic of predominantly wildland habitat which together forms the Table Mountain National Park (TMNP; 320 km²). Caracal density estimates vary widely across South Africa, but the likely Peninsula population size is 48–64 caracals at any one time (Avenant *et al.*, 2016). The Peninsula is geographically isolated by 2445 km² of dense urban development making up the city of Cape Town (Fig. 1a). TMNP receives on average 4.2 million visitors annually (sanparks.org), and recreational activities are permitted (e.g., walking domestic dogs and hiking) but with restrictions on such activities in the southern reserve section. The TMNP borders shift from predominantly urban in the north (Fig. 1a; 187 km² available wildlife habitat, 78% bordered by urban development) to more wildland habitat in the south (133 km² available wildlife habitat, 46% bordered by urban development). After exploring resource selection at the population level, we divided the study area (Table 1): urban-dominated in the north (hereafter 'urban region') versus wildland-dominated in the south (hereafter 'wildland region').

Protected areas are predominantly endangered Peninsula Sandstone fynbos, a dense shrubland providing medium-high cover. Land-use includes residential, light industrial, cultivated (pine plantations and commercial vineyards; Fig. 1a) and altered-open areas (e.g., golf courses and greenbelts).

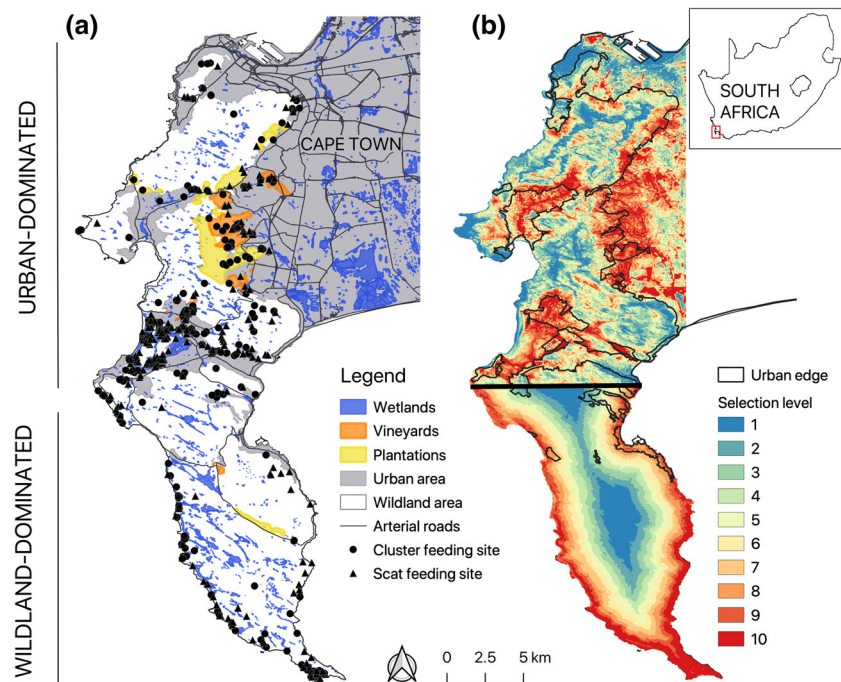


Figure 1 Cape Peninsula study area showing (a) feeding clusters (circles, $n = 326$) and back-traced scat feeding events (triangles, $n = 384$), and (b) selection surface for urban-dominated and wildland-dominated regions with estimates based on the land-use integrated-diet (scaled) RSF models for each region. Higher values indicate stronger positive selection.

Table 1 Summary of collared caracals ($n = 17$) on the Cape Peninsula, South Africa (*mean* \pm *SD*)

Region	Sex	Age	n	Days tracked	Home range area (km^2)	Proportion urban area	GPS cluster remains ($n = 326$)	Scat prey remains ($n = 377$)
Urban-dominated	Female	Adult	3	185.67 ± 96.67	14.04 ± 4.04	0.11 ± 0.05	18.00 ± 10.39	23.33 ± 17.90
		Juvenile	1	185.00	7.57	0.03	15.00	38.00
	Male	Adult	5	201.80 ± 68.29	72.89 ± 24.34	0.20 ± 0.09	19.40 ± 14.79	22.40 ± 18.72
		Juvenile	4	146.67 ± 29.47	54.43 ± 36.59	0.27 ± 0.02	17.75 ± 1.12	17.75 ± 13.20
Wildland-dominated	Female	Adult	2	138.75 ± 155.56	32.06 ± 22.68	0.01 ± 0.01	24.00 ± 28.28	16.00 ± 22.63
	Male	Adult	1	301.00	111.00	0.01	34.00	47.00
Relocated	Female	Adult	1	131.00	7.85	0.02	7.00	7.00

Sampling

We used standard cage-trapping techniques to capture and GPS-collar caracals between 2014 and 2016 (detailed capture and collaring method described in Serieys *et al.*, 2019). Individuals were fitted with GPS collars (FollowitTM Tellus, Lindesberg, Sweden) with a release mechanism and rot-off cotton spacer to ensure eventual drop-off. Collars recorded at two fix intervals: every 3 h, and on every 9–10th day at 20-min intervals for 24–36 h, for a maximum of 6 months.

Foraging datasets

Peninsula caracal diet was previously assessed by identifying and quantifying prey remains: (1) at GPS-clusters (hereafter

‘feeding clusters’); (2) in scat found at GPS-clusters; and (3) the integration of the clusters and scat to account for ‘missed’ feeding events (Leighton *et al.*, 2020). Feeding-cluster remains were biased towards birds (as discarded feathers are easy to detect), whereas scat prey remains were typically small species (<0.11 kg) that a caracal could consume over a duration too short for a GPS-cluster to form. For complete details and validation of the approach, see Leighton *et al.* (2020) and S1.

