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## Note

# Social Organization, Home Ranges, and Extraterritorial Forays of Black-Backed Jackals

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**ABSTRACT** We radio-tracked 15 black-backed jackals (*Canis mesomelas*) from 8 adjacent family groups on Benfontein Game Farm (i.e., Benfontein) in South Africa to investigate their movement patterns and social organization. Jackal family groups consisted of mated pairs (alphas), 0–3 nonbreeding adults (betas), and pups, depending on the season. Mean ( $\pm$ SE) home-range size of alphas ( $9.4 \pm 1.2$  km<sup>2</sup>,  $n = 6$ ) did not differ ( $P = 0.766$ ) from betas ( $9.8 \pm 0.7$  km<sup>2</sup>,  $n = 8$ ). Most beta jackals (8 of 10) remained philopatric on Benfontein, apparently because of the high density of springbok (*Antidorcas marsupialis*), their preferred prey. Three of 5 alphas and all 8 betas went on extraterritorial forays (i.e., forays). Generally, betas spent more of their active time on forays (2–20% of time) than alphas (0–3%;  $P = 0.048$ ), and betas went farther on forays (2–8 km) than alphas (2–3 km;  $P = 0.003$ ). The number of forays differed ( $P < 0.001$ ) among seasons; most forays occurred during summer (64%) when jackals visited neighboring livestock farms, apparently to predate on domestic sheep. Overall, our results indicate forays by jackals are affected by social status, seasonal availability of preferred prey, and the reproductive cycle of jackals. To reduce jackal predation on livestock farms near reserves, we recommend that preventative measures (e.g., use of herders, jackal control activities) be increased during summer when jackals are most likely to travel outside reserves. © 2019 The Wildlife Society.

**KEY WORDS** black-backed jackal, *Canis mesomelas*, excursion, extraterritorial foray, group formation, home-range overlap, social organization, South Africa.

Black-backed jackals (*Canis mesomelas*) are common mesocarnivores that have a wide distribution in eastern and southern Africa. Home ranges of black-backed jackals reportedly are 1–34 km<sup>2</sup> for territorial adults, with larger home ranges for subadults and smaller home ranges for juveniles, in Botswana (McKenzie 1990, Kaunda 2001), Namibia (Hiscocks and Perrin 1988, Jenner et al. 2011), Zimbabwe (Loveridge and Macdonald 2001), and South Africa (Rowe-Rowe 1982, Ferguson et al. 1983, Humphries et al. 2016). Black-backed jackals have a relatively complex social organization, which is based on the degree of territoriality and breeding status within groups. For example, black-backed jackals in South Africa were classified as resident and transient (Humphries et al. 2016), similar to that reported

for coyotes (*C. latrans*; Andelt 1985, Kamler and Gipson 2000, Kamler et al. 2005, Morin and Kelly 2017). Residents typically are family groups comprised of a mated pair (i.e., alphas) along with 0–6 other non-breeding adults (McKenzie 1990, Loveridge and Macdonald 2001, Walton and Joly 2003, Jenner et al. 2011). The non-breeding adults in the group, often called helpers (Moehlman 1979, 1983; Ferguson et al. 1983; Walton and Joly 2003), typically are grown offspring from the previous litter that help their parents raise the next litter (i.e., betas). It is not known if alphas and betas have the same home-range sizes, and little information exists about how often they travel together.

For beta jackals, there are several benefits and costs for remaining philopatric, instead of dispersing. The benefits of philopatry include increasing their survivorship, gaining experience raising pups, potential of inheriting the territory from their parents, and increasing their inclusive fitness via kin selection (Moehlman 1983, 1986). Regarding the last point, betas are typically full siblings to the pups in their parents' next litter; thus, betas are on average as closely

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related to the pups as they would be to their own offspring (Moehlman 1979, 1983). Because the presence of betas increases pup survival in black-backed jackals, betas increase their inclusive fitness via kin selection, in lieu of having their own pups (Moehlman 1979, 1983). The costs of betas remaining philopatric include delaying reproduction, and spending time feeding and guarding pups (Moehlman 1983, 1986). Despite the fact that the benefits of philopatry for both betas and alphas appear to outweigh the costs, only 24% of surviving young black-backed jackals remained philopatric as helpers in East Africa (Moehlman 1986). The costs and benefits of philopatry are likely affected by availability of food resources throughout the year and the availability of vacant territories (Moehlman 1986, Gese et al. 1996); thus, betas in other populations might remain philopatric at higher or lower rates. When betas do disperse, they presumably find mates and establish territories in vacant territories, although little information exists concerning group formation in black-backed jackals.

