Diet composition of black-backed jackals, *Canis mesomelas* in the Namib Desert

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Abstract. Black-backed jackals (*Canis mesomelas*, Schreber, 1775) survive in a wide range of environments. Their foraging strategies are highly variable in different habitats. Adaptations in foraging behaviour in relation to abundance and quality of food sources are expected to be highly pronounced in an extreme habitat like a desert. This study investigated the diet composition in black-backed jackals in the Namib Desert by analysing faecal samples collected between February 2004 and August 2005. Frequency of occurrence, relative dry mass and proportion of biomass consumed were calculated for different prey items. Insect parts, mainly of two species – the giant longhorn beetle (*Acanthophorus capensis*) and a locust (*Anacridium moestum*) – were found in 72.2% of the samples and were estimated to have contributed 22% to the biomass consumed. Mammals, predominantly rodents and ungulates, represented the highest proportion of biomass consumed (42%), although their remains were found in only one third of the samples. Based on biomass, mammals are assumed to be the jackal's preferred prey, but, probably due to lower abundance, more difficult to obtain than insects. More than 50% of the samples contained plant material, mainly seeds of !Nara plants (*Acanthosycios horridus*) and false ebony (*Euclea pseudebenus*), especially during their fruiting seasons. Although the abundance of *A. capensis* and of *A. moestum* varied annually, their remains were found in scats throughout the year, indicating a certain degree of specialization on these prey species.

Key words: diet frequency composition, prey abundance, foraging strategy, desert habitat

Introduction

Black-backed jackals (*Canis mesomelas*) are common and socially adaptive African carnivores (McKenzie 1997). They are distributed in a wide range of habitats, from desert areas to farmlands and villages, and often occur sympatrically with other carnivore species (Nel & Loutit 1986). Besides occurring throughout southern Africa up to the Zambezi River, they are also distributed in Eastern Africa, north and east of the Olduvai rift (Loveridge & Nel 2004). Several studies have documented the diet of black-backed jackals (Bothma & Du 1971, Stuart 1976, Moehlman 1978, Stuart & Shaughnessy 1984, Nel & Loutit 1986, Avery et al. 1987, Hiscocks & Perrin 1987, Dreyer & Nel 1990, Nel et al. 1997). These studies recorded highly variable proportions of mammals, arthropods and plants in the diet of different populations. In Kwazulu-Natal (South Africa), jackals fed mainly on carrion from antelopes in nature reserves, while in farming areas the main food source was carrion from sheep (Rowe-Rowe 1976, Nel & Loutit 1986). At the Namib Desert coast, birds were the main food source, followed by seals and invertebrates (Nel et al. 1997); at Cape Cross, the diet during some periods consisted almost 100% of seal (Nel & Loutit 1986). In the Natal Drakensberg (South Africa), about 55% of the food consisted of small mammals; only 11% was antelope. In the

Central Namib Desert (Namibia), food composition varied at different study sites. At Sandwich Harbour, the main food sources were mammals and birds, at Gobabeb they were plants and insects, and at Ganab they were small mammals (Stuart 1976). Finally, in the Serengeti National Park (Tanzania), scat analyses indicated that the jackals consumed more arthropod food in the wet and more mammalian food in the dry season (Lamprecht 1978). This flexibility in food choice is assumed to be the key to their success and wide distribution in eastern and southern Africa.

Optimal foraging theory predicts that prey choice is affected by prey abundance, the energetic value of a prey item and the costs of searching, handling and consuming the prey (MacArthur & Pianka 1966). The time and energy costs needed to search and successfully hunt a certain prey species have to be outweighed by the resulting energy intake (including specific nutrients like protein). Therefore, predators should be choosy in selecting their preferred prey, and their choice is predicted to be affected by changes in the abundance of specific prey species. This means that the most energy-rich food items should be taken at a constant rate, whereas the intake of less nutritional food should vary with the abundance of the food item. Field studies on several carnivore species have supported predictions of prey choice and hunting behaviour (Scheel 1993, Weber 1996, Krüger et al. 1999, Hernández et al. 2002).

