Reducing potential sources of sampling bias when quantifying the diet of the African wild dog through scat analysis

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To develop guidelines for the collection of independent field samples of scats for the quantification of wild dog (*Lycaon pictus*) diet we determined the passage rates of different wild dog prey items from feeding trials on a captive pack held at Marakele National Park, Limpopo Province. The minimum time to first detection was 5.5 hours after feeding (S.E. ± 1.52, $n = 5$) and prey items remained in the gut for an average of 79.4 hours (S.E. ± 6.00, $n = 3$). Differential passage rates of prey species were not pronounced. Observed passage rates were used to devise a sampling protocol for scats collected during a field study where scats were separated by a minimum period of 120 hours to ensure independence of samples. Comparison of the percentage occurrence of prey species in field-collected scats with the percentage occurrence from direct observations of kills illustrated the tendency for small prey to be underrepresented in the latter. However, the strong correlation between percentage occurrences in diet as determined by the two methods ($r_s = 0.85$, $P < 0.01$, 13 d.f.) suggests that both methods can reliably determine the relative importance of prey in the diets of obligate carnivores such as wild dogs. The determination of maximum passage rates and subsequent guidelines for collection of independent faecal samples in the field could be a valuable tool for reducing inherent biases in carnivore diet studies.

Key words: faecal analysis, *Lycaon pictus,* passage rates, sampling bias.

INTRODUCTION

Studies of food habits underpin research into many aspects of carnivore biology, including the role that large carnivores play in ecosystems, the effects of predation on community stability (Prugh 2005), the relative selection pressures predators exert on prey species (Husseman *et al.* 2003), range-wide prey preferences (Hayward *et al.* 2006), niche overlap among sympatric carnivores (Breuer 2005), seasonal variation in dietary composition (Begg *et al.* 2003), and the incidence of livestock predation (Marker *et al.* 2003; Woodroffe *et al.* 2005).

It has been argued that following carnivores for extensive periods is the best method to determine diet (Bertram 1979; Mills 1992; Weaver 1993). Opportunistically collected records, and those collected from radio-locations (as described by Mills 1992) contain several inherent biases. Small prey are consumed faster than large prey and are less likely to be located; small prey items are more difficult to locate even when carcass remains exist; prey items captured in accessible terrain are more likely to be located than those in inaccessible areas such as dense vegetation and rocky outcrops; and, some prey species are more likely to be captured at night when direct observations are difficult (Kruuk & Turner 1967; Kruger *et al.* 1999). To overcome these potential biases, partial direct observations, where because of the terrain visual contact is lost for extended periods, may be complemented by faecal analysis to assess under-representation of small prey items. Faecal analysis has played a much more important role in studies of the diets of smaller carnivores, (although there are exceptions, *e.g.* honey badgers *Mellivora capensis,* Begg *et al.* 2003; and African wild cats *Felis silvestris,* Herbst & Mills 2010) and has become progressively more sophisticated since Lockie (1959) first suggested correcting for

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Table 1. Common types of bias that can influence the results of wild dog scat analysis: causes, predicted effects and methods of avoidance.

Type of bias	Cause	Predicted effects	Method of avoidance
Detection	Multiple prey items of the same species in one scat	Effects are likely to be minimal if multiple predation is infrequent; common prey items may be under-represented if multiple predation is frequent	Use correction factor to account for bias
Replication	More than one scat contains the same prey item		
In space	The same prey item is present in scats from more than one individual	Random effects depending on sampling regime	Ensure samples from only one individual are collected at each time period
In time	The same prey item is present in consecutive scats from the same individual	Prey items with comparatively longer passage rates may be over-represented in the diet	Ensure enough time elapses between collection periods to allow for complete passage of all prey items

differential digestibility (*e.g.* Atkinson *et al.* 2002).

