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Original Investigation

Ecological relationships of black-footed cats (*Felis nigripes*) and sympatric canids in South Africa

Jan F. Kamler[a,*], Ute Stenkewitz[a], Alexander Sliwa[b], Beryl Wilson[c], Nadine Lamberski[d], Jason R. Herrick[e], David W. Macdonald[a]

[a] *Wildlife Conservation Research Unit, Department of Zoology, Oxford University, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, United Kingdom*
[b] *Cologne Zoo, Riehler Street 173, Cologne 50735, Germany*
[c] *McGregor Museum, PO Box 316, Kimberly 8300, South Africa*
[d] *Harter Veterinary Medical Center, San Diego Zoo Safari Park Veterinary Services, 15500 San Pasqual Valley Road, Escondido, CA 92027, USA*
[e] *Center for Conservation and Research of Endangered Wildlife, Cincinnati Zoo and Botanical Garden, Cincinnati, OH 45220, USA*

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ABSTRACT

The black-footed cat (*Felis nigripes*) is sympatric with several species of larger carnivores, although it is not known how this species partitions resources with potential competitors. From 2006 to 2008, we captured, radio-collared, and monitored 3 adult black-footed cats on Benfontein Game Farm in South Africa. We investigated their spatial, habitat, temporal, and dietary overlap with Cape foxes (*Vulpes chama*), bat-eared foxes (*Otocyon megalotis*), and black-backed jackals (*Canis mesomelas*) that were monitored during a concurrent study. Annual home range sizes of black-footed cats were 7.1 km^2 for the adult female, and 15.6 and 21.3 km^2 for the two adult males. Home ranges overlapped completely with the canid species, whereas core areas overlapped the most with jackals (79%), compared to Cape foxes (28%) and bat-eared foxes (21%). Within home ranges, black-footed cats selected habitats in proportion to availability, similar to Cape foxes, but in contrast to jackals and bat-eared foxes. Black-footed cats were primarily nocturnal, and their activity patterns significantly differed from jackals ($P < 0.001$), marginally differed from bat-eared foxes ($P = 0.082$), but did not differ from Cape foxes ($P = 0.717$). Dietary overlap of black-footed cats was high with Cape foxes ($R_0 = 0.83$), compared to jackals ($R_0 = 0.42$) and bat-eared foxes ($R_0 = 0.12$). Two black-footed cats were killed by predation, at least one of which appeared to be by jackals. We conclude that black-footed cats coexisted with jackals by using burrows during the day, and by partitioning activity and diets, but not space. In contrast, black-footed cats appeared to coexist with Cape foxes by partitioning space, but not habitats, activity, or diets. Black-footed cats exhibited relatively low amounts of overlap with bat-eared foxes across resources. Our results show that black-footed cats partitioned resources differently among the sympatric canids, which ultimately facilitated coexistence with these larger carnivores.

Introduction

Black-footed cats (*Felis nigripes*) are endemic to southern Africa and are listed as threatened by the IUCN (Sliwa 2008). They are one of the smallest felids in the world (1–2 kg), and their nocturnal and secretive nature makes them difficult to study. Black-footed cats are specialists of open short grassland, making this species rare compared to other small cats in southern Africa (Sliwa 2008). Previous research in South Africa showed that black-footed cats consumed primarily small rodents and birds, and that diets varied by season and sex (Sliwa 2006). Mean home range sizes of black-footed cats were nearly twice as large for males (16.1 km^2) than for females (8.6 km^2), with home ranges of males overlapping the ranges of several females (Sliwa 2004).

Despite the previous research on this species, nothing is known about the interspecific relationships of black-footed cats and other carnivores. For example, black-footed cats are sympatric with a high diversity of small and medium-sized carnivores in southern Africa, but how the former species partition resources and coexists with larger carnivores has not been studied. This information

* Corresponding author. Tel.: +44 0 1865 611100; fax: +44 0 1865 611101.
E-mail address: jan.f.kamler@gmail.com (J.F. Kamler).

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is important for their conservation, because predation and competition from larger carnivores may be an important threat to this small species (Sliwa et al. 2010).

In South Africa, black-backed jackals (*Canis mesomelas*; 7–10 kg) potentially could be the greatest competitor and predator of black-footed cats, based on the negative relationships between numbers of jackals and smaller carnivores (Blaum et al. 2009; Bagniewska and Kamler 2014), and the lethal and nonlethal effects jackals had on both Cape foxes (*Vulpes chama*; 3 kg) and bat-eared foxes (*Otocyon megalotis*; 3–4 kg; Kamler et al. 2013). For example, black-backed jackals were shown to kill both Cape foxes and bat-eared foxes, probably for territorial reasons (Kamler et al. 2012). Consequently, to coexist with jackals, Cape foxes spatially avoided jackal core areas when foraging and establishing den sites, and they selected habitats for den sites that were used least by jackals. Cape foxes also were more nocturnal than jackals, and they consumed primarily small rodents whereas jackals consumed primarily large ungulates (Kamler et al. 2012). Bat-eared foxes appeared to coexist with jackals by spatially avoiding jackal core areas when establishing den sites, consuming primarily insects and fruits, and by increasing group sizes to deter predation (Kamler et al. 2012). Additionally, both fox species had positive associations with each other while foraging and establishing den sites, likely because both were using the same areas outside of jackal core areas as refuges (Kamler et al. 2012). Thus, if black-footed cats also spatially avoid jackal core areas, then the potential exists for the cats to compete with foxes for limited resources in refugial areas. For example, black-footed cats may compete most with Cape foxes over food resources, as both species were shown to feed primarily on small rodents (Sliwa 2006; Klare et al. 2014).