This study investigates the diet composition of black-backed jackals in a desert area. The occurrence and relative dry mass of different food items in individuals' scat samples were analysed, compared between the wet and dry season and – in the case of insects – related to changes in prey abundance. The estimated proportion of biomass consumed was calculated for the main prey categories.

Material and Methods

Study site

Faecal samples were collected in a 6.25 km² area, stretching about 2 km south into the Namib Sand Sea from the Gobabeb Training and Research Centre (GTRC; S 23°33'40", E 15°02'14") and about 3 km along the Kuiseb River bed. The Kuiseb only carries water for several days per year (usually January to February), but the river bed provides groundwater throughout the year. Therefore, dense vegetation dominated by *Acacia erioloba*, *Faidherbia albida* and *Salvadora persica* develops in the river bed. Climate divides the year into a wet (October to March) and a dry season (April to September), the wet season containing the hottest months of the year.

The fruiting of the !Nara melon generates another annual cycle: low production from May to October, early fruiting season from November to January (medium production), and high production season, when most plants carry fruits, from February to April (Henschel et al. 2004).

Scat collection

Two-hundred samples of jackal faeces were collected between February 2004 and 2005. Sampling was carried out on 3 days per week in the morning by following recent jackal tracks (mean number = 13.2 scats/month). To exclude samples from other canids like dogs or foxes, jackal tracks were identified by the characteristic paw prints jackals leave in the sand. Jackal's paw prints are elongated, showing two long middle toes converging at the base and a triangular main pad. Domestic dog's paw prints are almost round with equally long toes, while cape foxes (*Vulpes chama*) have much smaller paws with hair between the toes, which obscures the track. Genetic analyses of 16 scat samples confirmed the species identification and distinguished a minimum of 16 different individuals, 9 males and 7 females, in the study area (Goldenberg et al. unpublished).

Scat analysis

The faecal samples were dried and weighed, and all food remains were separated and identified by macro-analysis (chitin extremities of insects and mammalian hair) following Stuart (1976), Lamprecht (1978) and Rowe-Rowe (1983). The GTRC curates an extensive collection of local insect and plant specimens, which, together with identification literature (Scholtz & Holm 1985), was used to analyse all prey items in the samples. Insect identification was possible to the species level because insect extremities are not digested. Counting the number of extremities, wings or heads in the scats provided an estimate of the number of individuals ingested. Hair in the scats was analysed by reflective polarization microscopy with a Zeiss Reflection Microscope (Perrin & Campbell 1980) using reference samples of the collection of the National Museum of Namibia in Windhoek. Species-typical patterns of the hair structure visible under the microscope according to Scholtz & Holm (1985) were used for analysis to the genus level; a more detailed identification was not possible with this method. Identified prey parts of insects, mammals and plants were sorted, counted and weighed. The Gobabeb herbarium collection was used to identify

plant remains (leaves) in the scats to species level.

Relative frequency of occurrence (percentage of samples containing each food item) was used as a measure of how common a food item is in the jackals' diet (Kelly & Garton 1997, Bartel & Knowlton 2005). Relative dry mass (percentage of total dry mass of all prey remains per scat) was calculated to take the relative amount of each prey category in the faeces into account (Angerbjörn et al. 1999, Elmhagen et al. 2002). In the case of insects, the mean number of individuals/scat and, for plant seeds, the mean number of seeds/scat was calculated. Black-backed jackal hair was occasionally found in the samples (5%) and was excluded from further analysis. To estimate the biomass of food consumed by the jackals (Reynolds & Aebischer 1991), dry weights of prey remains were multiplied by coefficients of digestibility (small mammals: 23, medium-sized mammals: 50, birds: 35, invertebrates: 5, plant material: 14), following Goszczyinski (1974) and Jedrzejewska & Jedrzejewski (1998). As carcasses contain a higher proportion of bones than fresh prey, we followed Jedrzejewski & Jedrzejewska (1992) and used a coefficient of 15 for antilope carcasses, due to the lower digestibility of bones (Floyd et al.1978, Kelly & Garton 1997). The method was previously used for different canid species such as golden jackals (*Canis aureus*), a closely related species of similar size (Jedrzejewski & Jedrzejewska 1992, Lanszki & Heltai 2002, Lanszki et al. 2006, Lanszki et al. 2009). We then calculated % biomass of the main food types (plants, insects, birds, mammals).

