Determining the diet of an African mesocarnivore, the caracal: scat or GPS cluster analysis?

Authors: Jansen, Corlé, Leslie, Alison J., Cristescu, Bogdan, Teichman, Kristine J., and Martins, Quinton

Source: Wildlife Biology, 2019(1) : 1-8

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00579

Wildlife Biology 2019: wlb.00579
doi: 10.2981/wlb.00579

Subject Editor: Al Glen. Editor-in-Chief: Ilse Storch. Accepted 29 August 2019

Determining the diet of an African mesocarnivore, the caracal: scat or GPS cluster analysis?

Corlé Jansen, Alison J. Leslie, Bogdan Cristescu, Kristine J. Teichman and Quinton Martins

C. Jansen, (https://orcid.org/0000-0002-8441-9639) ✉ (corlejansen@gmail.com) and A. J. Leslie, Dept of Conservation Ecology and Entomology, Stellenbosch Univ., Private Bag X1, 7602 Matieland, South Africa. – B. Cristescu and K. J. Teichman, The Cape Leopard Trust, Tokai, Cape Town, South Africa. BC also at: Inst. for Communities and Wildlife in Africa (iCWild), Dept of Biological Sciences, Univ. of Cape Town, Rondebosch, Cape Town, South Africa. KJT also at: Dept of Biology, Univ. of British Columbia, Kelowna, Canada. – Q. Martins, Audubon Canyon Ranch, Glen Ellen, CA, USA.

The caracal *Caracal caracal* is the largest of Africa's small felids (<20 kg). Across much of Africa, particularly where larger predators have been extirpated, caracal are one of the main carnivores contributing to livestock predation. Caracal dietary studies are outdated, typically have small sample sizes and have mainly relied on scat analysis. We used a combination of scat analysis (n = 250 scats) and GPS cluster visitation (n = 458 clusters visited; n = 91 clusters with feeding events) to estimate caracal diet in South Africa's Succulent Karoo, a global biodiversity hotspot. Based on both methods, rock hyrax *Procavia capensis* was the caracal's main prey. Small mammals accounted for 25.3% of total biomass consumed by caracal using scat analysis, however, were absent based on GPS cluster investigations. Domestic sheep *Ovis aries* biomass consumed was much higher (59.5%) when inferred from GPS cluster visitation than from scats (5%). Wild medium-to-large mammalian prey had little variation between the two methods. GPS telemetry did not enable detection of small prey (<1 kg) and possibly over-represented large prey items, including livestock. Scat analysis provided a broader representation of caracal diet, but scat investigations could have underestimated larger prey since caracals ingest only small amounts of hair from large-bodied animals. We recommend a combination of GPS cluster visitation and scat analysis to determine the diet of caracal and other mesocarnivores across a range of prey sizes.

Keywords: *Caracal caracal*, feeding ecology, mesocarnivore, predator–prey interactions, prey composition, Succulent Karoo, trophic spectrum

The caracal *Caracal caracal* is a solitary felid and the largest of Africa's smaller felids (<20 kg), with males weighing up to 15 kg and females up to 12 kg (Skinner and Chimimba 2005). Previous caracal diet studies mostly utilised the invasive method of stomach contents analysis of dead caracal, or alternatively non-invasive scat analysis (Grobler 1981, Stuart 1982, Palmer and Fairall 1988, Avenant and Nel 1997, Avenant and Nel 2002, Braczkowski et al. 2012). Scat analysis can overestimate the importance of smaller prey items, such as rodents and invertebrates, in a predator's diet (Klare et al. 2011); however, data analysis methods have been developed to decrease such biases (Ciucci et al. 1996, Marucco et al. 2008, Klare et al. 2011). Other methods used in dietary investigations include stable isotope and fatty acid analyses (Iverson et al. 2004, Thompson et al. 2005). However, these methods typically cannot differentiate between species–specific prey items for complex multi-prey systems (Hardy et al. 2010).

Global positioning system (GPS) technology has advanced carnivore research substantially (Cagnacci et al. 2010) with increased accuracy of kill site identification (Bacon et al. 2011, Martins et al. 2011), as well as providing valuable insight into other aspects of carnivore ecology including movement (Martins and Harris 2013, Odden et al. 2014), resting (Cristescu et al. 2013) and habitat selection (Cristescu et al. 2014, Fattebert et al. 2015). The use of GPS cluster visitation as a method to estimate carnivore diet has been reported to over-represent larger prey items (Pitman et al. 2012, Tambling et al. 2012, Clark et al. 2014). Svoboda et al. (2013) is one of the few studies wherein GPS radio-collars were used to determine and visit kill sites of a mesocarnivore, the bobcat *Lynx rufus*. This study, however, only focused on locating white-tailed deer *Odocoileus virginianus* kill sites. Studies in Africa utilising GPS clusters

to determine carnivore diet have been restricted to large carnivores, such as leopards *Panthera pardus* and lions *Panthera leo* (Tambling et al. 2010, Martins et al. 2011, Pitman et al. 2012). To our knowledge, mesocarnivore diet composition has not been reported using a combination of GPS cluster visitation and scat analyses outside of North America.

Caracal are reported to be one of the main mesocarnivores responsible for livestock predation in South Africa (Avenant and Du Plessis 2008, Van Niekerk 2010). The need to understand their feeding ecology has been emphasized in various past studies that have highlighted their potential for extensive damage to livestock (Avenant and Du Plessis 2008, Bergman et al. 2013, Du Plessis et al. 2015). Yet, management of caracal is often conducted based on assumptions and traditional knowledge, with little scientific evidence contributing to management decisions (Kerley et al. 2017).

