



## Acoustic territorial signalling in a small, socially monogamous canid

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Animals that actively defend all or part of their home range for the exclusive use of members of their social group are considered territorial. Defended areas may contain resources such as dens or nests, key foraging sites, or sexual partners that vary in value by season. We investigated territoriality and the function of long-ranging barking sequences in a wild population of swift foxes, *Vulpes velox*. We monitored space use and barking behaviour and combined this with experimental acoustic playback during the mating season. Mated male foxes used barking sequences mainly inside or close to the boundary of the pair's home range core (50% kernel contour isoline of estimated home range). Similarly, male resident foxes responded more intensely with barking if a playback simulating intrusion by a rival occurred inside of the core compared to outside of it. However, it was common for home range cores to be partly overlapped by neighbouring home ranges and therefore we cannot arbitrarily define 50% home range cores as territories. Still, pair home ranges had areas that were exclusive to the mated pair and their primary and secondary daytime sleeping dens were usually located inside these areas. These results suggest that the barking sequence is used in territorial defence and we conclude that at least male swift foxes are territorial in the mating season and they use a long-ranging acoustic signal in territory defence.

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Territoriality in animals is usually defined as the defence of a fixed physical space with the purpose of excluding individuals that are not members of the social group (see Maher & Lott 1995). It is widespread across taxa and involves a complex interplay between social and ecological factors (Brown & Orians 1970; Maher & Lott 2000). Territoriality accrues a cost to individuals. Therefore variation in the degree and nature of territoriality exists within species and between sexes depending on the benefits accrued by territory holders in particular seasons and on the types of encounters in which they are involved (e.g. Yasukawa & Searcy 1982; Raemaekers & Raemaekers 1985; White & Harris 1994; Jaeger et al. 1996; Alonso et al. 2004). That is, certain resources, such as mates, foraging sites, or nests/rearing dens may be worth defending only at certain times of year or against particular types of individuals in

the population, e.g. same-sex individuals versus opposite sex individuals and neighbours versus strangers.

Territories can be defended in several ways, spanning the range from aggressive physical contact with intruders to passive signals that announce territory borders to potential intruders (e.g. Gese 2001). In the case of the latter, signals are used indirectly to maintain exclusive areas by functioning to space animals by avoidance. In other instances, they may be used more directly during interindividual or intergroup encounters in an exchange of signals (e.g. Raemaekers & Raemaekers 1985; Jaeger et al. 1996). The signalling behaviour of animals can be used to examine the extent and nature of their territoriality. In the larger canids, long-ranging vocal behaviour has been shown to play roles in both indirect and direct territorial defence (Lehner 1978; Schassburger 1993; Gese & Ruff 1998), but also in simply maintaining social distances without reference to a particular area (Harrington & Mech 1983). Long-ranging vocal behaviour has received little attention in the smaller canids and the question of the existence of territoriality in these canids has only rarely been directly addressed (Frommolt et al. 2003).

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The swift fox, *Vulpes velox*, is a small, socially monogamous North American canid that, despite sometimes extensive overlap among neighbours, has exclusive areas within home range cores (see Moehrenschrager et al. 2004). Exclusive occupancy of an area, however, does not necessarily mean that individuals are territorial. Instead nonoverlap areas may exist simply because individuals exhibit mutual avoidance of each other or because individuals prefer food resources that have not been exploited (Brown & Orians 1970). Both of these explanations would particularly be the case in areas such as the core of an animal's home range where there is a higher likelihood of direct encounter and a higher rate of use per unit area. In a thorough study on relatedness and spatial structure in the swift fox, Kitchen et al. (2005) found that the degree of home range overlap among neighbouring foxes was positively correlated with the degree of relatedness. They also found a positive correlation between the simultaneous use of shared home range areas (overlap areas) by neighbours and their degree of relatedness. This is an indication of decreased mutual avoidance with increasing relatedness or increased tolerance as the authors suggest, but this does not directly address the issue of territoriality in this species.