African wild dogs (*Lycaon pictus*) are obligate carnivores preying mostly on large vertebrates (Carbone *et al.* 1999) but able to subsist on smaller prey in some areas (Woodroffe *et al.* 2007). Previous attempts to determine wild dog diet through scat analysis have assumed that the identified prey remains in each scat represented one individual (Kruger *et al.* 1999), based on feeding trials on wolves (Floyd *et al.* 1978). This assumption can be challenged for wild dogs on two grounds (Table 1). Firstly, wild dog packs routinely capture and consume multiple prey items of the same species in a single hunting period (Fuller & Kat 1990, 1993; Creel & Creel 1995; Woodroffe *et al.* 2005). Standard faecal analysis techniques preclude differentiation between individuals of the same species and so, when different prey items comprise the same species, this species may be under-represented in scat analysis. This is likely to occur when wild dogs hunt small prey species such as dik diks (*Madoqua kirkii*) (Woodroffe *et al.* 2007). A second source of sampling bias occurs when two or more scats contain the same prey item, either because different individuals deposited them or because the same individual deposited them consecutively. This bias can be further exacerbated by the differential passage of food items through the gut (Putman 1984), whereby items taking comparatively longer to pass through the gut will tend to be over-represented (see Reynolds & Aebischer 1991 for a review) (Table 1).

In this study, we examine the influence of detection and sampling bias by determining passage rates of different wild dog prey species, and developing guidelines for the collection of independent faecal samples in the field. These guidelines are then employed in a field-based diet study to assess the degree of correlation between frequency of occurrence of prey items as determined by scat analysis and partial direct observations of kills.

METHODS

Reference library

A reference library, compiled of cross-sections of hairs collected from 12 known wild dog prey species, was used as the basis for identification of hairs extracted from scats from passage rate trials and field-collected scats (Keogh 1983; Spaulding *et al.* 2000). Hair samples were taken from different parts of the body, from males and females, and from adults and juveniles. Various methods have been described for taking cross-sections of hairs (see Douglas 1989 for a review). The method we used was similar to that of Douglas (1989) and Maddock (1993) with some modifications (Rasmussen, pers. comm.). Approximately 20 hairs were inserted into the end of a thin, plastic Pasteur pipette and a small amount of molten beeswax was then drawn into the pipette. Once the beeswax had set, a thin slice (~0.2 mm) was sectioned off the pipette using a sharp razor blade. Two pipettes were prepared for each sample, thus sectioning

Table 2. Feeding trial schedule showing the minimum and maximum detection periods for each prey species.

Day	Time	Species	Age	Sex	Number fed	Positive identification in scats (hours since feed)	
						First	Last
1	06:20	Greater kudu	Subadult	Male	1	4.3	74.0
4	06:35	Warthog	Adult	Male	1	4.5	72.9
6	06:38	Impala	Adult	Male	1	6.7	91.4
9	06:34	Common duiker	Adult	Male	1	10.5	52.5*
10	06:45	Warthog	Adult	Male	2	1.3	28.3*

*The detection window for the last two trials was incomplete because identifiable remains were present in the last collected scats.

30–40 hairs. The sections were mounted onto a microscope slide and examined with a Zeiss Axiolab binocular microscope, and digital photographs taken with a Video Flex 2000 Explorer microscope camera (www.ken-a-vision.com) attached to a computer. Species were identified by cross-section form and shape as described by Keogh (1983). Blind identification tests were conducted (by H.D.M.) on 105 reference photographs, to determine the proportion of hairs correctly identified from this method.

Feeding trials

We conducted a feeding trial on a captive pack of wild dogs in a 1 ha holding boma at Marakele National Park to determine passage rates of four of the main wild dog prey species in southern Africa. The pack comprised seven adults (5 males, 2 females) and nine juveniles (5 males, 4 females), falling within the normal range of wild dog pack sizes in southern Africa (Fuller *et al.* 1992; Mills 1995). The four prey species selected for the study were chosen because (i) they are important wild dog prey items in most southern African systems, and (ii) they had different surface area: volume ratios. These were fed consecutively to the wild dog pack over a period of 10 days (Table 2).

