Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters

C. J. Tambling[1,2], S. D. Laurence[3], S. E. Bellan[4], E. Z. Cameron[1,5], J. T. du Toit[1,6] & W. M. Getz[1,4]

1 Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
2 Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa
3 Enviro-Insight, Murrayfield, Pretoria, South Africa
4 Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, USA
5 School of Zoology, University of Tasmania, Hobart, Tasmania, Australia
6 Department of Wildland Resources, Utah State University, Logan, UT, USA

Abstract

Scat analysis is one of the most frequently used methods to assess carnivoran diets, and global positioning system (GPS) cluster methods are increasingly being used to locate feeding sites for large carnivorans. However, both methods have inherent biases that limit their use. GPS methods to locate kill sites are biased towards large carcasses, while scat analysis overestimates the biomass consumed from smaller prey. We combined carcass observations and scats collected along known movement routes, assessed using GPS data from four African lion *Panthera leo* prides in the Kruger National Park, South Africa, to determine how a combination of these two datasets change diet estimates. As expected, using carcasses alone underestimated the number of feeding events on small species, primarily impala *Aepyceros melampus* and warthog *Phacochoerus africanus*, in our case, by more than 50%, and thus significantly underestimated the biomass consumed per pride per day in comparison with when the diet was assessed using carcass observations alone. We show that an approach that supplements carcass observations with scats that enables the identification of potentially missed feeding events increases the estimates of food intake rates for large carnivorans, with possible ramifications for predator–prey interaction studies dealing with biomass intake rate.

Quantifying carnivoran diets is an essential step in investigating carnivoran ecology (Mills, 1992), and provides the basis for understanding population-level impacts that carnivorans may have on prey populations (Owen-Smith & Mason, 2005; Owen-Smith, 2008). Numerous techniques are available for the assessment of carnivoran diets (Mills, 1992), including highly invasive stomach content analysis (Smuts, 1979), moderately invasive continuous direct observations (Mills & Shenk, 1992) and non-invasive faecal analysis (Andheria, Karanth & Kumar, 2007) and carcass observation (Lehmann et al., 2008). Each of the approaches is limited either due to inherent biases, or the feasibility and practicality of the technique.

Recent advances in global positioning system (GPS) technology permit the collection of animal location data at a scale that is sufficiently fine to provide a good approximation to the continuous movement path of individuals (Getz & Saltz, 2008). Despite this, a trade-off between the frequency of points collected and the total length of the movement path still exists owing to the limited battery life of most collars (Sand et al., 2005). Obtaining GPS fixes at an hourly interval for female lions *Panthera leo* in the Kruger National Park allowed the development of models that increased the probability of locating carcasses at GPS clusters in time (Tambling et al., 2010). However, small prey items might be entirely consumed by the predator (see Power, 2002), or scavengers might subsequently eliminate signs of some feeding sites. Similarly, the GPS approach has proved useful in dietary studies of mountain lions *Puma concolor* (Anderson & Lindzey, 2003), wolves *Canis lupus* (Sand et al., 2005; Franke et al., 2006) and leopards *Panthera pardus* (Martins et al., 2011), but the bias towards large prey has remained largely intractable (but see Martins et al., 2011).