Foraging-explicit resource selection functions (RSFs) assume precise knowledge of foraging locations. However, because feeding clusters and scat-based analyses were biased, we present a third approach that incorporated both small and larger prey, using gut-transit times to ‘back-trace’ likely foraging locations (‘integrated-diet’ approach; see S1 for

details). For each scat likely representing a missed feeding event, we leveraged the GPS-collar data against possible gut-transit times to estimate the location closest in time to the probable feeding event time. These back-traced locations were used in both scat-only and integrated-diet RSFs (see Table S3). We assessed the sensitivity of our approach by examining variable gut transit times including (1) minimum digestion time (0.5 days); (2) maximum digestion time (4 days); and (3) a scaled measure that accounted for the mass of the prey item, following estimates from the similar-sized jungle cat (*Felis chaus*; Chakrabarti *et al.*, 2016). See S1 for details of model comparisons for this approach. This resulted in seven foraging datasets (Table S3): feeding clusters, back-traced scat feeding events (for each digestion time) and integrated-diet feeding events (for each digestion time).

Behaviour at feeding clusters in a landscape of fear

We explored whether caracals increase nocturnality and reduce handling time and feeding site fidelity to mitigate risk of human detection. Specifically, we examined: (1) temporal partitioning (diel period based on local sunset and sunrise) of cluster initiation; (2) handling time (cluster duration, hours); (3) average and maximum (i.e., cluster radius) distance moved from the centroid; and (4) cluster fidelity, calculated as the inverse of the number fixes away from the cluster over the total number of expected fixes given the cluster duration (Table 2). Differences between diel periods (day and night) and region (urban or wildland) were tested using linear regression for continuous dependent variables (distance and time) and quasibinomial GLMs for proportional dependent variables (fidelity and *in situ* degree of cover; S1).

Landscape predictor variables

To control for both natural and anthropogenic influences on caracal habitat selection, we incorporated a suite of predictor variables in our models: animal age and sex, slope, NDVI, land use (urban, altered-open, vineyards, plantations, and wildland), vegetation cover (high and low), and distance to urban edge, wetlands, and coast (see Table S2). We assessed autocorrelation and retained only independent variables (Pearson correlation $|r| \leq 0.53$). Further details about predictor variables and collinearity can be found in S1 and Table S2.

Resource selection functions

Resource selection functions (RSFs) evaluate habitat selection through spatially explicit, predictive models that link

landscape features and the probability of animal presence (Manly *et al.*, 2002). We evaluated third-order selection (Johnson, 1980), by comparing used and available resources within estimated home ranges. We assessed caracal foraging-explicit RSFs using binomial generalized linear mixed models (GLMMs, where the binary response was observed location = 1 and available locations = 0) with 'individual' (i.e., caracal ID) as the random effect (Gillies *et al.*, 2006) using *glmmTMB* (Brooks *et al.*, 2017). We included a random effect term to handle the model variance between individuals, which may be especially problematic for the wildland-dominated region where sampling was limited to three caracals (but see S1 for methods on RSFs testing model sensitivity to additional individuals). We estimated resource availability by sampling 20 random points within home range for each observed GPS location to obtain a 1:20 ratio of used to available locations. Further details on methods for generating 95% *t*-LoCoH home ranges (Lyons *et al.* 2013) can be found in S1, and results are presented in Table 1, S4, and Fig. S5. We extracted landscape variables (Table S2) for each available location and for each real observation classified into (1) feeding clusters, (2) back-traced scat feeding events, and (3) integrated-diet feeding events. We ran separate models for urban and wildland-dominated regions for each of the seven foraging datasets (see Table S3 for the structure of the full models). We used no-intercept GLMMs with weighted available points (Muff *et al.*, 2020) and scaled and centred covariates at the Peninsula level to facilitate comparison between model estimates for each region.

We selected the top model using AICc (Burnham & Anderson, 2002) by fitting models with all predictor variable permutations (Table S3), and obtained values for the probability of selection w for a vector of n predictor variables ($x = x_1, \dots, x_n$) by substituting the parameter estimates β into the exponential model and normalizing:

$$w(x) = \exp(\beta_1 x_1 + \dots + \beta_n x_n) / \max(\exp(\beta_1 x_1 + \dots + \beta_n x_n))$$

We provide parameter estimates and 95% confidence intervals (from SE) on the logit scale, and plot $w(x)$ values.

Functional responses to the urban edge

Functional responses can reveal trade-offs between mortality risk and foraging success. To investigate this in caracal, we tested whether the distance of foraging sites to the urban edge varies as a function of its availability. We calculated a resource-selection proportion per individual by dividing the mean distance to the urban edge at used locations by the sum of the mean used and available locations within home range (i.e., mean used distance / [mean used + mean available]) following

Table 2 Behaviour at caracal GPS-clusters with prey remains on the Cape Peninsula, South Africa (*mean* \pm *SD*)

Region	Diel period	<i>n</i>	Duration (h)	Fidelity (%)	Radius (m)	Distance moved from centroid (m)
Urban-dominated	Day	152	22.87 \pm 23.51	87.95 \pm 2.72	61.37 \pm 36.79	28.71 \pm 13.31
	Night	85	24.40 \pm 26.61	85.71 \pm 4.01	59.99 \pm 32.71	30.17 \pm 13.59
Wildland-dominated	Day	23	12.82 \pm 11.85	89.84 \pm 6.30	52.87 \pm 39.94	24.39 \pm 13.63
	Night	59	24.64 \pm 21.93	59.11 \pm 6.40	48.32 \pm 29.27	30.88 \pm 12.03

Benson *et al.* (2016). We explored potential functional responses by modelling these resource-selection proportions (response variable) as a function of distance-based resource availability of the same resource (predictor variable, i.e., mean distance to the urban edge across home ranges) using quasibinomial GLMs which are appropriate for conducting regression on a proportional response variable.

Results

We captured 29 and GPS-collared 26 caracals between November 2014 and September 2016. We assessed resource selection for 17 individuals (≥ 1 month of movement data and ≥ 2 GPS cluster prey remains; $n_{\text{urban}} = 14$, $n_{\text{wildland}} = 3$; Table 1). Individuals were monitored for a mean of 154 ± 96.7 SD days (Table 1). One adult female was relocated by the City of Cape Town from the wildland to the urban region (Table 1).