Before each feed, the boma was cleared of all old scats. We did not starve the wild dogs before feeds because they are known to make more than one kill a day in the wild. After feeding the carcass remains were removed from the boma. The area was then scanned by two observers driving longitudinal transects spaced ~10 m apart. Scans took place at three-hourly intervals between 06:00 and 18:00. Those scats that were too liquid to be collected were designated as non-field collectable and discarded (Floyd *et al.* 1978). Each new collectible scat was collected and the time recorded. Scats deposited overnight were recorded as deposited at midnight to correct for the 12-hour period where no scats were collected. As none of the maximum detection windows were estimated from scats collected at 06:00 this six-hour error had no effect on our overall results. Scats were dried and then processed using techniques described above. As all animals in the pack fed on every carcass presented only one scat was analysed from each three-hour scat collection period. Prior to the feeding trials, passage rates had been predicted to be in the order of 24 hours (Greg Rasmussen, pers. comm.) and consequently the collection of samples was terminated before all identifiable remains from the last two prey items had passed through (Table 2).

Field samples

Faecal samples were collected over a period of three years from a free-ranging wild dog pack in Venetia Limpopo Nature Reserve (VLNR), Limpopo province. Fresh scats encountered during radio-tracking were collected whenever they were located. Scats were identified by their size, shape and proximity to fresh wild dog spoor (Smithers 1983). For each scat the date, estimated time of deposition based on scat consistency, and GPS location was recorded: scats for which this information could not be reliably determined were discarded. Scats were air-dried and then loosened by hand and thoroughly mixed, and a sample of *c.* 30 ml was taken. Tweezers were used to pick out all visible hairs (in the case of scats with few hairs) or approximately 40 hairs (in the case of scats with many hairs). Representatives of each hair type, determined from macroscopic observation, were included in the samples. Hairs were placed in sealed containers and labelled prior to processing (see above) and microscopic examination. Occurrence of ungulate hair was recorded and evaluated in terms of relative percentage occurrence, calcu-

lated by totalling all occurrences and expressing actual occurrence of each item as a percentage of all occurrences.

Direct observations

The diet of a single wild dog pack at VLNR was documented from direct observations of kills between January 2002 and December 2004, which were located by tracking radio-collared individuals during periods of hunting activity (at dawn and dusk) and occasionally through the night. Long-term direct observations for a minimum of three consecutive days were supplemented with short-term observations, which lasted a minimum of one full activity period, defined as the period of activity between two resting locations. Observations entailed locating the pack at rest and following closely by vehicle when the pack became active. Occasionally pack members became separated during hunts and in these cases, observations were focussed on a predetermined radio-collared individual. There were times when, because of inaccessible terrain, the dogs were out of visual contact for extended periods, and thus our records were only partial direct observations (as described above).

Cumulative species detection curves were generated by plotting the number of species detected by each method over time (in months), and per scat or observed kill.

Statistical procedures

Differences between proportions of each prey species from partial direct observations and faecal analysis were determined using the two-tailed *z*-ratio test, without applying sequential Bonferroni corrections (Moran 2003).The correlation between percentage dietary composition from scat analysis and direct observations was determined using the Spearman rank-order correlation coefficient (r_s). All statistical analyses were performed using the computer software SPSS 14.0.

RESULTS

Reference library

Each species exhibited a variety of cross-sectional characteristics among hairs from different parts of the body. Hairs were correctly attributed to a given species in 90% of blind identification tests on 105 reference photographs (95% C.I.: 0.83–0.95). When we excluded eland (*Taurotragus oryx*), which are outside the normal size range of wild dog prey and extremely unlikely to be missed in field observations, the proportion of correctly identified hairs rose to 0.93. Small species such as common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*) and scrub hare (*Lepus saxatilis*) were always correctly identified and thus the percentage occurrence in scats was assumed to represent reality for these species, assuming similar passage rates. Bushbuck (*Tragelaphus sylvaticus*) and greater kudu (*Tragelaphus strepsiceros*) could not be accurately differentiated and so these two species were grouped together as one category: greater kudu/bushbuck (following Reynolds & Aebischer 1991).