The analysis of large numbers of carnivoran scats offers a non-invasive estimate of carnivoran diets. Despite widespread use, this method over-estimates the biomass and underestimates the numbers of small species consumed (Karanth & Sunquist, 1995; Marker et al., 2003), although correction factors are available for some species to correct for this bias (Ackerman, Lindzey & Hemker, 1984). In addition, a problem
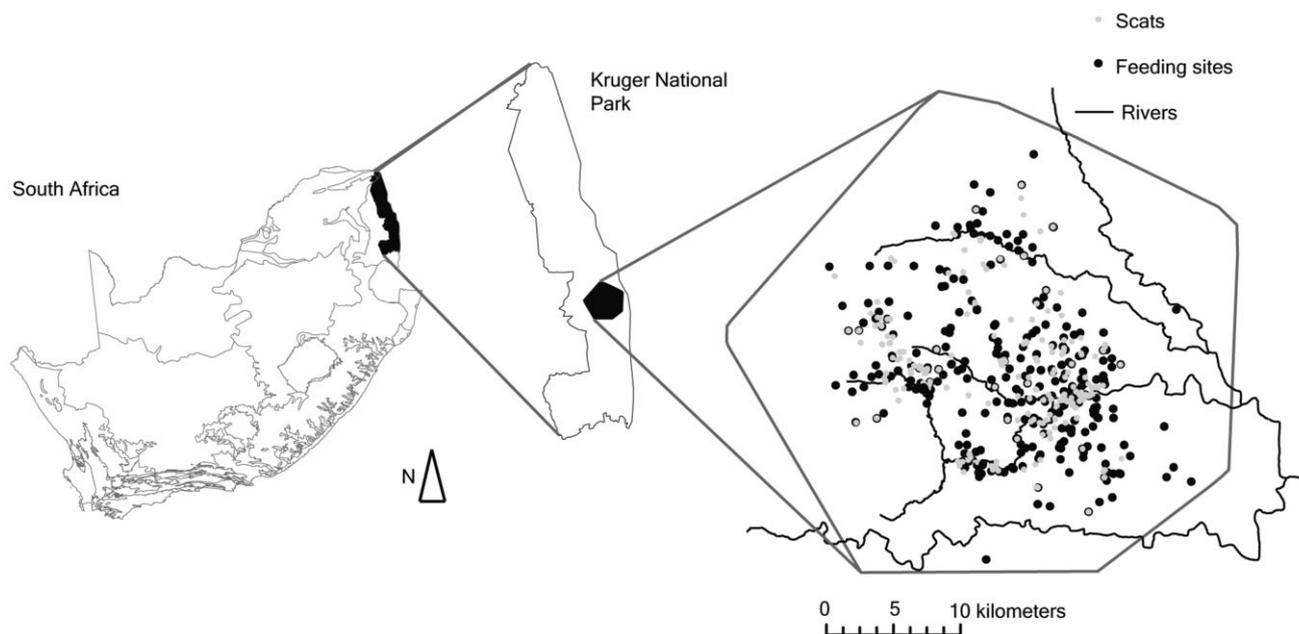
Figure 1 Study area in the central region of the Kruger National Park, South Africa, scats located at GPS clusters, and kills located at GPS clusters.

of autocorrelation occurs (Marucco, Pletscher & Boitani, 2008) when clusters of scats are produced by social carnivorans consuming prey items that are large in relation to their body size (e.g. wild dogs *Lycaon pictus*, lions, wolves). Despite the problems associated with both GPS cluster techniques and scat analysis, a combination of the two approaches can reduce possible pseudo-replication of correlated scats and identify small kills that are missed from direct observation (Marucco *et al*., 2008; Martins *et al*., 2011).

Although the most accurate method of quantifying lion diet composition is continuous observation of study animals, thereby allowing all predation activity to be directly observed (Mills & Shenk, 1992; Funston *et al*., 1998), this approach is not always logistically feasible (Hayward *et al*., 2009). Alternative methods, including scat and GPS approaches, have not been comprehensively tested; hence the bias inherent in results obtained through these methods is uncertain. Owing to their social nature, lions generally kill and consume prey items the same size as or larger than themselves (Radloff & du Toit, 2004; Hayward & Kerley, 2005), resulting in the possibility of correlated clusters of scats from a single large carcass. In this study, we investigated how the incorporation of scats into a GPS cluster approach might alter lion diet estimates, where diet estimates refer to both the composition and the total biomass of food consumed by lions.

