

Extension of the diet of an extreme foraging specialist, the aardwolf (*Proteles cristata*)

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The aardwolf, *Proteles cristata*, is a highly specialized myrmecophagous carnivore that feeds almost exclusively on termites of the genus *Trinervitermes*. Here we report data from an ongoing analysis of aardwolf diet, where we documented remains of sun spiders and scorpions in aardwolf scats. Although the prevalence of these items was low, with sun spiders recorded in nine and scorpion remains in one of 246 scats, our observations suggest that aardwolves opportunistically feed on larger prey than previously thought. However, our observations do not suggest that aardwolves utilized these large prey items as alternatives to their main food resource during periods of food scarcity. Therefore, we suggest that the adaptive advantages of such opportunism may be small, but that the observed behavioural plasticity could be advantageous under specific environmental conditions and therefore is maintained as a behavioural trait.

Key words: carnivore, solifugids, diet breadth, resource utilization.

Mammal dietary strategies range along a gradient from generalist to specialist foragers. Generalists feed on a broad spectrum of dietary items approximately in proportion to their immediate availability (e.g. Reid *et al.* 1997), while species that exhibit specialized strategies use a restricted part of available food resources, and typically feed on these more than what would be predicted from their relative availability (Anderson & Erlinge 1977). Therefore, while the adaptive advantages of generalist strategies seem intuitive, the development and maintenance of specialist foraging strategies are puzzling (Abrahams 1987; Abrahams 1999; Fox & Vasseur 2008).

The aardwolf (*Proteles cristata*) is a small (5–10 kg) insectivorous hyaenid that is generally regarded as one of the most specialized foragers within the Carnivora (Koehler & Richardson 1990). There are two subspecies with separate distributional ranges in East and southern Africa. The diet has been quantified for both subspecies (Smithers 1971; Kruuk & Sands 1972; Cooper & Skinner 1979; Bothma *et al.* 1984; Richardson 1987b; Kok & Hewitt 1990; Taylor & Skinner 2000; Matsebula *et al.* 2009), with all studies indicating that aardwolves are extremely specialized and feed almost exclusively on one genus of termite, *Trinervitermes*, occasionally supplemented with the harvester termite *Hodotermes mossambicus* in southern Africa (Richardson 1987a). Other taxa of invertebrates that have been recorded in their diet include beetles (Coleoptera), ants (Hymenoptera: Formicidae), and other termite genera such as *Odontotermes*, *Macrotermes* and *Lepidotermes*. (Kruuk & Sands 1972; Cooper & Skinner 1979).

Sun spiders (Arachnida: Solifugae) and scorpions (Arachnida: Scorpiones) are commonly found in southern Africa (Dean & Griffin 1993; Griffin 1998; Leeming 2003), and form part of the diet of many birds and mammals (Arlettaz *et al.* 1995; Nel & Kok 1999; Kopij 2002; Kok & Nel 2004; Kopij 2005; Kopij 2007; Pietersen & Symes 2010). Sun spiders are not venomous, but they possess strong chelicerae and it has been suggested that they mimic the hiss of adders by stridulating (Hrušková-Martišová *et al.* 2008), both of which act as a defence mechanism against potential predators. Scorpions in southern Africa vary in venom strength from the highly venomous *Parabuthus* to weakly-venomed species of *Hodogenes*. As far as we are aware, there has been only one previous record of sun spiders in

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aardwolf diets (Smithers 1971), and no records of scorpion remains.

Here we present data on rare or unrecorded incidences of sun spiders and scorpions in the diet of aardwolves from central South Africa, and discuss these occurrences in the light of the dietary strategies of this highly specialized forager.

