An integrated dietary assessment increases feeding event detection in an urban carnivore

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Abstract

Urbanisation radically changes habitats and alters available resources. Populations of large, highly mobile species are often extirpated at the urban-wildland interface, while species like mesocarnivores may thrive by capitalising on changes in prey abundance. We investigated the diet of the caracal (*Caracal caracal*), a medium-sized felid inhabiting patchy natural habitat isolated within the dense urban matrix of South Africa's second largest city, Cape Town. We systematically integrated two classic dietary methods (scat and GPS clusters) by accounting for gut transit times. As part of a larger caracal ecology study, we GPS-collared 26 individuals over a two-year period (2014–2016) to generate coarse (3-hour) and fine-scale (20-minute) GPS movement data. Using the movement data, we investigated 677 GPS-clusters for prey remains. We collected 654 scats, half of which were found at GPS-clusters and were linked with the individual sampled. By systematically correcting for a range of gut transit times, we determined whether scat at cluster sites was from the same or an earlier feeding event, thereby increasing the overall detection of feeding events by > 50%. Avian prey dominated GPS cluster findings while micromammals were overwhelmingly represented in scat. Although > 40% of feeding events occurred within 200 meters of the urban edge, caracals largely preyed on native species. Our findings have implications for understanding the ability of some species to persist in the face of rapid environmental change, human-wildlife conflict, pathogen transmission, and bioaccumulation of pesticides. Further, this approach could be incorporated into studies that estimate foraging-explicit resource selection and habitat preference.

Keywords urbanisation · *Caracal caracal* · scat · carnivore · GPS cluster analysis · methods

Introduction

Urbanisation leads to critical alterations in available resources through drastic habitat modification, affecting certain species disproportionately (McKinney 2002; Shochat et al. 2006). Populations of highly mobile carnivores with large resource requirements are often the first to be extirpated due to habitat loss and fragmentation (Crooks 2002; Ordeñana et al. 2010; Lowry et al. 2013). In contrast, generalist mesocarnivores (defined as predators with body mass < 34 kg and an average of 13–16 kg, Roemer et al. 2009; Wallach et al. 2015) may find more abundant smaller prey (Moss et al. 2016; Smith et al. 2016) and thus thrive at the urban edge (Prugh et al. 2009; Bateman and Fleming 2012). Consequently, these smaller predators may be more vulnerable to the spill-over of pathogens and the bioaccumulation of pesticides (Bradley and Altizer 2007; Riley et al. 2007; Serieys et al. 2019), making them valuable sentinels of ecosystem health (Jooste et al. 2013). Understanding the extent to which mesocarnivores are able to exploit human-derived food resources at the urban edge, and whether this facilitates their ability to persist in human modified landscapes, is critical to mitigate threats, alleviate human-wildlife conflicts, and promote biodiversity conservation globally as natural areas are increasingly transformed by urbanisation (Bateman and Fleming 2012; Allen et al. 2016; McPherson et al. 2016).

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Knowledge of the diet of free-ranging species is pivotal to understanding their ecology (Litvaitis 2000). For wild carnivores, a single unified approach to diet studies is not established (Litvaitis 2000; Bacon et al. 2011; Klare et al. 2011). Our understanding of the fundamental ecology of populations may therefore be biased by imperfect methodologies that do not provide comparable information (Litvaitis 2000; Klare et al. 2011; Morin et al. 2019). While there are many options for the diet analysis method, such as DNA metabarcoding (Shehzad et al. 2012; De Barba et al. 2014) and stable isotope analysis (DeNiro and Epstein 1978; Newsome et al. 2015a), an overwhelming number of carnivore diet studies analyse scat. Scat analysis may be preferred because samples can be cheaply, easily and non-invasively located on the landscape, whereafter undigested prey remains can be used to determine prey frequency and biomass (Klare et al. 2011). An inherent bias to this approach, however, is that small prey consumed in their entirety (i.e. including all bones and hair) will be overestimated. Conversely, large prey that have lower surface area-to-volume ratio have less indigestible matter per unit biomass, leaving little evidence in scat. The result is a diet assessment overrepresented by small prey species (Lockie 1959; Floyd et al. 1978; Marker et al. 2003).

An alternative, commonly used approach for carnivores relies on locating unconsumed prey remains from individual feeding events. Data collected via GPS-enabled collars can be mapped to locate clusters of GPS-points on the landscape which can form when an animal is feeding or at rest (Anderson and Lindzey 2003; Sand et al. 2005; Martins et al. 2011; Kindschuh et al. 2016). The GPS cluster approach is traditionally used for predators that consume large prey with long handling times (e.g. deer and elk, Anderson and Lindzey 2003; Knopff et al. 2009). The approach has been used on large predators that consume relatively smaller prey (e.g. mountain lions, *Puma concolor*, predating domestic cats, Smith et al. 2016). However, using GPS clusters is impractical to detect micromammal prey that have short handling times. Consequently, carnivore diet studies that rely on GPS clusters vastly underrepresent small prey (Bacon et al. 2011; Pitman et al. 2014).

For mesocarnivores that predominantly prey on smaller species, GPS clusters may not form with the longer fix rates traditionally used. Even if GPS clusters do form, few prey remains may be left behind. Often the potential to discover remains of small prey is assumed unfeasible and unimportant (e.g. prey 5–10 kg, Bacon et al. 2011; Elbroch et al. 2017; Knopff et al. 2009). Consequently, mesocarnivore studies that rely on scat-based assessments may overestimate the amount of small prey consumed while those that rely on GPS clusters may underrepresent small prey. To correct for the biases inherent to both the GPS cluster and scat approaches, Pitman et al. (2004) integrated the findings of the scat- and cluster-based methodologies to build a more complete understanding of the diet of the leopard (*Panthera pardus*), a large carnivore. Extending this approach further, we questioned whether implementing the conventional movement ecology methods (i.e. GPS data collection) may also shed new light on old questions of the diet of medium-sized carnivores (Svoboda et al. 2013; Kays et al. 2015; Vogt et al. 2018). Integrating scat and GPS cluster data while correcting for gut transit times to remove duplicate feeding events (see Methods, Fig. 2) may provide a more complete understanding of diet, particularly in medium-sized generalist carnivores with prey ranging considerably in size. This may increase resolution of carnivore diet by i) reducing pseudo-replication of correlated scats from the same feeding event, and ii) identifying small kills (< 0.5 kg) missed during GPS cluster investigations (i.e. missed feeding events; Marucco et al. 2008; Martins et al. 2011; Tambling et al. 2012; Pitman et al. 2014).