Foraging site sampling

In total, we investigated 677 GPS-clusters and recorded 326 prey items at 241 feeding clusters. We analysed a total of 654 scats containing 913 prey items (49.0% collected at clusters). Scats contained prey (mean = 0.72 kg) on average less than half the size of feeding cluster prey (mean = 1.54 kg). We detected 384 missed feeding events that represented 54.0% of foraging events modelled using integrated-diet RSFs (total $n = 710$). Logistical constraints including access to sites and permit restrictions resulted in more feeding cluster events (74.8%, $n = 244$; mean = 17.43 feeding clusters/individual) being sampled in the northern urban region, although more feeding events were recorded per individual in the wildland region (25.2%, $n = 82$; mean = 27.33 feeding clusters/individual; Table 1). We present findings from the wildland-dominated region, but acknowledge this difference in sampling may affect the interpretation of these results (but see S4 for results on RSFs testing model sensitivity to additional individuals).

Most feeding cluster prey were medium-sized birds (mass = 0.86 ± 0.52 kg; S4). Despite similar abundance along the Peninsula coastline (Brooks & Ryan, 2020), Cape cormorants (*Phalacrocorax capensis*) comprised 37% of feeding cluster detections in caracals in the wildland region, while only representing 0.9% of feeding events in the urban region ($n = 5$, integrated-diet). Caracals in the wildland region consume less small prey (mean_{wildland} = 0.8 kg, mean_{urban} = 0.4 kg, $F_{1,708} = 12.22$, $P < 0.001$). The majority of scat prey items were small rodents (0.11 ± 0.08 kg). Vlei rats (*Otomys irroratus*) represented only 9% scat detections in the wildland region, while they represented 24% in urban region.

Foraging habitat selection

Overall, both natural and anthropogenic landscape features influenced foraging habitat selection. Gentler slopes and greener vegetation were selected (higher NDVI; Fig. 2).

Inter-individual variation

We found very low inter-individual variation in foraging habitat selection (Hertel *et al.*, 2020; variance of caracal ID random effect: urban-dominated < 0.01), even in the wildland-dominated region where we had limited individuals (variance < 0.001), which is consistent with Leighton *et al.* (2020). Due to low number of individuals in the wildland-dominated region, we tested model sensitivity to additional individuals using GPS cluster centroid locations and found coefficient estimates to be robust (i.e., the addition of two individuals did not change our findings, see S1 and S4 for details), suggesting our results are representative of the larger subpopulation. Despite individual-level behavioural consistency within regions, we found differences in resource selection between regions. This suggests our findings are driven by landscape differences, rather than individual behavioural variation.

Urban region

Consistent across diet datasets (Figs 1b and 3a), caracals select to feed close to the urban edge ($\beta = -3.1 \pm 0.46$; Fig. 2, note that negative distance values indicate selection for habitat closer to the feature). While the distance of caracal feeding events ranged from 0 to 2095 m (median_{urban} = 273 m), 35.58% of feeding events were within 200 m and 58.21% and were within 500 m. Selection for the urban edge

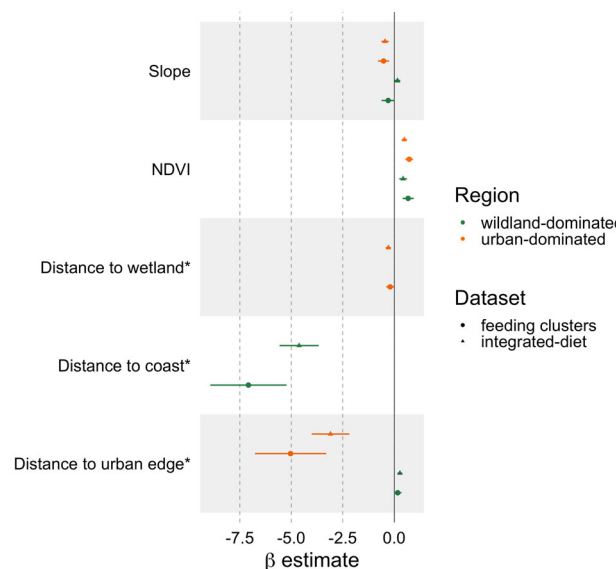


Figure 2 Continuous parameter estimates and 95% confidence intervals based on standard errors for RSFs (logit scale). *Feeding clusters* (circles) is the GPS cluster prey remains dataset; *Integrated-diet* (triangles) is the dataset with both cluster prey remains and scats. Estimates are shown for those parameters included in the top models (as determined by AICc) for the urban-dominated (orange) and wildland-dominated (green) regions. *Note that negative distance values indicate selection for habitat closer to the feature.

was stronger for adults than for juveniles ($\beta_{\text{adult}} = -4.76 \pm 2.94$; $\beta_{\text{juvenile}} = -28.02 \pm 3.36$).

Habitat selection differed across land-use types. Although selecting for the urban edge, caracals avoided foraging within the urban matrix itself (14.4% of feeding events; $\beta = -5.29 \pm 2.95$; Fig. 3b). Relative to availability in the landscape, caracals selected vineyards (3.5% of feeding events) and avoided plantations (2.7%), while wildland (76.1%) and altered-open (3.3%) areas were selected at similar levels (Fig. 3b). In vineyards, most feeding events (64%) were within greenbelts or bushy areas alongside the trellis vines. Caracals preferred high ($\beta = -5.33 \pm 2.95$; Tables S8 and S9) to low cover ($\beta = -2.06 \pm 2.96$; 88.5% high, 11.5% low). An interaction term revealed that high cover was selected closer to the urban edge, while low cover was selected further from it ($\beta = 7.24 \pm 0.67$; Fig. 3c; Tables S8 and S9).