The main objective of this study was to compare caracal diet estimation using scat analysis and GPS cluster visitation. We provide the first documentation on the comparative use of these two methods applied to a mesocarnivore species outside North America and hypothesize that the methods of sampling (scat versus field investigation of GPS location clusters) will influence the outcome of caracal diet estimation. We hypothesize that scat analysis will reveal a greater occurrence and biomass of small prey items than GPS cluster investigations, which will show diet to be dominated by large prey items. Based on the results of the methodological comparison, we formulate suggestions for future studies on mesocarnivore diet.

Material and methods

Study area

The 810 km² study area forms part of the Namaqualand District, Northern Cape, South Africa (Fig. 1). The area falls within the Succulent Karoo Biome, one of only two semi-arid biodiversity hotspots in the world (Mittermeier et al. 2005). Namaqualand makes up approximately a quarter of the Succulent Karoo and boasts 3500 floral species in 135 families and 724 genera, of which 25% are endemic (Driver et al. 2003, Desmet 2007). Namaqualand is classified as a winter rainfall region (Cowling et al. 1999), with a mean annual precipitation of 160 mm. The study area includes the eastern section of Namaqua National Park (30°16′62.7″S, 017°79′61.9″E) and surrounding commercial farms with free-ranging small-stock (sheep and goats) to the north, east and south of the national park. In addition to hosting naturally occurring small antelope species such as common duiker *Sylvicapra grimmia*, klipspringer *Oreotragus oreotragus* and steenbok *Raphicerus campestris*, the national park also re-introduced springbok *Antidorcas marsupialis*, gemsbok *Oryx gazelle* and red hartebeest *Alcelaphus buselaphus*. Black-backed jackal *Canis mesomelas* are the caracal's primary competitor but smaller carnivores such as Cape fox *Vulpes chama*, small-spotted genet *Genetta genetta* and Cape grey mongoose *Galerella pulverulenta*, as well as raptors may scavenge on caracal kills. The leopard *Panthera pardus*, an apex predator, also occurs within the study area.

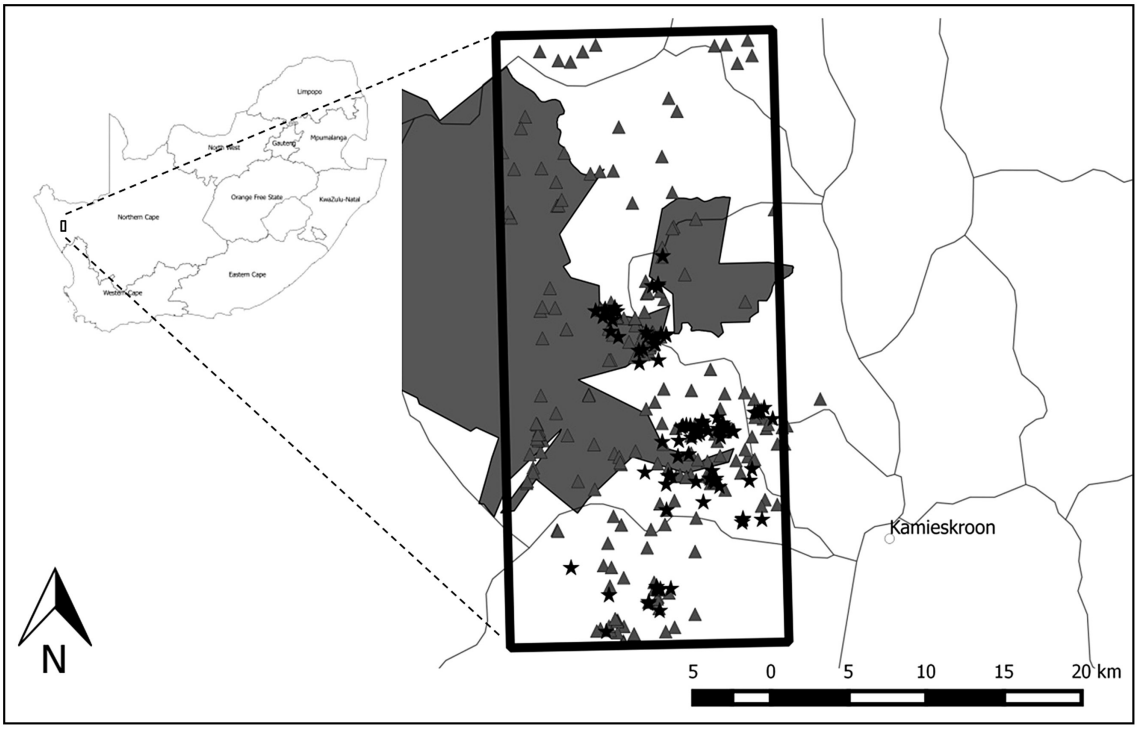

Figure 1. A map of South Africa (insert) showing the location of the study area in the Northern Cape. Locations of caracal *Caracal caracal* scats collected are indicated as a triangle and caracal clusters where prey remains were found using GPS cluster analysis are indicated as stars.

