SHORT COMMUNICATION

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Do black-backed jackals exhibit spatial partitioning with African wild dogs and lions?

Jan F. Kamler[1] ⓘ | Samantha Nicholson[2] | Ute Stenkewitz[3] |
Tazarve Gharajehdaghipour[4] | Harriet Davies-Mostert[2,5]

[1]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Abingdon, UK

[2]Endangered Wildlife Trust, Modderfontein, South Africa

[3]University of Iceland's Research Centre at Snæfellsnes, Stykkishólmur, Iceland

[4]Canadian Wildlife Services, Environment and Climate Change Canada, Edmonton, AB, Canada

[5]Department of Zoology and Entomology, Eugène Marais Chair of Wildlife Management, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

Correspondence: Jan F. Kamler, Wildlife Conservation Research Unit, Department of Zoology, Oxford University, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, UK.
Email: jan.f.kamler@gmail.com

1 | INTRODUCTION

Interspecific competition among mammalian carnivore species is common and results in a range of different behavioural mechanisms to partition resources and coexist. For example, sympatric carnivore species can coexist via spatial, dietary, habitat or temporal partitioning (Dröge, Creel, Becker, & M'soka, 2017; Kamler, Stenkewitz, Klare, Jacobsen, & Macdonald, 2012; Vanak et al., 2013). Spatial partitioning (i.e. spatial avoidance) is a common mechanism for some, but not all, smaller carnivores to coexist with large carnivores, especially when larger carnivores kill smaller carnivores (Kamler, Ballard, Gilliland, & Mote, 2003; Marneweck et al., 2019; Vanak et al., 2013). For example, black-backed jackals (*Canis mesomelas*), hereafter referred to as jackals, killed cape foxes (*Vulpes chama*), and thus cape foxes spatially avoided jackal core areas when foraging (Kamler et al., 2012). In contrast, although jackals also killed bat-eared foxes (*Otocyon megalotis*) and black-footed cats (*Felis nigripes*), these species did not spatially avoid jackal core areas when they foraged, although bat-eared foxes avoided jackal core areas when denning (Kamler et al., 2012, 2015). Among large carnivores, lions (*Panthera leo*) kill African wild dogs (*Lycaon pictus*), therefore the latter spatially avoided areas of high lion activity (Creel & Creel, 2002; Darnell, Graf, Somers, Slotow,

& Gunther, 2014; Marneweck et al., 2019; Vanak et al., 2013). In contrast, although lions kill cheetahs (*Acinonyx jubatus*) and spotted hyaenas (*Crocuta crocuta*; Périquet et al., 2016), spatial avoidance was not found to occur among these species (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Dröge et al., 2017; Vanak et al., 2013). Reasons for the differences in spatial avoidance of larger carnivores by smaller carnivores is not known, but could be due to the use of other behavioural mechanisms to facilitate coexistence (Broekhuis et al., 2013; Dröge et al., 2017; Kamler et al., 2012; Périquet et al., 2016; Vanak et al., 2013).

Compared to research on the relationships among large carnivores in Africa, the relationships between large carnivores and mesocarnivores have received little attention. This is surprising, given that large carnivores in Africa are sympatric with numerous mesocarnivores, such as jackals, throughout their distributions. Consequently, competitive interactions between large carnivores and mesocarnivores might be greater than is generally acknowledged. For example, jackals have reportedly been killed or consumed by lions (Schaller, 1972; Stander, 1992), spotted hyaenas (van Lawick & van Lawick-Goodall, 1970), brown hyaenas (*Hyaena brunnea*; Mills, 1982), leopards (*Panthera pardus*; Kamler, Loveridge, O'Donnell, & Macdonald, 2020), cheetahs (Hayward, Hofmeyr,

O'Brien, & Kerley, 2006) and African wild dogs (Kamler, Davies-Mostert, Hunter, & Macdonald, 2007), yet the spatial relationships between jackals and larger carnivores have never been studied.