Here we first use two classical approaches, scat and GPS-cluster analysis, to characterise the diet of a common medium-sized felid, the caracal (*Caracal caracal*, Skinner and Chimimba 2005), within South Africa's most rapidly urbanising city, Cape Town. Previous studies in protected natural and agricultural areas report the caracal opportunistically preys on a diverse range of species, typically 0.5–10 kg (e.g. Grobler 1981; Avenant and Nel 1998, 2002; Drouilly et al. 2019; Jansen et al. 2019). Next, with an understanding of the inherent biases of the GPS-cluster towards detecting large-prey (Knopff et al. 2009), and the scat approach towards detecting micro-mammal prey (Klare et al. 2011), we describe a third approach that refines our understanding of caracal diet. Specifically, we integrate the findings of the GPS-cluster and scat-based approaches by controlling for gut transit times and systematically verify and incorporate missed feeding events undetected with each approach in isolation (Pitman et al. 2014). We describe and quantify prey species detected using the two classical approaches. Additionally, we assess the relative proportion of wild indigenous; synanthropic; and exotic prey (see Methods Sect. 6) across the three approaches. We also compare prey detection using fine-scale (20-minute GPS intervals) and coarse (three-hour interval) GPS-collar sampling frequency, with the prediction that we would detect unconsumed smaller prey remains more frequently at 20-minute fix intervals. We predict that the two classical methods will differ substantially, with GPS cluster analysis underestimating small prey (< 1 kg) consumption and scat underestimating larger prey (> 5 kg). Finally, because the majority of GPS-clusters and scat were found within 500 meters of the urban edge, we predicted that exotic and synanthropic species would dominate caracal diet in our study area. We propose that the integrated approach described can be used to increase detection of feeding events and thus more accurately describe diet of a medium-sized carnivore. Understanding the diet of adaptable medium-sized carnivores is important in urbanising areas where conflict with humans and their pets is commonplace

(Bateman and Fleming 2012; Soulsbury and White 2015) and predators are vulnerable to bioaccumulation of toxicants through their prey (Serieys et al. 2015, 2019; Boyles and Nielsen 2017; Rodríguez-Estival and Mateo 2019).

Methods

Study area

We investigated caracal diet in the Cape Peninsula (hereafter Peninsula), a highly fragmented mosaic of urban, rural and natural land within the Cape Floristic Region, a biodiversity hotspot recognised as one of the most threatened ecosystems and a global priority for conservation (Underwood et al. 2009). The Peninsula comprised approximately 250 km² of available wildlife habitat, mostly within the Table Mountain National Park (TMNP) and the dense urban metropolis of Cape Town (Fig. 1). The national park has been fragmented by a variety of human land uses including residential and agricultural areas, roads, and altered open areas, such as golf courses and manicured school grounds. Prey species in the study area included indigenous synanthropic species (e.g.

Fig. 1 Boxplots with means (diamonds) of estimated caracal prey consumed biomass (kg, log transformed) using scat analysis, GPS cluster analysis, GPS-located prey remains integrated with minimum transit (0.5-day) and maximum transit time (4-day) scat samples for prey belonging to three prey categories (*wild, synanthropic* and *exotic*) from caracal (n = 22) on the Cape Peninsula, South Africa

Egyptian goose, *Alopochen aegyptiaca* and Helmeted Guinea fowl, *Numida meleagris*), exotic species (e.g. introduced brown rat, *Rattus norvegicus*, and Eastern grey squirrel, *Sciurus carolinensis*), and > 530 wild, indigenous species (Rebelo et al. 2011). Several species are especially abundant along the urban-wildland interface (i.e. TMNP areas that abut residential areas and vineyards), including Guinea fowl, Egyptian geese and hadeda ibis (*Bostrychia hagedash*; Serieys, *pers.obs.*).

Capture and GPS-collaring

We captured and GPS-collared 26 caracals between 2014–2016 using standardised cage-trapping techniques. Briefly, we custom built mesh wire cage traps or used Tru–catch traps (Bell Fourche, South Dakota) baited with a variety of visual, audio, and scent lures. Traps were checked a minimum of every 8-hours.

Once captured, individuals were immobilised using 7 mg/kg ketamine HCl and 0.08 mg/kg medetomidine HCl. We recorded age class, sex, weight, and morphological measurements. Individuals were classified as juveniles (< 2 years) or adults (≥ 2 years) based on body size, weight, tooth wear and eruption, and reproductive status (Schroeder et al. 2005). We collected a variety of samples at captures (blood, hair, etc.), including faecal samples (n = 12).

We fitted individuals with GPS-collars (FollowIt™ Tellus, Lindesberg, Sweden) equipped with a drop-off mechanism that activated within six months of collar fitting. We also fit all collars with a rot-off cotton spacer to ensure eventual drop-off. As part of a larger caracal movement ecology study, collars were programmed to collect GPS locations at two fix intervals: i) course scale: every three hours throughout the 24-hour cycle daily resulting in eight locations per day, and ii) fine scale: on every 9–10th day, 20-minute fixes were collected for 24–36 hours resulting in up to 108 consecutive 20-minute GPS locations. We recognise that our use of 3-hour fix intervals for the larger caracal study is likely too course to capture information about smaller prey. Animal capture, handling, and sampling followed ethical guidelines approved by the American Society of Mammologists, the University of Cape Town Animal Ethics Committee (2014/V20/LS), Cape Nature (AAA007-0147-0056), and South African National Parks (SERL/AGR/017–2014/V1). Finally, we opportunistically collected and necropsied caracal carcasses from which we recovered faecal samples (n = 3).
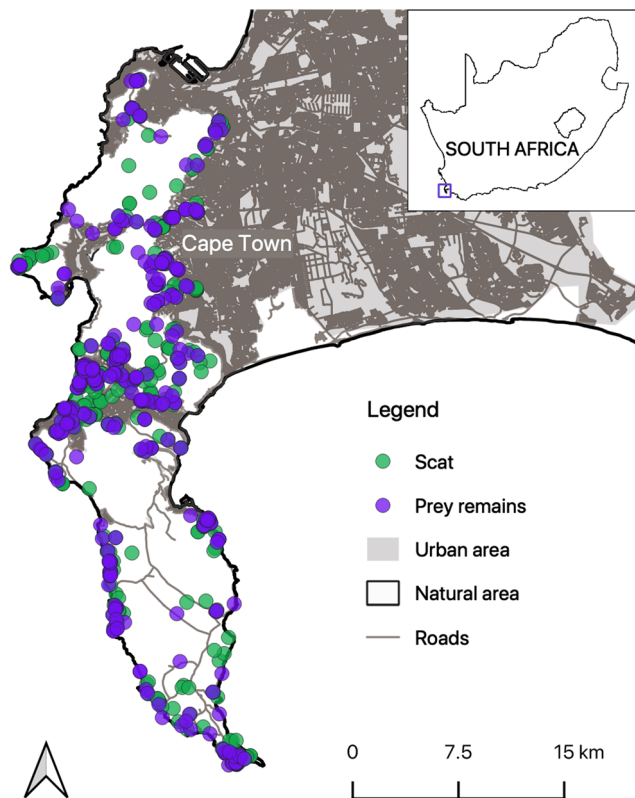
GPS cluster identification and search protocol

We downloaded GPS data weekly using the FollowIt™ GEO web interface. We used a rule-based Python algorithm (Python Software Foundation n.d.) to identify GPS clusters following

Knopff et al. (2009). The algorithm defined clusters as ≥ 2 GPS locations within 100 meters distance of each other within a 24-hour interval. To compare the effect of fix rate on prey size detected we used both three-hour and 20-minute fix intervals to identify clusters. We prioritised clusters using a set of decision rules implemented in Python that ranked each cluster as follows: a cluster ranked higher if it had i) a smaller cluster radius (< 50 m), ii) had a time span of > 3 hours, iii) had a cluster fix success of over 75%, and iv) had high site fidelity (i.e. the ratio of points spent away from the cluster/actual number of points in that time period was < 25%). We used the same rule-based algorithm on all the data, so clusters formed during the 20-minute fix schedule were ranked lower because there would be more GPS locations within closer proximity recorded for the same time period. The centroid, time elapsed, radius, number of points away from the cluster and fix success rate were generated and recorded for all clusters.