Territorial animals, from rodents to birds, sometimes travel outside of their territories for short periods, often called extra-territorial forays (i.e., forays; Soulsbury et al. 2011, Mayer et al. 2017). There appear to be 3 main purposes for forays: food acquisition, breeding adults seeking extra-pair copulations, and pre-dispersal exploratory movements by non-breeding subordinates that are seeking vacant territories and possible mates (Soulsbury et al. 2011, Mayer et al. 2017). Among canid species, forays have been reported in wolves (*C. lupus*; van Ballenberghe 1983, Messier 1985, Ballard et al. 1997, Mancinelli and Ciucci 2018), coyotes (Andelt 1985, Kamler and Gipson 2000, Kamler et al. 2004b, Morin and Kelly 2017), bat-eared foxes (*Otocyon megalotis*; Kamler et al. 2017), gray foxes (*Urocyon cinereoargenteus*; Deuel et al. 2017), other foxes (*Vulpes* spp.; Kamler et al. 2004a, Iossa et al. 2008, Soulsbury et al. 2011, Kamler and Macdonald 2014), and black-backed jackals (McKenzie 1990, Kaunda 2001, Jenner et al. 2011). Similar to that reported for other animal species, 1 of the main reasons for forays in black-backed jackals appears to be for food acquisition. For example, black-backed jackals went on forays to access marine food resources on the coast of Namibia (Jenner et al. 2011), to scavenge ungulate carcasses in the Kalahari (Nel 1984), and to form larger groups to hunt large ungulates in Botswana (McKenzie 1990). The seasonality of forays and degree to which alphas and betas use forays differently (e.g., extra-pair copulations vs. food acquisition) has not been studied in black-backed jackals.

Because of extirpations of large carnivores, black-backed jackals are the dominant predator over most of South Africa, including on small livestock farms where domestic sheep are often their main prey (Kamler et al. 2012a; Drouilly et al. 2018; Minnie et al. 2016, 2018). Consequently, jackals are heavily persecuted on small livestock farms because of their real or perceived predation on livestock (Du Plessis et al. 2015; Minnie et al. 2016, Drouilly et al. 2018). In contrast, on many nature reserves, jackals are not hunted, or are hunted at a much lower intensity compared to livestock farms (Kamler et al. 2013b,

Drouilly et al. 2018, Minnie et al. 2018). This has created a source-sink system of jackal populations in South Africa based on anthropogenic mortality, whereby reserves act as source populations of jackals for surrounding livestock farms, which act as sinks (Minnie et al. 2018). Furthermore, jackals living on some reserves may go on forays to surrounding livestock farms, apparently because of the abundance of food there (Kaunda 2001); sheep and other livestock have been reported in scats of jackals living in several different reserves (Bothma 1971, Rowe-Rowe 1976, 1983, Kaunda and Skinner 2003). In contrast, in other reserves there was no evidence that jackals left to predate on sheep in surrounding farms (Drouilly et al. 2018), although reasons for these differences among reserves are unknown. Detailed data are needed on movements of jackals between reserves and surrounding livestock farms because such information would help elucidate reasons for forays and therefore could be used to make recommendations for reducing livestock predation by jackals on farms.

Our objective was to investigate the movement patterns, social organization, and group formation of black-backed jackals, with an emphasis on comparing differences between alphas and betas on Benfontein Game Farm (i.e., Benfontein). We predicted that 1) alphas would have smaller home ranges than betas, 2) home ranges and core areas would overlap more within compared to between groups, and 3) most betas would disperse before their parents' next litter and would attempt to establish territories with other betas in vacant territories. Benfontein is surrounded by a mosaic of differently managed lands, primarily small livestock farms that raise sheep. Thus, we also compared the frequency, distance, and timing of forays between alphas and betas to help elucidate the purpose of the forays and the extent to which jackals used neighboring livestock farms, with the goal of making recommendations to reduce livestock losses. We predicted that 4) betas would go on forays more frequently and for longer distances than alphas, 5) alphas would mostly go on forays during the breeding season (winter) to search for extra-pair copulations within Benfontein, 6) betas would mostly go on forays during the breeding season to search for potential mates and vacant territories outside of Benfontein, and 7) both alphas and betas would go on forays to surrounding livestock farms to consume sheep during winter, which is the main lambing season (i.e., food pulse outside Benfontein).

## STUDY AREA

We conducted research on Benfontein (110 km<sup>2</sup>), near Kimberley, South Africa (28°53' S, 24°49' E). During our study, Benfontein was managed primarily for wild ungulate species, including springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas*), and black wildebeest (*Connochaetes gnou*), with a few domestic cattle. All large (>15 kg) carnivore species were extirpated from this area prior to 1900 (Skinner and Chimimba 2005). In addition to jackals, other carnivore species present on Benfontein included cape foxes (*Vulpes chama*), bat-eared foxes (*Otocyon megalotis*), aardwolves (*Proteles cristatus*), caracals (*Caracal caracal*), African wild