Insect abundance

A Long-Term Pitfall Trapping Project assesses the desert insect composition around the GTRC (Henschel et al. 2003). Sampling data collected in 8743 sampling days from 1976 to 2000 were available. Because suitable, more recent data was not available, we used the most recent five years with suitable data (1995-2000) to estimate insect abundance. The pitfall traps used consisted either of round tin cups or round plastic buckets (diameter 15 cm, 25 cm deep) placed in groups of three at several sites around GTRC consistent with our sampling area. Captured animals were released at the capture site if they could be identified or were taken to the laboratory for detailed examination before release (Henschel et al. 2003).

In total, animals of 228 taxonomic groups were identified in the traps. Tenebrionids made up 90% of the total capture (71 species), other beetles consited only 0.7%. Recorded insects also included antlions (Neuroptera), ants and wasps (Hymenoptera), crickets and grasshoppers (Orthoptera), earwigs (Dermaptera), fishmoths (Thysanura), springtails (Collembola), and termites (Isoptera). Other captured arthropods included spiders (Araneae, 0.3%), solifugids (Solpugida, 1.48%) and ten specimen of scorpions (Scorpionida, 0.08%), (Henschel et al. 2003, Henschel et al. unpubl. data).

Statistics

Statistical analysis (SPSS 16.0) employed non-parameteric tests. Mann Whitney-U-Tests and Wilcoxon-Tests were used to evaluate the differences between wet and dry season, and Spearman rank correlations to analyse relationships between the occurrence of insects in the pitfall traps and in the faecal samples. If not stated otherwise, means ± SD are shown. The three !Nara fruiting-periods and monthly changes were compared using Kruskal-Wallis Tests. Significance levels ($p \leq 0.05$) of post hoc tests are given after Bonferroni correction.

Results

Two insect species, the giant longhorn beetle (*Acanthophorus capensis*) and the locust *Anacridium moestum* were the most common prey items (Table 1). They were found in 72.2% of the samples. The giant longhorn beetle was found in about half of the samples (0.9 individuals/scat ± 1.43). Up to nine beetles were contained in individual scats. *A. moestum* was found in 41.5%, (1.1 individuals/scat ± 2.19). The maximum number was 15 beetles per scat. In 20.5% of the samples, both species were present. Other insects were found only occasionally (< 4%, Table 1). Mammal remains were present in about one third of the scats: rodent hair was identified in 11%, mainly from *Gerbillurus* sp.; 8.5% of the samples contained artiodactyl hair, with 2.5% identified as *Capra hircus*, the local domestic goat; 5% of the samples contained hair of shrews or hares. Seeds of three plant species were abundant in the scats (Table 1): 23.0% contained seeds of !Nara fruits (*Acathosycios horridus*, 3.8 seeds/scat ± 11.1), 18.5% of the scats contained seeds of the false ebony, *Euclea pseudebenus* (7.7 seeds/scat ± 26.1), 11% yielded *Salvadora persica* seeds (4.0 seeds/scat ± 1.0). The most common prey species, *A. capensis* and *A. moestrum*, accounted for almost 50% of total dry mass (Table 1). The less frequent occurrence of mammal parts was reflected in relative dry mass

Table 1. Food items found in black-backed jackal scats (n = 200). Frequency of occurrence (number of samples containing each food item), relative frequency of occurrence (percentage of samples containing each food item) and mean percentage of dry mass/scat (± SD) are shown. For the main prey categories (insects, mammals, birds, plants) the proportion of total dry mass is shown.

