Estimating lion's prey species profile in an arid environment

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Abstract

Information on large carnivore diet composition is important when conservationists seek to address stressors such as habitat encroachment, bush meat trade and retribution killing on the persistence of populations. Detailed diet sampling approaches can contribute to effective conservation management. We compare different approaches including GPS cluster analysis, scat analysis and opportunistic observations and describe lion diet profiles in the Kgalagadi Transfrontier Park (KTP). We determined that a sample size of between 65–69 lion feeding events out of 278 found by GPS cluster analysis and 55–59 lion scats out of 189 samples can provide a representative description of lion diet in the KTP. Our opportunistic observations ($n = 52$) were found to be too few for robust deductions. Scat analysis yielded the highest prey diversity ($n = 11$) and best representation of prey <50 kg, but required 160 scats at ∼ 263 km driven per scat collected. GPS cluster analysis provided good information for large prey, but underrepresented prey <50 kg. Kill remains were found at only 37% of the investigated GPS cluster points ($n = 823$). Even so, GPS cluster analysis yielded diet descriptions quicker than scat analyses. The use of GPS cluster and scat analysis in tandem is recommended for the estimation of lion diet in this arid environment.

Introduction

Several stressors affect large carnivore populations (Beschta & Ripple 2009). For lions (*Panthera leo*) these include direct stressors such as habitat degradation (Chardonnet *et al.*, 2010) and human-lion conflict (Bauer & van Der Merwe, 2004) but also indirect stressors that affect the prey base such as the bush meat trade (Lindsey *et al.*, 2013). Lion diet estimates provide important insights into predator-prey dynamics (Owen-Smith & Mills, 2008) and lion population demographics (Becker *et al.*, 2013) and thus provide important information for conservationists.

Traditionally the most common methods for defining lion diet estimates include stomach content analysis (Smuts, 1979), scat analysis (Mukherjee, Goyal & Chellam, 1994; Breuer, 2005), spoor tracking (Eloff, 1984), continuous follows (Schaller, 1972; Stander, 1992), and opportunistic observations (Mills, 1984). More recently, researchers have used GPS cluster analysis (Tambling *et al.*, 2010), isotopic analysis (Hilderbrand *et al.*, 1996; Newsome *et al.*, 2009) and DNA analysis (Reed, 2004; Shehzad, 2011) to investigate the diet of carnivores. Even so, all techniques have inherent bias (Mills, 1992; Tambling *et al.*, 2010; Shores, Mondol & Wasser, 2015).

Scat (faecal) analysis identifies undigested remains of prey that have passed through the digestive system (Mukherjee *et al.*, 1994) and allows estimates of consumed biomass (Ruhe,

Ksinsik & Kiffner, 2008). However, the approach, can over-represent smaller prey (Floyd, Mech & Jordan, 1978), is not able to identify age and sex, nor whether the prey was hunted or scavenged (Breuer, 2005). A sufficient number of scats representative of the population is required to depict the frequency of various prey items in the diet (Trites & Joy, 2005). Other lion dietary studies using scat analysis have used sample sizes of 74 (Davidson *et al.*, 2013), 96 (Ogara *et al.*, 2010) and 119 (Breuer, 2005).

GPS cluster analysis identifies kill sites by clustered geographical positions collated from individuals fitted with GPS collars (Tambling *et al.*, 2010; Bacon *et al.*, 2011). The technique is useful as it can provide insights into foraging behaviour such as the time spent on a kill, duration between kills, landscape utilization and age and sex of prey (Merrill *et al.*, 2010). However, GPS cluster analysis often presents an overestimation of large prey and may completely miss smaller prey that are consumed either too quickly to be detected using GPS cluster selection criteria, or are consumed whole without leaving detectable remains (Bacon *et al.*, 2011; Tambling *et al.*, 2012).

Continuous observations provide robust information on lion foraging, and identification of both small and large prey (Stander, 1992), but may influence lion behaviour and are dependent on the vigilance of the researchers (Mills, 1992). Using opportunistic observations of lion kills as an alternative skews

data towards large prey as small prey often go undetected (Mills, 1984). Tracking spoor, like continuous follows, has a high accuracy in determining diet, but can only be used in certain habitats and requires extensive efforts and specialized ground-tracking skills (Eloff, 1984; Mills, 1992).