The study presented logistical constraints that limited our ability to visit every GPS cluster. First, far more clusters were identified than we could feasibly investigate. Second, our field visitations were spatially restricted to areas that were considered safe (by local South African National Parks, SAN Parks, liaison officers) from violent crime. There were two small (< 3 km^2) urban crime hotspots adjacent to lower socio-economic status areas that we were unable to visit without armed guards (see Online Resource Fig. S1). While it is possible that avoiding these two unsafe areas may have biased our diet results, these areas were not ecologically distinctive and we sampled extensively in both habitat types in other areas, as well as directly adjacent to these sites. We coordinated field visitations to access multiple clusters in close proximity to each other only in areas classified as safe to conduct fieldwork. We navigated to the centroid of the selected clusters within an average of 16 ± 10 SD days and conducted a standardised search protocol (Svoboda et al. 2013). Briefly, a 50 meter radius around the cluster centroid was searched for a minimum of two hours, as has been used for ecologically similar species (Svoboda et al. 2013 bobcat, *Lynx rufus*; Podgorski et al. 2008 Eurasian lynx, *Lynx lynx*). We searched the area for prey remains (i.e. carcass, hair, feathers, etc.), scat, resting beds, and scratching posts. Prey remains were photographed *in situ* and collected. Remains were later identified macroscopically using reference feathers and guides (Hockey et al. 2005), hair samples, and taxidermic specimens housed at the University of Cape Town.

Scat collection and analysis

We identified caracal scats by their unmistakable size, shape, and visible content. Despite extensive fieldwork efforts, we rarely observed scat except during cluster investigations. A small section of the scat was left where it was found in the field in case it was an important mode of communication between individuals in the study area (Stuart 1981). Upon collection, scats were visually grouped into categories (from fresh to old and decomposed) based on visual characteristics (colour, dryness, etc.) and level of degradation. For those samples that plausibly matched the age of the cluster, we classified the scat as produced by that caracal at the start of the cluster formation. Those samples found at the clusters (i.e. within the 50-meter radius) that were too old or too fresh to belong to that cluster based on cluster duration and time to cluster investigation were classified as opportunistic. Scat were also classified as opportunistic if they were: i) collected in the field but not associated with clusters (i.e. outside of the 50-meter radius), ii) were collected during captures (n = 12), or iii) collected during necropsies (n = 3).

We washed scat samples to remove unidentifiable microfraction, after which the contents were oven dried at 30–40°C. We then used a combination of identification methods (Norton et al., 1986). The bones of birds and larger mammals were classified to the finest taxonomic level using osteological reference material at the Iziko South African Museum. Rodent postcranial bones were compared to reference material at the Iziko South African Museum and Monadjem et al. (2015). We counted the number of prey individuals in scats found in the same cluster using left and right bones (e.g. limb bones, clavicles, mandibles and coracoids) when possible. Using the hair impression methods described by Ott et al. (2007), we examined the microscopic characteristics of hair for the remaining samples. Reptile remains (e.g. scales) and insect fragments were identified to genus or family level where possible. To minimise pseudo-replication, scat samples collected in close proximity on the same day (i.e. in the same cluster) and containing the same prey species were combined (Tambling et al., 2012; Perilli et al., 2016), except where more than one individual prey item was identified using left and right bones.

Integrating scat and GPS cluster-located prey remains findings with gut transit times

We classified each prey item identified from a scat found at a GPS cluster as: i) consistent with the prey identified from prey remains at that cluster, ii) consistent with the prey identified at the previous cluster, or iii) inconsistent with prey identified at either that cluster or the previous cluster (i.e. a missed feeding event; summarised in Fig. 2). We then used gut transit times, as in Tambling et al. (2012) and Pitman et al. (2014), to further refine our classifications above. We set two extreme gut transit times, a minimum of 0.5 days and a maximum of 4 days for caracals, based on jungle cat (*Felis chaus*) feeding trial digestion rates (12–84 hours, Chakrabarti et al., 2016). The minimum and maximum gut transit times correspond to a high and low level of bias in terms of missed feeding events (Tambling et al. 2012). Scats produced at GPS clusters and within the gut
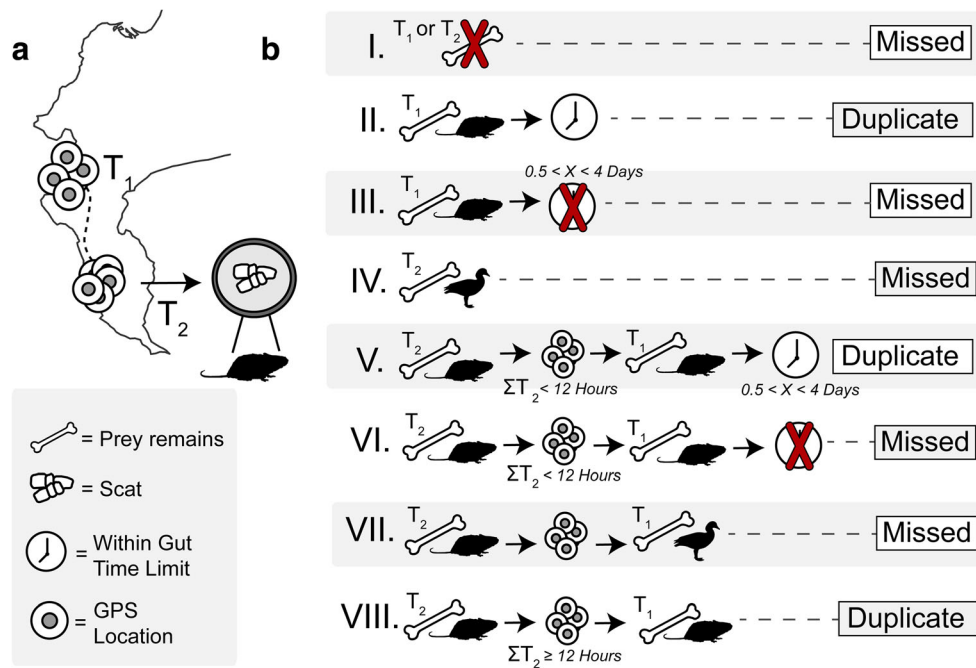
Fig. 2 Concept diagram used to classify prey items found in scats found at GPS clusters as i) a duplicate feeding event (either the product of prey remains at that cluster, or the product of prey remains at a previous cluster), or ii) a missed feeding event (i.e. a product of prey undetected by GPS cluster analysis). **a** Two hypothetical, chronological clusters in the study area generated by the same individual caracal on the Cape Peninsula. A scat is found at a GPS cluster (T_2). **b** The scat contains a prey item. If there were no prey remains at cluster T_1 or T_2 then this represents a missed feeding event (I). If prey remains are present at the previous cluster T_1 and they are from the same species as the scat prey item and within the gut transit limit (i.e. 0.5 or 4-day) then it is a duplicate feeding event (II). If prey remains are present at the previous cluster T1 and it is the same species as the scat prey item but it is outside the gut transit limit, the prey item could not have been digested in time and it represents a missed feeding event (III). If prey remains are present at T_2 and are from a different species from the scat prey item, then the scat prey item is a missed feeding event (IV). If there are prey remains present at T_2, they are the same species as the scat prey item, and the cluster time for T_2 is <12h, then the prey remains of the previous cluster T_1 was checked. If the scat prey item was the same species as the prey remains at T_1 and the time difference between the clusters was within the gut transit limit (i.e. 0.5 or 4 days), then the scat prey item was a duplicate feeding event (of the T_1 cluster prey remains; V). If the time difference was outside of the gut transit limit, then the scat prey item was a missed feeding event (VI). If the prey remains at T_1 were different from the scat prey item, then it was a missed feeding event (VII). If there are prey remains present at T_2 and they are the same species as the scat prey item and the cluster time for T_2 is >12h then it is a duplicate feeding event (of the T_2 cluster prey remains; VIII). If the scat prey item species was the same as both the T_1 cluster prey remains and the T_2 previous cluster prey remains then the age of the scat was used to decide which feeding event it belonged to: if the scat was old, then it was assigned to T_2 and if it was fresh then it was assigned to T_1