Thus, we examined whether swift foxes use long-ranging barking sequences, produced by both males and females (Darden et al. 2003), in defence of home range core areas. We timed our study to overlap with the swift fox mating period because this is the time of year that we expect foxes to benefit from territoriality by increased paternity assurance for males (see Kitchen et al. 2005) and increased paternal effort assurance for females (see Darden 2006). For the analysis, we used observational data of vocal behaviour and space use and an acoustic playback experiment to test our predictions. If core areas of the home range represent mated pair territories, we expect that these areas will be exclusive to the mated pair. If foxes are using barking sequences for territorial defence, we predict that calling behaviour will be concentrated in core areas of the home range rather than edge areas because edge areas are likely to be shared with neighbouring foxes (i.e. will not constitute part of the territory). We also predict that foxes will respond with barking to simulated intrusions in the home range core but not at their home range edges, again because edge areas are not likely to be defended. On the other hand, if foxes are using barking sequences primarily to facilitate mutual avoidance rather than deter an intruder or other types of communication with neighbours, we expect them to vocalize mainly in home range edge areas where they are most likely to encounter another fox and to respond equally to simulated intrusions in their home range irrespective of the simulated intruder's location.

## METHODS

### Study Site and Study Animals

The study was carried out on the Pawnee National Grassland and the Central Plains Experimental Range in

northeastern Colorado (40°49'N, 104°46'W; elevation 1650 m) from January to March 2004 to 2006 in an approximately 180-km<sup>2</sup> area that is part of the Great Plains short-grass prairie ecosystem. Twenty-seven adult foxes from 16 mated pairs were used in the study over the three-season period. We used single-door box traps (Tomahawk Live Trap Co., Tomahawk, WI) built with a 2.54 × 1.27-cm custom mesh size to avoid the risk of injury to trapped foxes in the form of broken teeth or jaws (Roell 1999). Traps were baited with chicken parts to live trap swift foxes in the early winter on precipitation-free nights between sunset and sunrise in temperatures no lower than -9°C. Traps were checked throughout the night at 4-h intervals to reduce the risk of injury while in the trap, including attack by coyotes (Moehrenschrager et al. 2003). Captured foxes were weighed, sexed and aged and all adults were fitted with a collar-mounted very high frequency transmitter (45 g, 40 ppm with mortality sensor; ATS, Isanti, MN, U.S.A.) that on average comprised 2.0% of each collared animal's body weight (range 1.5–2.4%). We also plucked a minimum of 10 guard hairs from each captured fox and collected any faeces left in the trap. We used the single-person handling procedure as detailed by O'Farrell (1987), which does not require the use of anaesthesia. For further details see Darden et al. (in press). Other than one adult fox that chipped the tip of a canine tooth from biting on the trap, none of the foxes sustained any injuries as a result of our trapping and handling procedures.

### Telemetry Data

Radiocollared foxes were located nightly by triangulation from a vehicle between 1800 and 0600 hours from January through March 2004, 2005, and 2006. We obtained a maximum of one location per fox per night and arranged the data collection to obtain 40 points per individual per season distributed evenly over the 12-h nightly tracking period. Point locations calculated from the triangulation data (Locate II v. 1.82; V. Nams, CA) were used to estimate individual and pair home ranges using a fixed kernel contour estimation method in Ranges 6 (Anatrack Ltd., ca. 2003; location density contours with a fixed smoothing multiplier of 1 and a 100-cell matrix). We calculated kernel contours at 5% intervals from 20 to 95% for each mated pair. As is standard for this species, we defined the home range boundary as occurring at the 95% contour isoline and the home range core as occurring within the 50% contour isoline (see Moehrenschrager et al. 2004). We used Arcview 3.2 (Environmental Systems Research Institute, Inc.) to examine home range contours for overlap among neighbours and to calculate overlap areas where applicable. Daytime locations of foxes were carried out to document their den use.

### Observations of Vocal Behaviour

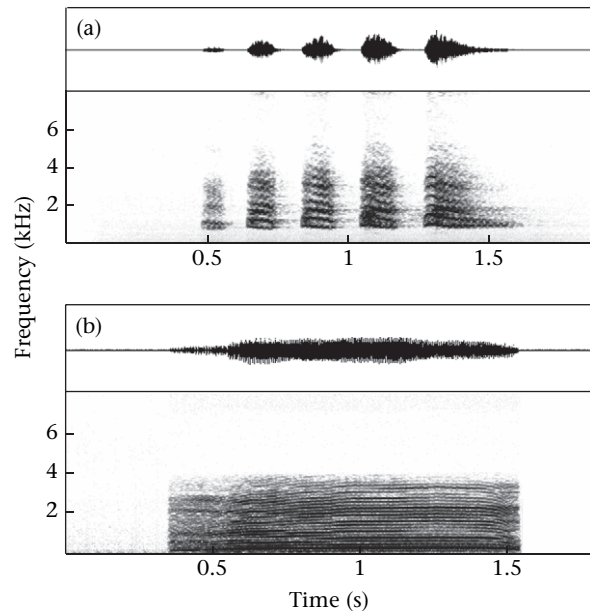
During the 2004 and 2005 seasons we conducted observations of swift fox vocal behaviour (barking sequence production) by radiotracking and following foxes