Caracal capture and immobilization

Eight male caracal were captured from March 2014–April 2015 using cage traps and padded foothold traps. Caracal were chemically immobilized using 3 mg kg^{-1} Zoletil (Tiletamine-Zolazepam) administered with a DanInject (DAN-INJECT ApS, Denmark) CO_2 pistol and fitted with satellite GPS radio-collars (Followit, Tellus Satellite Ultra-Light, Lindesberg, Sweden). These collars were chosen due to their light weight (±200 g), small size and Iridium satellite communication option. Collars were programmed to acquire a GPS location every 3 h, 24 h a day and transmit data remotely via e-mail every 33 h.

Methods used to capture and immobilize caracal for this study followed the ASM guidelines (Sikes et al. 2016). Research ethics approval was provided by Stellenbosch University (SU-ACUM14-00001), University of Cape Town (2013/V30/BC) and permits were obtained from South African National Parks (CRC-2013/029-2014) and the Northern Cape Department of Environment and Nature Conservation (FAUNA 1157/2013 and FAUNA 1158/2013). The study was conducted under the management of The Cape Leopard Trust, Cape Town.

GPS cluster investigations

The GPS radio-collar technology allowed for prompt identification of GPS cluster locations from e-mailed location data, based on a Python algorithm developed by Knopff et al. (2009). Clusters were defined as ≥2 locations occurring in a 50 m radius within six days of each other. Clustered locations, where a collared animal remained for more than 3 h, might indicate a kill or consumption site, bedding or resting site or a den site (Knopff et al. 2009, Cristescu et al. 2015a).

Cluster visitation occurred approximately eight days (7.61 days ± 0.18) after the initial GPS fix was recorded in the cluster. Each cluster site visited was searched systematically, using a 50 m radius from the cluster centroid identified by the algorithm. Total search time was standardized as two search-hours per site, with the exception of cluster sites where shrub cover was ≤50%, in which case total search time for the site was reduced to one hour. The search protocol followed a zigzag pattern, starting at the centroid and walking outwards to the edge of the 50 m radius. Searching was initiated on a random direction and covered a quarter of an imaginary disk of the given radius, then the centroid was revisited and the search was iterated three additional times to cover the remaining quarters of the disk.

Teams searched for prey remains which included carcasses, bone fragments, hair, rumen, feathers and drag marks. Where possible, carcasses were investigated for bite marks and/or method of feeding to confirm a caracal predation event. This was generally only possible for larger prey items, such as small to medium antelope and livestock. We do not know if caracal killed some of the other prey we found at clusters. However, because we only visited areas where caracal spent at least 3 h, we assumed that caracal spent at least some of that time consuming the respective prey that they either killed or scavenged.

The same method used to identify hair found in scat to species level was used to identify hair located at cluster sites. Prey species and when possible, prey sex and age (adult; sub-adult; and young-of-year [YoY]) were determined. Age assignment was done based on tooth wear (incisors and premolars) and gum recession line (Schroeder and Robb 2005).

The frequency of occurrence [FO] (per prey item) was calculated as the number of times a prey item was recorded divided by the total number of prey items and multiplied by 100 to calculate a percentage (Klare et al. 2011). Biomass was calculated by assigning an estimated weight to each prey item according to age (Morehouse and Boyce 2011, Pitman et al. 2013). Where the age was unknown, an average weight (from all age classes) of a prey species was calculated from available literature. To correct for biomass overestimation resulting from inclusion of full body weights of prey, a percentage estimation of consumption by caracal was applied to prey weights. The correction was based on photographic records of caracal's prey consumption patterns at feeding sites. The percentage of a prey item consumed differed between prey species. Prey weighing ≤4.5 kg, such as rock hyrax *Procavia capensis* and Lagomorpha, were consumed almost entirely (90%) with the exception of the rumen, viscera and fur. Larger bodied animals were only partially consumed, although this appeared dependent on the age of the prey. For example, a YoY sheep was consumed to greater extent (60%) than a subadult sheep (40%). A breakdown of percentage consumed for each prey item identified at GPS clusters is provided in Table 1 for prey items that contributed >5% to total biomass consumed.

Scat analysis

Caracal scats were collected opportunistically, along predetermined walking transects and at GPS cluster sites from radio-collared caracal. Walking transects were approximately 1 km in distance and were primarily set-up to search for livestock carcasses on farmlands, however these transects were also used to collect scats. Scats that were very old (collectively lost original shape, were dull in colour, porous and easily crumbled upon applied pressure) were not collected. To avoid pseudo-replication only two scats were collected at each cluster site (Bacon et al. 2011). Caracal scats were distinguished from those of other species based on segmentation, shape and size (Walker 1996). Because many felids use scat as a means of territorial marking, only half of each scat was collected (Martins et al. 2011).

Scat samples were autoclaved at 120°C for 20 min to allow for complete sterilisation, individually placed in a sorting tray and sorted under a fumehood, removing macroscopic fragments (e.g. bones, insects) before washing the remains of the scat in a sieve (Cristescu et al. 2015b) and drying the clean hair for 24 h in a fumehood. Hair samples were soaked in 70% ethanol for 24 h to ensure no particles were still attached to the hairs before further analysis. Hairs were then rinsed with distilled water and dried in a fumehood for an additional 24 h, or until dry.

Macroscopic and microscopic identification were used to identify prey items in each scat. Wild mammalian prey were grouped into four classes, differentiating based on body size: large mammals (>40 kg), medium- to large-sized mammals (10–40 kg), medium sized mammals (1–10 kg), and small mammals (<1 kg). Livestock was included as a

Table 1. Biomass of prey consumed by caracal estimated from feeding sites (n = 91) visited in Namaqua National Park and surrounding farmlands, Northern Cape, South Africa. Prey items that could not be identified to species level were not included in calculations. Only prey items that contributed >5% to the corrected biomass are included in the table. For a full list of prey items consumed, refer to Supplementary material Appendix 2.

