



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.

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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

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 km² (S. K. Darden & T. Dabelsteen, unpublished data), but can be up to 32 km² with the same estimation method in some parts of their range (Moehrenschrager 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 to 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-km² 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

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 (Moehrensclager et al. 2003). Captured foxes were weighed, sexed, and aged and all adults were fitted with a collar mounted VHF 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 sample of 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. In brief, the captured fox is transferred from the trap into a fabric handling bag by placing the mouth of the bag over the trap door and opening the door. The fox then generally sniffs at the bag and then enters it at which time the handler closes the bag so that the fox cannot escape. The fox remains in the bag for the remainder of the handling session. First it is weighed on a spring scale and the handler then kneels on the ground and places the fox on the ground between the legs at which point the remainder of the handling can be carried out by exposing the part of the fox necessary for the given procedure at the bag opening (mouth for ageing, neck for collaring, tail end for sexing, etc.). Once the handling procedure is done, the fox is released on site by opening the mouth of the bag and letting the animal leave the bag on its own. The bag is then weighed with the spring scale and the bag weight subtracted from the total weight to get the weight of the fox. S.K.D. handled all the foxes and the average handling time for individuals that were collared was 18 ± 2 min. 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.

Data Collection and Analysis

Telemetry data

Radiocollared foxes were located nightly by triangulation from a vehicle between 1800 and 0600 hours from January to March 2005 and 2006. We obtained a maximum of one location per fox per night and arranged the data collection so that we obtained 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.O. Nams) were used to estimate pair home-ranges using a fixed kernel contour estimation method in Ranges 6 (Anatrack, Ltd, c.2003, Poole, U.K.; location density contours with a fixed smoothing multiplier of 1 and a 100 cell matrix). A pair's home-range was defined as being within the 99% contour and a pair's core area as being within the 50% contour, which contain 99% and 50% of the location density, respectively. A third contour, 90%, was calculated only to aid in assigning latrines to a specific pair (see below).

Data on faecal deposits

In February and March 2005 we conducted transect searches on foot for swift fox faeces. Transects, which were

walked only once, were placed along landscape features such as tracks and fence-lines since we could see from pilot observations that this was where latrines were likely to be found. We also placed transects that crossed the open prairie without following any such feature. On a transect we recorded all occurrences of swift fox faeces using a Global Positioning System (GPS) unit (Garmin GPS 72) and scored their placement (on a trail, track, road, or fence-line, at the intersection of any of these or on the open prairie). All occurrences of a collection of two or more swift fox scats from at least two deposition events were labelled as a latrine. Some latrines contained one or more coyote scats and these were recorded and counted as well. The number of scats in a latrine and their relative age (NEW, from the current season as indicated by an intact surface, OLD, from a previous season as indicated by a missing surface) was recorded on site, but each latrine was also digitally photographed (Konica Minolta A200, 8.3 Megapixel) so the number of NEW scats in a latrine and whether or not there was any coyote faeces in the latrine could be evaluated in the lab by a single observer for the final analysis. Fifteen per cent of latrines were then randomly selected and re-counted from the photos by a separate observer to evaluate the reliability of the count. A Pearson product moment revealed a 0.91 correlation in the number of scats counted in a latrine independently by two different observers with an average difference of 1.7 ± 1.8 ($N = 90$) scats per latrine when scats were counted from photos. We therefore considered this to be a reliable method and used the latrine counts from photos for our analysis. In the short-grass prairie habitat it is relatively easy to spot carnivore faeces, however, to test for possible differences in the ability of different observers to locate faeces, we conducted a 1 km control count where each of the transect observers searched the same strip independently. We found that observers were equally likely to find latrines and single scats ($\chi^2 = 0.9821$, $df = 3$, $P = 0.8056$).