We aimed to estimate lion diet in the Kgalagadi Transfrontier Park (KTP) using opportunistic observations, GPS cluster analysis and scat analysis, and to assess the minimum sample size required for each technique. We evaluate biases in our techniques and use our results to make recommendations on approaches to effectively estimate lion diets in arid environments.

Materials and methods

Study area

The study took place between May 2013 and June 2015 across an area of 15 396 km² comprising the South African section of the KTP, and a 25 km band east of the Nossob River in Botswana (between 24° 15′ S and 26° 30′ S, and 20° 00′ E and 20° 45′ E, Fig. 1). The KTP receives summer rainfall mainly from December to April, varying between 185 mm to 230 mm annually (Anonymous, 2008). Evapotranspiration is high and natural surface water occurs only for short periods after heavy rain (Knight, 1995). Temperatures fluctuate daily and seasonally (Mills & Retief, 1984), reaching −10°C and 45°C during winter and summer respectively (Van Rooyen et al., 1990).

Dunes and riverbed habitats comprise the KTP within the Kalahari Duneveld Bioregion of the Savannah Biome (Rutherford, Mucina & Leslie, 2006). The dune habitats are sparsely vegetated with trees and shrubs, bare dunes, flat grasslands or tree savannahs (Bothma & De Graaff, 1973). The dune fields are bisected by two ephemeral riverbeds and scattered pans (van Rooyen et al., 1990). The riverbeds and pans support higher densities of herbivores than the dunes including springbok, *Antidorcas marsupialis*, blue wildebeest, *Connochaetes taurinus,* gemsbok, *Oryx gazella* and red hartebeest, *Alcelaphus buselaphus* (Mills & Retief, 1984). In the KTP gemsbok, blue wildebeest, ostrich, *Struthio camelus,* steenbok, *Raphicerus campestris,* and common duiker, *Sylvicapra grimmia* are sedentary, whereas springbok, eland, *Tragelaphus oryx,* and red hartebeest are nomadic (Mills, 2015).

Data collection

GPS clusters

We fitted seven adult female lions with GPS/VHF and satellite transmitter collars (African Wildlife Tracking[cc], Pretoria, South Africa) after catching lions using standard techniques employed by the South African National Parks (Smuts, Whyte & Dearlove, 1977). Two collars provided data for only 4 months while the other five collars provided reliable data for twelve months. Collars recorded lion localities at hourly intervals allowing extraction of lion movements (Tambling et al., 2010). We defined potential feeding sites as four or more consecutive
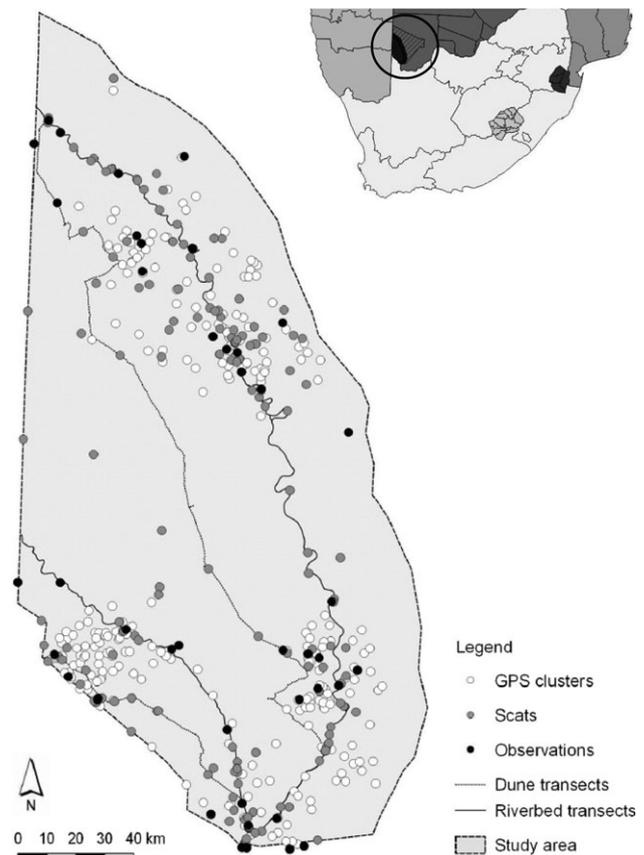
Figure 1 The study area in the Kgalagadi Transfrontier Park (indicated by diagonal lines), with markers indicating the independent locations of opportunistic observations of lion kills (*n* = 52), lion scats collected (*n* = 189) and lion prey remains located at GPS cluster points (*n* = 278).

