

# Seasonal Changes in Social Behavior and Movements of Bat-eared Foxes in South Africa: Disease Implications

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RH: KAMLER ET AL.—SEASONAL MOVEMENTS OF BAT-EARED FOXES

**Seasonal changes in social behavior and movements of bat-eared foxes in South Africa:  
disease implications**

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Bat-eared foxes (*Otocyon megalotis*) are the primary vector and maintenance host species for rabies in the western half of South Africa. Reported cases of rabies in this species peak during the dry season, although reasons for this annual peak are unknown. Rabies transmission is dependent on contact rates, thus seasonal differences in social behavior or movements may

facilitate increased contact rates in the dry season. During an ecological study of bat-eared foxes in South Africa from 2005-2008, we compared between the wet and dry seasons several aspects of the ecology of bat-eared foxes that presumably would influence contact rates. Bat-eared foxes had significantly larger group sizes in the dry season, which would presumably increase intra-group contact rates, and significantly greater home range sizes, greater home range overlap, and higher rates of excursions (i.e., short-term forays from their home range), which would presumably increase inter-group contact rates. Seasonal differences in behavior and movements of bat-eared foxes likely were related to their reproductive cycle and seasonal availability of food resources. In contrast to previous reports, we documented relatively high rates of physical contact between bat-eared foxes and dogs (*Canis familiaris*) and black-backed jackals (*Canis mesomelas*), suggesting there is potential for bat-eared foxes to transmit the rabies virus to larger canids in the region. We provide recommendations for control of rabies outbreaks in bat-eared foxes if it becomes a health or management concern.

Key words: bat-eared fox, contact rate, dispersal, excursion rate, group size, home range overlap, *Otocyon megalotis*, rabies, seasonal home range size

Rabies is an important zoonosis that, despite advances towards its control, remains a serious health hazard in developing regions, especially in Africa where the incidence of rabies has increased in recent decades (Bingham 2005; Sabeta et al. 2007). In southern Africa, canine rabies first spread through the region via domestic dogs (*Canis familiaris*) during the late 1940s and 1950s (Swanepoel et al. 1993). It soon thereafter appeared in wild canid species, most likely as a spill-over from domestic dogs; the first diagnosed rabies cases in bat-eared foxes (*Otocyon*

*megalotis*) in South Africa occurred in the mid-1950s (Swanepoel et al. 1993). Rabies was later detected in bat-eared foxes in many different regions, and was thought to be responsible for several population crashes of bat-eared foxes during the 1980s and 1990s (Maas 1993), including in central (Thomson and Meredith 1993) and northwestern (Nel 1993) South Africa, although other diseases might have been involved (Sabeta et al. 2007). In the relatively dry western half of South Africa, bat-eared foxes were shown to be the major vector for rabies (King et al. 1993; Nel et al. 1997; Sabeta and Nel 2003). In fact, bat-eared foxes are one of the few wild canid species that can maintain the virus cycle independent of domestic dogs and other wild species (Swanepoel et al. 1993; Bingham 2005; Sabeta et al. 2007). Consequently, bat-eared foxes in western South Africa are maintenance host populations for the disease (Bingham 2005), and could potentially infect populations of domestic dogs in the region, especially near human habitation where dog populations are higher (Thomson and Meredith 1993; Rhodes et al. 1998; Bingham 2005), thus resulting in a potential health hazard. Although molecular epidemiology studies indicated that the rabies virus in bat-eared foxes is phylogenetically distinct but closely related to the rabies virus found in dogs and black-backed jackals (*Canis mesomelas*; Sabeta et al. 2007; Bingham 2005), transmission of the rabies virus from bat-eared foxes to dogs does occur (Sabeta et al. 2007).