This study determined if spatial partitioning occurred at different scales between jackals and both lions and African wild dogs. Research was carried out on De Beers Venetia Limpopo Nature Reserve (VLNR), where jackals were confirmed to be killed by African wild dogs (Kamler et al., 2007). To our knowledge, this is the first study to investigate the spatial relationships between jackals and large carnivores. Our research will help determine whether jackals use spatial partitioning at different scales to coexist with large carnivores.

2 | METHODS

2.1 | Study site

We conducted research from on VLNR (316 km^2) in Limpopo Province, northeastern South Africa (22°15′–22°30′S and 29°12′–29°18′E). The VLNR has the full array of African large carnivores, including lions, leopards, cheetahs, spotted hyaenas and brown hyaenas, and is enclosed by an electrified predator-proof fence. African wild dogs were the only large carnivore previously extirpated from VLNR, and a pack of 16 individuals was reintroduced there in January 2002, and thereafter their numbers fluctuated annually between 11 and 25 individuals (Davies-Mostert, Mills, & Macdonald, 2013). Lion numbers fluctuated between 12 and 30 across years, whereas population sizes of cheetah, leopard and both hyaena species were low but stable (Davies-Mostert et al., 2013). See Davies-Mostert et al., (2013) for a more detailed description of the study site.

2.2 | Data collection and analysis

We captured jackals using padded foothold traps (see Kamler, Jacobsen, & Macdonald, 2008 for more details) and fitted radio collars (Advanced Telemetry Systems; 190 g) on three captured jackals (1 male, 2 females), which represented three different family groups. No nontarget species were captured during the study. During the first year of monitoring, the male jackal changed groups, and therefore, a total of four different family groups were monitored during the study. The total number of jackal groups in VLNR was unknown. In 2008, three individual African wild dogs were collared from a pack that consisted of 4 adults and up to 11 pups. For lions, at least one male and two females from each pride were collared. Three prides occurred on VLNR during 2018, and each consisted of 3–5 adults and 2–3 cubs. Two few locations were obtained from two lone male lions that were killed in early 2008, so they were excluded from the analysis. Our capture, handling and radio-collaring protocols were approved under permit (AG10610) from the Limpopo Province Department of Agriculture and Environment.

To obtain locations of study animals, Yagi antennas were used to home in on study animals from a vehicle until a visual observation was made, and then, a UTM coordinate was recorded, although if animals were in thick vegetation then sometimes triangulating from short distances was necessary. Study animals were radio-tracked continuously on nearly a daily basis throughout the study on a rotational basis, which typically consisted of two tracking sessions per day (one in morning, one in afternoon), although we used only the first location per tracking session to ensure independence of the location data. When several individuals were collared within the same group, we only used locations of one individual per group. We determined the annual home-range size of study animals using 90% fixed-kernel density estimates (KDE; Worton, 1989) and 50% KDEs to represent their core areas (Kamler et al., 2012; Kamler, Stenkewitz, & Macdonald, 2013). See Kamler, Rostro-García, and Macdonald (2017) for more details about kernel analyses.

We compared data at the home-range level (hereafter, broadscale) and within home ranges (hereafter, fine scale). At the broadscale, overlap of home ranges and core areas were compared between species. At the fine scale, we used utilisation distributions (UD) which provide a useful summary of an animal's use of space within its home range, by transforming the spatial data into a probability distribution (Fieberg & Kochanny, 2005). To measure overlap of intensity of use within home ranges, we used the utilisation distribution overlap index (UDOI; Fieberg & Kochanny, 2005). For two non-uniformly distributed UDs, UDOI values > 1 indicate a high degree of overlap, whereas values < 1 indicate less overlap than expected (Fieberg & Kochanny, 2005). The UDOI was calculated at both 90% and 50% UD isopleth levels based on all locations collected in 2018, to represent intensity of use within home ranges and core areas, respectively. See Kamler et al. (2017) for more details about UDOI analyses. The UDOIs (90% and 50%) were compared between jackals and both African wild dogs and lions using Mann–Whitney U tests, to determine whether jackals spatially avoided one species more than the other. Although some individuals were monitored over several years, only in 2008 were members of the four jackal groups and all three lion prides radio collared, and therefore, we only used data from 2008 in our analyses.