Prey item	Prey age class	Estimated prey weight (kg)[a]	Prey consumption (%)	Corrected biomass consumed (kg)[b]	Corrected biomass consumed as % of all consumption sites[c]
Sheep *Ovis aries*	YoY	21.7	60	195.3	34.6
	subadult	39.4	40	15.8	2.8
	adult	58	35	60.9	10.8
	unknown	40	40	64	11.3
Rock hyrax *Procavia capensis*	**unknown**	**3.03**	**90**	**98.2**	**17.4**
Goat *Capra hircus*	YoY	22.8	40	9.1	1.6
	subadult	78	40	62.4	11.1
Lagomorpha	**unknown**	**2.35**	**90**	**29.6**	**5.2**

[a] From Schoeman (2000), Lu (2001), Skinner and Chimimba (2005).
[b] Prey weight × Prey consumption (%).
[c] Prey weight × Prey consumption/Corrected biomass consumed × 100.

distinct prey class due to relevance to human-wildlife interactions and conflict potential. Non-mammalian prey were grouped taxonomically as birds, reptiles, invertebrates, fruit/seeds, and vegetation, with a separate category for unknown items. Mammalian prey was identified to species level by means of cross-sections of hairs. Cross-sections were made by randomly selecting hairs with a pair of forceps, placing them longitudinally in a 3 mm plastic Pasteur pipette and following Douglas's protocol (1989). A light microscope was used to photograph and examine slides at 20× magnification (where possible 40×). We used LAS Core ver. 4.0 software to measure cross-sections of the hairs for comparison with the reference collections (Rhodes University, Anita Meyer [The Cape Leopard Trust], Keogh (1979, 1983) and personal slides made from hair collected from carcass specimens encountered in the field). Teeth found in scat samples were used to identify rodents to species level (de Graaff 1981) to further validate hair-based identification.

The FO, corrected frequency of occurrence [CFO] (frequency of occurrence per scat) and percentage biomass were calculated. The use of CFO was recommended by Klare et al. (2011), where each scat has a total weighting of 1. If two prey items were present in one scat, each prey item would receive a weighting of 0.5 and less as the number of prey items per scat increases.

While both FO and CFO include rare food items, biomass establishes the importance of a food item in the diet of the target animal (Klare et al. 2011). To estimate the biomass of prey consumed by caracal we used Baker et al. (1993) linear regression equation developed for bobcat to calculate a correction factor for each prey item:

$$y = 16.63 + 4.09x$$

Where y is the weight of prey consumed per scat collected (kg scat^{-1}) and x is the average body weight of the prey item (kg) (Bacon et al. 2011). This equation is only applied to prey weighing ≤4.5 kg as this is the weight at which a bobcat would ingest the entire prey item. As with bobcats, caracals only feed on parts of larger prey species such as ungulates (Baker et al. 1993, Skinner and Chimimba 2005). To account for this, Baker et al. (1993) used a set correction factor of 27 for larger prey items to account for bobcats only feeding on part of the prey item. A linear regression equation developed for bobcat was used as no data exists for caracal, and bobcats are a felid species comparable both morphologically and ecologically to the caracal (Baker et al. 1993, Skinner and Chimimba 2005, Macdonald et al. 2010).

Predator diet was analysed from GPS cluster sites with confirmed prey remains (n = 91) and caracal scats (n = 250). Differences in prey species and prey categories between the two sampling methods were tested with Fisher's exact tests, reporting χ^2 goodness of fit statistics using the programme STATSoft Statistica 11 (Statsoft Inc.).

Results

Between March 2014 and April 2015, 458 caracal GPS cluster sites were visited. Of these, prey remains were located at 91 sites, with a 19.9% success rate of finding prey remains. Cluster visitation yielded a much lower variety of prey items when compared to the 250 scat samples analysed. Only 8 prey items were identified from GPS cluster sites (or consumption sites), whereas 31 prey items were identified in scat samples (Fig. 2, Supplementary material Appendix 1). Rock hyrax was the main prey item recorded from GPS cluster site visitations (39.6%), as well as scat analysis (31.2%). Based on body size classes, small mammals (<1 kg) were not identified at GPS clusters, but 29.1% were found in scats analysed ($\chi^2 = 71.45$, DF = 1, $p < 0.001$). Small mammals were the second most frequently occurring prey class as analysed from scat. However, according to GPS cluster analyses, livestock (28.6%) was the second most frequently occurring prey class, after medium mammals (56%) (Supplementary material Appendix 2). There was a significant difference in livestock occurrence between the two sampling methods ($\chi^2 = 22.72$, DF = 1, $p < 0.001$).

Sheep *Ovis aries* was the prey item occurring second most frequently at GPS cluster visits (25.3%), significantly higher than what was identified from scat analysis (2%) [$\chi^2 = 21.99$, DF = 1, $p < 0.001$] (Table 1). Medium to large mammals, including duiker, steenbok and klipspringer, showed no significant difference in occurrence in caracal diet between the two sampling methods ($p > 0.05$).