Wildland region

Although limited to three individuals, we found caracals in this region avoided the urban edge ($\beta = 0.27 \pm 0.06$; Fig. 3a). Feeding events occurred between 106 and 15 451 m from the

urban edge (median_{wildland} = 10 804 m) and only 3.66% of feeding events were within 200m of the urban edge. Rather, caracals selectively foraged on coastline up to 15 km from urban areas (Fig. 1b and Fig. 2). Most feeding events (52.5%) were within 200 m of the coast, with a median of 180 m (mean = 299 m, range = 15–2870 m). Further, the overwhelming majority of caracal feeding locations were in intact, wildland areas (wildland = 97.5%, plantations = 1.23%, urban = 1.23%) with high cover (high = 74.7%, low = 25.3%). Overall, trends varied by sex with selection being significantly stronger for the male ($\beta = -16.31 \pm 0.54$) than females ($\beta = -16.75 \pm 0.55$; Tables S6 and S9). The male's stronger selection for the coast may explain the dominance of seabirds in diet (male = 64.8%, female = 20.2%) and a less diverse prey base ($n_{\text{male}} = 18$, $n_{\text{female}} = 24$ species), although this trend may be specific to this individual.

Comparisons among feeding cluster, scat, and integrated-diet models

Incorporating all potential prey (integrated-diet) resulted in a more robust (lower SE) understanding of foraging-explicit

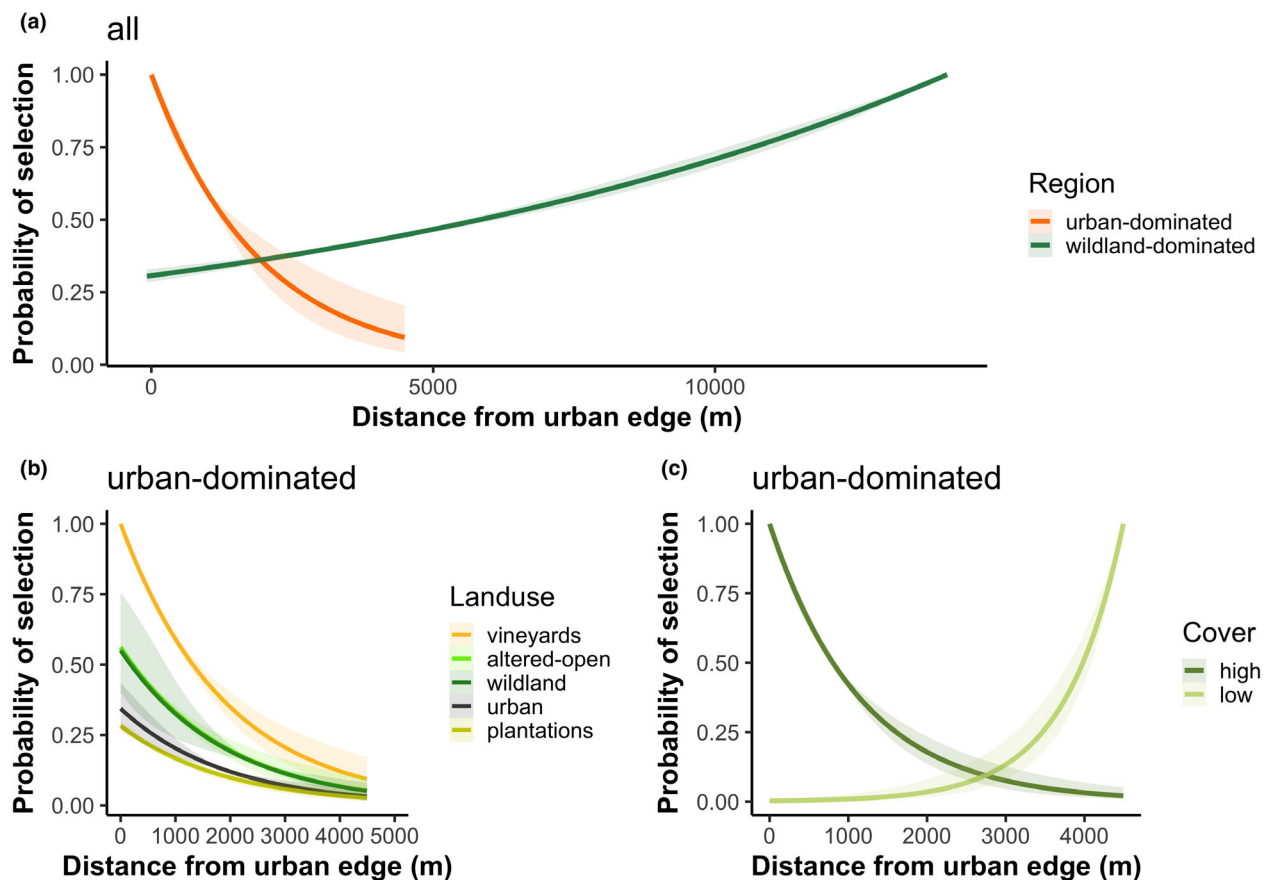


Figure 3 Probability of a caracal selecting habitat given distance to the urban edge based on RSFs, (a) caracals in both urban- and wildland-dominated regions and (b) urban-dominated region caracals for different land-uses, (c) at different levels of cover in the urban-dominated region for the scaled integrated-diet dataset (i.e., feeding events from both GPS cluster prey remains and scat, see *Methods*). The 95% confidence intervals are based on standard errors. Note that axes differ between plots.

habitat selection (Fig. 2) than when analysing feeding clusters or scat independently. Interestingly, we observed distinct trends in model optimisation when comparing region models.

For the urban region, feeding cluster and integrated-diet models were highly correlated ($r > 0.9$), with overwhelming similarity in direction and magnitude of coefficients. However, integrated-diet models did broaden resource selection estimates (i.e., moved estimates closer to zero, where zero indicates no selection). The exception was stronger selection for wetlands (more negative estimates, where negative distance values indicate selection for habitat closer to the feature; Tables S6 and S9). In the wildland region, where seabirds were the dominant prey, the integrated-diet approach added more unique prey species (particularly rodents and medium-sized mammals) and the distance to coast became less important (Fig. 2). Integrated-diet models also increased estimates of urban edge avoidance in caracals in the wildland region ($\beta = 0.27 \pm 0.06$).

