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Information transfer among widely spaced individuals: latrines as a basis for communication networks in the swift fox?

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In species where individuals are widely spaced instantaneous signals cannot readily form the basis of communication networks, that is several individuals within signalling range of each other. However, markings, signals that remain in the environment after the signaller has left, may fulfil this role. In this study, we have investigated the possible function of swift fox, *Vulpes velox*, latrines, collections of scat, urine and possibly other secretions, in a communication network context. We found that latrines had higher frequencies of occurrence inside the core (defined as the 50% kernel contour) of a pair's home-range when compared with outside the core and in areas of a pair's home-range that overlapped with neighbouring individuals when compared with those areas that did not overlap with neighbours. These were also the two areas where latrines were most likely to reoccur in the next consecutive breeding season. Furthermore, latrines in the exclusive part of a pair's home-range core and latrines in edge area overlap zones had the highest frequency of visits as determined by the rate of faecal depositions. Our interpretation of these results is that latrines possibly have a dual function. That is, they function in territory defence in the exclusive areas of a pair's core and as centres for information exchange in the outer areas of a pair's home-range that overlap with neighbouring foxes. We discuss the possible information content of latrines and the possibility of latrines forming the basis of communication networks in the swift fox.

Keywords: Canidae; communication networks; latrines; olfactory communication; scent marking; swift fox; *Vulpes velox*

The use of signals is central to animal social interactions. Signals function in, among other things, maintaining social distances, attracting mates and defending resources. Current research on animal communication emphasizes the importance of investigating signals and signalling interactions in a context that goes beyond the single signaller–receiver dyad in systems where several conspecifics are within signalling range of each other simultaneously, that is form communication networks (McGregor & Dabelsteen 1996). The presence of communication networks imposes at least one major constraint on signallers, namely through costs incurred by having unintended receivers (eavesdroppers). However, signalling individuals can also benefit from being within range of several receivers in terms of facilitating the publicizing of information (see Dabelsteen 2005).

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The notion of public information has been defined in studies of resource exploitation, where individuals use cues from the behaviour of conspecifics to select, for example, breeding habitat (e.g. Doligez et al. 1999), foraging areas (e.g. Coolen et al. 2003), and mates (e.g. Witte & Noltemeier 2002). Information is made available more directly however, in instances where signals or signalling behaviour have evolved to publicize information. Some examples include individuals from group foraging species emitting calls while foraging that indicate patch quality (Valone 1996), fallow bucks, *Dama dama*, producing post-copulatory vocalizations to advertise the pairing status of females with which they have just mated (McElligott & Hayden 2001), and female European robins, *Erithacus rubecula*, advertising their fertility to neighbouring males using begging calls (Tobias & Seddon 2002). In these examples, signalling individuals stand to gain direct fitness benefits by making information available to conspecifics within range of the signal without directing the signal at any particular individual, that is broadcast signalling. Fitness gains associated with this type of signalling are

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possible exclusively through the existence of communication network conditions.

The communication network literature has largely focused on acoustic and visual signals and has quantified signal transmission distances in these modalities to define the network. Still, it has been suggested that chemical signals, which generally persist in the environment after the signaller has left, in fact have evolved for communication in a network because of the selection pressure imposed by their nonspecificity in terms of who the receivers are (Hurst 2005). For species, such as carnivores, that occur at low densities or that have large home-ranges, the frequency of direct encounters or of individuals being within signalling range of acoustic and visual signals is likely to be very low. Because of this, the potential for communication networks to exist may have been overlooked. In this context, scent marks, that is signals that persist after the signaller has left, may be particularly important.