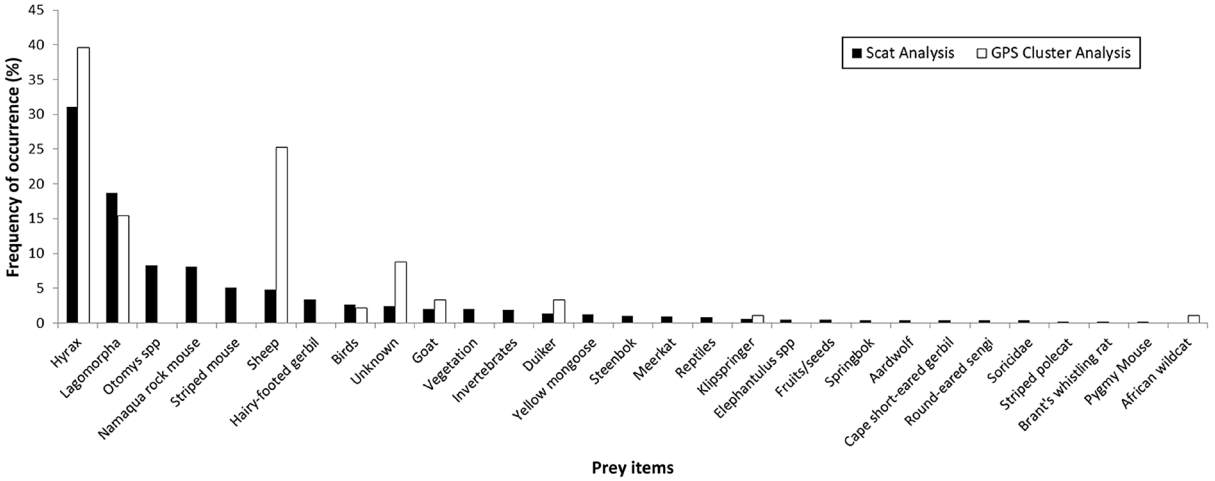

Figure 2. Comparison of prey items recorded in caracal *Caracal caracal* diet using scat analysis and GPS cluster visitation. Reptiles (Squamata) and invertebrates (Coleoptera, Orthoptera, Scorpiones and Solifugae) were grouped due to the low percentage of occurrence.

The total biomass consumed according to GPS cluster visitations was 564.4 kg, compared to 2344.9 kg from scat analysis. Sheep contributed a substantial proportion of biomass to caracal diet (59.5%) as analysed from GPS cluster sites, but only contributed 5% to the total biomass consumed based on scat analysis (Table 2, Supplementary material Appendix 3). Based on GPS clusters, rock hyrax contributed 17.2% to the total biomass consumed. However, rock hyrax contributed the bulk to the biomass from scat analysis (35.8%). *Otomys* spp. and Namaqua rock mouse *Aethomys namaquensis* were absent at GPS clusters but contributed 13.4% to the total biomass consumed as analysed from scats.

From the 250 scats collected and analysed, 89 (35.6%) scats were collected at GPS cluster sites (both feeding and non-feeding sites), 129 (51.6%) opportunistically across the study area and 32 (12.8%) along predetermined transects. Only 17 scats (6.8%) were collected at GPS cluster sites where prey remains were found. Prey classes identified in scats were generally evenly distributed between the manner in which these scats were collected (Fig. 3). From the 89 scats collected at GPS clusters, 36.1% of the prey classes identified were small mammals. The overall patterns of caracal diet remained consistent between the three scat collection methods, with medium mammals and small mammals being the main prey classes consumed by caracals in the study area.

Discussion

Prey composition identified from GPS cluster visitations and scat analysis differed, with a higher number of prey items identified through scat analysis. GPS cluster visitation findings represented primarily larger- and medium-sized prey items, such as rock hyrax and Lagomorpha, but smaller prey items were not recorded. Past studies found that small mammals, especially rodents, are prominent prey items in caracal diet (Stuart and Hickman 1991, Avenant and Nel 1997, Avenant and Nel 2002, Mellville et al. 2004). Scat analysis in our study further emphasizes the role of small mammals in caracal diet as an important prey item. The use of a corrected biomass consumed provided insight into which prey items are quantitatively important to the predator (Klare et al. 2011). In our study, smaller mammals (≤1–10 kg) identified

Table 2. Biomass of prey consumed by caracal estimated from scat (n = 250) collected in Namaqua National Park and surrounding farmlands, Northern Cape, South Africa. Only the relative biomass consumed and only prey items that contributed >5% to the biomass consumed are indicated. For a full list of prey items consumed, refer to Supplementary material Appendix 3.

Prey item	Prey weight (kg)[a]	Correction factor (kg scat^{-1})[b]	Number of occurrences (n = 297)	Prey items occurrence	Total biomass consumed (kg)[c]	Relative biomass consumed (%)
Rock hyrax *Procavia capensis*	3.03	29.02	86	28.96	840.39	35.84
Lagomorpha	2.35	26.24	52	17.51	459.45	19.59
Namaqua rock mouse *Aethomys namaquensis*	0.047	16.82	28	9.43	158.59	6.76
***Otomys* spp.**	0.131	17.17	27	9.09	156.05	6.66
Sheep *Ovis aries*	40	27	13	4.38	118.18	5.04
Striped mouse *Rhabdomys pumilio*	0.035	16.77	21	7.07	118.60	5.06

[a] From Skinner and Chimimba (2005).
[b] From Baker et al. (1993), $Y = 16.63 + 4.09x$; only for prey <4.5 kg.
[c] Correction factor × Prey items occurrence.