We found inconsistencies between the three digestion time methods (minimum, maximum, and scaled; Tables S6 and S9), particularly for feeding events in the wildland region. For instance, the scaled method revealed a stronger preference for steeper slopes than the other foraging datasets ($\beta = -0.15 \pm 0.07$), while slope was dropped from the maximum digestion time model.

Functional responses to the urban edge

Caracals exhibit a strong positive functional response to the urban edge at foraging sites. The selection for the urban edge increases with proximity to developed areas within individual home ranges ($\beta = 0.0001$, $t = 2.3$, $P < 0.05$; Fig. 4a), but especially within the urban region ($\beta = 0.004$, $t = 5.7$, $P < 0.001$; Fig. 4b). The relocated female was a clear outlier to the urban group, suggesting that foraging behaviour is maintained.

Behavioural strategies to mitigate risk of detection

We examined a suite of cluster characteristics to determine if caracals in urban and wildland regions employ different tactics to mitigate detection risk when foraging at the urban edge.

Diel period

Unexpectedly, individuals in the urban region initiated the majority (63.1%) of feeding clusters during the day ($\chi^2_1 = 16.79$, $P < 0.001$, Table 2). When accounting for small prey feeding events (integrated-diet), the trend was stable (diurnal = 61.1%; nocturnal = 38.9%). By contrast, only 28.0% of caracal feeding clusters in the wildland region were initiated during the day, while 72.0% began at night ($\chi^2_1 = 15.81$, $P < 0.001$; Table 2). Unlike individuals in the urban region, when incorporating small prey, caracal kills in the wildland region were more evenly spread over diel periods (diurnal = 46.9%, nocturnal = 53.1%).

Distance to the urban edge

Diurnal feeding clusters were closer to the urban edge ($\text{mean}_{\text{diurnal}} = 240$ m, range = 0–2010 m; $\text{mean}_{\text{nocturnal}} = 333$ m, range = 0–2095 m; $F_{1,235} = 3.88$, $P = 0.05$) for caracals in the urban region. To compare between regions, we filtered points to <5 km from the urban edge (maximum distance in the urban region). By contrast, diurnal feeding clusters in the wildland region were further from the urban edge (mean = 3412 m, range = 1953–4580 m), with nocturnal kills being closer on average (mean = 2088 m, range = 106–4538 m), although the difference was only marginally significant ($F_{1,19} = 3.3$, $P = 0.08$).

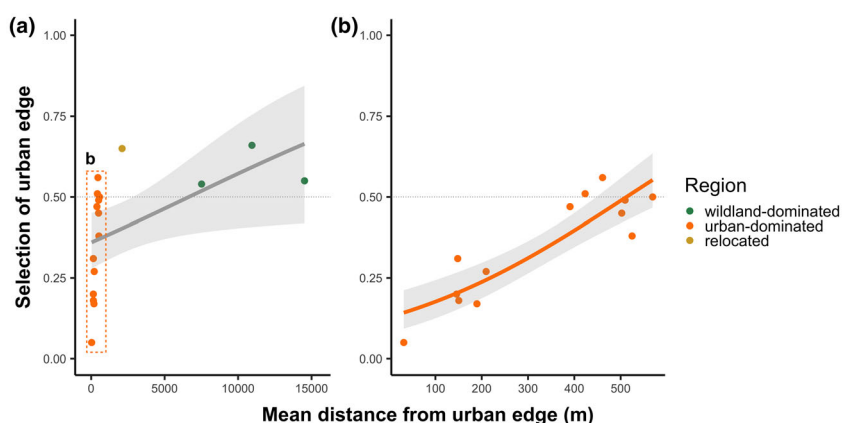


Figure 4 Functional response by (a) all caracals and (b) only caracals in the urban-dominated region of the Cape Peninsula, South Africa, relative to urban edge. Functional response is exhibited by the relationship between a selection proportion for the urban edge and the mean distance to the urban edge across each home range. Proportions of 0.5 represented no difference between used and available, whereas proportions <0.5 indicated caracals were closer to the urban edge than expected, and proportions >0.5 indicated caracals were further from the urban edge than expected.

Degree of *in situ* vegetation cover

As the distance from urban edge decreased, the degree of cover (0–100%, measured *in situ* at clusters) at feeding clusters increased ($\beta = -0.0001$, $t = -6.37$, $P < 0.001$; Fig. 5a). Further, the average feeding cluster in the urban region had a greater degree of cover (mean=69.1%) than the average cluster in the wildland region (46.1%; $\beta = -0.96$, $t = -3.63$, $P < 0.001$). Caracals predominantly established feeding clusters in areas with higher cover during the day (mean_{day} =

75.8%; mean_{night} = 45.4%, $\beta = -1.25$, $t = -5.88$, $P < 0.001$; Fig. 5a).

Handling time

Caracals in both regions spent similar amounts of time at feeding clusters (mean = 23.3 h, range=1–141 h; $F_{1,317} = 0.76$, $P = 0.38$; Table 2). However, handling time during the day was almost twice as long for caracals in the urban region ($F_{1,173} = 4.63$, $P < 0.05$; Table 2). This trend