	no. of samples	% of samples	% dry mass
Animal material	178	89.0	69.8
Insects	150	75.0	48.0
Acanthophorus capensis	102	51.0	25.7 ± 33.3
Anacridium moestum	83	41.5	20.2 ± 35.8
Acanthoproctus diademata	3	2.0	0.1 ± 0.8
Leptostaphus waltonii	2	1.0	1.1 ± 10.3
Unidentified tenebrionid beetles	5	3.0	0.9±6.6
Unidentified caterpillars	4	2.0	> 0.01
Other Arthropods	2	1.0	> 0.01
Unidentified Scorpions	2	1.0	> 0.01
Mammals	72	36.0	20.9
Artiodactyla	17	8.5	7.5 ± 19.2
Capra hircus	5	2.5	2.2 ± 14.3
Rodentia (mostly *Gerbillurus* sp.)	22	11	6.9 ± 21.9
Insectivora	6	3.0	1.9 ± 12.8
Lagomorpha	7	3.5	2.3 ± 14.2
Hyracoidea	3	1.5	0.1 ± 1.8
Birds	4	2.0	0.08
Plant material	101	50.5	31.2
Acathosycios horridus	46	23.0	14.7 ± 33.0
Euclea pseudebenus	37	18.5	12.0 ± 30.2
Acacia erioloba	2	1.0	0.5 ± 7.2
Salvadora persica	22	11.0	4.3 ± 16.6
Faidherbia albia	2	1.0	0.2 ± 3.3

(20%). This value per scat was negatively correlated with that of both *A. capensis* (r_s = -0.14, p = 0.03) and *A. moestum* (r_s = -0.29, $p < 0.001$). Hence, samples containing remains of mammals mostly lacked insect parts. Seeds of !Nara fruits or *E. pseudebenus* accounted each for more than 10% dry mass/scat. Biomass estimations showed that, although mammal remains were in fewer samples than insects and plants, their proportion of biomass consumed was highest (42%), followed by insects and plants (Fig. 1). Insects were consumed frequently but the estimated biomass was only half that of mammalian prey. Although more *A. capensis* were present in the pitfall traps in the wet versus dry season (dry season:

0.08 ± 0.3, n = 108; wet season: 0.60 ± 2.3, n = 108; Z = -2.16, p = 0.03), neither the number nor the relative dry mass of the beetles per scat differed significantly between the seasons. Beetles were present in the traps throughout the year but their abundance increased from December until February (Kruskal-Wallis Test, Chi² = 27.7, p = 0.003). We calculated the mean number of *A. capensis* per pitfall trap per month and correlated these values with the mean number of *A. capensis*/scat/month. No significant relationship was found between the number *A. capensis* in the scats and in the traps.

A similar result was found correlating the percentage of scats containing *A. capensis* with the number of *A. capensis* per trap/month (Fig. 2).

The numbers of *A. moestum*, both in the traps and in the scat samples, did not differ significantly between the wet and dry season. Abundances in the traps were quite constant from June until February, but peaked between March and May (Kruskal-Wallis Test, Chi² = 28.7, p = 0.002). The monthly occurrence in the scats did not correlate significantly with that in the traps (Fig. 3). Similar to the beetle, we found no significant relationship between the numbers of *A. moestrum*
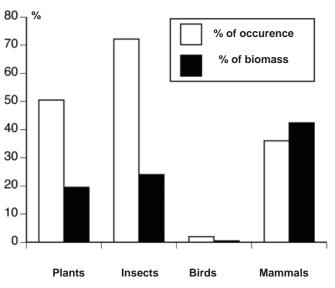

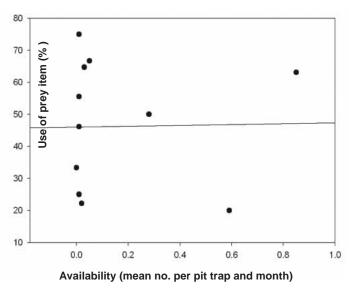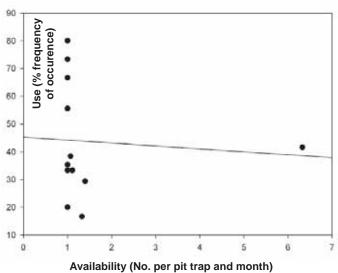Fig. 1. Estimation of ingested biomass for the four prey species groups consumed by jackals.