Latrines found during transect searches were revisited at the end of the season (last week in March) to get a final count of the number of scats so we could estimate deposition rate (number of scats deposited per day since the last count) and compare latrine sizes at the same time period in the season. Using the GPS coordinates of latrines and single scats, we measured nearest distances between occurrences on a transect to the nearest 5 m. From our home-range data we assigned faeces locations to individual pairs and defined their location as within the 50% contour of a pair's home-range or within the 99% contour, but outside the 50% contour. In areas where home-ranges overlapped between neighbouring pairs, we scored the latrine as being in an overlap area and assigned it to a pair, for statistical purposes only, according to the smallest contour line that it was inside since they would be the most likely pair to encounter that particular latrine. If a latrine was in an overlap area with equal contours (50%, 90%, or 99%), no ID was assigned. We assigned IDs to group latrines by ID in our analysis and thus control for possible pair differences in latrine use since we did not have an equal number of latrines sampled from each pair. In pairs where one or more of the home-range boundaries was

inhabited by uncollared foxes, we did not assign latrines in possible overlap areas as being or not being overlapped. We subjected our nearest neighbour and count data to a natural log transformation to approximate a normal distribution and used the transformed data for all tests and summary statistics. We used a GLIMMIX procedure grouped by pair ID in SAS 9.1 (SAS Institute c.2002–2003, Cary, NC, U.S.A.) to test for the effect of % contour (50% versus 99%), whether the latrine is in an overlap area, the interaction between these two and whether there was any coyote faeces in the latrine on faecal deposition rate, latrine size (number of NEW scats) and the distance to the nearest neighbouring latrine on the transect. A similar analysis was conducted for single fox scats found during transect searches, but we only tested for effects on the distance to the nearest neighbouring single scat on the transect.

We knew from our pilot work that latrines sometimes reoccurred in the next consecutive breeding season. Therefore, in January and again in March 2006 we revisited the latrines plotted in the 2005 season to document their status as reoccurring or not reoccurring. Again, the number of scats was counted on site and latrines were photographed using a digital camera. We classified latrines by location within the home-range as in the 2005 data set and tested for the effect of latrine location in the 2006 season (50% versus 99% core, overlap or nonoverlap area and the interaction between the two) on the reoccurrence of a latrine using Chi-squared tests of independence.

Since no description of swift fox behaviour at latrines exists, we monitored swift fox activity at 10 latrines in the study area using digital motion-detector infrared cameras (Leaf River IR-3BU, Vibrashine, Inc., MS, U.S.A.) during February and March 2006. Monitored latrines were in home-range overlap areas. Ninety-second video clips were recorded once the camera was tripped and from these we could observe and quantify the behaviour of foxes while visiting a latrine. We scored the video clips using one-zero sampling in the categories: sniff, urinate, defecate, and roll in or rub parts of the body on the latrine. We tested for differences in the number of times behaviours occurred in the given number of visits using a Fisher's exact test.

RESULTS

In 2005 we found a total of 580 latrines and 1630 old and new single scats on 212 km of transect. Not all of these were within the home-range boundaries of foxes in our study population (Fig. 1), but all pairs had transects running through parts of their home-range. The distribution of transect lines, single faeces and latrines across the home-ranges of pairs in the study population was as follows: (1) kilometres of transect that occurred on a given pair's home-range: 13.7 ± 2.9 km; (2) number of single faeces 'assigned' to a given pair: 89.2 ± 29.8 ; and (3) number of latrines 'assigned' to a given pair: 48.6 ± 10.8 . The size of a latrine, given as the number of scats in the latrine from the season of interest (5.9 ± 2.0 new scats per latrine; 7.8 ± 1.9 total scats per latrine), was not significantly affected by whether it was within or outside the pair's