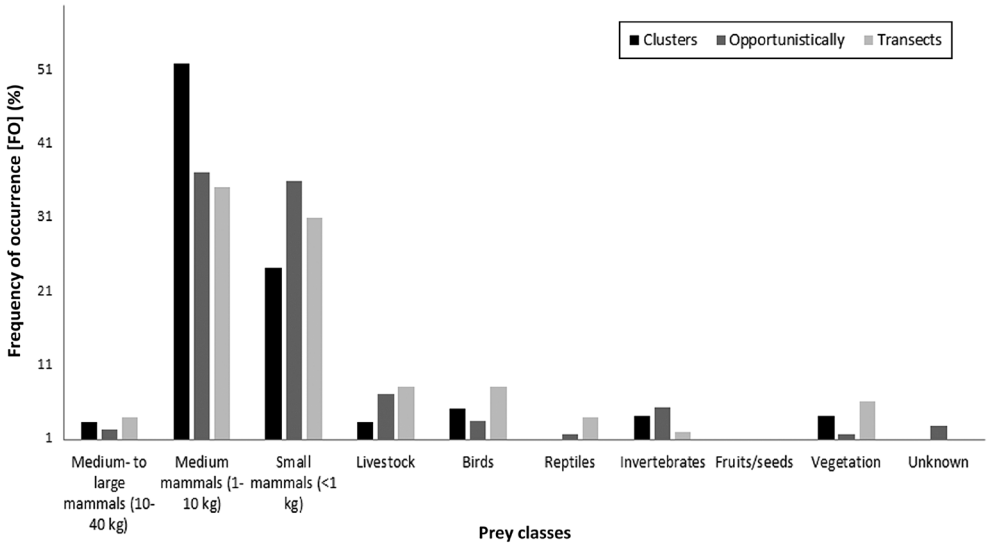

Figure 3. Comparison of scat collection methods showing the frequency of occurrence (FO) [%] of all prey classes identified from the 250 caracal *Caracal caracal* scats analyzed from Namaqua National Park and surrounding farmlands, Northern Cape, South Africa.

from scat analysis contributed 25.3% to the total biomass consumed, making it the second most important prey class in caracal diet. However, this prey class was completely absent from GPS cluster site analyses. Martins et al. (2011) used GPS cluster visitation and scat analysis to determine leopard diet in the Cederberg Mountains of South Africa. Leopards in the Cederberg are exposed to a limited and small-bodied prey base, consequently resulting in a preference for smaller prey items such as medium-sized ungulates, rock hyrax and even small mammals (Martins et al. 2011). Similar to our Namaqualand study, Martins et al. (2011) found that small mammals were absent from GPS clusters investigated, despite having 20% occurrence in scats.

We found a low contribution of medium-large wild ungulates to caracal diet based on both scat and cluster site analyses; however, sheep was a prey item that contributed substantially to the total biomass consumed by caracal in the study area. This might be a product of high numbers of sheep in the region (Jansen 2016) and in the hypothetical absence of small-stock, it is possible that caracal diet would include a larger proportion of wild ungulate prey than we documented (Grobler 1981, Braczkowski et al. 2012). According to GPS cluster visitations, sheep contributed 59.5% to the total biomass consumed, compared to only 5% as analysed from scats. If GPS cluster visitation was used as the sole method of dietary analysis, the importance of livestock as a prey item may have been overestimated. Our study only had male caracal collared, whereas caracal scat samples included males and females. Male felids have been generally found to be more predisposed to livestock predation than females (Loveridge et al. 2010). Male felids hold larger territories and young males disperse great distances to establish home ranges, making them more predisposed to contact with livestock (Linnell et al. 2001, Loveridge et al. 2010). In future work, DNA analysis of scats could be used to determine the sex of the individual that deposited each scat (Oyler-Mccance and Leberg 2012). This approach could answer the question as to whether in fact male caracal are mostly involved in livestock consumption in Namaqualand.

Several recent studies on large carnivore diet have used a combination of GPS cluster visitation and scat analysis (Bacon et al. 2011, Morehouse and Boyce 2011, Tambling et al. 2012, Pitman et al. 2013, Cristescu et al. 2015b). To our knowledge, only one study utilising GPS cluster visitation methods to determine the diet of medium-sized felids has been published to date (Svoboda et al. 2013). However, the Svoboda et al. (2013) study focused solely on bobcat predation on white-tailed deer and concluded that rapid visitation of cluster sites by researchers after the bobcat left the area should be a priority, especially to account for smaller prey species, such as white-tailed fawns. The success of finding prey remains when visiting GPS clusters for our study in Namaqualand was slightly higher (19.9%) than what Svoboda et al. (2013) found for bobcat kill clusters in general (17.4%). In Namaqualand we found it to be faster to locate ungulate carcasses at caracal consumption sites than finding rock hyrax or Lagomorpha carcasses, of which only the rumen, intestines and hair tufts were not consumed by caracal. The scavenger community likely influenced our estimation of caracal diet. Scavenger presence at caracal clusters presumably decreased detection of prey remains, or led us to overestimate biomass intake by caracal if the scavengers consumed large parts of a carcass. We suspect that scavenger effects on the reliability of our dataset were not overly extensive, because with the exception of black-backed jackal and some raptors, scavengers in our study area are small-bodied carnivores which caracal would likely displace at a kill.