fixes within a 100 m radius (Tambling et al., 2012; Davidson et al., 2013) between two hours before sunset and two hours after sunrise. GPS clusters occurring outside of these parameters were largely excluded from investigations, except for 165 randomly selected clusters used to verify the selection protocol. We searched GPS clusters for evidence of prey remains within a 100 m radius (Tambling et al., 2012) of the GPS fix for the start point and end point of each cluster. A feeding event comprised evidence of predation such as irregular soil disturbance and trampled vegetation along with prey remains such as rumen content, hair, bone, jaw, horn, blood or a carcass (Davidson et al., 2013). We used these biological remains to identify prey species (Tambling et al., 2012).

Scats

We opportunistically collected lion scats, identified by shape, diameter, colour, ingested hair as well as evidence of spoor (Breuer, 2005), and when encountered at GPS clusters. Scats collected at GPS clusters that had remains of the prey found at that cluster, or at a preceding cluster not older than 120 hours

were excluded (Tambling *et al.*, 2012). When encountered, the date and GPS location of scats were recorded and they were placed in brown paper bags to air dry.

To separate the organic components, we soaked scats overnight and then washed the samples under running water using a 2 mm sieve to collect hair, hoof, quill and bone (Ruhe *et al.*, 2008). We cleaned 25% of the undigested material with 16.5% sodium chloride sterilizing fluid and then allowed the subsample to air dry. Distributing the subsample evenly over an 8 × 8 cm gridded sectioning board allowed us to randomly select four hairs from each demarcated block (≥32 strands) and we soaked these in 90% ethanol for further cleaning. Once extracted, we assessed hair samples macroscopically for colour, width and length (Keogh, 1983) and microscopically using conventional light microscopy, for cuticular scale patterns and cross-sections of the medullary structure (Keogh, 1983). Samples were compared with a reference library of prey hair compiled from carcasses encountered in the field opportunistically as well from lion kills.

Observations

Opportunistic observations occurred when we encountered lions by chance across the study area (Mills, 1984). When we found lions feeding on a carcass we noted the date and location, as well as the prey species. Continuous follows were also attempted and involved observing lions for a continuous period of between 24–72 hours (Mills, 1992; Stander, 1992).

Data analyses

Defining lion diet

Lion diet was defined by the relative proportions of the different prey species represented in GPS cluster analysis, scat analysis and opportunistic observations, respectively. We converted the frequency of prey occurrence into relative biomass indices using the body mass of prey (Radloff & du Toit, 2004). We considered prey the size of springbok and smaller (≤50 kg) as small prey and the rest as large prey (>50 kg).

Assessing optimal sampling

The proportion of all prey species detected for GPS clusters, scats analysis and opportunistic observations served as a diet benchmark for each technique independently. To identify how sample size influenced the reliability of lion dietary profile estimates, we sub-sampled with replacement, at roughly 5% increments of the total number of samples collected for each technique. The similarity of the diet estimates at different sample size increments was calculated using the Bray-Curtis and Euclidean distance measures (Bray & Curtis, 1957; Danielsson, 1980) and were compared with the benchmarks. The Bray-Curtis distance measure is sensitive to the presence or absence of a species, whereas the Euclidian distance is sensitive to species abundance within a sample (Kindt & Coe, 2005). Smaller Bray-Curtis and Euclidian distances indicate similarity in diet profiles. We repeated this process 1,000

times (Monte Carlo simulations; Rollett & Manohar, 2004) for each technique.