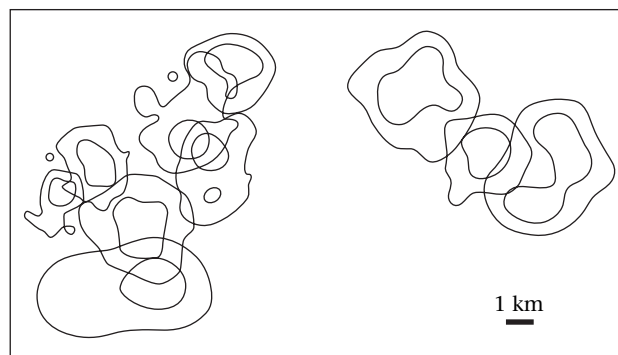


Figure 1. Fifty per cent (inner polygon) and 99% (outer polygon) range outlines for the estimated home-ranges of swift fox pairs included in the study in 2005 (Ranges 6 kernel location density contours with a fixed smoothing multiplier of 1 and a 100 cell matrix).

50% contour ($F_{1,182} = 0.03$, $P = 0.8733$), whether it was inside or outside an overlap area ($F_{1,182} = 0.18$, $P = 0.6712$) or whether there were any coyote scats in the latrine ($F_{1,182} = 3.41$, $P = 0.0663$). Similarly, the rate of faecal deposition in a latrine during the season of interest was not significantly affected by whether the latrine was within or outside the pair's 50% contour ($F_{1,390} = 1.03$, $P = 0.3107$), whether it was inside or outside an overlap area ($F_{1,390} = 0.32$, $P = 0.5736$), or whether there were any coyote scats in the latrine ($F_{1,390} = 2.22$, $P = 0.1374$). The interaction between the % contour and overlap or no overlap by a neighbouring range (i.e. whether the overlap area was over the 50% or 99% contour) had a significant effect on the rate of faecal deposition, that is rates were higher in nonoverlap areas of the 50% contour and in overlap areas outside the 50% contour ($F_{1,182} = 4.10$, $P = 0.0442$; see Fig. 2), but not on the size of the latrine ($F_{1,390} = 2.08$, $P = 0.1505$).

Latrines were significantly closer to each other within versus outside the pair's 50% contour ($F_{1,387} = 6.84$, $P = 0.0093$; Fig. 3a) and inside versus outside an overlap area ($F_{1,387} = 4.01$, $P = 0.0459$; Fig. 3b). There was

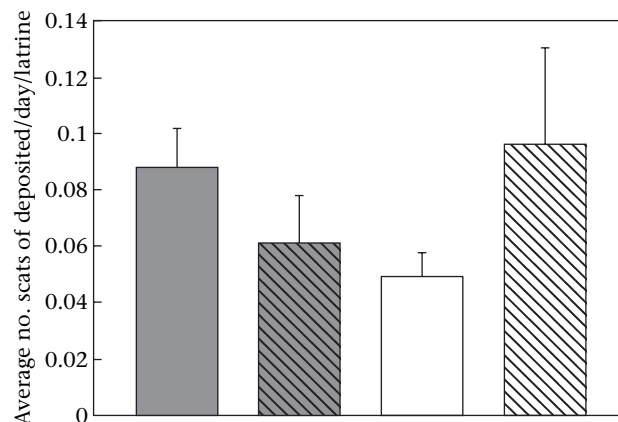


Figure 2. Average rates of faecal deposition in latrines inside the 50% core area and not in an overlap zone with neighbouring foxes (■); inside the 50% core area and in an overlap zone (▨); outside the 50% core area and not in an overlap zone (□); and outside the 50% core area and in an overlap zone (▩). Bars indicate standard error.

a tendency for the distance to the next latrine to be greater for latrines with coyote scats in them versus those without ($F_{1,387} = 3.67, P = 0.0561$) and no effect of the interaction between the % contour and whether or not it was an overlap area ($F_{1,387} = 0.48, P = 0.4869$). The distance to the nearest neighbouring latrine on a transect may be the result of clustering (i.e. latrines grouped in space so lower nearest neighbour distance) or of latrine density (i.e. a greater number of latrines per linear unit that would lead to lower nearest neighbour distances) so we counted the number of latrines per 100 m of transect within 50% contours and outside 50% contours within each pair's home-range. A paired t test showed that the density of latrines along transects within the 50% contour (0.65 ± 0.40 latrines/100 m) was higher than along transects in areas outside the 50% contour (0.33 ± 0.17 latrines/100 m) ($t_8 = 2.568, P = 0.0332$). We thus interpreted nearest neighbouring latrine distances as an indication of latrine density. For single scats, the distance to the nearest single scat on a transect was significantly affected by its location within or outside the 50% contour ($F_{1,655} = 9.61, P = 0.0020$). Interfaeces distances were smaller within 50% contours than outside these areas