Feeding trials

We collected 62 scats during the feeding trials. Identifiable hairs were first detected an average of 5.5 hours after feeding (range: 1.3–10.5 hours, S.E. ± 1.52, $n = 5$) and last detected an average of 79.4 hours (range: 72.9–91.4 hours, S.E. ± 6.00, $n = 3$). There was considerable overlap between the detection of consecutive prey despite the fact that frequency of feeds was lower than kill rates reported for field conditions (Fig. 1). The complete detection window could not be determined for the duiker or the second warthog (*Phacochoerus africanus*), as identifiable hairs of both species were still present when scat collection was concluded 244 hours after the commencement of the trial (28.3 hours after the last warthog was supplied). Differences in passage rates among species could not be tested statistically due to limited sample size, however, the data suggest that rates were slightly slower for impala than for either greater kudu or warthog (Table 2).

Comparing dietary composition from scat analysis with direct observations

As a result of these feeding trials we used only single fresh scats that were separated by a minimum of five days (120 hours) to determine dietary composition at VLNR, to ensure that faecal samples collected in the field represented independent dietary events. This period was longer than the detection window obtained from the feeding trials, but was chosen to allow for cases where the pack spent more than one activity period feeding on the same prey item. A total of 149 scats was examined for the three-year period, containing 207 different identified prey items in 11 prey species categories (Fig. 2). As bushbuck were rare at VLNR it was likely that most hairs assigned to

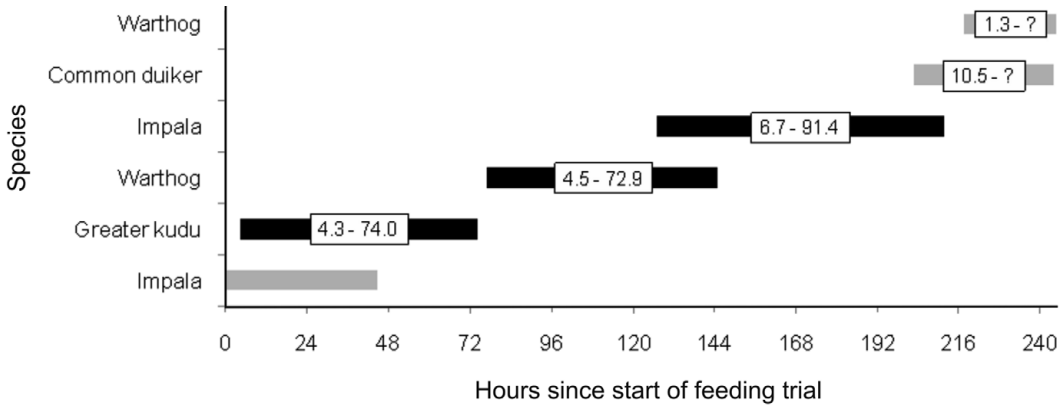

Fig. 1. Overlapping detection windows (hours) for wild dog prey items in scats from feeding trials at Marakele National Park. Shaded boxes indicate incomplete detection windows due to premature termination of scat collection. The lower impala was fed to the wild dogs two days prior to the feeding trial and is shown here to illustrate overlap in faecal content.

the greater kudu/bushbuck category were in fact greater kudu hairs. There was an average of 1.4 prey species/scat (range: 1–5).

