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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

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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 Moehrenschlager 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 longranging 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-km² 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 (Moehrenschlager 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 Moehrenschlager 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 Download English Version:

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