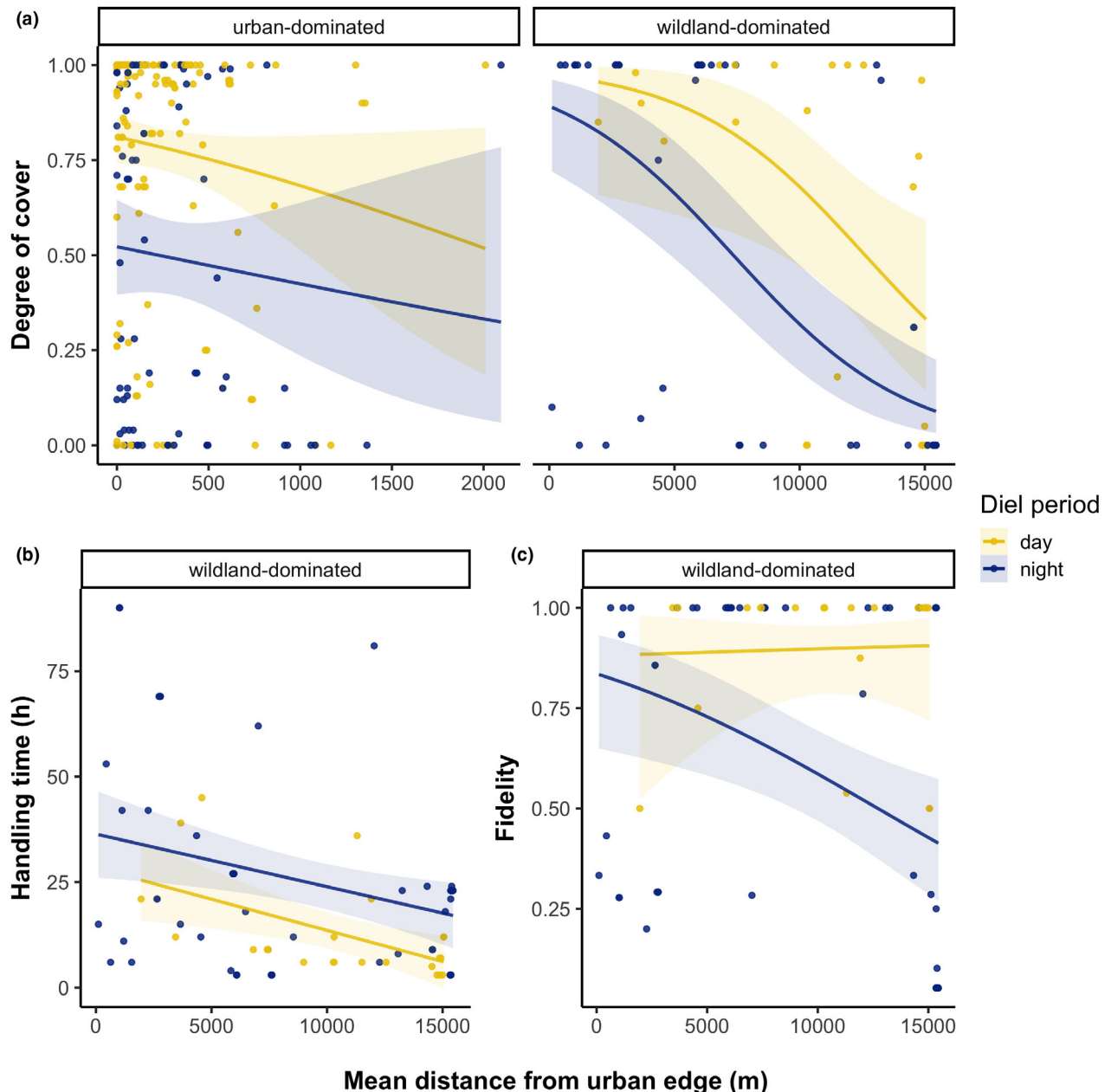


Figure 5 Caracal feeding cluster variables against distance from the urban edge between diel periods: (a) degree of cover measured *in situ* at clusters (b) handling time in the wildland-dominated region (c) cluster fidelity in the wildland-dominated region of the Cape Peninsula, South Africa. Note that axes differ between plots.

was stable when controlling for prey type (S4). Caracals in the urban region exhibited similar handling times during the day (mean = 23.8 h) and night (24.4 h; $F_1 = 0.03$, $P = 0.86$), regardless of distance from the urban edge (up to 2095 m from the urban edge, $F_{1,235} = 0.95$, $P = 0.33$). By contrast, with increasing proximity to urban areas, feeding clusters of caracals in the wildland region had longer handling time ($F_{1,80} = 12.19$, $P < 0.001$; Fig. 5b). Diel period and degree of cover significantly affected caracal handling time in the wildland region ($F_{2,79} = 8.36$, $P < 0.001$), but had no effect on caracals in the urban region ($F_{3,215} = 0.58$, $P = 0.63$). Handling time at diurnal feeding clusters in the wildland region was, on average, twice as long when in high cover areas (mean_{high} = 15.7 h; mean_{low} = 7.4 h; $F_{2,79} = 8.36$, $P < 0.001$). In the wildland region nocturnal clusters were longer than diurnal ones, particularly when in high cover (mean_{high} = 34 h; mean_{low} = 18.6 h; $F_{2,79} = 8.36$, $P < 0.001$; Fig. 5b).

Fidelity

Longer handling times with increasing proximity to the urban edge may reflect individuals seeking spatial refuge away from clusters when not actively feeding. Therefore, we examined fidelity to feeding clusters. Overall, caracals in the wildland region had lower fidelity (mean_{wildland} = 67.7%) than caracals in the urban region (mean_{urban} = 87.2%; $\beta = 1.18$, $t = 5.21$, $P < 0.001$), particularly at night ($\beta = -1.43$, $t = -4.60$, $P < 0.001$; Table 2). In the urban region fidelity was not related to diel period ($\beta = -0.19$, $t = -0.68$, $P = 0.50$) or degree of cover ($P > 0.05$). By contrast, caracals in the wildland region had 30.7% higher fidelity during the day (mean_{day} = 89.8%; mean_{night} = 59.1%; $\beta = 0.60$, $t = -3.0$, $P < 0.01$; Fig. 5c). Fidelity in the urban region remained very high ($\geq 80\%$) in all cases (up to 2095 m from the urban edge). There was no influence of urban edge distance in this region ($\beta = 0.0005$, $t = 0.92$, $P = 0.36$). By contrast, caracals in the wildland region had higher fidelity when closer to the urban edge ($\beta = -0.0001$, $t = -2.51$, $P < 0.05$), particularly at night ($\beta = -1.81$, $t = -3.03$, $P < 0.01$). During the day, fidelity was high across all distances from the urban edge (Fig. 5c). Further, when cover was high, fidelity increased ($\beta = 1.38$, $z = 2.63$, $P < 0.01$).