A total of 304 kills comprising 14 prey species was recorded at VLNR. The proportion of impala in the wild dog diet was consistent between methods (z = 0.083, P = 0.934). Impala are easily detectable, both in faecal contents and in field observations, with the exception of the impala lambing season (December–February) when small lambs of less than 10 kg are caught more frequently than at other times of the year (Davies-Mostert 2010). However, we did not detect a marked difference in the ability of the two methods to detect impala during the lambing season (z = –1.139, P = 0.255). Impala therefore provide a good benchmark for

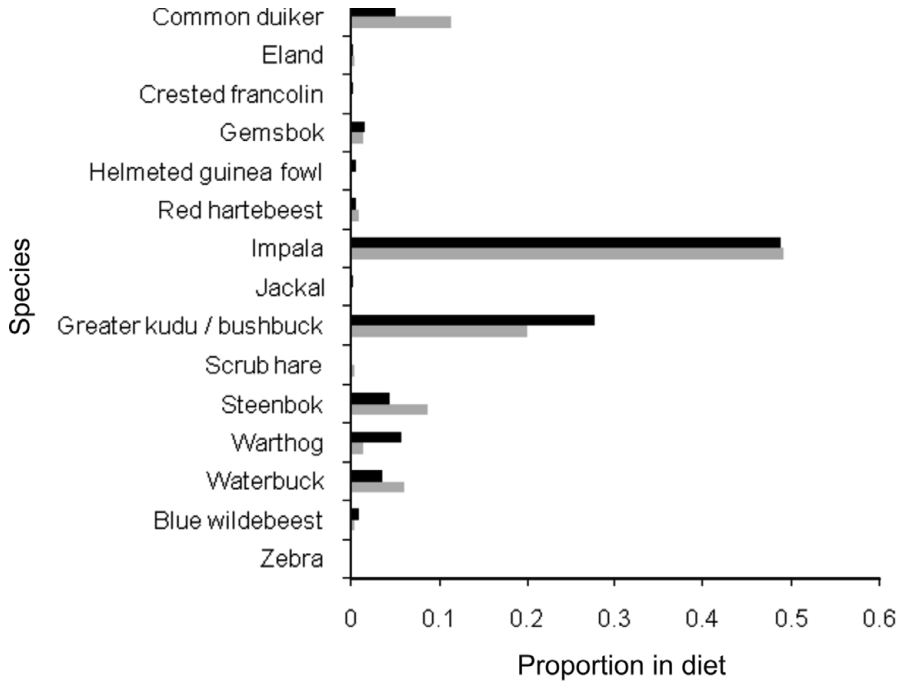

Fig. 2. The proportion of each prey species in the diet of wild dogs at Venetia Limpopo Nature Reserve as determined from direct observations (black bars, n = 304) and scat analysis (grey bars, n = 220).