Bat-eared foxes are thought to be especially susceptible to rabies, primarily due to their unique social behavior among canids, which includes relatively large group sizes, lack of territoriality (reported in some but not all regions), and relatively high rates of amicable behavior among group members, such as huddling and allogrooming (Maas 1993; Nel 1993). For example, allogrooming would potentially expose group members to each other's saliva, thereby increasing transmission rates if the rabies virus was present. In South Africa, the incidence of

reported rabies cases in bat-eared foxes peak during the dry season (Thomson and Meredith 1993), although reasons for this annual peak are unknown. Rabies transmission is dependent on contact rates, which may be determined by several factors including density, home range size, social behavior, and movements (Anderson et al. 1981; Macdonald 1982; Macdonald and Bacon 1982; Loveridge and Macdonald 2001). Thus, seasonal differences in the behavioral ecology of bat-eared foxes might facilitate increased contact rates, and therefore rabies transmission, during the dry season.

Understanding the behavioral ecology of a species is key to understanding disease spread and a prerequisite to scientifically sound management of disease (Macdonald 1993). Therefore, we investigated aspects of the behavioral ecology of bat-eared foxes in South Africa that could potentially contribute to higher contact rates, hence disease transmission. Specifically, we compared the home range sizes, home range overlap, group sizes, dispersal rates, and excursion rates between the wet and dry seasons. Our results will be useful for rabies management in South Africa, especially in the western half of the country where bat-eared foxes are the primary vector and maintenance host species for the disease.

## MATERIALS AND METHODS

*Study area.*—Research was conducted on Benfontein Game Farm (hereafter Benfontein; 110 km<sup>2</sup>; 28°53' S, 24°49' E) located 8 km southeast of Kimberley, South Africa. The area contained elements of 3 major biomes (savanna, Nama Karoo, and grassland), although Nama Karoo vegetation dominated (>65%) Benfontein. The area has a semi-arid continental climate, with a distinct cold and dry period during winter (Mar-Aug), and a hot and rainy period during summer (Sep-Feb). The mean ( $\pm$ SD) annual rainfall of nearby Kimberley Airport (1960-2007)

was  $419 \pm 134$  mm. Because annual rainfall during the study (2006: 497 mm, 2007: 539 mm) was within one standard deviation of the long-term mean, we considered rainfall during our study period to be typical for the area. 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, leaving only black-backed jackals, caracals (*Caracal caracal*), and aardwolves (*Proteles cristatus*) as the largest carnivore species, with jackals having the highest density of the 3 (Kamler et al. 2012). A more detailed description of the study site was provided by Kamler et al. (2012).

*Capture and monitoring.*—Bat-eared foxes were captured using wire box traps (50 x 50 x 120 cm) baited with meat scraps, which were placed along dirt roads and intersections throughout Benfontein, with >0.5 km separating each trap. Using 8-12 traps at a time, we set them in specific locations for approximately 1 week, then moved them so that all areas of the study site were covered during the trapping period. Trapping occurred only during the cold, dry season (May-Aug) to avoid capturing juveniles and pregnant females. We fitted captured foxes with radio-collars (Advanced Telemetry Systems, Inc., Isanti, Minnesota) weighing 1-2% of their body mass. All captured foxes were assigned to sex, weighed to the nearest 0.1 kg, and classified as adult ( $\geq 24$  months old), yearling (12-23 months old), or juvenile (<12 months old) based on tooth wear, body size, and reproductive condition, then released at the capture site. Adult females were considered breeders if they showed signs of nursing (i.e., dark and elongated teats) during or after the pup-rearing season. Adult males were considered breeders if they were associated (i.e., rested and foraged together) with adult females during the breeding season, and were associated with pups during the pup-rearing periods. For aging purposes, we assumed a

birth date of 1 November based on the approximate date of birth for the pups we observed at den sites during the study; this was the same as the middle of the birthing period recorded in other areas of southern Africa (Nel et al. 1984). Because gestation is 60-75 days (Nel and Maas 2004), we assumed mating peaked in late August and early September, which is the end of the dry season and start of the wet season. Our research and handling protocol (#0401/05) was approved by the Department of Tourism, Environment, and Conservation (now Department of Environment and Nature Conservation), Kimberley, South Africa, and followed the animal care and use guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Bat-eared foxes were radio-tracked at night 2-3 times per week from a vehicle using a null-peak system that consisted of dual 4-element yagi antennas. Radio-tracking occurred on a monthly basis throughout the year. When locating study animals, 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, Inc., 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). Den and diurnal rest sites were located by homing on foot using 3-element antennas. The activity patterns of bat-eared foxes changed significantly between the wet and dry seasons on Benfontein, primarily due to changes in activity of their main prey, northern harvester termites (*Hodotermes mossambicus*; Stenkewitz and Kamler 2008; Klare et al. 2011; Kamler et al. 2012). Therefore, unless otherwise noted, we classified data into 2 broad seasons: wet season (Sep – Feb) which occurs in summer, and dry season (Mar – Aug) which occurs in winter.