The variance of ecological distances calculated from these simulations, at different sample sizes, provided an indication of reliability (Leblois, Estoup & Rousset, 2003). We used the Hartley's *F*-max test for homogeneity of variance (Hartley, 1950) to identify a sufficient sample size. We considered a minimum sample size sufficient when homogeneity of variance was reached. This was achieved when the *F*-max value was less than, and remained less than the tabulated *F*-max value (Hartley, 1950) as sample sizes increased beyond the estimated minimum. Large sample sizes generated through simulations allowed us to evaluate *F*-max results against the tabulated critical value of 1.67.

Sample effort

We defined sample effort as the number of days it took to collect the samples using each method. For GPS clusters, sample days were represented by the number of days for which the five properly functioning GPS collars submitted locality data. For scat analysis and opportunistic observations, sample days were represented as the number of days spent looking for lions and their scats.

Comparison of techniques

We used the Pearson's Chi-square test (Pearson, 1900) to test if the relative contribution of each prey species varied across methods. Where small sample sizes hampered the use of Chi-square testing (Kindt & Coe, 2005) prey species were pooled. Kudu *Tragelaphus strepsiceros,* and ostrich, were pooled as 'other large prey' and all small prey (<50 kg) were grouped into a single category.

Results

Lion diet

We identified 823 GPS clusters and visited these on average 33 days after occurrence, finding prey remains at 36.5% of the sites (*n* = 278; Fig. 1). The 165 randomly selected clusters, not meeting our GPS cluster identification criteria, yielded only 29 kill records (17.6%). Collectively, gemsbok, wildebeest, hartebeest and eland contributed 92% of the species consumed (Table 1) and 98% of the biomass intake (Fig. 2).

Of the 221 lion scats that we collected 79 (39%) were at GPS clusters. Excluding scats that represented the same prey species as found at GPS clusters, a total of 189 (86%) scats remained (Fig. 1). Gemsbok, porcupine, springbok and blue wildebeest constituted 82% of lion diet extracted from scat analysis (Table 1). Small prey accounted for 32%, but comprised less than 4% of the biomass intake. Large prey contributed 96% to the lion biomass intake as derived from scat analysis data (Fig. 2).

Only 17% of all encounters with lions (*n* = 299) were when they were feeding (*n* = 52) (Fig. 1). Of the opportunistically observed lion feeding events, 92% constituted large prey (Fig. 2) to which gemsbok, wildebeest and eland contributed

Table 1 The percentage proportional contributions of prey species to lion diet derived from GPS clusters, scat analysis and opportunistic observations. Sample sizes are provided in brackets

		Cluster (278)	Scat (189)	Observations (52)
Large prey	Gemsbok	73 (203)	50.8 (96)	44.3 (23)
	Blue Wildebeest	10 (28)	8.5 (16)	25 (13)
	Eland	4.3 (12)	3.7 (7)	17.3 (9)
	Red Hartebeest	4.7 (13)	3.7 (7)	1.9 (1)
	Ostrich	3.6 (10)	0.5 (1)	1.9 (1)
	Kudu	1.1 (3)	0.5 (1)	0 (0)
	Cattle	0 (0)	0 (0)	1.9 (1)
Subtotal		96.7 (269)	67.7 (128)	92.3 (48)
Small prey	Porcupine	0 (0)	12.7 (24)	1.9 (1)
	Steenbok	2.5 (7)	7.4 (14)	1.9 (1)
	Springbok	0.4 (1)	9.5 (18)	0 (0)
	Kori Bustard	0.4 (1)	0 (0)	3.9 (2)
	Spring hare	0 (0)	2.2 (4)	0 (0)
	Jackal	0 (0)	0.5 (1)	0 (0)
Subtotal		3.3 (9)	32.3 (61)	7.7 (4)

86% (Table 1). Small prey comprised 8% of opportunistic observations, but contributed less than 0.5% to the biomass intake (Fig. 2).

We found that continuous follows was not suitable in the KTP. We conducted 21 days of continuous follows and found that navigating the dune landscapes by vehicle at night caused an unacceptably high level of disturbance to prey, potentially hampering lions foraging success.