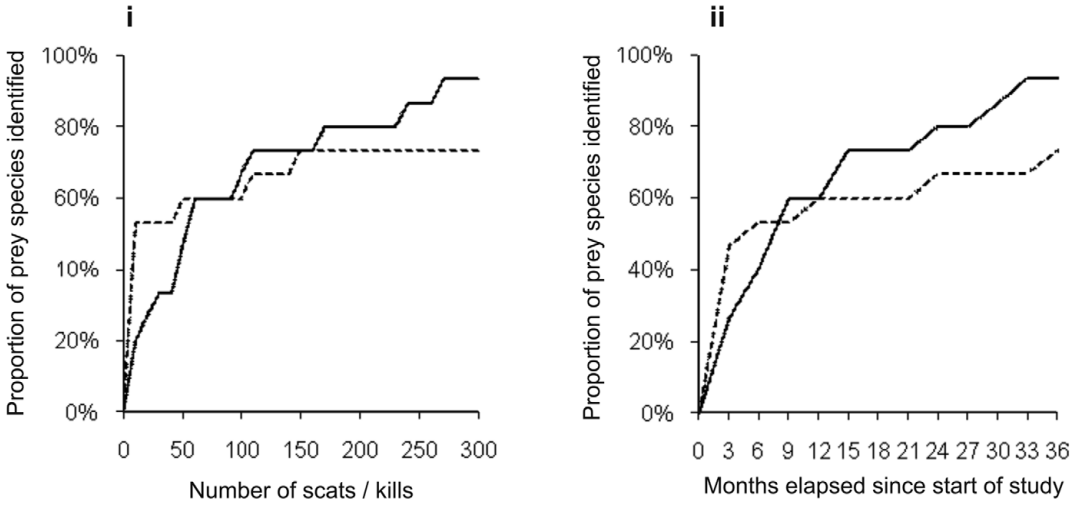

Fig. 3. Cumulative proportion of all prey species identified by (**i**) sample size (scats or kills) and (**ii**) elapsed time (months) in the diet of wild dogs at Venetia Limpopo Nature Reserve as revealed by scat analysis (dashed line) and direct observations of kills (solid line).

Table 3. Correcting scat results for multiple kills of the same species.

Species	Number taken in hunting period		Total hunts	Total items	Correction factor	Number in scats		Proportion in scats	
	One	Two				Counted	Corrected	Counted	Corrected
Common duiker	11	2	13	15	1.15	22	25	0.11	0.11
Impala	126	11	137	148	1.08	100	108	0.48	0.49
Greater kudu	71	4	75	79	1.05	42	44	0.20	0.20

the comparability of the two methods. As predicted, smaller species such as duiker and steenbok comprised a greater proportion of the diet from scat analysis than from direct observations (duiker, $z = -2.44$, $P = 0.015$; steenbok, $z = -2.25$, $P = 0.025$; Fig. 2). Conversely, greater kudu appeared to be under-represented in the scats, and warthogs appeared to be more highly represented in direct observations, although low sample sizes prevented statistical investigation.

Multiple kills of the same species during a single hunting period were recorded for just three species on 17 occasions: duiker, impala and greater kudu. Applying correction factors for multiple kills to the scat results for these species increased the total number of identified prey items in scats from 207 to 220, with negligible effects on the proportional representation of these species in the wild dogs' diet (Table 3). Despite the under-representation of smaller prey species in direct observations, there was strong correlation between the rank-order dietary composition of the wild dog packs as determined by the two methods ($r_s = 0.85$, $P < 0.01$, 9 d.f.).

Cumulative species curves show that 50% of all prey species were detected after analysing just 10 scats whereas 50 observations of kills were necessary before 47% of prey species were detected (Fig. 3). Four prey species – black-backed jackal (*Canis mesomelas*), cow (*Bos taurus*), helmeted guinea fowl (*Numida meleagris*) and crested francolin (*Dendroperdix sephaena*) – were detected by direct observation but not identified in scat analysis. One prey species (scrub hare) was identified in scats but not observed in kills. All of these species occurred at a frequency of <0.67% in the diet.

DISCUSSION

The determination of maximum detection periods for wild dog ungulate prey enables the application of methodical faecal collection to reduce sampling

bias in field studies. The time to first detection of wild dog prey species was similar to rates found for wolves (8 hours: Floyd *et al.* 1978), however, the detection window was longer, at 79.4 hours, than had been anticipated. The similarity in passage rates of the different prey species corresponds to earlier studies on wolves (Floyd *et al.* 1978). Wild dogs are strictly carnivorous and passage rates would be less uniform among food items of omnivorous canids such as red foxes (*Vulpes vulpes*) (Reynolds & Aebischer 1991) or side-striped jackals *Canis adustus* (Atkinson *et al.* 2002). The small sample sizes included in this study precluded any rigorous determination of interspecific variation in detection windows. We therefore advocate further passage rate studies to confirm the results of this study, and increase the number of prey species for which passage rate estimates are available.