Fig. 3. Relationship between the percentage of scats containing Anacridium moestum *and the number of* Anacridium moestum *per pit trap/ month, p = 0.35.*
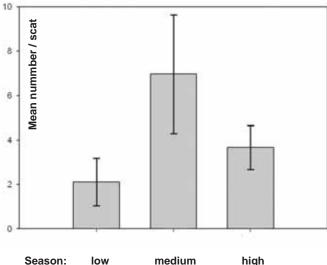

Fig. 2. Relationship between percentage of scats containing Acanthophorus capensis *and the number of* A. capensis *per pit trap/ month, p = 0.15.*

Fig. 4. Seasonal changes in the mean number ± SD of !Nara seeds per sample in the low (May to October, n = 66), medium (November to January, n = 39) and high fruiting season (February to April, n = 95).

individuals in the pitfall traps and in the scat samples. Mean dry mass of mammal remains in the scats did not differ significantly between the wet and dry season.

Both the number and the relative dry mass of *E. pseudebenus* seeds differed significantly between the two seasons. Dry season samples contained more *E. pseudebenus* seeds than those from the wet season (number: $mean_{dry}$ 16.3 ± 38.2, n = 63; $mean_{wet}$ 3.8 ± 16.7, n = 137, $p > 0.001$, Z = -3.75; dry mass: $mean_{dry}$ 7.3 ± 14.9, n = 63; $mean_{wet}$ 2.1 ± 8.4, n = 137, $p < 0.01$). We found no significant differences in the number of !Nara seeds per scat and relative dry mass between the dry and wet season, but the mean number per scat differed significantly between the !Nara growth periods (Kruskal-Wallis Test, $p = 0.04$). In the non-fruiting season, the faeces contained significantly fewer seeds than in the two other periods (Mann-Whitney-U-Test: low vs. medium fruiting season: $p = 0.004$, Z = 2.85; low vs. high season: $p = 0.01$, Z = -2.53; medium vs. high season: *n.s.*); (Fig. 4).

Discussion

Finding food is one of the most challenging tasks for survival in the harsh desert environment. This requires well-adapted strategies of food acquisition. One strategy is to specialize on one exploitable source, whilst the alternative is to generalise. Previous research shows that the flexibility of jackals in their food choice and their ability to adopt suitable foraging behaviours enables them to survive in different habitats (Rowe-Rowe 1976, Stuart 1976, Lamprecht 1978, Nel & Loutit 1986, Avery et al. 1987). This indicates that jackals are opportunistic feeders.

Our study demonstrates the broad range of potential prey items in the desert environment. It also provides evidence that jackals are not exclusively opportunistic but, as predicted by the optimal foraging theory, prefer highly nourishing, protein-rich food sources even in periods of low abundance (MacArthur & Pianka 1966). Similar results were obtained from coyotes in the Chihuahuan Desert (Hernández et al. 2002). Coyotes occupy an ecological niche in the American deserts similar to the one occupied by jackals in the African deserts.

Insects, in particular beetles, form a major part of the Namib Desert's biomass (Louw & Seely 1982). Since large beetles and locusts are protein rich and easy to catch, a rather large proportion was expected in the jackal scats. In fact, they were found in most of the samples and in a higher proportion than other prey items (e.g. the giant longhorn beetle *A. capensis* in more than half of all samples). This beetle (mean weight 1.8 g) has a very large abdomen and shows peak abundance after floods. The pit trap data clearly show consistent differences in occurrence between the wet and dry season. However, *A. capensis* occurred in the jackal scats throughout the year. This leads to the conclusion that jackals search for this specific beetle, digging it out during the dry season because of its high nutritional value. Although no detailed pit trap data were available for the year of the study, preliminary data collected in 2004-05 supported the consistent seasonal patterns in abundance for both *A. capensis* and *A. moestum* (Henschel et al. unpublished).

Another major insect component in the diet was the large locust *A. moestum* (mean weight of 2.6 g). These grasshoppers sit on the dunes and feed on grass and other detritus there. They are relatively slow in taking flight and can be easily caught by jackals. Similar to the beetles, the locusts were caught by the jackals throughout the year at a quite constant rate.