Materials and methods

We conducted the study between April 2005 and May 2007 in the Kruger National Park, in a 1000 km² area around the Satara rest camp (Fig. 1 and 31.77° E, 24.39° S) in the central region of the park. Rainfall in the area is highly seasonal, with

the majority falling between October and March, when there is also an increase in average temperature (Venter, Scholes & Eckhardt, 2003). As a consequence, faecal collection becomes more difficult during the rainy season as dung beetle (Coleoptera; Scarabaeinae) activity and rain reduce the number of collectable samples. The study area is an open tree savannah with a moderate to sparse shrub layer and dense grass layer, with marula *Sclerocarya birrea* and knob-thorn *Senegalia nigrescens* the dominant tree species, and red grass *Themeda triandra* and stinking grass *Bothriocloa radicans* the dominant grass species (Venter *et al*., 2003). Our study area includes the northern component of the wildebeest *Connochaetes taurinus* and zebra *Equus quagga* migrations, and high densities of these species occur in the wet months (Gertenbach, 1983). Resident buffalo *Syncerus caffer*, kudu *Tragelaphus strepsiceros*, giraffe *Giraffa camelopardalis* and waterbuck *Kobus ellipsiprymnus* occur in large numbers, all combining as a prey base for a high lion population density (Ferreira & Funston, 2010). Across the park, impala *Aepyceros melampus* are the most abundant prey species and provide the bulk of food for lions and the other large predators (Mills & Biggs, 1993; Radloff & du Toit, 2004).

Five female lions from four prides were collared with GPS/GSM units (i.e. GPS with mobile phone capabilities to access data; African Wildlife Tracking) between April 2005 and May 2007. Lions were captured and collared by South African National Parks (SANParks) veterinarians using standard SANParks protocols (Smuts, Whyte & Dearlove, 1977). The fix schedule of the collars (one fix per hour at night [18:00–06:00] when the lions are most active (Hayward & Slotow, 2009), and three fixes during the day [06:00–18:00] when lions tend to rest) provides a set of locations used to construct a

movement path over time for each collared lion. Along this movement path, we identified spatio-temporal clusters of GPS locations (hereafter referred to as clusters), where a cluster is defined as consecutive (i.e. 2 or more) GPS co-ordinates within 100 m of the previous GPS co-ordinate (see Tambling *et al.*, 2010). Investigated clusters were searched for carcasses and scats in a 50-m diameter around the GPS point, identified as the start of the cluster (accounting for GPS error – Tambling, 2010). If further GPS points identified as part of the cluster did not fall within the initial 50 m search diameter, new 50 m search diameters were created around those GPS positions. The duration of the search time was dependent on the vegetation cover of the area. Carcasses found at clusters were classified to species, age and sex based on the presence of identifiable material, such as horns, jaws, bones and hair. We defined the number of feeding events for each species for each pride based on the observed carcasses found at clusters as $n_{\text{car.sp.}}$. For all species-specific analysis, we removed carcasses that could not be identified to species level ($n = 3$).

Clusters (with and without observed carcasses) were searched for the presence of lion scats. Following collection, scats were washed under running water through a metal sieve to isolate all undigested distinguishable prey items (predominantly hair remains, but on some occasions hoof and horn remains as well). Hair was examined macroscopically (length, colour and texture) and microscopically (cross-section characteristics and cuticle-scale patterns) to identify prey species. Cross sections of hairs were made using the method outlined in Douglas (1989), and cuticle scale imprints were obtained by investigating inverse imprints under a light microscope (van Kesteren, 2006). Both cross-section and cuticle-scale imprints were compared against reference collections to identify the species consumed (Keogh, 1983; Buys & Keogh, 1984). If multiple scats were found at GPS clusters, and if the same prey species occurred in more than one scat, we used the collection of scats containing remains of that prey species as a single sample unit to avoid over-representation of prey items from multiple scats (Marucco *et al.*, 2008).