Optimal sample size

Mean ecological distances for GPS clusters from the GPS cluster diet benchmark, ranged from 0.4 to 0.5 (Bray-Curtis, mean = 0.49) and 0.0 to 0.05 (Euclidean, mean = 0.05) across all sampling intensities. Results from scat analysis were similar, with Bray-Curtis distances ranging from 0.3 to 0.5

(mean = 0.46), while Euclidean distances ranged from 0.0 to 0.4 (mean = 0.06) from the scat analysis diet benchmark. For opportunistic observations we noted a mean Bray-Curtis distance of 0.39 (range 0.0–0.5) and Euclidean distance of 0.15 (range 0.0–1.3). The mean point estimates for opportunistic observations were further from the diet benchmark than for the other techniques (Fig. 3).

The variance of ecological distances at different increments of sample sizes reached homogeneity at sample sizes of 55–59 for scats ($F\text{-max}_{bc} = 0.96$; $F\text{-max}_{eu} = 1.138$) and 65–69 ($F\text{-max}_{bc} = 1.019$; $F\text{-max}_{eu} = 1.119$) for GPS cluster analysis (Table 2). At 65–69 samples, mean ecological distances between the derived diet profile and the GPS cluster diet benchmark were 0.49 (Bray-Curtis) and 0.05 (Euclidean), while for scat analysis at 55–59 samples mean ecological distances were 0.45 (Bray-Curtis) and 0.09 (Euclidean). Homogeneity of variance was not obtained for opportunistic observations at 45–50 samples ($F\text{-max}_{eu} = 1.71$; $F\text{-max}_{bc} = 0.17$). The sample size of 52 opportunistic observations was thus insufficient to provide an accurate representation of lion diet.

Sample effort

We drove 49,784 km in search of lions and signs of their activities. Effort for opportunistic observations (957 km/sample) was higher than for lion scat collection (263 km/sample). We drove 4,200 km searching for prey remains at GPS clusters, with an average distance of 5 km between clusters, and an average of 15 km between clusters where we found prey remains.