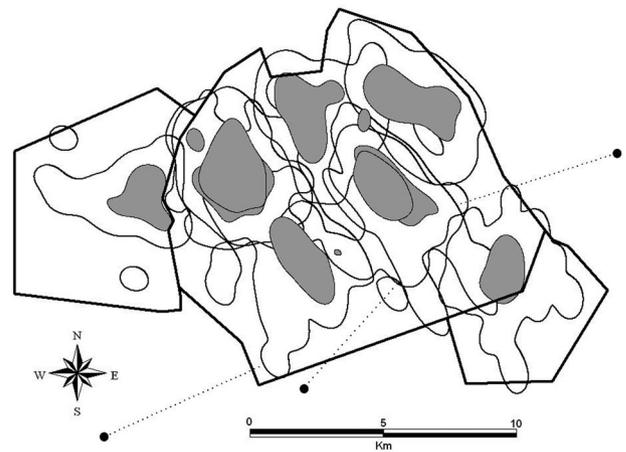
cats (*Felis silvestris*), black-footed cats (*Felis nigripes*), small-spotted genets (*Genetta genetta*), striped polecats (*Ictonyx striatus*), and  $\geq 5$  species of Herpestidae. Aside from 1 or 2 annual culls for ungulates on Benfontein, there is relatively little human activity. Carnivore species were not heavily persecuted on Benfontein during the study, although jackals were occasionally shot ( $<3$  jackal/yr) during culling operations for ungulates. On other game farms in South Africa, jackals often are heavily persecuted because of their perceived predation on game species (Minnie et al. 2018). Because jackals were not systematically persecuted in Benfontein, this site functioned as a reserve rather than a typical game farm; thus, we considered Benfontein as a reserve for the purposes of this paper. In contrast, jackals were heavily persecuted on surrounding livestock farms, to the extent that territorial jackals were almost completely excluded on the livestock farms (Kamler et al. 2013b). Surrounding livestock farms contained mostly sheep, in addition to small herds of domestic goats and cattle (Kamler et al. 2012a). Many owners of livestock farms also managed small herds of wild ungulates, such as springbok, impala (*Aepyceros melampus*), or gemsbok (*Oryx gazella*), to supplement their incomes with safari hunting (Kamler et al. 2012a). Vegetation on Benfontein and surrounding lands contained elements of 3 major biomes, Savanna, Nama Karoo, and Grassland, although the most dominant was Nama Karoo vegetation (66% of study area; Kamler et al. 2012b). 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; Kamler et al. 2012b). Kamler et al. (2012b, 2013b) provide more detailed information about the study site.

One male and 1 female jackal captured and collared on Benfontein had home ranges that occurred partially and mostly outside of Benfontein, respectively. The male jackal had a home range that extended onto Banksfontein Farm, which was an adjacent small game reserve along the southeastern border of Benfontein (Fig. 1). A female jackal had a home range that was almost entirely within the Mauritzfontein Farm, which was an adjacent game reserve along the western border of Benfontein (Fig. 1). The fences between both reserves and Benfontein were porous; thus, jackals could easily move between the properties. Both of these adjacent reserves had similar game species as Benfontein. Additionally, these reserves did not contain sheep, jackals were not persecuted, and both were managed similarly to Benfontein; thus, we considered them to be part of the Benfontein study site.

## METHODS

### Capture and Monitoring

We captured black-backed jackals using padded foothold traps (Woodstream Corp., Lititz, PA, USA) set along dirt roads and intersections throughout Benfontein (Kamler et al. 2008). We set padded foothold traps with a high pan tension to exclude species smaller than jackals (Kamler et al. 2008).



**Figure 1.** Home ranges (95% fixed kernel density estimates [KDE]; thin black outlines) and core areas (50% KDE; solid gray polygons) of 9 black-backed jackals, comprising 7 family groups, that were monitored simultaneously on Benfontein Game Farm and 2 smaller adjoining game reserves (thick black outlines), South Africa, 2006–2007. Note that the smaller ovals represent disjunct parts of jackal home ranges and core areas. The 3 dots and connected dashed lines are examples of extraterritorial forays taken by 3 different jackals to neighboring sheep farms.

Trapping occurred only during winter (May–Aug) to avoid capturing pups younger than 9 months old. We set traps just prior to sunset, checked them at least once during the night, and closed them at sunrise. We fitted captured jackals with radio-collars (Advanced Telemetry Systems, Isanti, MN, USA) weighing 190 g (i.e.,  $\sim 2\%$  of body mass). We sexed all jackals, weighed them to the nearest 0.1 kg, aged them according to tooth wear and reproductive condition, then released them immediately at the capture site. If jackals showed heavy wear on incisors (Gier 1968) and had large testes ( $n = 4$  males) or dark elongated teats (indicating previous nursing;  $n = 1$  female), then we considered them to be adults ( $>12$  months old) when captured and we classified them as alphas. All other jackals (5 male, 5 female) had minor wear on incisors and small testes or small pink teats; therefore, we considered them to be 9–12 months old when captured and classified them as betas. For aging purposes, we assumed a birth date of 1 September based on the approximate date of birth for the pups we observed at den sites during the study. We pulled 1 lower canine tooth from the skulls of 4 jackals (2 alphas, 2 betas) that died during the study, and sent teeth to Matson’s Laboratory (Milltown, MT, USA) to count cementum annuli and determine ages. The cementum annuli counts indicated that the age at capture was 5 years for an alpha male, 4 years for an alpha female, and 1 year for the betas (1 male, 1 female), indicating our age classifications based on tooth wear were accurate. We followed the animal care and use guidelines of the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016) and our research protocol (number 0401/05) was approved by the Department of Tourism, Environment and Conservation (now Department of Environment and Nature Conservation), Northern Cape Province, Kimberley, South Africa.