*Home ranges.*—We determined seasonal home range size of collared foxes using 95% fixed-kernel home ranges (Worton 1989). We also calculated 100% minimum convex polygon

(MCP) to allow comparisons with previous studies. Seasonal home ranges were calculated for individuals that had a minimum of 30 independent locations within a single season (Seaman et al. 1999). We made 1 exception for an individual fox with 28 locations, because an area observation curve, which plotted home-range size against number of locations, showed home range size plateaued before 28 locations. We quantified MCPs, kernel density estimates (KDEs), isopleths and areas (km<sup>2</sup>) in the Geospatial Modelling Environment (GME; Beyer 2012). Gaussian KDEs were calculated using the kernel density command in GME (Beyer 2012) and plug-in bandwidth estimator algorithm in the “ks” package of R (R Core Team 2013). For foxes that were monitored in 2 consecutive seasons, we compared mean home range sizes (95% KDE) between seasons using paired *t*-tests. For 2 foxes, home ranges were calculated for 2 different wet seasons, so we took the average home range of the wet seasons to compare to the home range in the dry season. We did not compare home range sizes between sexes because movements of collared foxes represented movements of entire family groups that typically consisted of a mated pair and adult offspring from previous litters, at least until young foxes dispersed from their natal group.

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. We used the utilization distribution overlap index (UDOI) which compares the 3-dimensional UD between the intersecting and exclusive areas of 2 home ranges (Fieberg and Kochanny 2005). In other words, the index compares the heterogeneity of use within each animal's home range where they overlap and quantifies how much they use the shared space (Maletzke et al. 2014). The UDOI equals 0 when



2 home ranges do not overlap, and 1 if both animals' UD have 100% overlap with uniformly distributed locations. For 2 non-uniformly distributed UD, 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) that assumes 2 animals use space independently of one another, which is likely true in the case of non-territorial canids such as bat-eared foxes. We investigated the spatial overlap between every possible pair of neighboring foxes that were monitored simultaneously during the same season using the UDOI. The UDOI was calculated at both 95% and 50% UD isopleth levels, to represent home ranges and core areas, respectively, using the `kerneloverlap` function of the `adehabitatHR` package in R (Calenge 2014). This function produces an index for the UD of both the intersecting and exclusive areas of 2 home ranges. The UDOI was calculated between neighboring foxes only if they were monitored during both seasons, and results were compared between seasons using Mann-Whitney U-tests.

*Group size, dispersal, and excursions.*—Mean number of adult-sized bat-eared foxes per group was determined by walking in on collared foxes on a monthly or bimonthly basis and counting other adults within the group. Adults in un-collared groups within the trapping area also were counted opportunistically. Mean group size was compared between seasons using 2-sample *t*-tests. Because we obtained  $>100$  observations of group size, we separated the data into 4 periods for a more detailed illustration of group size changes throughout the year: early dry (Mar-May), late dry (Jun-Aug), early wet (Sep-Nov), and late wet (Dec-Feb) seasons.

The dispersal date was assumed to be the median between the last location within their initial home range and first location outside their home range or the first time that contact was

lost. If contact was lost for foxes, we assumed they dispersed if we never visually observed them on Benfontein again, and if collars were not sounding impaired prior to loss of contact. We defined excursions of foxes as short duration forays (1-5 days)  $\geq 2$  km away from their home range boundary (Kamler and Gipson 2000). Total number of dispersals and excursions were compared between the dry and wet seasons using chi-square goodness-of-fit tests.