on foot at a distance of 300–500 m for the first 6 h of their active period (0600 to 0000 hours). Each fox was followed one to three times during the season. During these observation sessions we noted any vocal behaviour made by the focal fox, its location (by triangulation) and, where applicable, the location (by triangulation) of its mate at the time of the vocal event. A single vocal event consisted of a fox making one or more barking sequences from the same location. We also noted any vocalizations made by foxes other than the focal fox. Pair mates and their closest neighbour(s) were followed simultaneously by separate observers. We did not detect any effect of our presence on the behaviour of focal foxes in the form of, for example, foxes moving away from the direction of the observer. Observations of vocal behaviour were also noted ad libitum during regular radiotracking sessions.

We characterized the locations of vocalizing foxes according to four parameters: (1) shortest distance to the 50% contour isoline (home range core) of the pair's estimated home range (negative if foxes were inside the contour and positive if foxes were outside the contour); (2) shortest distance to the 95% contour isoline (home range edge) of the pair's estimated home range (negative if foxes were inside the contour and positive if foxes were outside the contour); (3) distance to the primary den (see below) and (4) distance to the pair mate in cases where the pair mate was collared. These parameters were tested using permutation tests with the mean distance of each parameter as the test statistic (Manly 1991). That is, for parameters 1–3 the grand mean values were each tested against mean values calculated from 1000 permutations of randomly assigned locations of each observed vocal event. Random locations of each individual were taken from our database of locations collected for the home range analysis (i.e. all telemetry locations for that season). For parameter 4, distance to the pair mate, we randomly assigned distances from our database of interindividual distances of the focal pair mates from simultaneous and consecutive point locations collected for the home range analysis. In these tests the number of grand mean proximities from the permuted data sets that were less than or equal to the grand mean of the observed data set was used to calculate our *P* value (i.e. number of randomly generated means less than or equal to observed mean/1000).

### Acoustic Playback Experiment

We used acoustic playback to simulate the intrusion of a strange male fox into a pair's home range and measured the behavioural responses of resident male foxes. We subjected 10 male foxes in our marked study population in the 2005 and 2006 seasons combined to two playback stimuli, barking sequences from a strange male fox for experimental trials (Fig. 1a) and moos from local cows, *Bovis domesticus*, for control trials (Fig. 1b). The purpose of the control trials was to play a sound that was likely to be neutral to a fox (neither aversive nor attractive) to be able to control for any effect of the logistics of the playback procedure on the measured response variables used



**Figure 1.** Spectrograms with waveforms of sound types used as acoustic stimuli in a playback experiment simulating the intrusion of a strange male swift fox into a pair's home range (Avisoft SASLab Pro 3.2; Hamming window, 512-point FFT, 100% frame size, 87.5% overlap, 43 Hz and 2.9 ms resolution). (a) Male swift fox barking sequence with five barks, representative of the experimental acoustic stimuli used. (b) Single moo of a cow, representative of the control acoustic stimuli used.

for the experimental trials. The barking sequences used as playback stimuli were recorded in a captive swift fox population in Cochrane, Alberta, Canada with a directional microphone (AT815b; Audio-Technica Ltd., Leeds, U.K.) and a digital audiotape (DAT) recorder (TCD-D8; Sony Corp., Tokyo, Japan) (see Darden et al. 2003 for details). We used high-quality recordings from nine male foxes to create a unique strange male playback stimulus for each experimental trial, each consisting of six different barking sequences from a single fox looped once to give a stimulus with 12 complete barking sequences. We did not use calls from foxes in our study population because it was not possible to obtain high-quality recordings (i.e. recorded very close to the vocalizing animal) from wild foxes that were needed for this type of playback. Also, by using calls from strange male foxes for the simulated intrusions, we avoided the effects of previous experience with the simulated intruder. Cow moos were recorded from pastured cows in the study area (MKH 70 P48 U-3 directional microphone; Sennheiser Electronic Corp. and a Sony TCD-D8 DAT recorder). Moos that were close in duration to swift fox barking sequences were chosen and looped 11 times to give control stimuli each with 12 identical moos. Barking sequences and moos were spaced 25 s apart (average spacing of barking sequences as measured from a captive fox colony, S. K. Darden, unpublished data) and gave a playback stimulus that lasted 5 min including the 25-s silent intervals. We normalized the amplitude of vocalizations so that they had equal peak RMS values (SIGPRO; S. B. Pedersen) and recorded them onto the Sony TCD-D8 DAT recorder.