transit widow of a caracal are expected to contain the remains of the species found at that cluster or at previous clusters for that caracal individual within the gut transit time limit (Fig. 2). Scat samples found outside of the gut transit times and/or consisting of species other than the prey remains found at the cluster were considered missed feeding events. If a cluster had the same species in the scat and the prey remains but the cluster time span was < 12 hours, then we classified it as a missed feeding event, as the prey could not have been digested within the assigned gut transmit limit. Similarly, if the cluster was formed over > 12 hours, then the scat was classified as corresponding to that cluster (i.e. a duplicate record of a feeding event). If the cluster scat prey item was the same species as the prey remains at both current and previous clusters, then the age of the scat was used to decide to which cluster it belonged. The integrated scat and GPS cluster-located prey remains databases therefore contained all prey remains found at GPS clusters together with the missed feeding events identified from the scats found at GPS clusters at 0.5-day and 4-day

gut transit limits. The duplicate feeding events (i.e. those prey items in scat that were the product of prey remains at the cluster or a previous cluster) were discarded.

Prey classification, occurrence and biomass calculation

We classified all prey species into three categories: i) *wild* prey species indigenous to the Peninsula, ii) *synanthropic* prey species that are indigenous but which are known to thrive in human-modified landscapes (e.g. Egyptian goose and Helmeted Guinea fowl, *sensu* Johnson et al. 2005) and iii) *exotic* introduced prey species such as domestic dogs (*Canis lupus familiaris*) and cats (*Felis catus*), livestock such as goats (*Capra aegagrus hircus*), sheep (*Ovis aries*), various poultry, and rodents (e.g. brown rats and grey squirrels). We calculated corrected frequency of occurrence (CFO) per scat and for both scats and clusters. We also calculated a mean biomass for each

of the three prey categories. We calculated proportion edible mass of found prey remains using proportions scaled to equivalent prey mass categories (see Funston et al. 1998, Appendix 1). We adapted the proportions for use in caracals based on Grobler's (1981) feeding observations. Specifically, prey species with a mass < 0.05 kg were 100% consumed, 0.05–0.25 kg were 90% consumed, 0.26–2.5 kg were 67% consumed and > 2.5 k g were 60% consumed. We determined prey masses by multiplying mean adult female mass (Skinner & Chimimba 2005, Hockey et al. 2005) by 0.75 to account for an assumed proportion of predation on juveniles, as used for previous carnivore diet studies (e.g. African lion, *Panthera leo*, Hayward & Kerley 2005; leopard, Hayward et al. 2006). Where the exact species identification was unknown, the average mass for that prey group was used.

The prey items present in the scat are reported as measures of frequency of occurrence to allow for comparison with previous studies (Klare et al. 2011). This included frequency of occurrence per food item ('relative occurrence', RO) and corrected frequency of occurrence per scat (CFO). To estimate consumed biomass, we used the generalised felid biomass model developed by Chakrabarti et al. (2016). The model requires only the mean predator mass (calculated as the mean mass of the caracals in the diet study), number of scats containing the prey item (calculated by summing the proportional amounts of each prey item found in the scat, i.e. CFO) and 0.75 mean female prey mass (from Skinner & Chimimba 2005, Hockey et al. 2005) as inputs.

Statistical analyses

To examine diet sampling efficiency we used the R package *vegan* (Oksanen et al. 2013). We used the bootstrap method to calculate extrapolated species richness in the species pool for each method (species identified through GPS cluster and scat analysis). To compare the similarity in the corrected frequency of occurrence (CFO) of prey items between scat and clusters, a Bray-Curtis similarity index was calculated, as it reflects quantitative similarity between communities (Bloom 1981). Equivalent frequencies of prey between methods represent a Bray-Curtis similarity coefficient of 1.

We used Chi-squared tests to determine if species composition differed between i) scat samples collected opportunistically versus those found at GPS clusters, ii) prey remains located at GPS clusters versus all scat samples found, and iii) prey remains found at GPS clusters versus prey remains found at GPS clusters that are integrated with scat samples using both minimum and maximum gut transit times. To test for differences in biomass consumed between the two methods (scat and GPS cluster analysis) and the three urban prey categories (wild, synanthropic and exotic) we used unbalanced Type III two-way ANOVAs for: i) prey remains found at GPS clusters versus all scat samples found, ii) prey remains found at GPS clusters versus prey remains found at GPS clusters integrated with scat samples collected at GPS clusters for minimum and maximum gut transit times. To test for differences in biomass consumed between the three GPS cluster fix rates (3-hour, 20-minute, and a combination of both) we used an unbalanced Type III one-way ANOVA. The consumed biomass data was non-normal and lacked homogeneity of variance and was therefore log transformed to fulfil ANOVA assumptions. Tukey HSD post hoc tests were performed for each ANOVA to find means for the categories that were significantly different.

We compared the proportion of scat, GPS clusters with prey remains, and feeding events from the integrated method (4-day) at 50 m bins of distance from urban edge. We measured the availability of protected available habitat on the Peninsula by laying a grid of 10 m cells on the clipped area of non-urban habitat patches in ArcGIS (v. 10.1). We calculated the number of 10 m cells which fell into the same bins of Euclidean distance from the urban edge.

Finally, to test for specific bias in each method we used, we resampled (1000 iterations) the prey group of interest (i.e. wild, synanthropic and exotic) by caracal to quantify if sampling was biased by specific individuals (Balme et al. 2019). We additionally resampled by binned (100 m) distances to urban edge to evaluate if site accessibility and safety biased our findings. We further investigated potential spatial bias in the clusters we managed to investigate compared to those we did not by testing for a difference in distance from the urban edge using a bootstrap hypothesis testing approach (10,000 iterations). All analyses were conducted in R v3.5.1 (R Core Team 2018) using preloaded packages.