## RESULTS

From May 2005 to March 2008, we captured, radio-collared, and monitored 23 bat-eared foxes (13 males, 10 females) on Benfontein. There were sufficient data to calculate seasonal home ranges for 16 foxes, all of which were from different family groups. However, only 10 foxes had home ranges calculated in consecutive seasons, thus only these were used for the comparison of seasonal home range sizes (Table 1). Mean home range sizes were larger ( $t_9 = 2.288$ ,  $P = 0.048$ ) in the dry season compared to the wet season (Table 1, Fig. 1). Home-range overlap (UDOI 95) between foxes of neighboring groups was higher ( $Z = 2.267$ ,  $n = 48$ ,  $P = 0.023$ ) during the dry ( $\bar{X} \pm SE = 0.249 \pm 0.066$ ) than during the wet ( $0.132 \pm 0.030$ ) season (Fig. 1). The core-area overlap (UDOI 50) between foxes of neighboring groups was similar ( $Z = 0.907$ ,  $n = 48$ ,  $P = 0.364$ ) during the dry ( $\bar{X} \pm SE = 0.012 \pm 0.005$ ) than wet ( $0.008 \pm 0.003$ ) season.

Mean ( $\pm SE$ ) group size differed ( $t_{106} = 4.469$ ,  $P < 0.001$ ) between the dry ( $4.95 \pm 0.23$ ) and wet ( $3.29 \pm 0.29$ ) seasons. More detailed analysis showed group sizes decreased gradually throughout the year, with the largest group size in the early-dry season ( $5.26 \pm 0.40$ ) and the smallest group size in the late-wet season ( $2.27 \pm 0.34$ , Fig. 2). There were 14 dispersals during the study from 5 adults (1 male, 4 females) and 9 yearlings (7 males, 2 females). The number of

dispersals was similar ( $\chi^2_1 = 1.143$ ,  $P = 0.285$ ) between the dry ( $n = 9$ ) and wet ( $n = 5$ ) seasons. Twelve foxes (6 males, 6 females) made 43 excursions during the study, and there were significantly more ( $\chi^2_1 = 3.93$ ,  $P = 0.047$ ) excursions during the dry season ( $n = 28$ ) than during the wet season ( $n = 15$ ).

## DISCUSSION

Bat-eared foxes had larger group sizes in the dry season, which presumably would have increased intra-group contact rates. In the dry season, bat-eared foxes also had greater home range sizes, greater home range overlap, and higher rates of excursions, which presumably would have increased inter-group contact rates because foxes would have had more encounters and opportunities for physical contact with individuals of other groups. The seasonal changes in behavior and movements that likely increased contact rates help explain why reported rabies peaks during the dry season (Thomson and Meredith 1993). The seasonal differences in movements and group sizes, hence contact rates, of bat-eared foxes may have been primarily due to their reproductive cycle and the seasonal availability of food resources, such as termites and fruit (see below).

Seasonal changes in group sizes have been previously reported for bat-eared foxes (Lamprecht 1979; Nel et al. 1984; Mackie and Nel 1989); these authors noted that the largest groups occurred just prior to mating season before the family groups had broken up. The same was found in this study, with the largest group sizes in the dry season, just prior to the peak mating season at the start of the wet season. In fact, group sizes continually declined throughout the year (Fig. 2), suggesting that seasonal changes in group sizes was likely influenced by the reproductive cycle of the foxes. Recruitment of grown offspring into the group was likely the

main factor contributing to the largest group sizes in the early dry season, whereas the smallest group sizes in late wet season indicated groups mostly comprised of mated pairs when young were born. Deaths and emigration would have caused group sizes to continuously decline throughout the year. Larger groups in the dry season would have led to higher intra-group contact rates, especially given that bat-eared foxes have relatively high rates of amicable behavior among group members (Maas 1993; Nel 1993).