Comparing frequency distributions of carcasses of prey species across the four prides revealed that two of the six pairwise comparisons were significantly different. Therefore, we conducted analyses at the pride level and averaged results (mean ± SE) across prides ($n = 4$) to estimate the diet at the population level. Carcasses and scats found at each cluster occurred at known dates and times along the movement path of each pride, and these data were used to create a history of feeding events related to either (1) a carcass alone, (2) a scat alone, or (3) a combination of a carcass and a scat from the same feeding event. Since no estimate for transit times through the guts of lions exists (Breuer, 2005), based on cheetah *Acinonyx jubatus* transit times (48–111 h: Marker *et al.*, 2003), we assumed a minimum of 2 days and a maximum of 5 days. The minimum and maximum gut transit times correspond to a high and low level of bias in terms of missed feeding events. The low bias assumes a long (120 h) gut transit time, with all scats produced within 5 days of an observed carcass being the result of that carcass. The high bias assumes a 48 h gut transit time with all scats produced within 2 days of an observed

carcass being the result of that observed carcass. Therefore, if species A was consumed on day 1, and 3 days later, species A was found in the scats for the same pride of lions, we assumed that the scat originated from the observed carcass of species A for the low bias estimate, but that we had missed a feeding event of species A for the high bias estimate. For each pride, we defined the number of missed feeding events for each species based on the inclusion of scats as $n_{\text{scat.sp.}}$, and this value is calculated for both the low and high biases for missing feeding events.

To investigate the temporal relationship between observed carcasses and scats found for the same lion group following a feeding event, we tracked the presence and identity of scats found at subsequent clusters for each lion group for 10 days after the observed feeding event. We then plotted the daily proportion of scats containing the species identified at the feeding site against the proportion of scats containing a different species over the 10-day period. Scats at a carcass site are a function of previous carcasses consumed and/or the observed carcass. Scats found at clusters not associated with a carcass are a function of the most recently observed carcass (within the range of days delineated by gut transit times) and/or possible missed feeding events that occurred once the lions had moved away from the last observed carcass. However, during the observed movement path for each lion pride, there exists a possibility that the same prey species contributes two consecutive feeding events, with either the first or second carcass not detected during cluster investigations. When this happens, the scats found at a cluster could belong to a more recent feeding event of the same species that was missed, and thus our estimates for $n_{\text{scat.sp.}}$ are an underestimate. To quantify the possible magnitude of this underestimation, we calculated how often the same species was found consecutively at clusters in a two-day window (average kill rate of female lions in Kruger National Park = 1.8 days, Funston *et al.*, 1998) as a proportion of all feeding events within a two-day window. We multiplied the proportion of same-species consecutive feeding events by $n_{\text{scat.sp.}}$ for each prey species for each pride to estimate the number of missed feeding events per prey species per pride resulting from undetected consecutive feeding events, defined as $n_{\text{con.sp.}}$. The final corrected number of individuals of each prey species consumed by each pride is then calculated as $n_{\text{sp.}} = n_{\text{car.sp.}} + n_{\text{scat.sp.}} + n_{\text{con.sp.}}$.

For each pride, as well as for all averaged prides, we used *G*-tests (Zar, 1999) to test if adding missed feeding events through scat-supplementation (using both the high- and low-bias levels of missed feeding events) changed the diet composition of lions as opposed to when the diet is estimated from observed carcasses alone. Using the log unit weight (taking into account the range of age and sex categories in the prey population) of each prey species (Coe, Cumming & Phillipson, 1976), we investigated if missed feeding events (using both high- and low-bias estimates) were related to the size of the prey species. We calculated the total biomass of each species consumed by each pride as the product of the unit weight of the species (Coe *et al.*, 1976), the proportion of edible meat for that species (see Funston *et al.*, 1998, appendix 1) and the number of individuals of that species consumed by each pride.
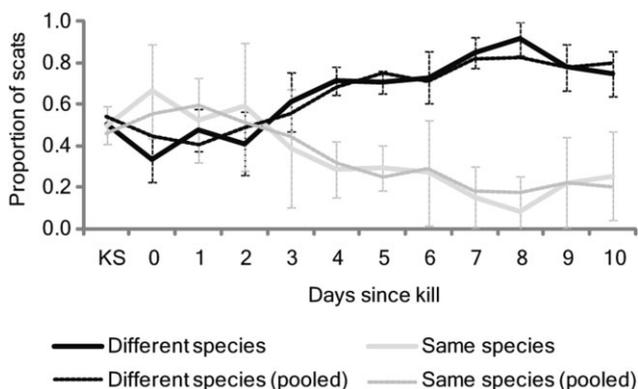
Figure 2 Proportion of scats (±SE) containing remains of the same prey species (grey) or a different species (black) as the focal kill (at the kill site [KS] and each day thereafter), based on the investigation of GPS clusters in the central region of the Kruger National Park, South Africa, between April 2005 and May 2007.