Results

Sampling

We captured 29 individuals and GPS-collared 26 individuals over 3466 trapping nights distributed across the Peninsula. The mean time that individuals were collared was 154 ± 96.7 SD days. Of these, 22 caracals produced clusters that were feasible to visit given the safety constraints of our study area (Table 1). A total of 4202 clusters were generated between November 2014 and November 2016 with a mean fix success of 99.2%. We investigated 677 GPS clusters (mean fix success = 98.9%), which represented a total of 16.11% of the overall clusters generated. We found a high proportion of all generated clusters were ≥12 hours (29.53%), while almost half (45.4%) of investigated clusters were ≥12 hours. Most generated clusters (56.47%) were formed during 3-hour sampling intervals. Twenty-minute locations (for a consecutive 24–36 hours) were collected only every 9th – 10th day, and we rarely documented multiple clusters within a 24–36-hour period.

Nevertheless, 27.15% of clusters were formed during the 20-minute sampling interval and 15.17% were a combination of both schedules. The mean time difference between when cluster formation and investigation date was 16 days ± 10 SD (range: 1–83 days). Of the 677 GPS clusters investigated, 36.3% of GPS clusters were for females and 63.07% were for males; 89.21% were for adults and 10.79% were for juveniles (Table 1). We located feeding sites at 241 clusters (35.75% of all clusters; Table 1). At clusters, we also identified sleeping sites and scratching posts (Table 2). At 37.08% of GPS clusters we did not find evidence of feeding, resting or territorial behaviour (Table 2). Of the 242 GPS clusters with prey remains, 66.4% were formed on the 3-hour GPS fix interval, 13.7% on the 20-minute fix interval and 19.9% were a combination of both fix intervals. Of all clusters investigated 51.55% were within 500 meters of the urban edge. Of these clusters within 500 meters of the urban edge, 60.99% had prey remains. We found 40.79% of clusters with prey remains were within 200 meters of the urban edge (Fig. 3, purple line), although the amount of available protected natural habitat within 200 meters was 12.55% (Fig. 3, black dotted line).

We collected a total of 654 caracal scat samples, of which 177 scat samples were found at GPS clusters with prey remains, 151 scat samples from GPS clusters without prey remains and 326 scat samples from locations not associated with GPS clusters (i.e. opportunistically, Table 1). We found a marginally significant difference in dietary composition (i.e. proportion wild, synanthropic and exotic prey) between scat samples collected at GPS cluster sites and those collected independently of GPS cluster investigations (i.e. opportunistically, $\chi^2_2 = 5.72$, $P = 0.06$), as the proportion of exotic and synanthropic prey was marginally higher in cluster scat than opportunistic scat. This may be the result of insufficient sampling of opportunistic scat.

Given that we visited only a fraction of generated clusters, we evaluated our dataset for potential biases that may have arisen from a lack of representative sampling. Our resampling suggests that there is little evidence of individual bias in the three methods (GPS cluster prey remains, scat and integrated method). Prey group proportions remained similar to those we found across resampling, with low variance, suggesting that individual caracals did not bias these prey group categories (Online Resource Table S2). Similarly, our resampling by binned distance from urban edge resulted in similar prey group proportions (Online Resource Table S3), which suggests that distance from the urban edge did not bias these prey categories. Additionally, there was little evidence to suggest a significant difference in distance from the urban edge between all generated (mean = 2602.8 m) and investigated clusters (mean = 2930.9 m; bootstrapped [10,000 iterations] t = -0.243, $P = 0.56$).

Occurrence, biomass and species richness estimates using scat and GPS cluster methods

There were significant differences in both dietary composition ($\chi^2_2 = 737.58$, $P < 0.001$, Fig. 5) and biomass ($F_1 = 76.9$, $P < 0.001$, Fig. 6) estimates of prey types for GPS clusters and scats with a relatively low overall similarity between the methods (Bray-Curtis = 0.64). In terms of biomass, there was no significant difference between exotic, synanthropic and wild prey types ($F_2 = 1.2$, $P = 0.30$, Fig. 6). However, the interaction between the method and prey type was highly

Table 1 Diet data collected for collared caracals for which GPS clusters were investigated (n = 22), and opportunistically on the Cape Peninsula, South Africa

Sample type	Total count of prey items	Adult female (n = 8)	Juvenile female (n = 1)	Adult male (n = 8)	Juvenile male (n = 5)
SCAT	**654**				
Scat at clusters	**328**	**97**	**22**	**186**	**23**
With prey remains	177	55	6	144	2
Without prey remains	151	42	16	72	21
Opportunistic scat	**326**	**NA**	**NA**	**NA**	**NA**
Field	311	NA	NA	NA	NA
Capture	12	3	2	5	2
Necropsy	3	1	0	0	2
CLUSTERS	**677**	**226**	**30**	**360**	**61**
With prey remains	241	81	10	134	16
Without prey remains	436	145	20	226	45
PREY REMAINS	**385**				
Prey remains at clusters	**331**	111	15	190	15
Opportunistic prey remains	**54**	NA	NA	NA	NA

Table 2 Data collected for collared caracals (n = 22) for which GPS clusters (n = 677) were investigated on the Cape Peninsula, South Africa; mean ± SD (n)

Group	Days tracked	Clusters investigated	Scats collected	Prey remains collected	Sleeping sites	Scratching posts	Empty GPS clusters
Adult female (n = 8)	149.3 ± 114.8 (1350)	28.3 ± 32.3 (226)	12.1 ± 12.4 (97)	16 ± 16.9 (82)	5.6 ± 5.9 (37)	0.4 ± 0.7 (3)	11.9 ± 15.8 (95)
Juvenile female (n = 1)	185.0 (185)	30.0 (30)	22.0 (22)	16.0 (16)	2.0 (2)	2.0 (2)	5 (5)
Adult male (n = 8)	210.6 ± 102.8 (1900)	45.0 ± 31.5 (360)	23.3 ± 22.5 (186)	25.0 ± 20.4 (133)	7.8 ± 4.9 (58)	1.0 ± 1.1 (8)	16.9 ± 11.5 (135)
Juvenile male (n = 5)	97.2 ± 32.3 (586)	12.2 ± 12.1 (61)	4.6 ± 5.7 (23)	4.6 ± 5.7 (16)	2.0 ± 2.0 (10)	0.0 ± 0.0 (0)	3.8 ± 3.3 (19)

significant ($F_2 = 10.22$, $P < 0.001$). A Tukey HSD post-hoc test showed that for scat analysis there was only significantly higher biomass between wild and synanthropic prey ($P < 0.001$), while there were no significant differences between any other prey categories, nor between any prey categories for the GPS cluster analysis (Fig. 6).