We used the Sony DAT recorder to playback stimulus recordings through a Denon DCA-600 power amplifier (Denon Electronics, LLC) and JBL Control 5 speaker (JBL Professional, Northridge, CA, U.S.A.). All vocalizations were played back so that their peak readings on a sound pressure level (SPL) meter (2236 SPL meter; Brüel and Kjær Inc., Nærum, Denmark) were  $68 \pm 2$  dB SPL at a distance of 10 m, which corresponds to the level measured in the captive swift fox population (S. K. Darden, unpublished data). Playback trials were carried out only on nights with low wind velocity ( $<2\text{--}3$  m/s) between 2000 and 2300 hours. Once a subject male had been located and the equipment set up within 500 m of that male, a playback trial lasting 20 min was initiated. Since we knew from our observations that barking sequences could be heard by a human observer at a distance of 500 m in low wind, we chose this as our maximum playback distance to insure that focal foxes would be able to hear the playback. We made audiorecordings of all playback trials (Sennheiser MKH 70 P48 U-3 directional microphone and an HHB PDR 1000 Portadat recorder; HHB Communications Ltd., London, U.K.) and two stationary observers used radiotelemetry to track the movements of the focal male during the 5-min playback period and of the focal male and his mate (if possible) during the 15 min following the end of the playback stimulus. To control for the possible effects of female proximity and possible vocal response on the measured male response, we initiated a playback trial only if pair mates were separated by a distance of at least 500 m and it was possible to conduct the playback at least 500 m from the female's location and still remain inside the pair's home range. We also did not initiate a playback trial if a neighbouring fox was within 500 m of the playback location to avoid responses that would confound our results. Control and experimental stimuli were played back to the same focal individual on separate days and the order of presentation of the two stimuli was balanced among focal animals.

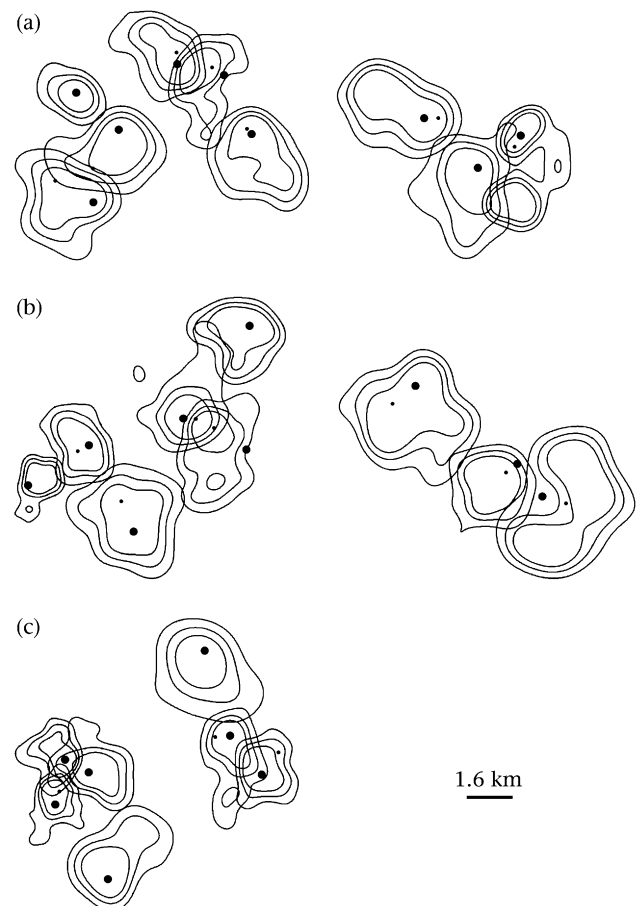
We measured two types of behaviour for each focal animal during the 20-min control and experimental trial periods: vocal behaviour and movement relative to the playback location. Our vocal response measures were (1) the number of barking sequences made during a trial after the start of playback and (2) the latency to respond with barking sequences. Our movement response measures were (1) the latency to approach the speaker (i.e. a decrease in distance between the focal animal and the speaker) after the start of playback and (2) the closest approach to the speaker (i.e. the closest distance of the fox to the speaker resulting from movement towards the speaker). In all instances where the focal individual did not exhibit a specified response within the 20-min trial period, a latency of 1200 s was assigned. We initially tested for a measurable effect of our experimental trials (simulated intrusion of a strange male fox) on our two sets of response variables by comparing values for experimental and control trials within individuals (Wilcoxon signed-ranks test). We then tested our variables for an effect of the location of the simulated intrusion (Mann–Whitney *U* test). In this case, our main effect was whether the speaker was in the core of a pair's estimated home range (inside the 50%