We radio-tracked individual jackals 2–3 times/week throughout the year from a vehicle using a null-peak system consisting of dual 4-element Yagi antennas. We also radio-tracked on foot using 3-element hand-held antennas to locate den sites. When locating jackals, observers took  $\geq 2$  readings from known telemetry stations  $< 5$  minutes apart. We calculated location estimates using the maximum likelihood estimation option in the Program Locate II (Pacer, Truro, Nova Scotia, Canada). Mean ( $\pm$ SE) error of estimated locations was  $57.3 \pm 6.3$  m when using reference collars ( $n = 29$ ) placed at known locations 0.8–1.5 km from observers (i.e., typical distance when tracking animals). We assumed locations for jackals were independent because we obtained only 1 location/animal during 6 to 8-hour tracking sessions. During each tracking session, we located jackals in a random order at random times. When we located a jackal, we checked if other jackals were traveling with it. We determined group size by observing natal dens of collared jackals several times per month during spring (Sep–Nov) to count the number of adult jackals that visited or associated with the pups. We observed dens with binoculars from  $> 100$  m away to avoid disturbing jackals. For collared jackals within the same group, we determined the percent time they traveled together by counting the number of times they were located within 100 m of each other when foraging, and dividing by the number of locations for each jackal.

### Home Ranges

We determined the home-range size of collared jackals using 95% fixed-kernel density estimates (KDE; Worton 1989). We also calculated 50% KDEs for each jackal to represent their core areas, which are areas of concentrated use within home ranges (Laundre and Keller 1981, Springer 1982). To allow for comparisons with previous studies, we also calculated home ranges and core areas using the 95% minimum convex polygon (MCP) and 50% MCP, respectively. We calculated home ranges and core areas for jackals with 40–100 locations and 6–12 months of tracking. If we monitored a jackal in multiple years, then we included in the analysis only the home range from the first year, unless the jackal changed social status or shifted ranges between years. We quantified KDEs, MCPs, isopleths, and areas ( $\text{km}^2$ ) in the Geospatial Modelling Environment (GME; Beyer 2012). We calculated Gaussian KDEs using the kernel density command in GME (Beyer 2012) and plug-in bandwidth estimator algorithm in the ks package (Duong 2018) of R software (R Version 3.3.2, www.r-project.org, accessed 17 Dec 2016). We compared mean home-range sizes between alphas and betas using independent  $t$ -tests.

The utilization distribution (UD) provides a useful summary of an animal's use of space within its home range, by transforming the spatial data into a probability distribution (Fieberg and Kochanny 2005). The UD also provides a more informative measure of overlap between individuals through indices that are a function of the UD. To measure home-range overlap, we used the utilization distribution overlap index

(UDOI), which compares the 3-dimensional UD between the intersecting and exclusive areas of use (Fieberg and Kochanny 2005). For 2 non-uniformly distributed UDs (the most common situation), UDOI values  $> 1$  indicate a high degree of overlap, whereas values  $< 1$  indicate less overlap than expected relative to uniform space use (Fieberg and Kochanny 2005). The biological interpretation of UDOI is similar to that of Hurlbert's index of niche overlap (Hurlbert 1978), which assumes 2 animals use space independently of each other. We investigated the spatial overlap between all jackals within the same group, and between jackals of neighboring groups. We calculated the UDOI in R software at both 95% and 50% UD isopleth levels to represent home ranges and core areas, respectively, using KernSmooth (Wand 2015) and adehabitatHR (Calenge 2015) packages, and code from Fieberg (2014). We calculated the UDOI between neighboring jackals only if they were monitored during the same period, and we compared results between seasons using Mann-Whitney  $U$  tests. To allow comparisons with previous studies, we also calculated percent area overlap using 95% and 50% MCPs. We determined percent area overlap for 2 jackals by multiplying the area overlap by 2, and then dividing by the area of both polygons (Cole 1949).

### Forays

We defined forays of collared jackals as solitary movements of short duration (1–3 days)  $\geq 2$  km from their home-range boundary (Kamler and Gipson 2000). Nearly all known forays were to surrounding livestock farms outside of Benfontein, or to the core areas of neighboring jackal groups within Benfontein. We did not include foray locations in home-range calculations (Andelt 1985, Kamler and Gipson 2000). We determined the length of known forays by measuring the distance between the foray location and the jackal's home-range boundary, as calculated by 95% KDE. Of 36 forays recorded during the study, we could not calculate distance for 10 forays because the beta jackals traveled too far away to obtain a location (we did not have permission to radio-track on all surrounding properties). Thus, our estimates of foray distances should be considered conservative, at least for the beta jackals. We calculated the percent time that each jackal went on forays by dividing the number of forays by the number of active locations. We compared the percent time alphas went on forays with that of betas using a Mann-Whitney  $U$  test.

We assessed seasonal differences in number of forays and divided the year into spring (Sep–Nov), summer (Dec–Feb), autumn (Mar–May), and winter (Jun–Aug), to parallel major changes in climate and vegetation, and different biological periods for jackals and their main prey (Klare et al. 2010). For example, the 2 birthing periods of springbok, the main prey of jackals on Benfontein, occurred during spring and autumn (Klare et al. 2010). Winter was the main lambing season for sheep on surrounding livestock farms (Kamler et al. 2012a). Jackals gave birth during early spring; thus, their breeding season occurred in winter given their gestation lasts 60–65 days (Walton and Joly 2003). We grouped the number of forays

from all jackals and compared them among seasons using a chi-square goodness-of-fit test.