We used *G*-tests to assess whether the percent diet composition based on the biomass of each prey species consumed changes after implementing the scat-supplemented approach. Finally, using these biomass estimates, we investigated the difference in consumed biomass per pride per day between the three approaches (carcass observations, high bias of missing feeding events and low bias of missing feeding events) using ANOVA with a Tukey *post hoc* test to identify significant differences between approaches.

Results

Between April 2005 and May 2007, we investigated 59.5% (1447 out of 2433) of all clusters identified, finding 236 carcasses (103, 70, 41 and 22 carcasses per pride respectively) and 208 scats (91, 48, 50 and 19 scats per pride respectively). Clusters were investigated a median of 24 (range 0–331) days after lions occupied the clusters. Scats were found at clusters that were investigated a median of 16 (range 0–195) days after lions occupied the clusters. Scats were found both at carcass sites ($n = 47$) and at resting sites not associated with a carcass ($n = 161$). In 50% (±9%) of the scats found at carcass sites, the detected species was the same as the consumed species at that cluster (Fig. 2). For all consecutive feeding events within the two-day window ($n = 60$), the same species was found consecutively 16% (±7%) of the time. Therefore, two-thirds (50 + 16% = 66%) of all scats found at carcass sites probably originated from a carcass fed on prior to the feeding event, where the scat was collected. Once lions moved away from a known carcass, 52–66% of scats found at subsequent clusters in the following 2 days contained remains of the same species as that carcass and this level declined to ~20% in days 4–10 (Fig. 2).

Numerically, the dominant prey species identified from carcasses located at clusters were zebra (24.6 ± 4.3%), wildebeest (18.8 ± 5.6%) and impala (15.4 ± 7.1%; Table 1). The most

important prey species in terms of percent consumed biomass were giraffe (30.6 ± 9.5%), zebra (21.8 ± 2.7%) and buffalo (17.9 ± 6.2%; Table 1). Assuming gut transit times of 2 and 5 days, respectively, and consecutive kills were from the same prey species in 16% of kills made within 2 days of each other, we estimated that we missed 147 and 111 feeding events ($n_{scat.sp.}$ + $n_{con.sp.}$) for the high- and low-bias levels respectively. Therefore, we detected 383 and 347 feeding events in total for the high- and low-bias levels, respectively. Assuming a high bias of missing carcasses, detected feeding events increased by 69% (±13%), and, assuming a low bias of missing carcasses, detected feeding events increased by 52% (±7%). Following scat-supplementation, impala (19.6 ± 5.1% and 17.3 ± 3.6% for the high- and low-bias estimates respectively) became numerically the second most consumed prey species, but no change in the order of importance was evident in terms of the consumed biomass (Table 1). Following scat supplementation, we found no significant changes in the estimated diet composition calculated from prey numbers ($G < 13.9$, $P > 0.08$ for all prides) or biomass ($G < 9.3$, $P > 0.42$ for all prides).