Overall, mean group sizes of bat-eared foxes in our study were higher than the 2.1-3.2 foxes per group previously reported for this species (Lamprecht 1979; Nel et al. 1984; Malcolm 1986; Mackie and Nel 1989; Maas and Macdonald 2004). In fact, the maximum group size of 12 foxes in our study was the highest ever reported for this species, as previous studies reported a maximum of 7-9 foxes (Lamprecht 1979; Nel et al. 1984; Malcolm 1986; Mackie and Nel 1989). We feel that the relatively large groups of bat-eared foxes on Benfontein, especially those with >9 foxes per group, were the result of the temporary joining of at least 2 different family groups that would sometimes forage and rest together for several weeks at a time. Thus, larger groups during the dry season were not only the result of recruitment of grown offspring into family groups, but also due to the temporary joining together of different family groups. The extra protection afforded by larger groups may have been especially important on Benfontein because this site had a relatively high number of black-backed jackals, who were the main predator and largest cause of mortality for bat-eared foxes (Kamler et al. 2012; Kamler et al. 2013b). In fact, larger groups of bat-eared foxes on Benfontein had lower predation from jackals, confirming larger groups provided increased protection (Kamler et al. 2012). That bat-eared foxes had smaller group sizes in the absence of jackals on an adjacent site indicated that larger group sizes on Benfontein were an adaptive behavioral response to jackal predation (Kamler et al. 2013b).

Nevertheless, we feel our results are applicable to other populations of bat-eared foxes, at least in western South Africa, because seasonal changes in group size of bat-eared foxes should be consistent across populations regardless of jackal density. For example, although the overall group size of bat-eared foxes may be affected by jackal density, the gradual decrease in group size from the early dry to the late wet season should not be affected by jackals because it appears to be most related to the reproductive cycle of bat-eared foxes.

The seasonal home range sizes in our study using MCP were similar to the seasonal home ranges reported (0.3-3.5 km<sup>2</sup>) for bat-eared foxes in southern (Mackie and Nel 1989) and eastern Africa (Lamprecht 1979; Malcolm 1986; Maas and Macdonald 2004; Wright et al. 2010). However, seasonal changes in home range size and overlap of bat-eared foxes had not been studied in detail. Our results showed that home range size and overlap increased during the dry season, which coincided with the larger group sizes in the dry season. The greater home range size and overlap during the dry season could have been the result of larger group sizes, which might have needed to forage over larger areas to accommodate the extra group members. Alternatively, home range sizes could have been larger in the dry season due to changes in available food resources, as the diet of bat-eared foxes on Benfontein changed significantly throughout the year (Klare et al. 2011). Arthropods dominated the diet of bat-eared foxes in Benfontein, and the most consumed arthropod was northern harvester termites (Klare et al. 2011). Northern harvester termites are most active during the dry season (Coaton 1958), and live colonially underground yet forage in unpredictable locations above ground (Wilson and Clark 1977). Consequently, bat-eared foxes may have foraged over larger areas in the dry season to take advantage of the more abundant but unpredictable northern harvester termites. Furthermore, fruits were an important alternative food resource for bat-eared foxes on Benfontein, and

consumption of fruits peaked during the dry season, when foxes apparently searched for and visited known places with higher fruit abundance (Klare et al. 2011), which likely increased their overall movements. Regardless of the reason, larger home range sizes and greater home range overlap between neighbors during the dry season would have increased inter-group contact rates, thereby contributing to greater transmission of rabies if the disease was present. Similarly, seasonal increases in home range size and overlap of jackals (*C. mesomelas* and *C. adustus*) was shown to increase contact rates and rabies transmission during the dry season in Zimbabwe (Loveridge and Macdonald 2001). Among *Vulpes* species in North America and Europe, contact rates were shown to peak during the mating season in winter (White and Harris 1994; Murdoch et al. 2008; Ralls et al. 2013), suggesting peaks in contact rates typically occur during the winter or dry season in canids worldwide.

There were significantly more excursions during the dry season than wet season, although the number of dispersals were statistically similar between seasons. That the number of dispersals was nearly twice as high in the dry season compared to the wet season suggested the difference might have been significant if sample size was higher. Although timing of dispersal was not previously studied in bat-eared foxes, other fox species were shown to have higher dispersal rates during the dry or winter season (Harris and Trehwella 1988; Koopman et al. 2000; Kamler et al. 2004; Gosselink et al. 2010), including Cape foxes (*Vulpes chama*) on Benfontein (Kamler and Macdonald 2014), probably because young foxes tend to disperse before the next birthing season. Similarly, excursion rates often occur just prior to dispersal as young foxes begin to explore surrounding areas (Kamler et al. 2004), thus higher excursion rates of bat-eared foxes during the dry season were not unusual. Although we most often did not get visual observations on bat-eared foxes that went on excursions, on 3 occasions collared foxes during

excursions were observed to associate with other groups of bat-eared foxes, suggesting excursions also may been used to find new mates or increase mating opportunities.