## RESULTS

We captured, radio-collared, and monitored 15 black-backed jackals from 8 adjacent family groups from July 2005 to March 2008 (Fig. 1). At the time of capture, we classified jackals as 5 alphas and 10 betas. Two betas later formed a mated pair on Benfontein and had pups; thus, we classified them as alphas after they left their respective natal territories and began associating with each other. Jackal family group consisted of 2–5 adults, which included the mated pair (alphas) and 0–3 nonbreeding adults (betas). The only jackal group that we observed that did not have betas was the new group formed by the 2 former betas mentioned above. Within the same group, betas traveled with other betas or alphas only 4.0% (range = 2.1–5.4%,  $n = 5$ ) of the time when foraging, although all monitored betas and alphas often associated with each other at natal dens when pups were present. Two alphas traveled with each other 23.9% of the time when foraging.

There was sufficient data to calculate home ranges for 11 of 15 jackals because 2 jackals were killed by humans 1–3 months after being collared and 2 jackals dispersed from the study site about 2 months after being collared. The mean ( $\pm$ SE) home-range size for all jackals was  $9.67 \pm 0.63 \text{ km}^2$  using KDE, and  $8.57 \pm 0.78 \text{ km}^2$  using MCP. Mean home-range sizes (KDE) were not significantly different ( $t_{12} = -0.304$ ,  $P = 0.766$ ) between alphas and betas (Table 1). Similarly, mean core-area sizes (KDE) were not significantly different ( $t_{12} = -0.715$ ,  $P = 0.486$ ) between alphas and betas (Table 1). Home-range overlap (UDOI 95) between individual jackals was higher ( $Z = -3.450$ ,  $n = 30$ ,  $P < 0.001$ ) within groups ( $\bar{x} \pm \text{SE} = 1.177 \pm 0.113$ ) than between groups ( $0.010 \pm 0.003$ ; Fig. 1). The mean ( $\pm$ SE) core-area overlap (UDOI 50) for jackals within the same group was  $0.538 \pm 0.139$ , whereas core areas never overlapped between jackals in adjacent groups. When using MCP, individual home ranges overlapped 79.2% (range = 64.0–90.0%,  $n = 4$ ) within groups and 1.6% (0.0–16.1%,  $n = 25$ ) between groups, whereas core areas overlapped 68.8% (53.2–90.9%) within groups but never overlapped between groups.

A male (13-M) and female (16-F) beta from neighboring groups formed a pair when they were both about 18 months old, and thereafter used a home range in the area between their respective core areas (Fig. 2). The subsequent home range of 13-M ( $6.1 \text{ km}^2$ ) over the next 12 months was the smallest we recorded for any jackal, and the home range of the 16-F ( $6.4 \text{ km}^2$ ) was only slightly larger (Table 1). Their new home ranges overlapped extensively with jackals from both his natal home range (MCP = 14.2–19.4%) and her natal home range (26.9–31.0%; Fig. 2). This pair produced  $\geq 1$  litter of pups, but then 16-F died because of a non-traumatic cause, possibly disease. Thereafter, 13-M joined the natal group of 16-F, presumably as the new alpha male, and his home range expanded to  $11.0 \text{ km}^2$  (Table 1).

We recorded 36 forays during the study. Most jackals went on forays, including 3 of 5 alphas and all 8 betas that were monitored  $>2$  months. Overall, betas spent more of

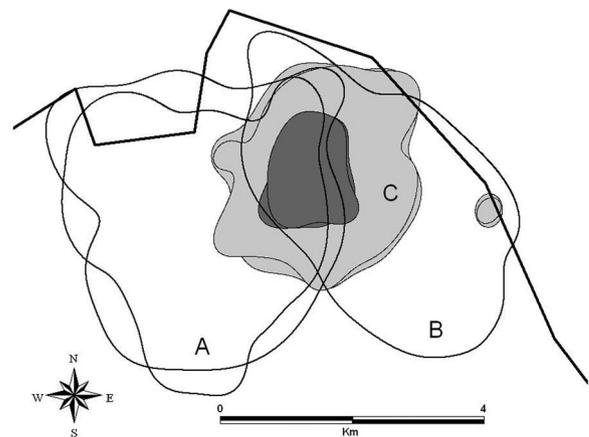
**Table 1.** Home-range sizes (95%) and core-area sizes (50%) of 11 black-backed jackals that we monitored on Benfontein Game Farm, South Africa, 2005–2008 (KDE = fixed kernel density estimate, MCP = minimum convex polygon). For alphas (breeding adults) and betas (non-breeding adults), nomenclature includes the individual's assigned number (ID) and sex (male [M] or female [F]).