We had records from 2,028 collar days (each day a lion had a working collar). There were on average 7 days between identifiable feeding events. We achieved the minimum sample of 65 within 90 sample days, using five GPS collars and investigating 97 cluster points. Getting a minimum sample size of 55 lion scats required 93 sample days, during which we drove 14,487 km. The 52 opportunistic observations of lions feeding took 317 field days.
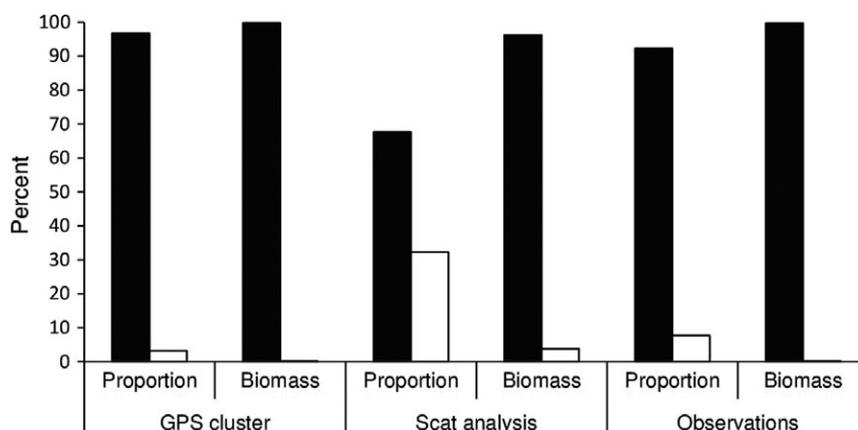
Figure 2 Proportional lion diet composition and biomass contributions of large prey (≥50 kg; black bars) and small prey (≤50 kg; white bars) as calculated using three different techniques in the Kgalagadi Transfrontier Park.
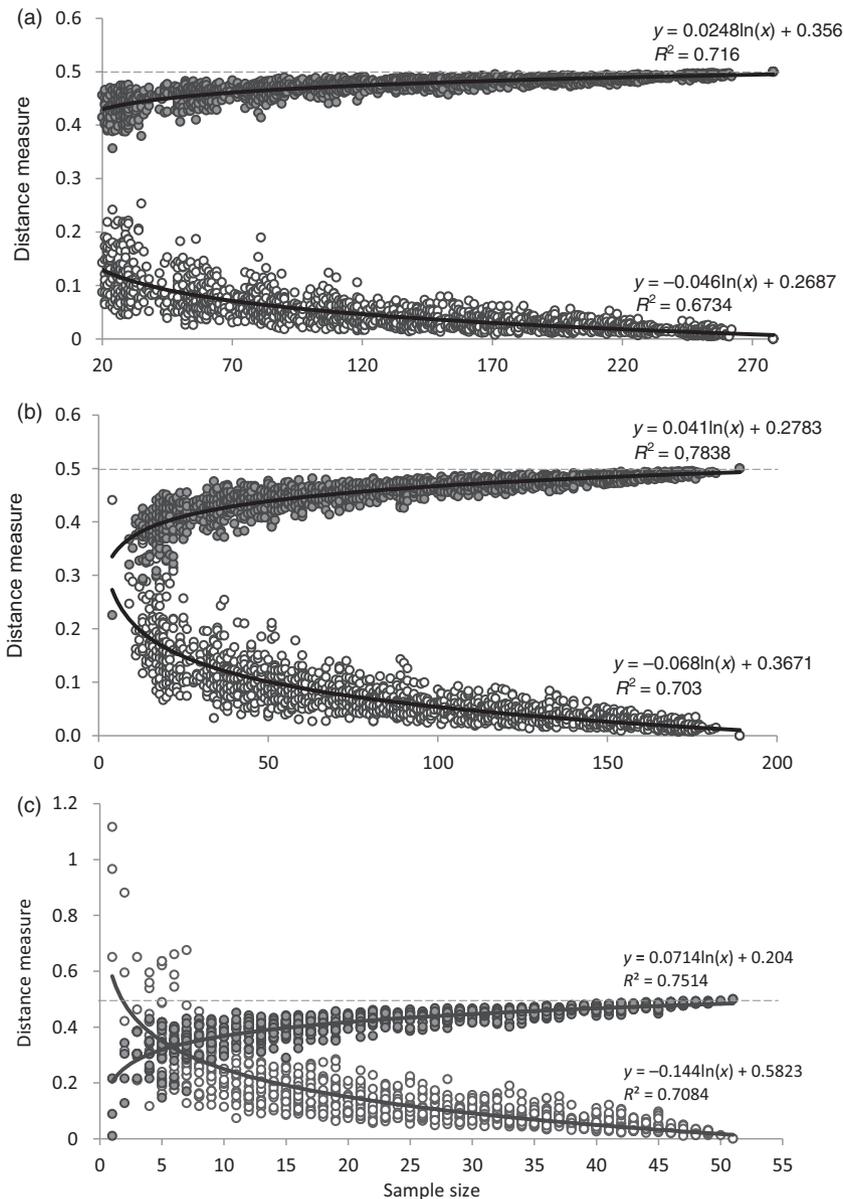
Figure 3 The difference in 1,000 Monte Carlo simulation calculations of lion diet composition at different sample intensities, as reflected by Bray-Curtis (grey symbols) and Euclidean (white symbols) distance estimations for GPS cluster analysis (a), scat analysis (b) and opportunistic observations (c). The reference samples are represented at '0.5' for the Bray-Curtis distance and at '0' the Euclidean distance. Logarithmic trendlines (black lines) represent the fitted relationship between ecological distances and the rate of change in data by indicating the general course or tendency. The ecological distances were greater within smaller sample sizes, indicating that diets were less similar to the benchmarks, and decreased as the sample size increased, indicating that diets became more similar as the sample sizes increased.

We needed to collect 160 lion scat samples traveling 42,145 km over 270 sample days to identify all 11 prey species noted through scat analyses. To detect all the prey species identified through GPS cluster analysis ($n = 9$) required finding prey remains at 250 clusters over 350 collar days, using five GPS collars, and travelling 3,500 km. Identifying a total of nine species using opportunistic observations took 310 sample days travelling 47,869 km.