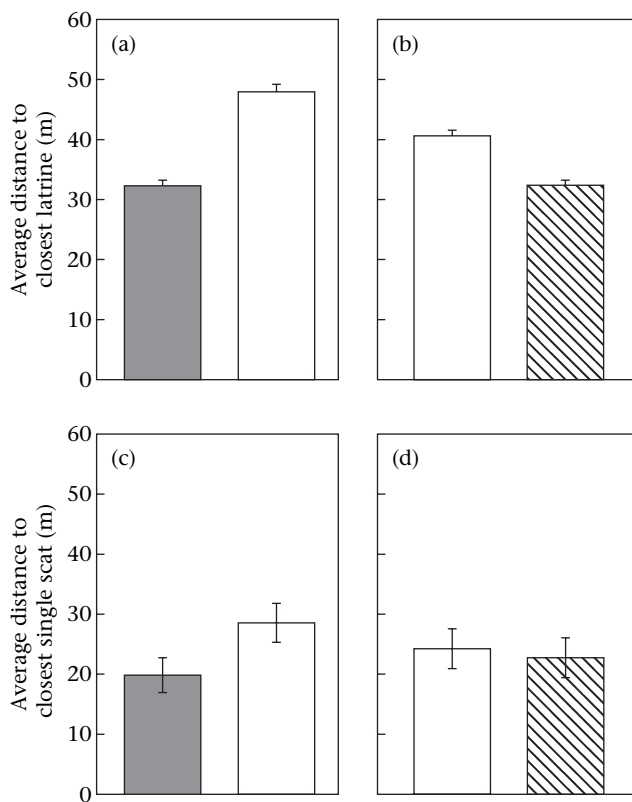


Figure 3. (a) Average distances from a latrine to the closest neighbouring latrine inside the 50% core area (■); and outside the 50% core area (□). (b) Average distances from a latrine to the closest neighbouring latrine in a nonoverlap zone (□); and in an overlap zone with neighbouring foxes (▨). (c) Average distances from a single faecal deposit to the closest neighbouring single faecal deposit inside the 50% core area (■); and outside the 50% core area (□). (d) Average distances from a single faecal deposit to the closest neighbouring single faecal deposit in a nonoverlap zone (□); and in an overlap zone with neighbouring foxes (▨). Bars indicate standard error.

(Fig. 3c). There was no significant effect of whether or not the area was an overlap area between neighbouring fox pairs ($F_{1,655} = 3.32, P = 0.0690$; Fig. 3d) or the interaction between overlap and location inside or outside the 50% contour ($F_{1,655} = 0.0, P = 0.9897$). Again, with a paired t test we found that single scats occurred at higher densities (scats/100 m of transect) within 50% contours (1.11 ± 0.37 single scats/100 m) than outside 50% contours (0.85 ± 0.40 single scats/100 m; $t_7 = 3.13, P = 0.0166$).

In our analysis of the reoccurrence of latrines in the 2006 season in relation to pair space use in that season, we found that latrines were more likely to reoccur in an overlap area versus a nonoverlap area ($\chi^2 = 17.097, df = 1, P < 0.0001$; Fig. 4a) and less likely to reoccur outside the 50% contour of a pair's home-range than inside it ($\chi^2 = 4.857, df = 1, P = 0.0275$; Fig. 4b). We also found that the effect of the nonoverlap area is greatest outside the 50% contour ($\chi^2 = 21.061, df = 3, P = 0.0001$).