We conducted the study on Benfontein Game Reserve in the Northern Cape Province, South Africa (28°50'S, 24°50'E), between June 2008 and December 2009. We collected aardwolf scats weekly from middens located within the territories of ten radio-collared aardwolves. Although our study has suggested a substantial home range overlap in aardwolves, most of these ten animals had discrete ranges in relation to each other. We therefore believe that our scat analysis is reflecting the diet of at least 10 animals. Because the area has a distinct seasonal rainfall pattern, we divided each year into a wet and a dry season based on data received from the South African Weather Bureau, and scats were categorized by season. We randomly selected 246 of 521 collected scats, including 128 scats from the wet and 118 scats from the dry season.

We dried scats at 70°C for a period of 24 h and then washed them through a series of sieves to remove excess soil. We analysed washed scats for the presence of arthropod remains, such as termite and ant heads, beetle elytra and any other skeletal remains. To estimate the size of sun spiders and scorpions we measured the length of each sun spider chelicera and scorpion pincer recorded in scats. These were then compared to the same parts from intact specimens collected during a concurrent pitfall survey in the area.

We found remains from the termite *Trinervitermes trinervoides* in all but one of the 246 scats analysed, supporting the expected dietary specialization of aardwolves within our study population. In addition we found remains of sun spiders in nine of the 246 scats (3.7%), and remains of scorpions in one scat (0.4%). Two of the scats containing sun spiders were collected during the dry season and seven during the wet season, while the scat containing the scorpion remains was collected during the wet season. The scats were collected from middens in the home ranges of five different aardwolves, suggesting that they may have been deposited by at least five individuals. The length of sun spider chelicerae varied from 3–5 mm, indicating that the individuals consumed were between 20 and 40 mm in length. The scorpion pincers were 8 mm

long which translates to a scorpion of about 70 mm in length.

Since both the scorpion and most of the sun spider remains were recorded in the scats from the wet season, which is when termites are most available as prey, our observations suggest that neither sun spiders nor scorpions were utilized as alternative prey during periods of food scarcity, but rather were consumed opportunistically. Since sun spiders are active and can deliver a painful bite (Leeming 2003; Hrušková-Martišová *et al.* 2008), it seems unlikely that they were ingested accidentally. We identified the scorpion as *Opisthophthalmus* sp. (Scorpionidae). These scorpions are sit-and-wait predators (Leeming 2003), similarly suggesting that their consumption was unlikely to be accidental.

Our observations suggest a degree of opportunism in aardwolf foraging behaviour, since both sun spiders and scorpions appear to have been actively preyed upon. Such opportunism can be regarded as adaptive if it helps specialized foragers sustain themselves during periods of food scarcity. However, these large prey items were consumed when the main prey items were most available rendering this explanation unlikely. Alternatively, behavioural plasticity in diet selection may be advantageous to individuals, since using a variety of food items may help individuals survive periods of food shortage, and may also be advantageous at other times, providing extra nutrition during, for example, breeding seasons. We therefore believe that such opportunism may be regarded as latent behavioural plasticity that may only become directly advantageous under specific environmental conditions, but is still retained within the population because it carries low evolutionary costs.