contour isoline) or at the edge of a pair's home range outside this core. This effect was balanced among experimental trials so that five males received playback inside the core area and five males received playback outside the core area. We adjusted our *P* values for multiple testing using an improved ad hoc Bonferroni correction that takes into account the correlations among dependent variables (D/AP procedure: Sankoh et al. 1997), which is useful in cases where a principle component analysis is not possible.

## RESULTS

### Space Use

Swift fox pairs used home ranges that ranged in size from 3.4 to 15.8 km<sup>2</sup> (mean  $\pm$  SE:  $8.7 \pm 0.8$ ,  $N = 12$  mated pair home ranges where both individuals were collared) with core areas that ranged from 0.9 to 6.8 km<sup>2</sup> ( $2.9 \pm 0.4$ ) (Fig. 2). Comparing neighbour–neighbour overlap in ranges where both members of the mated pair were radiocollared (15 instances of overlap occurring on the 12 home ranges; totalling 30 overlap area calculations



**Figure 2.** The 95% (outer polygon), 75% (middle polygon) and 50% (inner polygon) home range kernel contours calculated for paired foxes in the 3 years: (a) 2004, (b) 2005 and (c) 2006 (January through March). The locations of primary (●) and secondary (●) dens are shown also well (see text).



since each instance of overlap creates an overlap of a certain percentage of each home range in the overlap dyad), 43.3% of the overlap areas included part of a mated pair's 50% core area ( $25.4 \pm 4.7\%$  of the 50% core area was overlapped). In the remaining 56.7% of the overlapped areas, the pair's home range was overlapped on average at the  $74 \pm 4\%$  contour isoline. In documenting den use across years, 84% of primary dens (highest frequency of use;  $N = 25$  primary dens) were within the 50% core area of the home range and 76% of secondary dens (second highest frequency of use;  $N = 21$  secondary dens) were also within the core area (Fig. 2). Primary and secondary dens on average accounted for  $88 \pm 3\%$  of a mated pair's den use, with the remaining den use comprising primarily one-time visits to other dens in the home range.

## Barking Sequence Use

### Observations

We observed 49 events of swift fox natural vocal behaviour using the barking sequence where we could identify the vocalizing individual. In 44 of these events, representing samples from 12 unique pairs, we were able to get a location estimate for the vocalizing individual using triangulation, and, in 40 of these events, representing samples from 10 unique pairs, we were also able to get a location estimate of the focal individual's mate. The proximities of vocalizing foxes to their pair mate and to the 95% contour isoline of the pair's home range were not significantly different from that expected by chance ( $P = 0.132$  and  $0.861$ , respectively) (Fig. 3a, b). The distance of vocalizing individuals to a pair's primary den was lower than that expected by chance ( $P < 0.0001$ )