On Benfontein, mean dispersal distance for bat-eared foxes was 4.5 km for males and 22.7 km for females (Kamler et al. 2013b), with a maximum dispersal distance of 42 km. Bat-eared foxes exhibited both straight-line and transient-like dispersals (Kamler et al. 2000), with several male dispersers “floating” around areas near their natal home range for several months (Kamler et al. 2013b). Similar to some foxes that went on excursions, young males that floated in areas near their natal range were sometimes observed foraging and resting with foxes from other groups, indicating that dispersing foxes increased inter-group contact rates. Bat-eared foxes can live up to 9 years in the wild (Kamler and Macdonald 2006), although the longevity of bat-eared infected with rabies virus is unknown. Nevertheless, the relatively long dispersal distances and greater movement of bat-eared foxes outside of their home ranges during the dry season likely would have increased contact rates with both neighbors and non-neighbors, thereby contributing to greater transmission of rabies if the disease was present. In general, high contact rates in canid species are often linked to dispersal periods (Macdonald 1980; White and Harris 1994; Loveridge and Macdonald 2001).

Molecular epidemiology studies showed that the rabies virus in dogs and black-backed jackals was phylogenetically similar, with no distinction between host species, whereas the rabies virus in bat-eared foxes was related but distinct (Sabeta et al. 2003, 2007). Sabeta et al. (2007) concluded that transmission of the rabies virus by bat-eared foxes was primarily intraspecific, with rather low rates of interspecific transmission. Nevertheless, they noted that rabies transmission from bat-eared foxes to dogs did occur, and degree of transmission was dependent on human and dog density, and dog vaccination coverage (Sabeta et al. 2007). We

conclude that in our study site, and probably in other areas of the region, there was relatively high potential for bat-eared foxes to transmit rabies to both jackals and dogs. Firstly, although Sabeta et al. (2007) reported that interspecific physical contact between bat-eared foxes and jackals was not common, the same was not true on our study site. Predation from jackals was the primary cause of mortality in bat-eared foxes on Benfontein, and 5-7 of the 23 bat-eared foxes we radio-collared on Benfontein were killed by jackals (Kamler et al. 2012), indicating physical contact between these species was relatively high. Secondly, we also documented several cases of physical contact between bat-eared foxes and dogs: 1) a radio-collared bat-eared fox was killed by dogs on private land after dispersing from Benfontein; 2) on an adjacent small livestock farm where jackal density was 94% lower than on Benfontein (Kamler et al. 2013b), we observed a dog run into a group of bat-eared foxes and kill a subadult while the other bat-eared foxes scattered, and; 3) we suspected dogs were responsible for the death of at least 1 radio-collared adult bat-eared fox on the adjacent small livestock farm. Consequently, transmission of the rabies virus between bat-eared foxes and larger canids might be higher in areas with relatively high interspecific killing of bat-eared by jackals and dogs, which may be dependent on canid densities, food resources, and habitat. That bat-eared foxes reportedly have been killed by all large carnivore species in southern Africa (Kamler and Macdonald 2006) indicates that bat-eared foxes have the potential to transmit the rabies virus to a wide diversity of larger carnivores in areas where they are sympatric.