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REFERENCES

- ABRAHAMAS, P.A. 1987. Alternative models of character displacement and niche shift 1. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution* **41**: 651–661.
- ABRAHAMAS, P.A. 1999. The adaptive dynamics of consumer choice. *American Naturalist* **153**: 82–97.
- ANDERSSON, M. & ERLINGE, S. 1977. Influence of predation on rodent populations. *Oikos* **29**: 591–597.
- ARLETTAZ, R., DÄNDLIKER, G., KASYBEKOV, E., PILLET, J., RYBIN, S. & ZIMA, J. 1995. Feeding habits of the long-eared desert bat, *Otonycteris hemprichi* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* **76**: 873–876.
- BOTHMA, J.D.P., NEL, J.A.J. & MACDONALD, A. 1984. Food niche separation between four sympatric Namib desert carnivores. *Journal of Zoology (London)* **202**: 327–340.
- COOPER, R.L. & SKINNER, J.D. 1979. Importance of termites in the diet of the *Proteles cristatus* in South Africa. *South African Journal of Zoology* **14**: 5–8.
- DEAN, W.R.J. & GRIFFIN, E. 1993. Seasonal activity patterns and habitats in solifugae (Arachnida) in the southern Karoo, South Africa. *South African Journal of Zoology* **28**: 91–94.
- FOX, J.W. & VASSEUR, D.A. 2008. Character convergence under competition for nutritionally essential resources. *American Naturalist* **172**: 667–680.
- GRIFFIN, R.E. 1998. Species richness and biogeography of non-acarine arachnids in Namibia. *Biodiversity and Conservation* **7**: 467–481.
- HRUŠKOVÁ-MARTIŠOVÁ, M., PEKÁR, S. & GROMOV, A. 2008. Analysis of the stridulation in solifuges (Arachnida: Solifugae). *Journal of Insect Behaviour* **21**: 440–449.
- KOEHLER, C.E. & RICHARDSON, P.R.K. 1990. *Proteles cristatus*. *Mammalian Species* **363**: 1–6.
- KOK, O.B. & HEWITT, P.H. 1990. Bird and mammal predators of the harvester termite *Hodotermes mossambicus* (Hagen) in semi-arid regions of South Africa. *South African Journal of Science* **86**: 34–39.
- KOK, O.B. & NEL, J. A.J. 2004. Convergence and divergence in prey of sympatric canids and felids: opportunism or phylogenetic constraint? *Biological Journal of the Linnean Society* **83**: 527–538.
- KOPIJ, G. 2002. Food of the lesser kestrel (*Falco naumanni*) in its winter quarters in South Africa. *Journal of Raptor Research* **36**: 148–152.
- KOPIJ, G. 2005. Diet of some insectivorous passerines in semi-arid regions of South Africa. *Ostrich* **76**: 85–90.
- KOPIJ, G. 2007. Seasonal and annual dietary changes in lesser kestrels *Falco naumanni* wintering in Lesotho. *Ostrich* **78**: 615–619.
- KRUUK, H. & SANDS, W.A. 1972. The aardwolf (*Proteles cristatus* Sparrman 1783) as a predator of termites. *East African Wildlife Journal* **10**: 211–227.
- LEEMING, J. 2003. *Scorpions of Southern Africa*. Struik Publishers, Cape Town.
- MATSEBULA, S.N., MONADJEM, A., ROQUES, K.G. & GARCELON, D.K. 2009. The diet of the aardwolf, *Proteles cristatus* at Malolotja Nature Reserve, western Swaziland. *African Journal of Ecology* **47**: 448–451.
- NEL, J.A.J. & KOK, O.B. 1999. Diet and foraging group size in the yellow mongoose: a comparison with the suricate and the bat-eared fox. *Ethology Ecology & Evolution* **11**: 25–34.
- PIETERSEN, D.W. & SYMES, G.T. 2010. Assessing the diet of Amur Falcon *Falco amurensis* and lesser kestrel *Falco naumanni* using stomach content analysis. *Ostrich* **81**: 39–44.
- RICHARDSON, P.R.K. 1987a. Aardwolf: the most specialized myrmecophagous mammal? *South African Journal of Science* **83**: 643–646.
- RICHARDSON, P.R.K. 1987b. Food-consumption and seasonal variation in the diet of the aardwolf *Proteles cristatus* in southern Africa. *Zeitschrift für Säugetierkunde* **52**: 307–325.
- REID, D.G., KREBS, C.J. & KENNEY, A.J. 1997. Patterns of predation on noncyclic lemmings. *Ecological Monographs* **67**: 89–108.
- SMITHERS, R.H.N. 1971. *The Mammals of Botswana*. National Museum of Rhodesia, Bulawayo, Zimbabwe.
- TAYLOR, W.A., SKINNER, J.D. 2000. Associative feeding between aardwolves (*Proteles cristatus*) and aardvarks (*Orycteropus afer*). *Mammal Review* **30**(2): 141–143.

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