We had a total of 56 video clip recordings with fox activity at the camera stations during 270 camera trap nights. In 19 of these clips (33.9%), the fox did not approach the latrine so they were excluded from the further analysis of fox latrine behaviour. From the remaining 37 clips where foxes approached and sniffed the latrine, 75.7% of the visits resulted in a deposition. Of these visits with deposition, 28.6% had faecal deposition (21.6% of all visits) while 89.3% had urine deposition (67.6% of all visits), so urination had a much higher frequency of occurrence at latrines than defecation (Fisher's exact, $P = 0.0001$). There were only two instances where the fox rubbed on the latrine.

DISCUSSION

In this study of faecal-marking patterns in the swift fox we found that faeces were not deposited randomly within home-ranges. Single scats and latrines were placed at higher densities within core areas of a pair's home-range, when compared with outside of these areas. In addition, latrines had a higher frequency of occurrence in areas

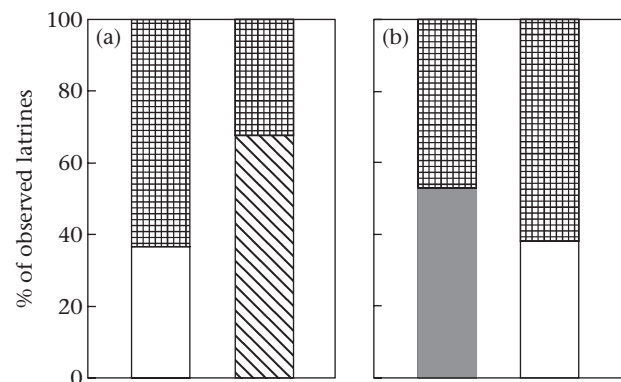


Figure 4. Proportion of latrines reoccurring and not reoccurring (▨) in the consecutive breeding season when located (a) in a nonoverlap zone in the new season (□) versus in an overlap zone with neighbouring foxes in the new season (▨) and (b) inside the 50% core in the new season (■) versus outside the 50% core in the new season (□).

where the home-ranges of two neighbouring fox pairs overlapped than in areas where they did not overlap. The higher density of single scats within core areas could be because individuals simply spend more time per unit area in core areas (e.g. *Canis lupus*, Zub et al. 2003), but it may also be because the deposition of single scats functions in territory announcement (Gosling 1982). The first is unlikely since the occurrence of single scats did not increase in neighbour–neighbour overlap areas where there are more foxes using the same area and we would expect more faecal events than in nonoverlap areas if occurrence was exclusively an indicator of use. The pattern for latrines was somewhat different. They did occur at a higher frequency in overlap versus nonoverlap areas, suggesting a difference in function from that of single scats. Their density may be an indication of the amount of use an area gets, but it is very likely that their density is associated with function. This spatial importance in latrine location is particularly emphasized by the observation that latrines were less likely to reoccur in the next consecutive breeding season if they were located in a nonoverlap area versus an overlap area in the new season. The tendency for latrines that contained coyote faeces to be further from the nearest neighbouring latrine than those without, may be simply because these latrines were established because of the presence of the coyote faeces, rather than because of social factors. It may also be that the increased detectability of latrines with heterospecific faeces (see Roberts & Gosling 2001) allows them to be spaced further from other marking sites.

We found that the highest deposition rates in latrines occurred in the exclusive part of a pair's home-range core and in outer areas of the home-range that overlapped with neighbouring fox pairs. This pattern indicates that latrines in a pair's exclusive area of the home-range core and outer overlap areas with neighbouring pairs receive the most visits in a single breeding season. From our camera work we saw that not all visits to a latrine resulted in a deposit of any kind; about one fourth of visits only involved sniffing (information gathering) and only some resulted in a faecal deposit. In fact, urination was the most common mark used. We see similar patterns in other species (e.g. Bailey 1974; Gorman & Mills 1984; Stewart et al. 2002) and it may be that faeces per se are not the most important information component of a latrine. They may, however, be the important long-term components of a latrine because of their persistence in the landscape.