Although insects were frequently eaten by the jackals, their contribution may be over-estimated when using a simple frequency of occurrence measure (Angerbjörn et al. 1999). This is indicated in the biomass estimation, where insects represent about 20% of biomass consumed. Similar results were found using other methods to estimate biomass (Floyd et al. 1978, Putman 1984, Weaver 1993). Some of these calculations have shown discrepancies in estimating bird remains (Reynolds & Aebischer 1991), but as bird parts were present in only 2% of our samples, this problem was negligible here. Previous studies on *C. mesomelas* did not use biomass estimations, hence the diet composition of different jackal populations cannot be compared on this level. However, the insect proportion of consumed biomass in our species was up to tenfold higher compared to certain other canids like golden jackals (Lanszki et al. 2009) or coyotes (Neale & Sacks 2001).

Mammals, like rodents and ungulates, are apparently another major food source with high nutritive value. The occurrence of rodent remains in jackal scats was similar to earlier studies in the same area. Stuart (1976) reported rodent parts in 13.3% of the samples, compared to 11% in our study. In both periods the frequency of occurrence did not differ between wet and dry season. Rodents can appear in cyclical outbursts and are usually taken in higher proportion during peak years (Krebs & Myers 1974). We did not

measure seasonal changes in rodent abundance in this study, but the scat analysis indicated that rodents were hunted by the jackals throughout the year. Negative relationships between dry mass of insect and mammal remains in individual scat samples suggest that when the jackals were able to feed on rodents or scavenge on larger mammal carcasses they did not search for insects. Considering the biomass proportions, mammals are assumed to be the preferred prey of the jackals but, probably due to lower abundance, less frequently eaten.

Compared with an earlier study on jackal diet carried out at Gobabeb (Stuart 1976), the recent data indicate that plant parts have declined markedly in scats (from 92.6% in 1976 to 50.5% in 2004/05) while the number of insect parts has increased (from 49.6% to 72.2%). The number of ungulate parts has slightly decreased (from 11% to 8.5%). Although the number of goats has increased in the area (Directorate of Extension and Engineering Services 2004), their remains were present in only 2.5% of the scats, indicating that jackals very rarely fed on domestic stock. Jackals are probably unable to kill springbok (*Antidorcas marsupialis*) or oryx (*Oryx gazella*). In grassland habitats, groups of jackals are known to kill antelopes (Lamprecht 1978), but in the Namib Desert, they seem to forage alone or in pairs (Goldenberg et al. unpublished). Hence, another food source for the jackals is carcasses of large prey.

The large melons of the !Nara plant provide moisture which seems to be readily sought by jackals. During the fruiting season, melon leftovers were abundant and scats sometimes exclusively contained !Nara seeds. This preference makes jackals a key distributor of !Nara seeds: they can travel far distances and their carnivorous digestion system cannot digest the seeds (versus donkeys and oryx antelopes, which destroy the seeds and prevent later germination; Müller 2000). During the !Nara melon's non-fruiting season, jackals lick moisture from the !Nara plants on foggy mornings. Potentially, the jackals survive in the Namib Desert without access to open water sources by licking fog and using the moisture of fruits.

Another fruit eaten in large quantities is *E. pseudebenus*, a small, round fruit growing on trees along the Kuiseb river bed. They ripen seasonally and are consumed in vast numbers by birds and mammals. During their fruiting period in the dry season, they are frequently eaten by jackals. Both the !Nara melons and the *E. pseudebenus* fruits appear to be an important part of the jackals' diet.

Overall, this study indicates that nutritive prey items that are easy to catch, like the giant longhorn beetle, are an important component of the jackal diet throughout the year, independent of its seasonal changes in abundance. Mammals, particularly rodents, represent a major part of the biomass consumed, but seem to be more difficult to obtain. On the other hand, the seasonal variation of plant parts in scats demonstrates the opportunistic aspect of their foraging behaviour. This flexibility enabled jackals to inhabit the entire southern African continent. The extremely limited resources in the desert demand efficient foraging strategies for reproduction and survival.

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