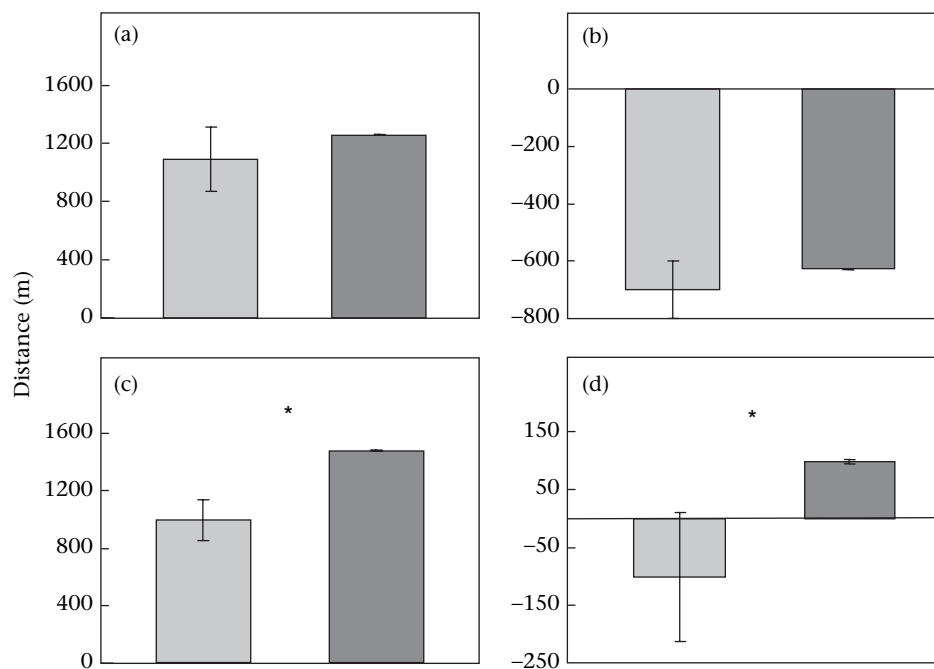
(Fig. 3c) and its average proximity to the pair's core area was also lower than that expected by chance ( $P = 0.020$ ) (Fig. 3d).

### Playback

We found a significant effect of our experimental playback compared to the control playback on both of our vocal response variables (Spearman rank correlations:  $r = -0.91$  for correlation between the two vocal behaviour variables) and we used both of these variables for further analysis of the effect of intruder location on response (Table 1). The only movement response variable that differed significantly from control trials was the latency to approach, but males also tended to approach the speaker more closely during experimental trials ( $r = 0.41$  for correlation between the two movement variables) and we therefore retained both variables for further analysis of the effect of intruder location on response (Table 1). In the analysis of the effect of playback location, focal foxes responded with more barking sequences and tended to have a shorter latency to a vocal response when the simulated intrusion occurred within the pair's home range core area compared to when the simulated intrusion occurred outside of the core area ( $r = -0.60$ ) (Table 1). There was no significant effect of playback location on the focal individual's latency to approach the simulated intruder or its closest approach ( $r = 0.10$ ) (Table 1).

## DISCUSSION

In our analysis of the use of a long-ranging vocalization, the barking sequence, in the swift fox, we found direct evidence for territorial defence in this species. From our



**Figure 3.** Average observed (□) and randomized (■) (see text) distances of male swift foxes making barking sequences to (a) their mated female partner, (b) the edge of the pair's home range (95% kernel contour isoline), (c) the pair's primary den and (d) the pair's core area boundary (50% kernel contour isoline). Asterisks indicate a significant difference between columns; bars indicate standard error.

**Table 1.** Male responses to acoustic playback

Response variable		Control (N=10)	Experimental (N=10)	Adjusted <i>P</i> (Wilcoxon signed-ranks test)	Inside core (N=5)	Outside core (N=5)	Adjusted <i>P</i> (Mann–Whitney <i>U</i> test)
Vocal behaviour	No. barking sequences	0 (0–4)	4 (0–20)	0.0083**	9 (3–20)	1 (0–6)	0.0354*
	Latency to bark (s)	1200 (960–1230)	246 (57–1200)	0.0083**	221 (57–326)	471 (230–1200)	0.0609
Movement	Latency to approach (s)	450 (120–1200)	90 (60–240)	0.0118*	180 (60–240)	60 (60–120)	0.4714
	Closest approach (m)	500 (80–550)	150 (60–470)	0.0584	150 (60–340)	150 (120–470)	0.8206

Summary of results from experimental and control trials in an acoustic playback experiment simulating the intrusion of a strange male swift fox into the home range of mated fox pairs (inside the 50% core and outside the 50% core). Values represent median with the range in parentheses. *P* values adjusted for multiple testing.

observations of the natural occurrence of barking sequences, we found that male foxes were most likely to produce barking sequences within or close to the 50% core area contour isoline of their home range. Furthermore, our playback experiment showed that the intensity with which a male fox responded with barking to a simulated intrusion by a strange male fox was greatest if the intrusion occurred within the 50% core area of the home range. There was also a tendency for males to respond more quickly with barking when the simulated intrusion was in the core area as opposed to outside of it. This higher intensity and apparently shorter latency of responses suggest a higher level of aggression in the vocalizing animal. This is likely to represent a greater willingness on the part of the sender to risk escalation and possible physical contact and this type of threat behaviour would be expected only if the area was defended (e.g. Schradin 2004).