ID-sex	KDE (km <sup>2</sup> )		MCP (km <sup>2</sup> )	
	95%	50%	95%	50%
<b>Alphas</b>				
13-M II <sup>a</sup>	6.11	1.54	5.22	1.33
13-M III <sup>b</sup>	10.95	2.37	9.81	2.74
16-F II <sup>a</sup>	6.38	1.47	5.39	1.49
17-M	11.87	2.84	8.84	3.90
53-M	8.80	1.45	9.50	1.16
54-M	12.55	2.60	11.25	2.51
$\bar{x} \pm \text{SE}$	$9.44 \pm 1.24$	$2.05 \pm 0.28$	$8.34 \pm 1.11$	$2.19 \pm 0.47$
<b>Betas</b>				
13-M I	10.60	2.49	7.28	1.64
16-F I	10.41	3.07	7.53	2.05
35-F	7.85	1.51	5.11	1.53
45-F	6.23	1.40	5.17	0.58
52-F	11.96	3.50	9.37	3.00
48-M	8.95	2.18	9.29	1.37
49-M	10.92	2.19	14.24	1.74
51-M	11.73	2.11	12.01	1.73
$\bar{x} \pm \text{SE}$	$9.83 \pm 0.71$	$2.31 \pm 0.25$	$8.75 \pm 1.13$	$1.70 \pm 0.23$

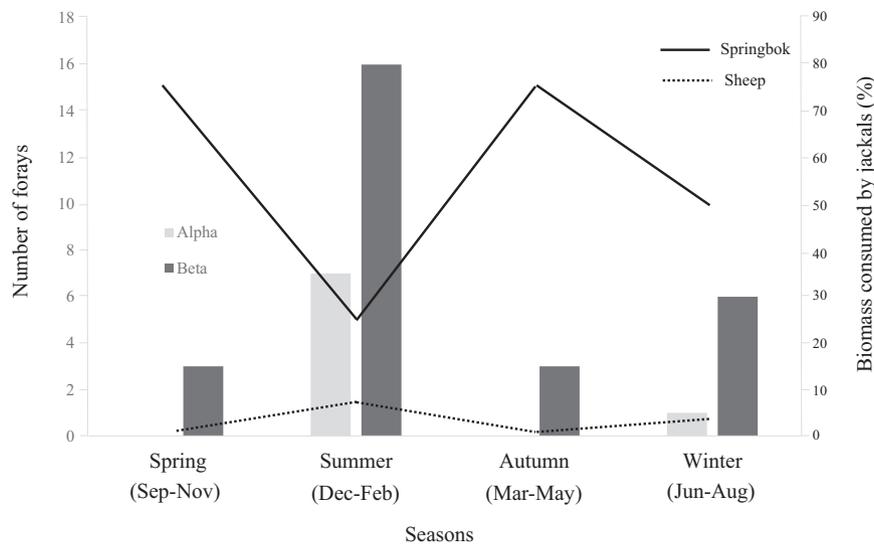
<sup>a</sup> Home ranges of 13-M II and 16-F II were included as alphas during the second year of the study because they formed a mated pair and produced pups in an area of overlap between their respective natal ranges.

<sup>b</sup> The home range of 13-M III during the third year of the study was included as an alpha because after his mate (16-F) died, he joined the natal group of 16-F, presumably as the new alpha male.

their active time on forays (2–20% of time) than alphas (0–3%;  $P = 0.048$ ), and betas went farther on forays (2–8 km) than alphas (2–3 km;  $P = 0.003$ ). The number of forays differed ( $P < 0.001$ ) among seasons; most forays



**Figure 2.** Group formation by black-backed jackals on Benfontein Game Farm (thick black outline), South Africa. During the initial year of monitoring (2005–2006), a beta (non-breeding adult) male and alpha (breeding adult) male occupied similar home ranges (95% fixed kernel density estimate [KDE]) that represented a family group (A; thin black outlines), whereas a beta female occupied a home range that represented an adjacent family group (B; thin black outline). During the second year of monitoring (2006–2007), the beta male and beta female formed a mated pair and produced pups within the overlap area of their respective family groups (C; light gray represents their home ranges [95% KDE], whereas dark gray represents their core areas [50% KDE]). Note that the smaller ovals represent disjunct parts of jackal home ranges.



**Figure 3.** Number of extraterritorial forays by season for alpha (breeding adult) and beta (non-breeding adult) black-backed jackals on Benfontein Game Farm, South Africa, during 2005–2008. Also shown is the seasonal amount of springbok and domestic sheep consumed by black-backed jackals on Benfontein during the same period, taken from Klare et al. (2010).

occurred during summer (63.9%) followed by winter (19.4%; Fig. 3). In summer, 22 of 23 forays occurred when alpha and beta jackals visited neighboring livestock farms. In winter, 5 of 7 forays occurred when beta jackals visited core areas of neighboring jackal groups. There was only 1 foray recorded by an alpha during winter, and that was to feed on the carcass of a springbok that had been shot in a culling operation on Benfontein. During spring and autumn combined, there were 6 forays: 3 to livestock farms and 3 to neighboring jackal groups. Within the same family group, some betas rarely went on forays (2–4%), similar to alphas, whereas other betas went on forays more frequently (12–20%). Only 2 betas dispersed during the study, and both occurred during winter when the jackals were 11–12 months old.