Comparison of methods used to identify lion diet

Scat analysis had a lower proportional representation of gemsbok, ostrich and kudu than GPS cluster analysis (Table 1, Table 3). Small prey contributed significantly more to the lion diet profile of scat analysis than that of GPS cluster analysis ($\chi^2 = 77.22$, d.f. = 5, $P = <0.01$) or opportunistic observations

Table 2 A summary of variance between the Euclidean and Bray-Curtis distances at ascending increments of sample size (d.f. = 1) for scat analysis and GPS cluster analysis. Large sample sizes generated through simulations allowed us to identify homogeneity of variance when the F-max value was identified to be less and remained less, across all larger sample sizes, than the F-max tabulated value of 1.67 for both the Bray-Curtis and Euclidean distances. The point at which homogeneity of variance was obtained for both scat analysis and GPS cluster analysis are presented in bold. Opportunistic observations did not reach homogeneity and are thus not presented

| No. samples | Scat | | GPS cluster | |
	F-max value: euclidean distance	F-max value: bray-curtis distance	F-max value euclidean distance	F-max value: bray-curtis distance
40–44	1.059	1.187	1.613	1.250
45–49	1.168	1.036	1.134	1.030
50–54	1.833	1.681	1.270	1.304
55–59	**1.138**	**0.960**	1.353	1.097
60–64	1.324	1.295	**2.390**	**2.417**
65–69	0.823	0.917	1.019	1.119
70–74	1.559	0.580	0.503	0.523
75–79	1.559	1.051	0.517	0.584
80–84	1.101	1.051	0.527	0.479

Table 3 Comparison of the scat analysis (Scat), GPS cluster (Cluster) methods used to identify lion diet in the KTP indicating the Degrees of Freedom (d.f.) and depicting results for Chi-square test (χ^2) and P-value (P). Significant differences ($P \leq 0.05$) are highlighted in bold

| | Scat vs. cluster | | | Scat vs. observed | | | Cluster vs. observed | | |
	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P
Gemsbok	38.29	1	**<0.01**	44.78	1	**<0.01**	143.4	1	**<0.01**
Blue wildebeest	3.27	1	0.07	0.31	1	0.58	5.49	1	**0.02**
Eland	1.32	1	0.25	0.25	1	0.62	0.43	1	0.51
Red hartebeest	1.8	1	0.18	4.5	1	**0.04**	10.29	1	**<0.01**
Other large prey	8.07	1	**<0.01**	0.33	1	0.56	10.29	1	**<0.01**
Small prey	38.63	1	**<0.01**	47.51	1	**<0.01**	1.14	1	0.29
Total	77.22	5	**<0.01**	29.27	5	**<0.01**	30.54	5	**<0.01**

(χ^2 = 29.27, d.f. = 5, P = <0.01). Eland and blue wildebeest contributed more frequently to the lion diet profile using opportunistic observations, while gemsbok contributed more using GPS cluster analysis compared with opportunistic observations (Table 1).

Discussion

Arid environments of the Kalahari have limited natural resources resulting in low densities of lions and their prey (Eloff, 1984; Mills, 2015). This provides challenges to estimate lion diets. The methods we used needed intensive sampling and recorded different contributions of species, as well as number of species.

Researchers may prefer techniques that identify more species in animal diets. Scat analyses typically identifies more species (Breuer, 2005; Davidson et al., 2013) and a sufficient sample size may thus provide a species rich lion diet (Mills, 1992), but it may over-represent small prey (Floyd et al., 1978; Ruhe et al., 2008). In our case, 55–59 lion scats gave a representative lion diet profile, similar to the 59 required to define Steller sea lion (Eumetopias jubatus) diet (Trites & Joy, 2005), but lower than the 70 scats required for lion diet estimations in northern Cameroon (Breuer, 2005). Sample effort (263 km/scat) is high and may be site and season dependent through

factors such as scat deterioration by coprophagous insects and rain (Tambling et al., 2012; Davidson et al., 2013).

The difference in the contribution of species to lion diet profiles between methods is of concern. A potential reason for this might be a disproportional contribution of certain prey species to a particular methods' dataset. If lions from a particular area specialize on specific prey species it can bias comparisons between methods. Our sample collection points do not support this notion as no particular area contributed disproportionally to the datasets of either GPS cluster or scats analysis (see Fig 1). The northern, south-eastern and south-western parts of the 15 396 km^2 study area provided roughly 37%, 33% and 30%, respectively to the 278 GPS cluster samples. While 48% of the 189 scat samples came from the northern part, 34% from the south-west and 18% from the south-east.