We detected strikingly different results using scat compared to GPS clusters. Small mammals (mainly rodents 0.005–0.11 kg) were the dominant species detected in scat. Birds (0.02–1.12 kg) were the dominant prey detected at clusters. Unexpectedly, the smallest prey species detected at 3-hour interval clusters were < 0.02 kg for mammals and < 0.03 kg for birds. Although we detected small prey items at clusters, given the coarse sampling intervals, it is likely we missed more feeding events with prey of similar size. Using the GPS cluster method (n = 296), we detected 58 unique prey species (see full list in Online Resource Table S1) with an additional 10 species that were likely undetected following

the species accumulation bootstrap. Dominant avian species included Helmeted guinea fowl (17%), Cape cormorant (*Phalacrocorax capensis*, 11%) and Egyptian goose (10%) (Fig. 4). Frequency of occurrence (RO) estimates per prey item revealed that synanthropic birds were the most consumed (44.94%), while biomass estimates show wild mammals to be most common (44.85%, Table 3). Exotic prey comprised < 20% using both prey remains RO (12.73%) and biomass (15.79%) estimates (Table 3). In contrast, when examining scat, we detected 59 species with bootstrap estimates indicating only five species were likely undetected. Rank abundance indicated that vlei rat (*Otomys irroratus*, 22%), Cape cormorant (10%), and rock hyrax (*Procavia capensis*, 8%) were the most dominant species in scat (Fig. 4). According to all scat estimation methods (RO, CFO and biomass) the majority of prey were wild mammal species (Table 3) and exotic prey were < 10% (Table 3). Prey biomass in scat revealed higher use of wild prey (20.8% more), while caracal prey remains found in the field revealed greater use of urban (8.4% more)
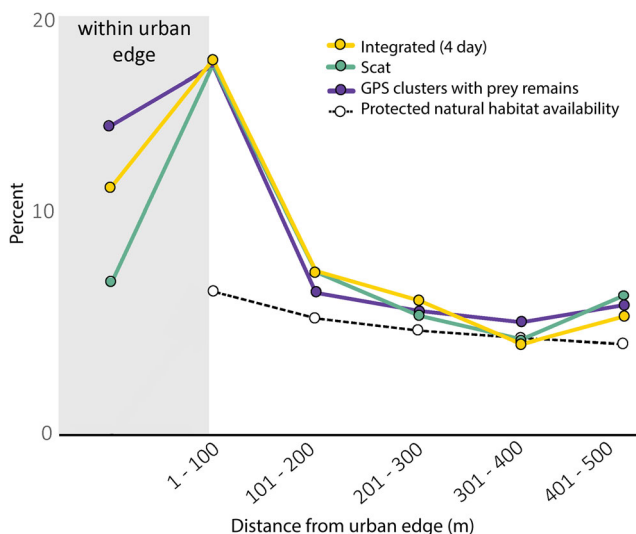

Fig. 3 Percentage of prey items found at binned distance from the urban edge (m) for each method (GPS clusters with prey remains, scat and the integrated method with the maximum 4-day gut transit time) for caracal (n = 22) on the Cape Peninsula, South Africa. The dotted black line shows the percentage of protected natural habitat availability (see Methods)
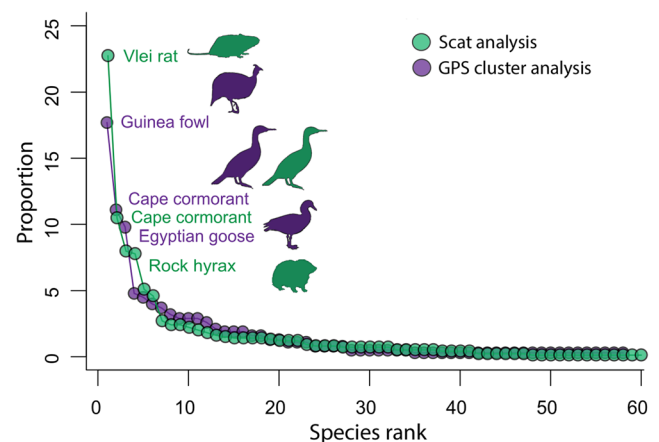

Fig. 4 Rank abundance plots for prey items identified to species level per GPS cluster with prey remains (n=296) and per scat (n=590) for caracal on the Cape Peninsula, South Africa. Helmeted guinea fowl (*Numida meleagris*), Cape cormorant (*Phalacrocorax capensis*) and Egyptian goose (*Alopochen aegyptiaca*) were the most dominant species for prey remains. Vlei rat (*Otomys irroratus*), Cape cormorant and Rock hyrax (*Procavia capensis*) were the most dominant species present in scat

Table 3 Caracal prey on the Cape Peninsula, South Africa as determined by scat analysis and unconsumed prey remains identified using GPS cluster analysis for three prey categories (*wild, synanthropic and exotic*). 'All scat' includes scat found at GPS clusters and opportunistically; 'all prey remains' includes prey remains found at GPS clusters and opportunistically. The results of the integrated method are presented at both minimum 0.5-day gut transit and maximum 4-day gut transit limits (see Methods)

Prey group	ALL SCAT (n = 913)				ALL PREY REMAINS (n = 385)			INTEGRATED (0.5-day, n = 739)			INTEGRATED (4-day, n = 731)		
	Count of prey items	RO	Corrected FO	% Biomass consumed	Count of prey items	RO	% Biomass consumed	Count of prey items	RO	% Biomass consumed	Count of prey items	RO	% Biomass consumed
wild	**772**	**84.56**	**82.37**	**81.02**	**163**	**42.34**	**60.25**	**481**	**65.09**	**59.03**	**476**	**65.12**	**58.78**
amphibian	2	0.22	0.33	0.21	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
bird	207	22.67	25.61	27.32	112	29.09	15.32	174	23.55	15.92	172	23.53	22.16
insect	13	1.42	0.98	0.52	0	0.00	0.00	7	0.95	**0.08**	7	0.96	0.08
mammal	513	56.19	53.01	49.76	50	12.99	44.85	279	37.75	42.57	276	37.76	36.09
reptile	37	4.05	2.45	3.21	1	0.26	0.08	21	2.84	0.45	21	2.87	0.46
synanthropic	**76**	**8.32**	**9.79**	**11.57**	**173**	**44.94**	**23.97**	**186**	**25.17**	**27.27**	**183**	**25.03**	**28.13**
bird	76	8.32	9.79	11.57	173	44.94	23.97	186	25.17	0.00	183	25.03	0.00
exotic	**65**	**7.12**	**7.84**	**7.42**	**49**	**12.73**	**15.79**	**72**	**9.74**	**13.70**	**72**	**9.85**	**13.09**
bird	3	0.33	0.39	0.29	23	5.97	2.57	21	2.84	2.99	21	2.87	2.94
mammal	62	6.79	7.45	7.13	26	6.75	13.21	51	6.90	10.71	51	6.98	10.15

and synanthropic avian prey (12.4% more, Table 3). Specifically, we find that from all prey remains found in the field, 6.23% of caracal diet was made up of domestic animals, while in scat only 1.53% of caracal diet was represented by domestic animals.

A post-hoc Tukey HSD test showed a significant difference ($P < 0.05$) in prey biomass between GPS clusters identified using the combined fix intervals and the fine scale (20-minute) fix interval. There was no significant difference in the prey biomass between the course (3-hour) and fine scale (20-minute) fix clusters, or the course and combined fix interval clusters (Online Resource Fig. S2).

Integrating scat and GPS cluster analysis data with gut transit times

Prey items found in scat samples collected at GPS clusters (n = 443), and the prey remains detected at GPS clusters rarely matched (match: only 6.09% [n = 27] of the time). Prey items found in scat matched a carcass found at previous GPS cluster feeding sites only between 1.8% (minimum transit 0.5 day, n = 8) and 3.61% (maximum transit 4-day, n = 16) of the time, indicating that scat found at GPS clusters would reflect missed feeding events rather than duplication of feeding events. In total we recorded between 7.90% (minimum transit, 0.5-day, n = 35) and 9.71% (maximum transit, 4-day, n = 43) duplicate feeding events. Using the integrated method, we estimate the number of missed feeding events to be 400 and 408 for maximum and minimum gut transit times, respectively. Therefore, after using this integration approach, feeding events increased by 54.71% (maximum transit, 4-day, n = 731) and 55.21% (minimum transit, 0.5-day, n = 739). According to both RO and biomass estimates at both gut transit time limits the majority of prey were wild mammal species, and exotic prey were < 15% of all biomass consumed (Table 3).