Discussion

We explored caracal foraging in a risky landscape and present a novel data approach that incorporates a suite of diverse prey feeding locations into resource selection analysis. Level of exposure to urbanisation determined individual foraging behaviour, with low interindividual variation but marked differences between urban and wildland regions. Caracals living in the urban-dominated northern region adjacent to the city of Cape Town demonstrate an attraction to the urban edge. Here they develop unique strategies to mitigate risk: opting to 'hide in plain sight' to avoid detection, rather than spatial or temporal partitioning to avoid human-associated risk altogether. This strategy may lend caracals,

and potentially other carnivores that adopt similar strategies, greater resilience in increasingly urbanizing areas; however it carries a suite of associated risks.

Caracals in the urban-dominated region selectively forage close to the urban edge, despite disturbances that may be perceived as risky, such as the presence of hikers, park rangers, as well as deadly threats such as vehicles (>72% of deaths), poachers (7%) and domestic dogs (3%). In assessing foraging habitat selection that may be used in downstream management for generalist, urban-tolerant mesocarnivores, it is critical that the full suite of foraging events is included in RSF analyses. As for other carnivores (e.g., Bacon *et al.*, 2011; Tambling *et al.*, 2012; Pitman *et al.*, 2014; Perilli *et al.*, 2016; Studd *et al.*, 2021), we have found that scat analysis overestimates smaller prey, while GPS cluster analysis overestimates larger prey (Leighton *et al.* 2020), highlighting the need to integrate these methods, particularly for smaller carnivores that feed across a range of prey sizes. Importantly, integrated-diet data improved model resolution, particularly with respect to the relative importance of natural and anthropogenic landscape features. For instance, in the urban region wetlands were more important for foraging, and the urban edge was less strongly selected when smaller prey was incorporated. This we attribute to the inclusion of vlei rats (*Otomys irroratus*, wetland habitat specialists; Curtis & Perrin, 1979) only represented in scat sampling. In the wildland region, integrating diet datasets added prey species other than seabirds, reducing the strength of selection for the coast. Additionally, this novel approach revealed selection for steeper slopes. This is perhaps due to the inclusion of hyrax (*Procavia capensis*), a medium-sized mammal inhabiting rocky outcrops and cliffs (Kotler *et al.*, 1999), also only recorded in scats. This suggests selection of particular mammalian prey habitat patches that would be missed by cluster analysis alone, and that using digestion time scaled to prey mass is likely the most appropriate integrated-diet method for RSFs in mesocarnivores.

The positive functional response to the urban edge reveals that caracals are able to modify their foraging habitat-selection patterns depending on the landscape in which they find themselves. We observed that caracals, particularly in the urban-dominated region, selected for urban edge habitats more as they became more available, as documented in other carnivores for other urban features (McKenzie *et al.*, 2012; Knopff *et al.*, 2014; Zimmermann *et al.*, 2014). Notably, selection of the urban edge depended on land-use and not all transformed areas were selected equally. While commercial pine plantations do not apparently provide adequate resources, cultivated vineyard properties were strongly selected, as they likely provide higher prey availability. Additionally, unlike plantations, vineyards provide patches of closed cover between and alongside vines not often frequented by people, where most feeding events were located. Retaining adequate greenbelts may therefore facilitate caracal foraging. Yet there may be hidden risks to foraging in vineyards. Caracal proximity to vineyards was significantly associated with anticoagulant rodenticide exposure and was implicated in the death of at least two study animals (Serieys *et al.*, 2019).

Caracals in the urban region, like other felids (Riley *et al.*, 2003; Athreya *et al.*, 2013), generally mitigate risk by avoiding the urban matrix, remaining on the periphery. Attraction to the urban edge is likely due to greater resource availability as a product of lower elevation and added resource input through human activities (Fleming & Bateman, 2018). In our study area, development is concentrated in low-lying areas with productive soils (Rebello *et al.*, 2011), while intact wildland areas predominantly comprise low nutrient quality fynbos vegetation and few palatable grasses for prey (van Hensbergen *et al.*, 1992). Habitat disturbance at the urban edge, such as frequent anthropogenic fires (Forsyth & Van Wilgen, 2008), alien clearing and maintenance of fire breaks, greenbelts and golf courses may increase secondary succession grasses (Milton, 2004), which are favourable habitat for select prey, principally vlei rats, striped mice and Egyptian geese (MacKay *et al.*, 2014). While local prey distribution data are limited, commonly consumed avian prey are more abundant at the urban edge (e.g., pigeons, *Columba livia*, and Guinea fowl, Suri *et al.*, 2017).

Although juveniles had proportionally more urban area in their home ranges compared with adults (Table 1; S4), they showed weaker selection for the urban edge relative to its availability. This may be due to competitive exclusion by larger, older conspecifics favouring the urban edge. Indeed, at least two Peninsula juveniles have died due to conspecific aggression (Serieys, unpubl. data). Similar results have been documented in peri-urban populations of bobcats and pumas (Riley *et al.*, 2003; Benson *et al.*, 2020). The mortality risk from adults is likely exacerbated in this population, where dispersal by juveniles is restricted by the dense urban matrix. These results suggest that while optimal foraging may be focussed at the urban edge, there is likely intense competition between individuals.