3 | RESULTS

The annual home-range sizes (90% KDE) for the four jackal groups ranged from 2.7 to 9.0 km^2 ($\overline{X}$ = 6.4 km^2). The annual home range of the pack of African wild dogs was 339.5 km^2 in 2008. The annual home ranges of the three lion prides ranged from 112.8 to 208.5 km^2 ($\overline{X}$ = 167.4 km^2).

At the broadscale, all home ranges (90% KDE) of jackals were completely overlapped by those of African wild dogs and lions (Figure 1). Similarly, 3 jackal core areas (50% KDE) were completely overlapped by those of African wild dogs and lions, whereas 1 jackal core area did not overlap either species (Figure 1). At the fine scale, overlap of the UDs within home ranges was low between jackals and
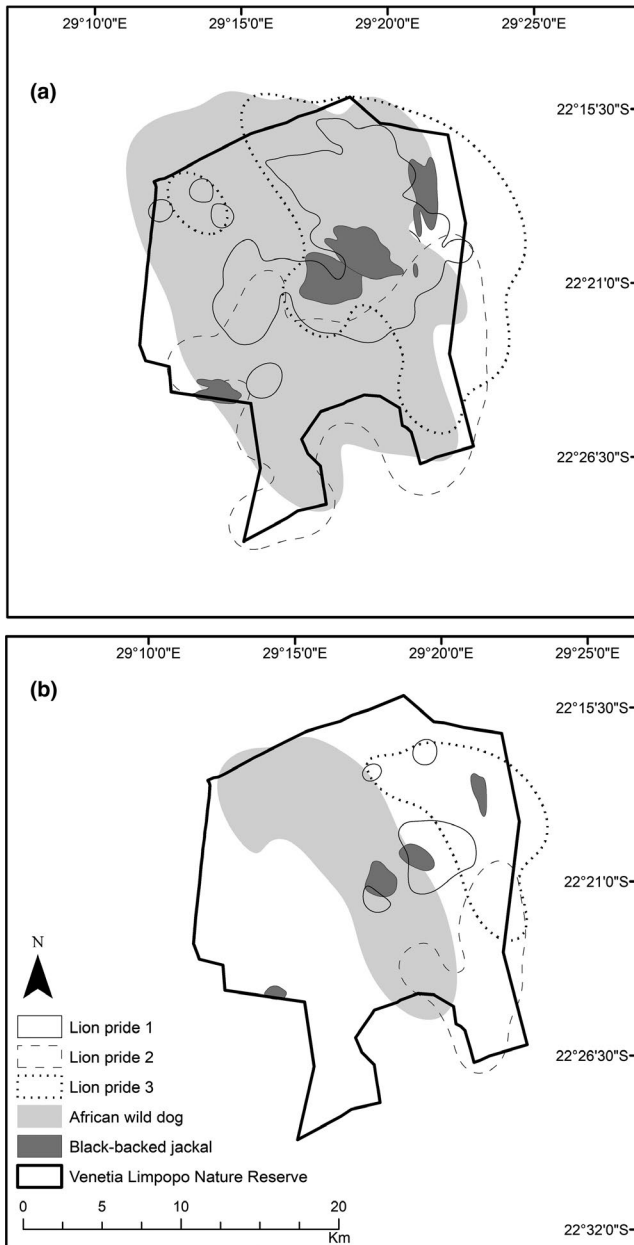
FIGURE 1 The annual (a) home ranges (90% kernel density estimate [KDE]) and (b) core areas (50% KDE) representing four groups of black-backed jackals, one pack of African wild dogs, and three prides of lions that were monitored simultaneously during 2008 in De Beers Venetia Limpopo Nature Reserve, South Africa

African wild dogs ($\overline{X} \pm SE$ = 0.011 ± 0.008; range = 0.001–0.036) and between jackals and lions (0.034 ± 0.021; range = 0.000–0.255), and there was no significant difference in overlap between jackals and both African wild dogs and lions (Z = 0.672, n = 16, p = .501). We excluded the jackal core area that did not overlap either species, and the overlap of the UDs within the remaining core areas was low between jackals and African wild dogs ($\overline{X} \pm SE$ = 0.006 ± 0.006; range = 0.000–0.018) and between jackals and lions (0.011 ± 0.008; range = 0.000–0.063), and there was no significant difference in overlap between jackals and both African wild dogs and lions (Z = 0.000, n = 12, p = 1.000).