The inclusion of missed feeding events altered the estimation of urban prey consumed. There was a significant difference between estimated dietary compositions when comparing GPS cluster analysis with the integrated method at both maximum (4-day: $\chi^2_2 = 184.26$, $P < 0.001$, Fig. 5) and minimum gut transit times (0.5-day: $\chi^2_2 = 185.46$, $P < 0.001$, Fig. 5). We found that for both minimum (0.5-day) and maximum (4-day) gut transit limits there were significant differences in biomass between the GPS cluster method and the integrated method ($F_2 = 6.98$, $P < 0.01$, Fig. 6), with mean biomass estimates being lower for the integrated method. The majority of missed feeding events were prey items weighing < 0.5 kg (57.70% at minimum [0.5-day] and 58.60% at maximum [4-day] gut transit limit). Overall, there was no significant difference in biomass between exotic, synanthropic and wild prey ($F_2 = 2.97$, $P = 0.40$, Fig. 6). However, the interaction between method used (i.e. GPS cluster analysis or the integrated method at either gut transit limit) and prey category was highly significant ($F_4 = 14.24$, $P < 0.001$). Importantly, Tukey HSD post-hoc tests showed significantly higher exotic than wild prey biomass ($P < 0.001$) and higher synanthropic than wild prey biomass ($P < 0.001$) when integrating methods at both
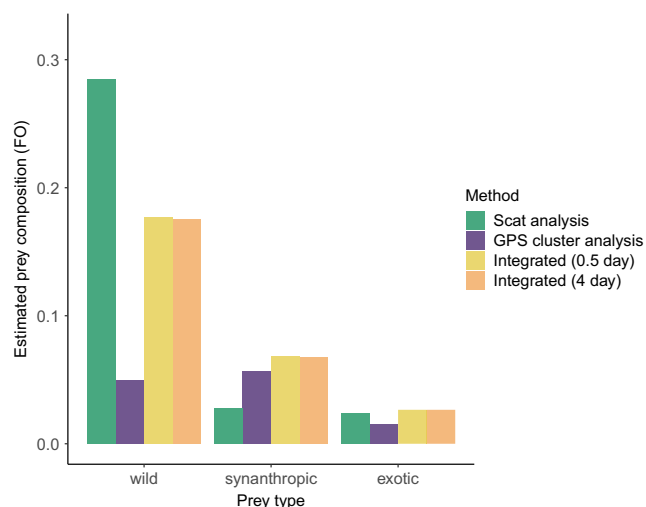
Fig. 5 Bar plot of estimated caracal dietary composition (FO, frequency of occurrence) using scat analysis, GPS cluster analysis and GPS-located prey remains the integrated method with minimum transit (0.5 day) and maximum transit time (4 day) scat samples for prey belonging to three urban categories (*wild, synanthropic* and *exotic*) from caracal (n = 22) on the Cape Peninsula, South Africa

minimum and maximum gut transit limits (Fig. 6). In contrast, there were no significant differences in biomass between prey categories for the GPS cluster method (Fig. 6) at either gut transit limits, indicating that these differences only arose using the integrated approach.

Discussion

Caracals are generalist and opportunistic predators that thrive in the Western Cape province of South Africa (Avenant and Nel
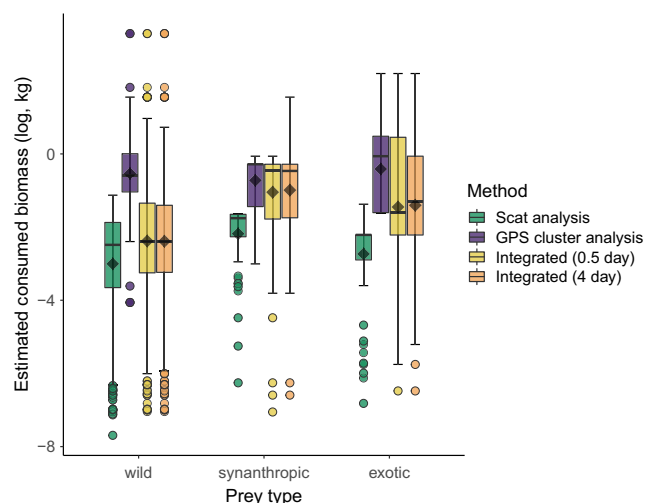
Fig. 6 Boxplots with means plotted (diamonds) of estimated caracal prey consumed biomass (kg, log transformed) using scat analysis, GPS cluster analysis, GPS-located prey remains integrated with minimum transit (0.5 day) and maximum transit time (4 day) scat samples for prey belonging to three prey categories (wild, synanthropic and exotic) from caracal (n = 22) on the Cape Peninsula, Western Cape, South Africa

2002). In our study we find caracals forage in areas on Cape Peninsula heavily impacted by human activities, and we investigated the diet of these caracals using multiple approaches. Interestingly, we found that > 40% of GPS clusters with prey remains were within 200 meters of the urban edge, while the available natural habitat also within 200 m was at 12% (Fig. 3). Overall, we observed that caracals consume a diverse prey base, as has been described in other studies based on scat and stomach contents (Palmer and Fairall 1988; Stuart and Hickman 1991; Avenant and Nel 2002; Melville et al. 2004; Braczkowski et al. 2012; Drouilly et al. 2017). The integrated approach elucidated caracal use of smaller prey items that were likely to be missed by GPS cluster investigations and overestimated using scat analysis alone. Caracals are frequent sources of human-wildlife conflict (Inskip and Zimmermann 2009; Minnie et al. 2016; Drouilly et al. 2017, 2019). In our urban system, they are persecuted for predating pets and domestic fowl. However, given frequent reports of caracal predation of domestic animals, we were surprised that caracals in our study area rarely consumed common exotic prey (e.g. domestic cats, livestock, brown rats), and rather predate native species that themselves likely capitalise on increased resources at the urban edge. Our integrated approach reveals that < 4% of caracal diet was represented by domestic animals.