Investigating carcasses alone and prior to scat-supplementation, we found 62% (±10%) and 57% (±12%) less impala feeding events in comparison to when carcasses and scats were combined, depending on whether we implemented a short or long gut transit times (Fig. 3a,b). Similarly, without scat-supplementation, we detected 68% less warthog *Phacochoerus africanus* feeding events for both the short and long gut transit times (Fig. 3a,b). For medium-sized species (100–300 kg [2–2.5 on the log scale]), the failure to detect carcasses declined to 25–45%, whereas for larger species (>300 kg [>2.5 on the log scale]), we increased our detection of feeding events by 10–20% (Fig. 3a,b), by incorporating scats and carcasses. As a result, there is a significant negative relationship between the log unit weight of each prey species and the percentage of missed feeding events between the two approaches of estimating diet for both the high bias of missing carcasses ($F_{1,9} = 48.5$, $R^2 = 0.84$, $P < 0.005$, Fig. 3a) and the low bias of missing carcasses ($F_{1,9} = 70.5$, $R^2 = 0.89$, $P < 0.005$, Fig. 3b).

There was a significant difference in the estimated biomass of meat consumed by the prides per day when diets were assessed using the three different approaches ($F_{2,9} = 7.2$, $P < 0.05$, Fig. 4). *Post hoc* tests revealed that this difference was driven by the detection of a significantly higher biomass of consumed meat by lion prides per day, when calculating diet estimates assuming a high bias of missing feeding events (46.0 ± 3.3 kg/day/pride) as compared with estimating consumed biomass from carcasses alone (31.2 ± 2.6 kg/day/pride, $P <$ 0.05, Fig. 4). The same trend was evident when we calculated consumption rates based on a low bias of missed feeding events (41.0 ± 3.3 kg/day/pride), although the difference to the biomass consumed from carcasses alone was no longer statistically significant ($P = 0.079$, Fig. 4).

Discussion

Adequate knowledge of the movement paths of carnivorans determined by GPS (our study) or spoor tracking (Melville,

Table 1 Mean percent representation (± SE) of prey species in the diet (numerical and biomass consumed) of lions in the central region of Kruger National Park, South Africa, between April 2005 and May 2007, utilizing three approaches to estimate the diet

	Numerical diet estimate			Biomass diet estimate		
	Carcasses	Scat-supplemented		Carcasses	Scat-supplemented	
	Av.	High bias	Low bias	Av.	High bias	Low bias
Buffalo	10.1 (3.9)	7.8 (3.3)	7.8 (3.3)	17.9 (6.2)	15.3 (6.2)	16.5 (5.9)
Elephant	0.2 (0.2)	0.1 (0.1)	0.1 (0.1)	1.6 (1.6)	1.1 (1.1)	1.2 (1.2)
Giraffe	10.6 (3.9)	8.9 (3.4)	7.1 (2.3)	30.6 (9.5)	28.4 (9.4)	26.4 (8)
Impala	15.4 (7.1)	19.6 (5.1)	17.3 (3.6)	3.9 (1.7)	5.4 (1.3)	5.5 (1.3)
Kudu	7.4 (2.5)	7.9 (2.1)	7.2 (1.5)	4.8 (1.7)	5.6 (1.5)	5.8 (1.4)
Warthog	2.2 (1.4)	4.4 (0.8)	3.8 (0.5)	0.5 (0.3)	1.3 (0.1)	1.3 (0.1)
Waterbuck	7 (1.4)	9.1 (3.4)	7.5 (2.3)	5.4 (1.5)	8.6 (4.3)	7.5 (3.1)
Wildebeest	18.8 (5.6)	17.8 (5)	16.4 (4.4)	11.6 (4.6)	12.2 (4.4)	12.2 (4.2)
Zebra	24.6 (4.3)	20.9 (3.7)	20 (3.5)	21.8 (2.7)	20.6 (2.6)	22 (2.3)
Ostrich	0.6 (0.6)	0.6 (0.3)	0.6 (0.3)	0.3 (0.3)	0.3 (0.2)	0.4 (0.2)
Porcupine	0.6 (0.6)	1.4 (0.5)	1.4 (0.5)	0 (0)	0.1 (0)	0.1 (0)
Unknown	2.5 (2.2)	1.5 (1.3)	1.5 (1.3)	1.6 (1.4)	1.1 (1)	1.2 (1.1)