Based on the latrine distribution and use patterns we found in our study, we suggest that latrines most likely have a dual function in the swift fox. In exclusive core areas they probably function in territory maintenance, while in outer and nonexclusive areas of the home-range they probably function as information centres for neighbouring individuals. As a scent-marking strategy for territory defence, latrines are most likely quite economical. An accumulation of marks in a small area is likely to increase signal strength and thus detectability. For example, Ralls & Smith (2004) found a tendency for dogs trained to locate San Joaquin kit fox, *Vulpes macrotis mutica*, faeces by scent to locate collections of scat from

further away than single scats. Signallers that want to announce a territory should then be able to reduce the spatial frequency of marks, which may otherwise be a strategy for increasing the likelihood of detection, and thereby the amount of mark replenishment (see Roberts & Gosling 2001). Increasing latrine density will further augment the likelihood that intruders will encounter a mark when entering a defended area. In terms of information exchange, latrines are likely to be economical for information gathering and therefore benefit both signaller and receiver as a predictable area for information exchange: a type of established information centre. That is, latrines have the potential to form the basis of communication networks in the swift fox, which would otherwise be difficult to achieve since their other signals are only seldom likely to be available to more than one receiver in the time period that the signal is present.

If edge area latrines act as information centres in a network of interacting individuals in the swift fox, what would we expect regarding the types of information exchanged at latrines during our season of interest, the mating season? When a fox leaves a deposit at a latrine, it most likely at a minimum provides information on individual identity (e.g. Sun & Müller-Schwarze 1999) and gender and reproductive state (Raymer et al. 1986). An individual visiting a latrine can thus gather absolute information on conspecifics. When a second fox visits a latrine and leaves a deposit, we can define this as an interaction between two individuals (a signal and a response). An individual visiting a latrine at this point, can now get two types of information: (1) that an interaction has occurred between two particular individuals and (2) any relative information provided by the two marks, for example order of events. We know from a study by Kitchen et al. (2006) that there can be high rates of extrapair paternity in swift fox populations. In terms of absolute information, females may be able to facilitate extrapair mating opportunities by advertising their presence and fertility at latrines, that is publicizing information on location and reproductive state. Males may likewise publicize their presence and provide odour for scent matching (Gosling 1982) at latrines to obtain extrapair mates, but also to defend their paternity with their social partner as a form of intimidation (Richardson 1993). The information provided by latrines on intraspecific interactions may also signal the relative quality of the interacting individuals, for example competitive countermarking (Hurst & Rich 1999), and can be used by females that have the opportunity to eavesdrop on these interactions in making mating decisions (e.g. Otter et al. 1999). The social unit for this species during the winter months is the mated pair and they have high levels of den sharing (daytime sleeping dens; Moehrenschrager et al. 2004), which probably functions to maintain the pair bond and exchange information such as reproductive state within the pair. In this respect, latrines are not likely to be central to within pair communication for the maintenance of social cohesion.

We can see from the patterns of latrine placement and use observed in this study, that home-range edge area latrines may form the basis of communication networks in the swift fox. With the occurrence of latrines in overlap

areas, neighbouring foxes, plus any transient foxes, make up the communication network of a swift fox pair and information of particular importance to reproduction may be exchanged within the network by the use of latrines. To look at the role of latrines in mediating social interactions, future research should quantify the timing of latrine visits by resident males and females and nonresident foxes and what occurs on these visits, that is sniffing only or sniffing and deposition, scent-over marking, etc. By investigating these patterns, we will be able to test hypotheses of the types of information that foxes are interested both in broadcasting and in gathering at latrines. Further study on latrine use and function in the swift fox, should also include the use of other marking media in addition to faeces, especially if experimental methods are applied.

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Supplementary Material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2007.05.007](https://doi.org/10.1016/j.anbehav.2007.05.007).

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