The observed pattern of response in our study population of swift foxes differs from that seen in group-living grey wolves, *Canis lupus*. In the wolves, responses to simulated intrusions (simulated wolf howls) were independent of the location within the home range of the simulated intruder (Harrington & Mech 1983), and the authors suggest a spacing function of wolf howls. The responses that we observed in the swift fox, however, are similar to those of a socially monogamous primate species, lar gibbons, *Hylobates lar* (Raemaekers & Raemaekers 1985), and those authors interpreted a high response rate to simulated intrusions at the home range centres compared to home range borders as territorial responses. Foxes were also observed to bark closer to a pair's primary den than expected by chance, but the average proximity of barking foxes to the den was close to 1 km. Since primary dens were usually located within the 50% core area, the greater proximity to the den may be an effect of this rather than actual defence of the den.

Although our observational and experimental data suggest that the primary function of the barking sequence is territorial defence, it is likely to have other functions also. In our playback experiment, most foxes responded with some barking to the simulated intrusion at the edge

of their home range and approached the loudspeaker as closely as when the intrusion was simulated inside the core area. The close approach indicates that there is equal interest in the vocalizing, strange fox in both types of intrusion and that the resident fox may gain something from approaching closely. For example, by approaching the vocalizing, strange fox, the receiver may be able to facilitate the extraction of information about the intruding individual from its barks that could be important in determining the appropriate response (see McGregor 1993). Resident males that responded vocally to intrusions at home range edges may have been trying to elicit more information about the simulated intruder, such as its location or motivation (level of aggression, etc.), or to provide this information about itself. In this sense, the barking sequence may function in spacing individuals for mutual avoidance (e.g. Harrington & Mech 1983) or exchanging information without close contact, which may otherwise be likely to lead to an aggressive encounter (e.g. White & Harris 1994). Our observational data, however, do not support this as the main function of the barking sequence during this time of year because barking was not concentrated in edge areas of pair home ranges.

In this study and in other studies of swift fox space use (see Moehrensclager et al. 2003), most or all of the 50% core areas of swift fox home ranges tend to be exclusive to the mated pair or single individuals occupying the range. However, the frequency of overlap of the 50% core area by the home range of a neighbouring fox was quite high in our study (43%) and, as such, the 50% core area is not necessarily the best way to define the exclusive area of the home ranges of swift fox pairs. It is, however, the area where foxes tended to have their main dens, which are likely to be an important resource (e.g. Koopman et al. 1998), and we have evidence from the scent marking behaviour of swift foxes that core areas are marked with faeces more intensively than the area outside of the core area, independent of use (Darden et al., in press).

Our study was carried out during the months that include the swift fox mating period (mid-February to early March in our study area). Given the high reported incidence of extrapair paternity in a swift fox population in

southern Colorado and the high likelihood for neighbours to be the extrapair partners (Kitchen et al. 2005), we expect that this is also a time of year where mated male foxes benefit from being territorial. If females are in danger of losing male parental care to extrapair females, they would also benefit from being territorial during this time period (e.g. Yasukawa & Searcy 1982) because male care can be quite substantial (Darden 2006). In either case, the defended resource is the mated partner. We did not investigate female response to barking sequence playback and, although females also produce barking sequences (see Darden et al. 2003), we did not observe any instances of females barking in our study where we were sure of the identity of the caller. Therefore we cannot address, based on barking behaviour, whether females show territoriality in this species. There is some evidence of direct mate guarding in the swift fox population that we studied (Leick 2007), but by defending an area where the female is likely to spend a lot of her time, such as the core of the home range and the den area, males may be able to guard their mates indirectly (e.g. Eason & Hannon 2003). These questions can be addressed further with barking sequence playback and observations of natural vocal behaviour conducted at times of year where the defended resource, or its value, is likely to change (e.g. pup rearing or dispersal seasons) and we would expect differences in the degree and nature of territory defence (e.g. Jaeger et al. 1996; Gese & Ruff 1998; Gese 2001). By comparing among populations and other canids, we will be able to gain valuable insight into the role of territoriality in maintaining social organization in these species.

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