The uncorrected estimate uses only carcasses found at GPS clusters, whereas the scat-supplemented approach combines scats and kills observed at GPS clusters along a known movement trajectory for each collared lion. The high bias assumes a gut transit time of two days and the low bias assumes a gut transit time of five days, which are used to identify feeding events that have been missed.
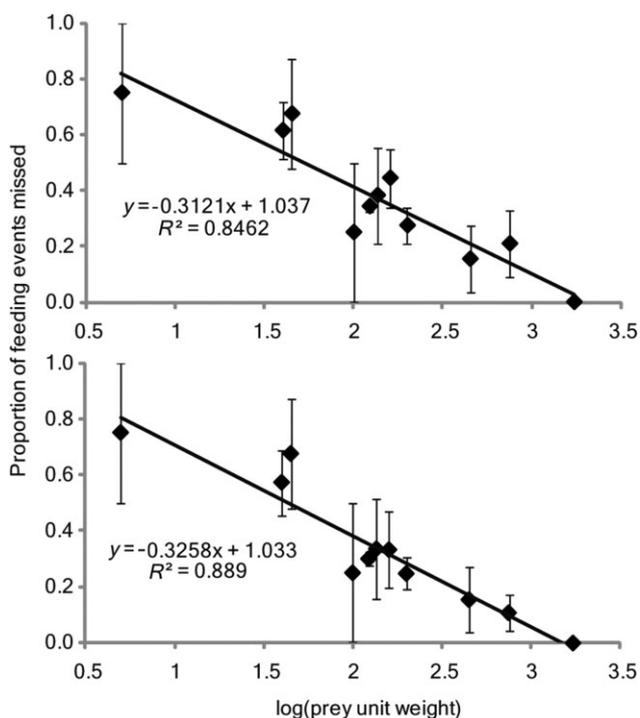

Figure 3 Relationship between the log unit mass of prey species and the estimated percent of missed kills, using the scat-supplemented approach in the central region of the Kruger National Park, South Africa, between April 2005 and May 2007 (Top: high bias of missing feeding events, Bottom: low bias of missing feeding events).

Figure 4 Daily food consumption by female lion groups in the Kruger National Park, South Africa, calculated using carcasses against carcasses and scats for short and long gut transit times.

carcass observations to help define independent feeding events (Marucco *et al.*, 2008); (2) by locating carcasses and then collecting scats to reduce the bias against smaller species in the final diet estimates (current study, Jedrzejewski *et al.*, 2000; Martins *et al.*, 2011).

GPS tracking of large carnivorans results in datasets of carcasses located at clusters and these datasets are increasingly being used to estimate prey selection and feeding rates in large carnivorans (Knopff *et al.*, 2010). However, it must be recognized that small prey species are under-represented in such data sets (Franke *et al.*, 2006). Suggestions to counter this bias include reducing the time between GPS fixes (Sand *et al.*, 2005; Webb, Hebblewhite & Merrill, 2008), using alternate movement metrics for model development (Webb *et al.*, 2008), increasing the number of clusters investigated in the field (Sand *et al.*, 2005; Knopff *et al.*, 2009), or collecting scats independently of carcass observations (Martins *et al.*, 2011).

Bothma & Mills, 2004; Marucco *et al.*, 2008) enables data from scats and carcasses to be combined chronologically to identify feeding events. This can be achieved through two different approaches: (1) by collecting scats and then using
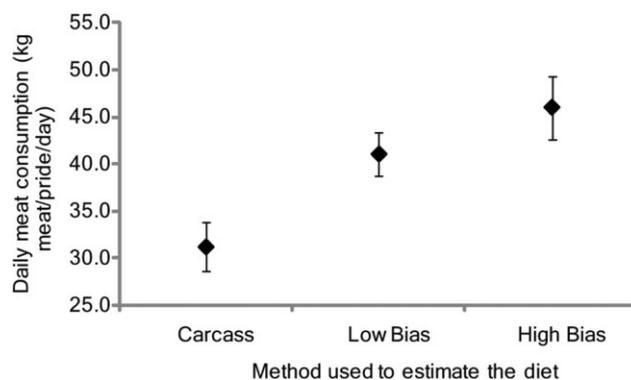
However, until now, none has suggested using scats collected at GPS clusters to adjust the bias.