## DISCUSSION

The home-range sizes of alphas and betas were similar, which did not support our first prediction that alphas would have smaller home ranges than betas. Nonetheless, betas went on forays more frequently and farther than alphas; consequently, most betas did have more wide-ranging movements than alphas. Thus, if we had not removed forays from home-range calculations, then some betas would have had much larger home-range sizes. When foraging, the alphas spent more time with each other than with betas, although all jackals spent a majority of their time foraging alone. Home-range and core-area overlap was higher within groups than between groups (Fig. 1), which supported our second prediction. Our results were similar to those previously reported for black-backed jackals, in which overlap between neighboring groups was <10%, whereas overlap within groups was >50% (Rowe-Rowe 1982, Ferguson et al. 1983, Loveridge and Macdonald 2001). Although betas seldom traveled with alphas, betas often visited natal dens and associated with pups, whether or not

alphas were present, similar to that reported in other jackal studies (Moehlman 1983). We could not confirm if betas brought food to pups, although we assumed they did because food provisioning by betas was previously reported in black-backed jackals (Moehlman 1979, 1983). Additionally, the presence of betas at natal dens likely provided extra protection for the pups, especially when the alphas were absent (Moehlman 1979, 1983; Jenner et al. 2011). In contrast to other studies, we did not record transient jackals during our study, probably because of the high rates of philopatry by the beta jackals.

Most beta jackals (8 of 10) stayed on Benfontein within their natal groups beyond 12 months of age, and after their presumed parents had the next litter, which did not support our third prediction that most betas would disperse before their parents' next litter. Additionally, 2 betas (both females) stayed within their natal territory beyond 24 months of age without producing pups. This was surprising given that betas made numerous forays to surrounding livestock farms, yet none attempted to establish territories there. Although the rate of philopatry by betas was higher than that observed in East Africa (24%; Moehlman 1986), our results were consistent with those reported by Minnie et al. (2016) in South Africa, who reported that on reserves with low human-caused mortality, only about 50% of female black-backed jackals that were 3–4 year old had become pregnant, suggesting a relatively high proportion of older jackals were betas. Beta females staying in their natal ranges for 2 subsequent litters to help their parents was reported previously for black-backed jackals (Moehlman 1979, Ferguson et al. 1983) and coyotes (Andelt 1985, Gese et al. 1996, Kamler and Gipson 2000), so it may not be unusual behavior for medium-sized canids. Because black-backed jackals can reproduce at 12 months of age (Minnie et al. 2016), there must have been substantial benefits for beta jackals on Benfontein to

forego their own reproduction and remain within their natal range beyond 12 months old.

There are several possible explanations for the high rates of philopatry and lack of group formation by betas outside of Benfontein. First, because all philopatric betas associated with the next litter of their presumed parents, the betas likely benefited from gaining experience with raising pups while increasing their inclusive fitness via kin selection (Moehlman 1979, 1986). Second, although betas made numerous forays to livestock farms, they probably did not meet potential mates during their short trips there because many of livestock farms lacked territorial groups owing to high rates of human persecution (Kamler et al. 2013*b*). Third, the preferred prey and most highly consumed species of jackals on Benfontein was springbok, which had a relatively high density (22 springbok/km<sup>2</sup>; Klare et al. 2010). In contrast, surrounding livestock farms either did not contain springbok, or had a relatively low density (5 springbok/km<sup>2</sup>; Kamler et al. 2012*a*). Additionally, although sheep were consumed by jackals on surrounding livestock farms, wild ungulates were selectively consumed over sheep in most seasons (Kamler et al. 2012*a*), and densities of sheep (16 sheep/km<sup>2</sup>) were lower than that of springbok on Benfontein (Kamler et al. 2012*a*). Therefore, the higher density of preferred prey on Benfontein may have caused most betas to remain philopatric, instead of dispersing into relatively unknown areas with much lower preferred prey. Lack of dispersal by subordinate group members, despite the existence of vacant neighboring territories, has been observed in other canid species (Macdonald et al. 2004), although the reasons for this behavior are not always clear. In a review of helping behavior, Emlen (1982) indicated that grown offspring can delay dispersal even if breeding opportunities or vacant territories exist, if the cost of rearing their own young is perceived to be prohibitive. Thus, beta jackals might have perceived the livestock farms as too risky to establish territories, either because of the lower abundance of preferred prey or to lack of other jackals. Nonetheless, perhaps with a larger sample size of betas, some betas might have established territories on the livestock farms.

Betas spent more of their active time on forays, and went farther on forays, than alphas, which supported our fourth prediction. More extensive forays by betas has been reported in other mammal species (Mayer et al. 2017), including coyotes (Kamler and Gipson 2000, Kamler et al. 2004*b*) and gray wolves (Messier 1985), likely because forays allow betas to become familiar with surrounding areas and search for potential mates and vacant territories. Overall, the number of forays differed among seasons; most forays for alphas and betas occurred during summer, which did not support our fifth, sixth, and seventh predictions. We predicted that both alphas and betas would go on forays mostly in winter, which is the jackal breeding season, because we assumed alphas would search for extra-pair matings in neighboring groups (prediction 5) and betas would search for new mates in vacant areas outside of Benfontein (prediction 6). Additionally, most sheep lambing on surrounding farms occurred