4 | DISCUSSION

The extent of spatial partitioning between jackals and both African wild dogs and lions depended on scale. At the broadscale, jackals did not exhibit spatial partitioning with either African wild dogs or lions. In contrast, at the fine scale, jackals appeared to exhibit spatial partitioning with both African wild dogs and lions because the UDOI overlap was relatively low, which indicated that the likelihood of animals occurring in the same area within their home ranges was relatively small. The fine-scale spatial partitioning between jackals and African wild dogs and lions was not surprising, given that both large carnivores kill jackals. Although our sample size of collared jackals was relatively small, we assumed our study animals exhibited typical behaviour and movements of other jackals on VLNR, and thus we feel that our results adequately represent the mechanisms of spatial partitioning between jackals and both large carnivores. That being said, our results should be viewed with caution because our study occurred within a relatively small fenced reserve, so our results might not be applicable to large or unfenced reserves where movements of carnivores are less confined. Also, our study occurred during 1 year, therefore it does not represent the dynamic spatial relationships that might occur between carnivores over the long term. Furthermore, spatial relationships between carnivores likely differ among areas based on differences in large carnivore densities, prey abundance and diversity, and habitat (Gigliotti et al., 2020; du Preez, Hart, Loveridge, & Macdonald, 2015; Rostro-García, Kamler, & Hunter, 2015). Nonetheless, our results provide the first evidence of spatial partitioning between jackals and large carnivores, and we hope future researchers examine spatial partitioning between these species under a variety of environmental conditions across Africa, to help build a more complete understanding of their interactions.

The lack of spatial partitioning between jackals and both African wild dogs and lions at the broadscale was likely due to the excessively large home ranges of the latter two species. The annual home range of the African wild dog pack covered the entire area of VLNR, whereas the home ranges of the lion prides each covered most of VLNR, and thus there was not adequate space in VLNR for jackals to avoid the large carnivores at the home-range level. In comparison, the low overlap of UDs was likely facilitated by the wide-ranging movements of African wild dogs and lions, which allowed jackals to have small areas of concentrated use within the larger home ranges and core area of both large carnivores. The movements and annual home ranges in our study were typical of that previously reported for jackals (Kamler, Stenkewitz, Gharajehdaghipour, & Macdonald, 2019), African wild dogs (Davies-Mostert et al., 2012; Pomila, McNutt, & Jordan, 2015) and lion prides (Loveridge et al., 2009), therefore similar spatial relationships probably occur in other areas where these species are sympatric. In addition to lions and African wild dogs, other large carnivores also kill jackals, so future research should investigate whether spatial partitioning occurs between jackals and leopards, cheetahs and hyaenas.

In addition to spatial partitioning at the fine scale, jackals may have avoided African wild dogs and lions via other mechanisms not investigated during this study. For example, jackals may have used habitat, dietary or temporal partitioning to facilitate coexistence with African wild dogs and lions, similar to that previously reported for other African carnivores (Broekhuis et al., 2013; Dröge et al., 2017; Kamler et al., 2012; Marneweck et al., 2019; Périquet, Fritz, & Revilla, 2015; Périquet et al., 2016; Vanak et al., 2013; Vogel, Somers, & Venter, 2019). Future research should investigate whether jackals use these additional mechanisms to coexist with African wild dogs, lions and other large carnivores.

DATA AVAILABILITY STATEMENT

Data are available on request.

ORCID

Jan F. Kamler iD https://orcid.org/0000-0003-4148-2088

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