We found that both the scat analysis and GPS cluster approaches had inherent biases. The scat approach overestimated small mammal prey, while the GPS cluster approach overestimated large, particularly avian, prey. The GPS cluster approach was likely further biased by the use of 3-hour fix intervals, which were likely too course to detect small prey. An intuitive solution to the detection bias inherent in GPS cluster analysis would be to increase the fix interval of GPS-collars and investigate more clusters formed during shorter time intervals. We acknowledge that our 3-hour sampling interval provided only a crude estimate of the cluster centroid, and to compensate for uncertainty in the 'activity centroid' of each cluster, we dispersed our search efforts over an area of 7,854 m² (i.e. 50 m radius from centroid estimate). Higher intensity sampling frequency is becoming more feasible with advancing technology, and movement data can now be collected in by-the-minute resolution, even for medium-sized carnivores (Svoboda et al. 2013; LaPoint et al. 2015; McCann et al. 2018; Serieys and Wilmers 2019). With higher resolution 5- to 10-minute sampling intervals, we may have been more successful in locating the true centroid of activity, and thus been able to concentrate our search efforts to a smaller area and discover minute remains of smaller prey. Further, with extremely fine-scale data, each cluster investigation takes less time because search efforts are reduced (Serieys, Matsushima, and Wilmers, unpubl. bobcat data), thus facilitating the investigation of substantially more clusters. Despite these potential advantages to finer-scale GPS data to locate feeding sites, we did not find a significant difference in estimates of biomass consumed when comparing

coarse- and fine-scale GPS fix intervals for Peninsula caracals. These findings suggest that finer-resolution sampling on the order of 20-minute fix intervals did not aid in the detection of smaller prey items for caracals in our study area, although we had less opportunity to investigate 20- minute clusters given that 20- minute data was collected infrequently (every 9–10th day) compared with daily collection of 3-hour locations. However, going forward, for those studies heavily focused on the diet of smaller carnivores, we would recommend finer-scale sampling on the order of minutes rather than hours. An additional constraint that may have affected our cluster sampling is the avoidance of two small unsafe areas. While we found little evidence to suggest the subsample of clusters we investigated were non-representative, we cannot rule out that this safety issue may have influenced our assessment of diet.

While urban development is associated with high extirpation rates of indigenous fauna (McKinney 2002), select native synanthropic species (e.g. Guinea fowl and Egyptian geese) may thrive. The increased abundance of a few synanthropic species may be sufficient to support numerous predatory species – coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), Eurasian badgers (*Meles meles*), bobcats, and mountain lions benefit from the increased abundance of indigenous and synanthropic prey at the urban edge (Bateman and Fleming 2012), while rarely predating domestic animals (MacCracken 1982; Quinn 1997; Fedriani et al. 2001; Contesse et al. 2004; Morey et al. 2007; Riley et al. 2010). Empirical data on prey abundance across the Peninsula study area that would explain where and what caracals forage are unfortunately limited. However, at the urban-wildland interface of Cape Town, vegetation is regularly transformed to create fire breaks and remove invasive alien plant species. Moreover, frequent arson in national park land close to the urban edge regularly transform the landscape further. There has been an increase in short-interval fires in recent years (Forsyth and Van Wilgen 2008), particularly over the course of this study (Serieys, *pers. obs.*). Native and alien grasses that benefit important prey species (i.e., vlei rats and four-striped grass mouse, *Rhabdomys pumilio*, Curtis and Perrin 1979) are dominant secondary succession species in fire-impacted areas (Milton 2004; Yelenik et al. 2004; Reinecke et al. 2008). Consequently, the frequent human disturbances may increase the net abundance of small mammal prey at the urban edge. Empirical evidence does show that commonly consumed avian prey are more abundant at the urban-wildland interface (e.g. rock pigeons, *Columba livia*, and Guinea fowl, Suri et al. 2017). Opportunistic generalist predators, such as caracals, prey most frequently on what prey species are most abundant on the landscape (Avenant and Nel 2002) and predatory species forage in areas that offer resources for

their prey (Newsome et al. 2015b; Smith et al. 2019). Overall, our findings suggest that food resources are more abundant on the urban edge in the Peninsula, and that transformed Peninsula landscapes support higher densities of indigenous prey species including vlei rats, Guinea fowl, and Egyptian geese.

Although our integrated approach confirmed that caracals are generalist, opportunistic predators (e.g. Avenant and Nel 2002; Braczkowski et al. 2012), our study design facilitated several added insights into the diet of a medium-sized carnivore. First, even with coarse (3-hour) fix intervals, GPS clusters formed on the landscape, and we detected avian prey remains that were underrepresented in scat. Caracals, like many other medium-sized felids (Elbroch 2003), pluck feathers prior to consuming avian prey (Grobler 1981) and large, easily visible feathers remained at clusters long after consumption. The act of plucking feathers means they ingest few that would be detected in scat or stomach contents (e.g. Stuart and Hickman 1991). Second, when implementing the integrated approach, the total count of feeding events more than doubled. Further, duplicate feeding events were rare, suggesting the integrated approach seldom results in pseudo-replication. Rather, a substantial number of missed feeding events are revealed. Finally, there were significant shifts in biomass estimates of each prey category (exotic, synanthropic and wild) when the integrated approach was used, and the differences in biomass became significant only with the addition of scat prey items, specifically due to improved detection of smaller prey. A potential issue with the integrated method is the marginally significant difference between scats found at GPS clusters and those found opportunistically (i.e. without caracal individual information), indicating there may be an issue with excluding these scats. A solution may be genetically testing scat to determine their source individual but this may be cost prohibitive (Taberlet et al. 1999; Farrell et al. 2000; Adams and Waits 2007). Overall, as reported by other studies comparing scat and cluster findings (Martins et al. 2011; Tambling et al. 2012; Pitman et al. 2014; Perilli et al. 2016; Drouilly et al. 2019), we find that each approach offers unique information. Therefore, systematically integrating both GPS-collar cluster data with scat data, and correcting for gut transit times, yields a more comprehensive diet assessment than either approach in isolation, despite the increased costs (to the animal and financially) of deploying GPS-collars.

While Peninsula caracals rarely consumed exotic species, a recent study showed that 92% of caracals (n = 24) were exposed to the ubiquitous second-generation rodenticides in and around Cape Town (Serieys et al. 2019). Thus, our results on limited consumption of exotic prey, specifically very few

targeted exotic rodents, point to widespread exposure of native prey species (like vlei rats) to these rat poisons, or to caracal tertiary exposure via other more urban-associated carnivores that frequently consume exotic rodents (e.g. large-spotted genets, *Genetta tigrina*; Widdows and Downs 2015, 2018) and are also exposed to poisons (Serieys et al. 2019). Disease spillover may also occur between domestic and free-ranging carnivores (Riley et al. 2004; Bevins et al. 2012; Carver et al. 2015) and within the Peninsula, we have observed alarming mortality rates that we suspect are linked with both pesticide (e.g. Serieys et al. 2019, Leighton et al., unpublished data) and pathogen exposure (Serieys et al., unpublished data). Although we show that caracals rarely prey on domestic cats or dogs, what limited spillover does occur during predation events may substantially threaten Peninsula caracals.

Overall, our findings highlight the importance of an integrated approach to diet studies, particularly for medium-sized carnivores. We found that not only do the independent scat and GPS cluster methods produce consistently different estimates of caracal diet, but a valuable proportion of feeding events go undetected. Diet studies have important implications for research that may form a foundation of management practices. Dietary data are often used to calculate resource selection functions (RSFs; Manly et al. 2002; Benson et al. 2016; Smith et al. 2016) that are influenced by the model input, specifically the location of feeding events and the prey species. Diet estimations, such as those we obtained from either scat analysis or GPS cluster analysis alone, could inherently skew resource selection estimates. Mesocarnivore species are often used as landscape species (Sanderson et al. 2002; Redford et al. 2003), particularly in urbanising, fragmented landscapes. The integrated approach we propose, while not entirely eliminating bias, could nevertheless provide a more complete understanding of mesocarnivore diet. Caracal are a potentially valuable indicator of trophic dynamics and threats in this global biodiversity hotspot (Myers et al. 2000; Sergio et al. 2006). Their conservation in this urbanising landscape is a priority, and the improved understanding of their diet we provide will facilitate informed management decisions.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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