Due to the sensitive nature of human–wildlife conflict concerning depredation, it is important to report results with caution. Had this study only presented GPS cluster results, it would have indicated that sheep make up the bulk of caracal diet in Namaqualand – an outcome which could lead to increased persecution of caracal. We contend that for medium-sized felids it is important to also include scat analysis if GPS cluster investigations are being used to report predator diet composition. By itself, scat analysis would have likely underestimated the contribution of large prey items to caracal diet. Furthermore, GPS cluster technology can also

be used to investigate individual diet/specialization (Elbroch and Wittmer 2013) as well as identify habitat preferences for prey consumption (Cristescu et al. 2019), making it a critical tool in studies on the effects of predators on wild and domestic prey.

Acknowledgements – The authors thank South African National Parks (Namaqua National Park) and private landowners for supporting the project and for allowing us to work in the area. We thank Woolworths Holdings Limited, Conservation South Africa, The Cape Leopard Trust, and additional sponsors (ABAX Foundation, Afrihost, Bridgestone, K-Way, Mica, Supa Quick, Ultra Dog) for providing funding and/or in-kind support. Karoo PEACE (Predator Ecology and Coexistence Experiment) team volunteers assisted with data collection and processing. Anita Wilkinson (née Meyer), of the Cape Leopard Trust assisted with the identification of mammal species from hair cross-sections. Dan Parker provided access to the Rhodes University reference collection of mammalian hair cross-sections. Justin O'Riain, University of Cape Town provided valuable suggestions at various stages of the research.
Funding – BC was supported by a Claude Leon Foundation Postdoctoral Fellowship at the University of Cape Town and KJT was supported by the Natural Sciences and Engineering Research Council Canada Graduate Scholarship – Doctoral at the University of British Columbia.
Conflicts of interest – One of the authors (Bogdan Cristescu) is a Subject Editor for Wildlife Biology. There are no other potential conflicts of interest.
Permits – Research ethics approval was provided by Stellenbosch University (SU-ACUM14-00001), University of Cape Town (2013/V30/BC) and permits were obtained from South African National Parks (CRC-2013/029-2014) and the Northern Cape Department of Environment and Nature Conservation (FAUNA 1157/2013 and FAUNA 1158/2013). The study was conducted under the management of The Cape Leopard Trust, Cape Town.

References

Avenant, N. L. and Du Plessis, J. J. 2008. Sustainable small stock farming and ecosystem conservation in southern Africa: a role for small mammals? – Mammalia 72: 258–263.
Avenant, N. L. and Nel, J. A. J. 1997. Prey use by four syntopic carnivores in a strandveld ecosystem. – S. Afr. J. Wildl. Res. 27: 86–93.
Avenant, N. L. and Nel, J. A. J. 2002. Among habitat variation in prey availability and use by caracal *Felis caracal*. – Mamm. Biol. 67: 18–33.
Bacon, M. M. et al. 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. – Wildl. Soc. Bull. 35: 409–415.
Baker, L. A. et al. 1993. Bobcat prey digestibility and representation in scats. – Proc. 47th Annu. Conf. Southeastern Fish Wildl. Agen. 47: 71–79.
Bergman, D. L. et al. 2013. The need to address black-backed jackal and caracal predation in South Africa. – In: Armstrong, J. B. and Gallagher, G. R. (eds), Proc. 15th Wildlife Damage Management Conference, pp. 86–94.
Braczkowski, A. L. et al. 2012. The diet of caracal, *Caracal caracal*, in two areas of the southern Cape, South Africa as determined by scat analysis. – S. Afr. J. Wildl. Res. 42: 111–116.
Cagnacci, F. L. et al. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. – Phil. Trans. R. Soc. B 365: 2157–2162.
Ciucci, P. L. et al. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. – Wildl. Biol. 2: 37–48.
Clark, D. A. et al. 2014. Cougar kill rates and prey selection in a multiple-prey system in northeast Oregon. – J. Wildl. Manage. 78: 1161–1176.
Cowling, R. M. et al. 1999. Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem. – Plant Ecol. 142: 3–21.
Cristescu, B. et al. 2013. Perception of human-derived risk influences choice at top of the food chain. – PLoS One 8: 1–12.
Cristescu, B. et al. 2014. Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing. – Anim. Behav. 92: 133–142.
Cristescu, B. et al. 2015a. Predicting multiple behaviors from GPS radiocollar cluster data. – Behav. Ecol. 26: 452–464.
Cristescu, B. et al. 2015b. Grizzly bear diet shifting on reclaimed mines. – Global Ecol. Conserv. 4: 207–220.
Cristescu, B. et al. 2019. Habitat selection when killing primary versus alternative prey species supports prey specialization in an apex predator. – J. Zool. <https://doi.org/10.1111/jzo.12718>.
De Graaff, G. 1981. The rodents of southern Africa. – Buttersworth, Pretoria, South Africa.
Desmet, P. G. 2007. Namaqualand – a brief overview of the physical and floristic environment. – J. Arid Environ. 70: 570–587.
Douglas, R. M. 1989. A new method of cross-sectioning hair of larger mammals. – S. Afr. J. Wildl. Res. 9: 73–76.
Driver, A. et al. 2003. Succulent Karoo Ecosystem Plan biodiversity component technical report. – Cape Conservation Unit, Botanical Society of South Africa, Cape Town, South Africa.
Du Plessis, J. J. et al. 2015. Quality and quantity of the scientific information available on black-backed jackals and caracals: contributing to human–predator conflict management? – Afr. J. Wildl. Res. 45: 138–157.
Elbroch, L. M. and Wittmer, H. U. 2013. The effects of puma prey selection and specialization on less abundant prey in Patagonia. – J. Mammal. 94: 259–268.
Fattebert, J. et al. 2015. Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. – Ecol. Appl. 25: 1911–1921.
Grobler, J. H. 1981. Feeding behaviour of the caracal *Felis caracal* Schreber 1776 in the Mountain Zebra National Park. – S. Afr. J. Zool. 16: 259–262.
Hardy, C. M. et al. 2010. Carbon source accounting for fish using combined DNA and stable isotope analyses in a regulated lowland river weir pool. – Mol. Ecol. 19:197–212.
Iverson, S. J. et al. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. – Ecol. Monogr. 74: 211–235.
Jansen, C. 2016. Diet of key predators responsible for livestock conflict in Namaqualand, South Africa. – MSc thesis, Stellenbosch Univ.
Keogh, H. J. 1979. An atlas of hair from southern African species with reference to its taxonomic and ecological significance. – PhD thesis, Univ. of Pretoria, Pretoria, South Africa.
Keogh, H. J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. – S. Afr. J. Wildl. Res. 13: 89–131.
Kerley, G. I. H. et al. 2017. Livestock predation in South Africa: the need for and value of a scientific assessment. – S. Afr. J. Sci. 113: 1–3.
Klare, U. et al. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. – Mamm. Rev. 41: 294–312.
Knopff, K. H. et al. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. – J. Wildl. Manage. 73: 586–597.
Linnell, J. D. C. et al. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. – Anim. Conserv. 4: 345–349.