in winter, and we assumed jackals on Benfontein would take advantage of this food pulse and travel to the livestock farms to consume lambs (prediction 7). Instead, most forays occurred in summer when jackals visited surrounding livestock farms. On Benfontein, summer coincided with 2 important aspects of the jackal diet: the lowest amount of springbok consumed (26% of biomass consumed), and the highest amount of sheep consumed by jackals (8%; Fig. 3; Klare et al. 2010). Sheep did not occur on Benfontein, so the consumption of sheep by jackals in summer had to occur during their forays to surrounding livestock farms, similar to that reported on other reserves (Bothma 1971; Rowe-Rowe 1976, 1983; Kaunda and Skinner 2003). Similar movements of jackals were reported in Namibia, where resident jackals often went on forays of up to 20 km to feed on pups of Cape fur seals (*Arctocephalus pusillus*) along the coast (Jenner et al. 2011).

On Benfontein, consumption of springbok by jackals peaked during the 2 springbok birthing seasons in spring and autumn, indicating jackals consumed mostly springbok fawns (Fig. 3; Klare et al. 2010). During summer, only subadult and adult springbok would have been available to jackals on Benfontein, decreasing the accessibility of this prey species to jackals. Although jackals can kill adult springbok (Krofel 2008, Klare et al. 2010), they are clearly more difficult and dangerous to bring down compared to small fawns. Thus, it appears jackals chose to consume more subadult and adult sheep on surrounding livestock farms in summer when springbok fawns became unavailable, probably because adult sheep are easier and less dangerous to bring down than adult springbok. Our results indicate that food consumption was the main purpose of forays for alphas and betas, and that the number of forays peaked during low availability or accessibility of preferred prey within Benfontein (summer), but not during a major food pulse outside of Benfontein (winter). Our results are consistent with previous studies that reported forays in jackals, coyotes, and wolves occurred more during periods of food stress (Bekoff and Wells 1980, Messier 1985, McKenzie 1990, Ballard et al. 1997).

During winter, the jackal breeding season, there was a secondary peak in number of forays (Fig. 3). Most forays during winter were by beta jackals visiting neighboring groups within Benfontein, indicating the primary purpose for forays during this season was to seek mates or inter-group breeding opportunities. In other canid species, alphas sometimes went on forays to neighboring groups during the breeding season in search for extra-pair copulations (Gese et al. 1996, White et al. 2000, Iossa et al. 2008, Deuel et al. 2017), although this was not recorded on Benfontein, which could have been because of the low sample size of alphas. Betas sought breeding opportunities within Benfontein instead of the livestock farms, and consequently this resulted in pair bonding and group formation by 2 neighboring betas within Benfontein (Fig. 2). Group formation by betas on the edge of or in between their natal territories was not reported in previous studies of jackals, although it was reported in other canid species, including gray wolves (Mech and Boitani 2003), red foxes (*Vulpes vulpes*; Baker et al. 2000), and

crab-eating foxes (*Cerdocyon thous*; Macdonald and Courtenay 1996). Such territorial division within canid family groups often leads to clusters of related individuals (Kamler et al. 2013a) and may serve to reduce conflict and infanticide between neighboring groups (Macdonald and Courtenay 1996). Our results support the conclusion that territorial inheritance or sharing in canids is one of the benefits for betas remaining philopatric (Bekoff and Wells 1980, Moehlman 1986, Gese et al. 1996, Macdonald et al. 2004).

## MANAGEMENT IMPLICATIONS

If predation by black-backed jackals on sheep is too high on livestock farms near reserves, our results can help managers identify several preventative measures to reduce livestock losses, because forays in black-backed jackals were affected by social status, seasonal availability of preferred prey, and the reproductive cycle of jackals. We recommend caution, however, when extrapolating our results to other areas because forays onto livestock farms by jackals likely vary spatially and temporally. Nonetheless, we recommend several preventative measures to reduce livestock losses based on the results of our study. First, because there was a strong seasonal variation of forays onto livestock farms, managers of livestock farms could implement seasonal measures to reduce livestock predation during summer, the peak season when forays occurred. For example, most livestock farms in the area used rotational grazing, and thus sheep could intentionally be moved to fields farther away from reserves during summer. Additionally, herders could be seasonally employed during summer, thereby reducing the cost of annually employing them. Furthermore, hunting of jackals on livestock farms could increase during summer. Second, several of the livestock farms in the area maintained small herds of springbok, a small hider species (Klare et al. 2010), to supplement their income with safari hunting. Springbok are the most preferred prey of black-backed jackals (Klare et al. 2010); thus, maintaining herds of this species on their property is likely to attract jackals, potentially more so than the sheep. Instead, livestock managers could switch to ungulate species that are less preferred by jackals, such as follower species (e.g., blesbok) or hidiers with larger body sizes (e.g., gemsbok; Klare et al. 2010). Finally, other alternative methods such as using livestock guarding dogs might be particularly effective (Potgieter et al. 2013), especially if this reduces forays onto livestock farms and discourages beta jackals from establishing territories there. Realistically, it may be impossible to completely prevent jackal predation on sheep, especially on farms that are near to reserves, but using one or more of the above preventative measures could help reduce livestock losses to acceptable levels.

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