Carnivore success in transformed landscapes is increasingly linked to their ability to either avoid or accommodate human activities through flexible behaviour (Knopff *et al.*, 2014; Suraci *et al.*, 2019b). The human apex predator creates disturbance stimuli that can have far-reaching spatial effects (Andersen & Aars, 2008; Suraci *et al.*, 2019b). While feeding, the perceived presence of predators can likewise lead to shifted behaviour: large carnivores reduce handling times and flee more frequently in response to anthropogenic disturbance (Kerley *et al.*, 2002; Smith *et al.*, 2017). Here, we compare foraging behaviour in regions with differing levels of anthropogenic risk. Despite the low number of individuals in the wildland-dominated region, these results provide a valuable baseline expectation. However, we acknowledge that these trends could be specific to these individuals and therefore focus our interpretation on the caracals in the urban-dominated region. We found that when in urban-dominated landscapes during the day, caracal handling time and fidelity to clusters was greater compared with those of caracals in the wildland region. Remarkably, caracals in the urban region had consistently high fidelity (>80%) to feeding sites and similar handling times, suggesting that they perceived similar risk regardless of diel period or distance from the urban edge. Contrastingly, caracals less exposed to urbanisation appear to mediate behaviour based on perceived

risk: at night, when risk of detection is lower, is the only time they forage close (<1 km) to the urban edge, and it is only when close to the urban edge that they leave feeding sites less and extend handling time. The lack of spatial avoidance by caracals in urban- compared with wildland-dominated areas points to behavioural plasticity and habituation to human presence (Schell *et al.*, 2018), likely due to frequent exposure to non-lethal encounters.

In urbanized areas with few green spaces, species may instead adopt temporal avoidance of humans (Gaynor *et al.*, 2018). However, in the urban region temporal patterns in caracal foraging appear to strictly track prey activity (>60% diurnal clusters), corroborating recent evidence that mesocarnivores do not always increase nocturnality (Frey *et al.*, 2020). While the trend was unexpected, the most important caracal prey items in the urban region are more active during daylight: vlei rats are mainly crepuscular, and Guinea fowl and striped grass mice are diurnal. By contrast, in the wildland region, more feeding events were nocturnal (>50%). Here the dominant prey, cormorants, are diurnal but regularly forage 10–20 km offshore (Ryan *et al.*, 2010) while at night, they roost in large coastal colonies, where they may be more vulnerable to predation. Thus, caracal foraging activity is dictated by optimal hunting success (Avenant & Nel, 2002), and not temporal avoidance of the human apex predator.

In lieu of temporal or spatial refugia, caracals in the urban region reduce movement and make use of vegetative cover to 'hide in plain sight' in high-quality patches. As the human apex predator seems to appear randomly on the landscape, the most effective predator-avoidance tactic is to remain stationary, although this is traditionally attributed to herbivore prey species (Broom & Ruxton, 2005; Laundré, 2010). We observe that, like other carnivores (Boydston *et al.*, 2003; Llaneza *et al.*, 2016), caracals select high cover to improve concealment when foraging at the urban edge, relying on their reddish-brown coat for camouflage (Sunquist & Sunquist, 2002). Additionally, as an ambush predator, selection of higher cover may also improve ability to stalk prey (Smith *et al.*, 2020). The availability of dense fynbos, or natural vegetation patches in and around trellis vineyards and greenbelts, lends success to this strategy as urbanisation expands. Remaining hidden could also have energetic benefits. Caracals move off kills less and therefore do not have to increase their kill rate (Smith *et al.*, 2015) or increase the duration or intensity of movement (Ordiz *et al.*, 2014; Oriol-Cotterill *et al.*, 2015). However, long periods spent at the urban edge may increase competition with other species (e.g., large-spotted genet, *Genetta tigrina*, Widdows & Downs, 2015) or increase exposure to anthropogenic threats (e.g., poachers and domestic dogs).

Foraging at the urban edge is likely to have numerous adverse consequences, even when wildlife employ ecologically adaptive risk-avoidance strategies. Dense road systems are a major cause of wildlife mortality (Seiler & Helldin, 2006; Hill *et al.*, 2020), particularly for Cape Town's caracals (Serieys *et al.*, unpubl. data) and peri-urban mesocarnivores globally (e.g., Poessel *et al.*, 2014; Litvaitis *et al.*, 2015; Garrote *et al.*, 2018; Serieys *et al.*, 2021). As for other felid mesocarnivores (e.g., Riley *et al.*, 2004; Mateo *et al.*,

2012; Serieys *et al.*, 2015; Boyles & Nielsen, 2017), exposure to pollutants (e.g., rodenticides, Serieys *et al.*, 2019, and pesticides, Leighton *et al.*, unpubl. data) and diseases (10% of deaths; Serieys, unpubl. data) that are uniquely associated with human-modified areas may also exacerbate risks (Murray *et al.*, 2019). Despite the low incidence of caracal predation on domestic animals (Leighton *et al.*, 2020), exposure to tick-borne pathogens in the study population points to possible pathogen spillover (Viljoen *et al.*, 2020). When the costs outweigh the benefits, human-modified areas may become population sinks or ecological traps, where continued use of attractive, but harmful, environments often leads to local extinction (Battin, 2004). Mitigative conservation measures to prevent a potential trap include reduced use of pesticides and maintenance of cover, particularly around vineyards and at the urban edge, and traffic calming measures where roads bisect frequent crossing points. Further to reducing anthropogenic mortality of wildlife, the work of local government and conservation agencies in maintaining and restoring connectivity between foraging habitats is essential for the continued ecological success of mesocarnivores like caracals, which persist despite extensive urbanisation of our cities.

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Data Availability Statement

Data will be available from the Dryad Digital Repository.

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Supporting information

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

Data S1. Supplemental Methods

Table S2. Description and sources of all predictor variables

Table S3. Full models considered for caracal foraging habitat selection analyses

Data S4. Supplemental Results

Fig. S5. Cape Peninsula study area showing home ranges

Table S6. Top model results for LAND-USE/AGE/SEX RSF models

Table S7. Top model results for LAND-USE/SEX RSF models

Table S8. Top model results for COVER/AGE/SEX RSF models

Table S9. Top model results for COVER/SEX RSF models

Table S10. Top model results for LAND-USE/SEX RSF models

Table S11. Top model results for COVER/SEX RSF models