Loveridge, A. J. et al. 2010. People and wild felids: conservation of cats and management of conflicts. – In: Macdonald, D. W. and Loveridge, A. J. (eds), Biology and conservation of wild felids. Oxford Univ. Press, pp. 161–195.
Lu, C. D. 2001. Boer goat production: progress and perspective. – Proc. 2001 Int. Conf. Boer Goats China.
Macdonald, D. W. et al. 2010. *Dramatis personae*: an introduction to the wild felids. People and wild felids: conservation of cats and management of conflicts. – In: Macdonald, D. W. and Loveridge, A. J. (eds), Biology and conservation of wild felids. Oxford Univ. Press, pp. 3.
Martins, Q. and Harris, S. 2013. Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. – Afr. J. Ecol. 51: 571–579.
Martins, Q. et al. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. – J. Zool. 283: 81–87.
Marucco, F. et al. 2008. Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. – J. Mammal. 89: 665–673.
Mellville, H. I. A. S. et al. 2004. Prey selection by caracal in Kgalagadi Transfrontier Park. – S. Afr. J. Wildl. Res. 34: 67–75.
Mittermeier, R. A. et al. 2005. Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. – CEMEX, Mexico City.
Morehouse, A. T. and Boyce, M. S. 2011. From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. – Front. Ecol. Environ. 9: 440–445.
Odden, M. et al. 2014. Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. – PLoS One 9: e112044.
Oyler-Mccance, S. J. and Leberg, P. 2012. Conservation genetics and molecular ecology in wildlife management. – In: Silvy, N. J. (ed.), The wildlife techniques manual. John Hopkins Univ. Press, pp. 526–526.
Palmer, R. and Fairall, N. 1988. Caracal and African wild cat diet in the Karoo National Park and the implications thereof for hyrax. – S. Afr. J. Wildl. Res. 18: 30–34.
Pitman, R. T. et al. 2012. Predictive modelling of leopard predation using contextual global positioning system cluster analysis. – J. Zool. 288: 222–230.
Pitman, R. T. et al. 2013. Global positioning system-located kills and faecal samples: a comparison of leopard dietary estimates. – J. Zool. 292: 18–24.
Schoeman, S. J. 2000. A comparative assessment of Dorper sheep in different production environments and systems. – Small Ruminant Res. 36: 137–146.
Schroeder, M. A. and Robb, L. A. 2005. Criteria for gender and age. – In: Braun, C. E. (ed.), Techniques for wildlife investigations and management. The Wildlife Society, USA, pp. 303–338.
Sikes, R. S. and Animal Care and Use Committee of the American Society of Mammalogists 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. – J. Mammal. 97: 663–688.
Skinner, J. D. and Chimimba, C. T. 2005. The mammals of the southern African subregion. – Cambridge Univ. Press.
Stuart, C. T. 1982. Aspects of the biology of the caracal (*Felis caracal* Schreber 1776) in the Cape Province, South Africa. – MS thesis, Univ. of Natal. Kwazulu-Natal, South Africa.
Stuart, C. T. and Hickman, G. C. 1991. Prey of caracal *Felis caracal* in two areas of Cape Province, South Africa. – J. Afr. Ecol. 105: 373–381.
Svoboda, N. J. et al. 2013. Identifying bobcat *Lynx rufus* kill sites using a global positioning system. – Wildl. Biol. 19: 78–86.
Tambling, C. J. et al. 2010. Methods for locating African lion kills using global positioning system movement data. – J. Wildl. Manage. 74: 549–556.
Tambling, C. J. et al. 2012. Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters. – J. Zool. 286: 102–109.
Thompson, D. R. et al. 2005. Stable isotope in ecological studies. – Oecologia 144: 517–519.
Van Niekerk, H. N. 2010. The cost of predation on small livestock in South Africa by medium-sized predators. – MS thesis, Univ. of the Free State, Bloemfontein, South Africa.
Walker, C. 1996. Signs of the wild. – Struik Publishers.

Supplementary material (available online as Appendix wlb-00579 at <www.wildlifebiology.org/readers/appendix/wlb-00579>). Appendix 1–3.