Latrines are collections of scent marks, usually faeces and at least one additional marking medium, namely urine or glandular secretions, that occur in a range of carnivore species (river otters, *Lontra canadensis*: Ben-David et al. 2005; San Joaquin kit foxes, *Vulpes macrotis mutica*: Ralls & Smith 2004; hyaenids: Gorman & Mills 1984; honey badgers, *Mellivora capensis*: Begg et al. 2003; Eurasian badgers, *Meles meles*: Stewart et al. 2002 and bobcats: Bailey 1974) and several other mammalian taxa (Woodroffe & Lawton 1990; Sneddon 1991; Irwin et al. 2004). Latrines provide a medium for an accumulation of information, including a timeline of signalling events and allow for a time delay between sending and receiving signals. In these respects, latrines can act as 'information centres' and may be an important component of information broadcasting and gathering in networks of interacting individuals. In systems where several individuals visit and use common latrines, latrines have the potential to form the basis of communication networks among these individuals.

The term 'information centre' has most commonly been applied to roosting sites, where individuals gain information on, for example, novel food (e.g. Ratcliffe & ter Hofstede 2005) or foraging sites (e.g. Wright et al. 2003), by observing or interacting with other individuals. However, the concept can also be applied to assemblages of signals designed for the transmission of information. For example, in a recent study, Wronski et al. (2006) hypothesized that latrines (termed 'localised defecation sites' in their study) function as centres for intersexual information exchange in a system where males and females do not occupy common home-ranges. They suggest that these sites provide a medium for males to get information on female reproductive state, without having to come into physical contact with the female, which in turn, minimizes female harassment by males. Females concentrate their use of latrines to peripheral areas of the home-range and as such, resident females and neighbouring males are part of a communication network on the basis of these latrines.

We know from pilot observations that our study species, the swift fox, *Vulpes velox*, a socially monogamous mesocarnivore that inhabits the short-grass prairies of North America, uses latrines scattered throughout the landscape. The relative ease with which an observer can detect faecal deposits in the sparse vegetation of their habitat makes the species well suited for studying latrine use in carnivores. The foxes generally occupy large home-ranges, which in our study area average about 8 km^2 (S. K. Darden & T. Dabelsteen, unpublished data), but can be up to 32 km^2 with the same estimation method in some parts of their range (Moehrenschlager et al. 2004). Pair mates share a common home-range (up to 100% overlap) and neighbouring pairs and individuals have home-range overlap that can be quite extensive (up 55% overlap; S. K. Darden & T. Dabelsteen, unpublished data). Pair mates do have exclusive areas that they use, usually at home-range cores, which is taken as evidence for territoriality (e.g. Schauster et al. 2002). The foxes have at least one long-ranging acoustic signal, the barking sequence, that has the potential to be simultaneously broadcasted to several conspecifics, but it is unlikely that it ranges far enough during most signalling events to form the basis of communication networks in this species (S. K. Darden, T. Dabelsteen, O. N. Larsen & S. B. Pedersen, unpublished data).

In this study we investigate latrine function and its possible role in a communication network context by analysing the distribution and use of latrines in the framework of the spatial organization of swift fox social units. If we adhere to the hypothesis supported in a study by Mills & Gorman (1987) with the spotted hyaena, *Crocuta crocuta*, we would expect that the large size of swift fox home-ranges and the dynamic nature of their spatial environment, with patterns of extensive home-range overlap among individuals, will lead to a distribution of scent marks throughout the home-range. Latrines, however, will be likely to show a more limited distribution because of their potential to act as information centres. We predict that latrines will be concentrated in home-range overlap zones between neighbouring individuals and pairs rather than in home-range areas that only members of the resident social group are likely to frequent. In these overlap areas, latrines would provide predictable places for individuals from neighbouring social groups to exchange socially relevant information.

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 2005 and 2006 in an approximately 180-km^2 area that is part of the Great Plains short-grass prairie ecosystem. Twenty-two adult foxes from 12 mated pairs were used in the study over the 2-year period. We used single-door box traps (Tomahawk Live Trap, Co., Tomahawk, WI, U.S.A.) built with a custom mesh size measuring 2.54 × 1.27 cm 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 the hours of sunset and sunrise in