The purpose of this paper was to examine resource partitioning and the potential for competition between black-footed cats and sympatric Cape foxes, bat-eared foxes, and black-backed jackal in South Africa by determining their spatial, habitat, temporal, and dietary overlap. We also identified mortality factors to determine the potential for interference competition. Based on our previous research (Kamler et al. 2012, 2013), we predicted that black-footed cats would: (1) spatially avoid jackal core areas, and have high overlap of core areas with the fox species; (2) exhibit habitat partitioning with jackals; (3) exhibit temporal partitioning with jackals, but not the fox species, and; (4) exhibit dietary partitioning with jackals and bat-eared foxes, but not Cape foxes.

Material and methods

This research was part of a larger study investigating the ecology and interactions of Cape foxes, bat-eared foxes, and black-backed jackals in South Africa (Kamler et al. 2012). One of the main goals of the larger study was to determine how the fox species partitioned resources and coexisted with black-backed jackals (Kamler et al. 2013). Consequently, all mated pairs of Cape foxes and all family groups of jackals were radio collared and monitored on the study site. Bat-eared foxes were the most numerous canid species, so only a sample of their family groups was collared and monitored. During the study period, members of the Black-footed Cat Working Group (A. Sliwa, B. Wison, N. Lamberski, J. R. Herrick) conducted a concurrent project in which 4 black-footed cats were captured and radio collared. By monitoring the black-footed cats with radio-telemetry, we collected data to allow a post hoc investigation of the niche partitioning between black-footed cats and the sympatric canids.

Study area

We conducted research on Benfontein Game Farm (hereafter, Benfontein; 110 km^2; 28°53′S, 24°49′E), located 8 km southeast of Kimberley, South Africa. At that time, Benfontein was managed primarily for wild ungulate species, including springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas*), and black wildebeest (*Connochaetes gnou*), along with some domestic cattle (*Bos taurus*). All large (>15 kg) carnivore species were extirpated from this area prior to 1900 (Skinner and Chimimba 2005). In addition to black-footed cats and the canid species, other carnivore species present included aardwolves (*Proteles cristatus*), caracals (*Caracal caracal*), African wild cats (*Felis silvestris*), small-spotted genets (*Genetta genetta*), striped polecats (*Ictonyx striatus*), and 5 species of Herpestidae. Aside from one or two annual culls for ungulates on Benfontein, there is relatively little human activity. No carnivore species was heavily persecuted on Benfontein during the study. Vegetation on Benfontein contained elements of 3 major biomes, Savanna, Nama Karoo, and Grassland, although the most dominant was Nama Karoo vegetation (66% of study area). The area had a semi-arid continental climate, with a distinct cold and dry period during winter (Jun to Aug) and a hot and rainy period during summer (Dec to Feb), with intermediate rainfall and temperatures during spring (Sep to Nov) and autumn (Mar to May; Sliwa 1996). The mean (±SD) annual rainfall at nearby Kimberley Airport (1960–2007) was 419 ± 134 mm, although the annual rainfall for 2006 (497 mm) and 2007 (539 mm) was above the long-term mean (unpublished data, South African Weather Service).

Capture and monitoring

Black-footed cats were captured by detecting them with a spot light at night from a vehicle, then either following them to a hole where they were dug out, or throwing a net over them when they squatted on the ground. One cat was anesthetized with a mixture of 0.1 mg/kg of medetomidine and 8 mg/kg of ketamine, and antagonized with 2 mg/kg of atipamezole. The remaining cats were anesthetized with a mixture of 0.1 mg/kg of medetomidine, 5–6 mg/kg of ketamine, 0.1–0.2 mg/kg of Midazolam, and 0.4–0.5 mg/kg of butorphanol, whereas they were antagonized with 1 mg/kg of atipamezole and 1–2 mg/kg of Naltrexone (Lamberski 2015). Cats were fitted with radio-collars (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) weighing 40 g (i.e., ~2% of body mass). The capture and handling protocol for the canid species is given by Kamler et al. (2012). In summary, foxes were captured in wire box traps baited with meat scraps, whereas jackals were captured in padded foothold traps baited with commercial lures. Canids were fitted with radio-collars weighing 1–2% of their body mass. All study animals were sexed, weighed to the nearest 0.1 kg, and aged according to tooth wear, body size, and reproductive condition, then released at the capture site. We classified black-footed cats as adult (>1.5 yr) or subadult (1–1.5 yr). Capture and handling methods followed the animal care and use guidelines of the American Society of Mammalogists (Gannon et al. 2007), and our research protocol for black-footed cats (OBD 2466/2006, Permit 0880/06; OBD 537/2007, Permit 0246/07, OBD 1937/2007, Permit 0756/07) was approved by the Department of Tourism, Environment and Conservation, Kimberley, South Africa.

We located all study animals 2–3 times per week primarily during late afternoon, crepuscular, and nocturnal hours when most were active. We radio-tracked from a vehicle using a null-peak system consisting of dual four-element Yagi antennas. We also radio-tracked on foot using 3-element hand-held antennas to home in on signals during the day to locate den sites. When locating study animals, observers took ≥2 readings from known telemetry stations <5 min apart. We calculated location estimates using the maximum likelihood estimation option in the program Locate II (Pacer, Inc., Truro, Nova Scotia, Canada). Mean (±SE) error of estimated locations was 47.3 (±6.3) m when using reference collars (n = 29) placed at known locations 0.8–1.5 km from observers (i.e.,