Our results confirm previous GPS-based studies in the northern hemisphere on mountain lions (Anderson & Lindzey, 2003; Knopff *et al.*, 2009) and wolves (Sand *et al.*, 2005; Franke *et al.*, 2006; Webb *et al.*, 2008) that the use of carcasses alone underestimates the presence of smaller prey species in the diet of large carnivorans. In the Kruger National Park, impala (45–50 kg) and warthog (45–100 kg) were under-represented by as much as 50%. Similarly, in Hwange National Park, small species (common duiker *Sylvicapra grimmia* [15–20 kg] and reedbuck *Redunca arundinum* [30–70 kg]) were considerably under-represented when diets were based on carcass observations estimated from GPS cluster investigation (van Kesteren, 2006).

Despite the considerable underestimation of these smaller prey species, their inclusion did not significantly alter the estimated composition of the lion diet. This is contrary to findings that wolf diet estimates changed significantly once scat-supplementation was applied in an additive approach (Marucco *et al.*, 2008), but the size of the sample of observed carcasses (51 for wolves vs. 236 for lions) could be a key factor. The effect of small sample size will be exacerbated if some prey species inhabit inaccessible regions (Marucco *et al.*, 2008). In our open savannah study area, our diet estimate based on carcasses alone is based on a large sample size, such that detecting an additional 30–37 impala carcasses only resulted in a compositional increase of 1.8–4.2% in the diet.

We did, however, find a significant effect of missed kills on the estimation of biomass consumed by the lion prides. The biomass of food contributed by each prey species is important for the estimation of kill rates, which in turn is important for the conservation and management of carnivorans (Hebblewhite *et al.*, 2003). Predator kill rates are calculated by taking into account all kills over an extended monitoring period (Merrill *et al.*, 2010), but the majority of studies on African carnivorans do not estimate kill rates, because finding the majority of kills over long periods requires continuous observation (Funston *et al.*, 1998), which is often logistically not possible (Martins *et al.*, 2011). Combining data from scats and carcasses over periods, during which researchers are frequently (but not necessarily continuously) monitoring the study animals in the field, may provide a better chance to estimate kill rates for African carnivorans, and as such allow the development of functional response curves that will increase the understanding of the link between predators and prey (Merrill *et al.*, 2010). Additionally, accurate knowledge of the biomass consumption by large carnivorans is beneficial for the development of carrying-capacity models (Hayward, O'Brien & Kerley, 2007).

Although this approach deals with correlated clusters of scats associated with social carnivorans, other aspects of sociality are important to consider. Scats could be produced by other individuals not associated with feeding sites, reducing the confidence in combining scats and feeding events into single sample units. Nevertheless, female lions in southern Africa have a high group fidelity (females remain together 87–94% of the time – Funston *et al.*, 1998; Tambling & Belton,

2009; Valeix *et al.*, 2009), and pride females in the study site have limited interaction with each other (C.J. Tambling, unpubl. data), reducing the chance of the scat samples being contaminated by interlopers. Males, on the other hand, join females intermittently (detected at 23 [9.7%] of female kills) and could contaminate clusters to cause an overestimation of missed feeding events, although the use of genetic testing could verify the origin of scats (Marucco *et al.*, 2008).

Where direct continuous observation of lions is not possible, the use of the scat-supplemented approach, through a combination of GPS point investigation and serial collection of scats, results in much improved estimates of lion dietary consumption. In the case of social carnivorans with fission–fusion societies, genetic identification of individuals producing each scat can improve efforts to obtain a fine-scale representation of diets. Our study demonstrates how, as ecological methods become more diverse, there are increasing opportunities to combine and analyse collected data collected, using multiple techniques to yield less biased and more accurate results to advance large carnivoran research.

Acknowledgements

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