In general, group cohesion in bat-eared foxes appeared fluid, because different family groups sometimes foraged and rested together for several weeks at a time, and foxes that dispersed or went on excursions sometimes joined other groups temporarily. Such behavior may help explain why bat-eared foxes appear to be so prone to rabies epizootics, and why this is one



of the few species that can maintain the virus cycle independent of dogs. If rabies epizootics in bat-eared foxes in western South Africa become a health or management concern, then we recommend oral vaccination programs for bat-eared foxes during rabies outbreaks. Several reliable oral vaccinations have been developed, and this would seem to be the most ecologically viable option, especially given its widespread success in Europe (Loveridge and Macdonald 2001; Mahl et al. 2014), North America (Sidwa et al. 2005; Slate et al. 2009), and northern Africa (Hayden et al. 2006). Economic and logistical constraints often prevent year-round baiting, thus peak periods of rabies incidence could be targeted. In western South Africa, we recommend coverage of the bat-eared fox populations during late wet and early dry seasons (Feb-May), as this would effectively reduce the population of susceptible individuals just prior to the annual peak in incidence of rabies in the late dry season when movements, group sizes, contact rates, and disease transmission are highest.

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Table 1. Seasonal home range sizes (km<sup>2</sup>) of 10 bat-eared foxes (*Otocyon megalotis*) that were monitored in consecutive seasons on Benfontein Game Farm, South Africa, 2005-2007 (KDE = fixed kernel density estimate, MCP = minimum convex polygon).

ID-sex	Wet season		Dry season	
	95% KDE	100% MCP	95% KDE	100% MCP
B2-F	6.60	3.90	6.75	3.74
B4-M <sup>a</sup>	5.81	3.06	5.73	2.88
B6-F <sup>a</sup>	3.85	2.44	3.14	1.85
B12-M	1.64	0.93	6.29	4.08
B27-M	2.49	1.72	6.22	3.56
B37-M	2.81	1.85	3.93	2.31
B55-F	4.71	2.26	11.31	6.38
B56-F	6.71	3.19	8.24	3.94
B60-M	2.93	1.64	5.37	2.55
B62-M	8.98	5.18	7.80	4.68
Mean ± SE	4.65 ± 0.74	2.62 ± 0.40	6.48 ± 0.73	3.60 ± 0.42

<sup>a</sup> Home ranges were calculated for 2 different wet seasons; the home range size shown was an average of those 2 seasons.

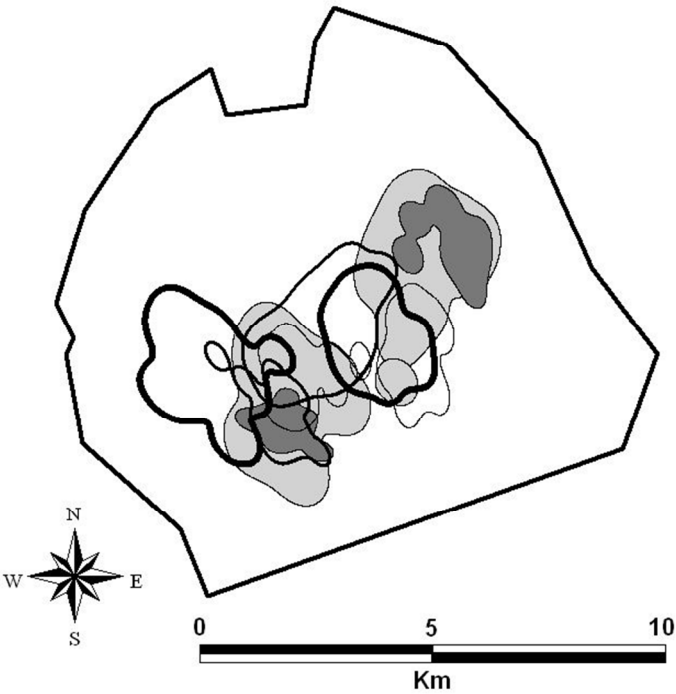


### Figure legends

Fig. 1.-Home ranges (95% fixed kernel density estimate [KDE]) of 10 bat-eared foxes (*Otocyon megalotis*) monitored during consecutive wet (A) and dry (B) seasons on Benfontein Game Farm, South Africa, illustrating the expanded home ranges and greater overlap of home ranges during the dry season.

Fig. 2.-The mean ( $\pm$  SE) adult group size of bat-eared foxes (*Otocyon megalotis*) among seasons on Benfontein Game Farm, South Africa, 2005-2008.

A



B