The variable probability of correctly attributing a hair to a given species raised some concerns about the ability of faecal analysis to determine accurately the diet of large carnivores preying on ungulate prey. To our knowledge, blind tests of hair identification have not been performed in other faecal studies. Further work to estimate the extent of researcher error will help to quantify the effects of misidentification of prey remains. Fortunately we were able to identify accurately those species of particular interest to this study – namely the small prey items that we postulated would be underrepresented in direct observations – and were thus able to proceed with our comparison of the dietary composition obtained from each method.

Kruuk (1972) found a strong correlation between dietary composition from faecal analysis and direct observations in spotted hyaenas (*Crocuta crocuta*), although the relationship was less clear for brown hyaenas (*Hyaena brunnea*) because of the numerous very small items they eat, such as insects (Mills & Mills 1978). The strong rank-order correlation between methods found in this study suggests that scat analysis can disentangle the relative importance of various prey in the wild dog diet which, in southern Africa, is comprised mainly of medium-sized ungulates (Hayward *et al.* 2006). For some individual prey species, however, the differences between the two methods were pronounced: duiker and steenbok were more than twice as common among scats than direct observations, and scrub hares were detected once among scats but not among kills. The under-representation of small prey items is likely to be more pronounced among pack animals that consume their prey quickly.

Our method of ensuring independence of samples means that these differences are likely to reflect the real inability to detect small prey by direct observation where relatively long periods are spent in inaccessible habitats where direct observation is impossible, or when prey are caught at night. However, as impala and greater kudu/bushbuck were the only species to comprise greater than 11% by percentage occurrence of the total diet, the differences observed for less common species were unlikely to have an important quantitative effect on estimation of wild dog diet overall. It is worth noting that warthogs were unusual in that they were detected 3.9 times more frequently in observed kills than in scats. This is attributed to the fact that warthogs are difficult prey to capture, take longer to kill, are highly vocal when attacked, and are thus more likely to be located during follow periods. They are also not very hairy, which reduces the frequency of occurrence of – and thus the ability to detect – identifiable remains in scats.

Independent faecal sampling quickly identifies the most important species in the diet. However, species accumulation curves illustrate the potential shortcomings of faecal sampling to detect uncommon species. If the determination of dietary diversity is an important objective, it may be necessary to analyse a greater number of non-independent samples to ensure that rare species are detected. In this study, all species undetected in scats occurred at low frequencies (<1%) in direct observations and predation on these species was therefore assumed to be unimportant in terms of overall provision of biomass.

Percentage occurrence is, by its very nature, likely to overestimate items in low proportions and underestimate those at high proportions (Lockie 1959). Floyd *et al.* (1978) derived an equation to improve estimates of the relative mass of large and small prey consumed, and this method has been used in a number of studies to convert percentage occurrence into relative biomass consumed (Reynolds & Aebischer 1991; Weaver 1993; Marker *et al.* 2003). This method is problematic for wild dogs and other carnivores that prey on a wide range of species in different age and sex classes. Many ungulates exhibit marked sexual dimorphism and size differences among age classes (Smithers 1983), and as scat contents do not allow for differ-

entiation between these the presence of identifiable remains in a scat provides little information about actual biomass killed and consumed. Added to this is the impracticality of calculating meaningful biomass correction factors for a multitude of prey size categories: in this study prey sizes ranged through numerous classes from crested francolin (<0.5 kg) to adult female cow (~460 kg). We therefore contend that direct observation, which enables differentiation between age and sex classes, remains the most reliable way to obtain estimates of relative biomass consumed by wild dogs, and even condition of prey. Differential selection for certain sex or age or condition categories influences the population effects of predation and so is an important consideration.

We conclude that direct observations can underestimate the consumption of small prey when conditions prevent full visual contact at all times. Under these circumstances faecal analysis can provide complementary information for a reconstruction of diet. Our study pack happened to eat relatively few small prey and so this bias had little effect on our overall understanding of wild dog diet, however, in areas where small prey form a significant proportion of the diet, the effects are likely to be significant (*e.g.* Laikipia, Kenya; Woodroffe *et al.* 2007).

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