Lag effects might also bias comparisons between methods, for instance we investigated GPS clusters typically 33 days after a feeding event. However, in Kruger National Park there was no difference in the likelihood of detecting prey remains between 28 and 98 days after the feeding event occurred (Tambling et al., 2010).

An additional source of differences in lion diets between methods may originate from differences in sex-specific diets (Funston et al., 1998). For instance, our GPS cluster analysis may be skewed towards female diet as adult males only

associated 31% of the time with our collared females. This potential bias is unlikely to realize for scat analysis in our study, as scats would have been collected from both sexes, and at the time of this study the lion sex ratio was at parity (Beukes, Radloff & Ferreira, 2017). It is unlikely that the potentially larger contribution of male lion data to the scat analysis results can explain the larger proportion of small prey detected with this method. Male lions tend to feed on prey larger than that utilized by females and not smaller (Radloff & du Toit, 2004), although no in depth study on male lion diet has been conducted in the KTP.

Opportunistic observations may be biased toward certain micro-habitats like riverbeds, where tourist roads concentrate, increasing the survey effort conducted and thus the detectability of lion kills (Mills, 1984). Even so, opportunistic observations of lions feeding are rare in the KTP averaging 28 records per annum (Mills, 1984), and in this study only 52 records were obtained over 317 field days. Nonetheless, opportunistic observations of lion feeding events, collected over long periods in order to obtain a sufficient sample, can provide useful insights into lion diets (Mills, 1984; Radloff & du Toit, 2004).

Much of the differences in lion diet come from the contributions of large versus small prey. Despite that opportunistic observations (Mills, 1984; Rapson & Bernard, 2007) and GPS cluster analysis (Bacon et al., 2011; Tambling et al., 2012) typically miss small prey, although these techniques provide additional opportunities to study other aspects such as the sex and condition of prey killed (Merrill et al., 2010). In addition, as we have shown in the Kalahari, GPS cluster analysis can yield the highest number of kills over the shortest time frame, alleviating the low return problems associated with opportunistic observations. GPS cluster analysis, however, requires the costly and logistically challenging capture of animals and fitting of GPS collars (Hebblewhite & Haydon, 2010).

As supported by our findings lions prefer large prey in the weight range of 150–650 kg including wildebeest and gemsbok (Radloff & du Toit, 2004; Hayward & Kerley, 2005). Small prey (<50 kg) such as steenbok, porcupine and springhare are included in lion diets (Eloff, 1984; Stander, 1992), although small prey and megaherbivores (≥1000 kg) are generally avoided (Owen-Smith, 1988 Hayward & Kerley, 2005). Resource limitations in arid areas result in carnivores developing specialized hunting techniques for specific prey species (Mills, 2015). We found that gemsbok were the primary prey of lions in the KTP and are the most widespread and abundant of the large prey (Mills & Retief, 1984). Dynamics of large prey, specifically gemsbok, are likely to be key drivers of the lion population in the KTP. Elsewhere, changes in the dynamics of large prey species influence lion density, demography and pride dynamics (Valeix et al., 2009).

Alternatively, even though small prey contributed to less than 4% of the total biomass intake of lion noted in our study, smaller prey species serve as 'top-ups' to lion diet between large kills (Eloff, 1984). This could be important for lions hunting alone, as hunting success generally increases with increased pride size (Packer & Pusey, 1997). Small prey items may also be of particular significance during droughts when several large herbivores migrate out of the KTP (Knight,

1995). It is thus possible that the contribution of small prey to lion diet might be higher during drought years, not experienced during this study, but are unlikely to meet the daily food requirements of lions (Stander, 1992).

Our study highlighted different results for different techniques to estimate lion diets in arid environments. This mostly associates with identifying large and small prey. The importance of both large and small prey suggest that GPS cluster points supplemented with scat analysis found at cluster points could provide a comprehensive lion diet profile (Tambling et al., 2012). We thus recommend using both GPS cluster and scat analysis (Tambling et al., 2012) if resources are available to support the high sample efforts required.

Acknowledgments

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