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ARTICLE

Seasonal and sex differences in urine marking rates of wild red foxes *Vulpes vulpes*

John K. Fawcett · Jeanne M. Fawcett · Carl D. Soulsbury

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Abstract Understanding the role of urine marking in the territorial systems of wild mammals can be difficult, especially for nocturnal cryptic species. Even for common species, such as the red fox *Vulpes vulpes*, a comprehensive analysis of seasonal and sex differences has not been carried out. Using 6 years of infra-red video monitoring, we compared marking rates between months and between sexes. Urine marking was significantly lower during summer (June–August). Males urine marked significantly more frequently than females during late summer and autumn, but not winter. Males marked more frequently than females also during March. There was no increase during the breeding season for either sex. Our results correlate with previous partial data but demonstrate how urine marking rates vary across the year. They also further support the greater role of males in fox territorial maintenance. Urine marking is lowest during summer when territorial intrusions are least, whilst the higher male urine marking rate in March reflects the period when females are denning. Overall, our results provide the first comprehensive analysis of red fox urine marking rates, contributing to a greater understanding of territoriality and olfactory communication.

Keywords Scent marking · Territoriality · Dispersal · Home range · Semiochemistry · Red fox

J. K. Fawcett · J. M. Fawcett
14 Forest Glade Close, Brockenhurst,
Hampshire SO42 7QY, UK

C. D. Soulsbury (✉)
School of Life Sciences, Riseholme Campus,
University of Lincoln, Lincoln LN2 2LG, UK
e-mail: csoulsbury@lincoln.ac.uk

Introduction

Scent marking plays a fundamental role in communication in many mammal species, allowing information such as the species, sex, individual identity, health, and reproductive status of a signaller to persist in the environment (Johansson and Jones 2007; Wyatt 2003). Many mammalian taxa use urine as the primary source of scent, because it is a waste product and so its use as a scent mark does not incur additional metabolic costs (Eisenberg and Kleiman 1972; Ralls 1971), but understanding usage of urine as scent marks in wild animals can be difficult.

Direct observation of urine marking provides the best opportunity to study patterns, but data are particularly difficult to obtain for nocturnal or crepuscular free-ranging species. Whilst faecal marking is easier to study because faeces are often displayed on or in latrines (e.g. badgers *Meles meles*; Roper et al. 1986) or on prominent substrates (e.g. wolves *Canis lupus* on plants; Barja et al. 2005), urine marking is more problematic. Urine marking can be studied where it leaves a visible trace (e.g. stains: Smith et al. 1989), where habituated individuals are directly observed (Begg et al. 2003; Jordan 2007) or where enhanced with biomarkers (e.g. Hutchings et al. 2001), but urine marking is studied less commonly than faecal marking for cryptic species. The use of video cameras can provide a non-invasive method to allow greater study of fine-scale behaviours, e.g. fox–badger interactions (Macdonald et al. 2004), and therefore could be used to monitor urine marking. In addition, long-term monitoring can be beneficial to examine seasonal patterns that otherwise might be missed using techniques limited to particular seasons, e.g. snow tracking (Henry 1980; Goszczyński 1990).

Red foxes (*Vulpes vulpes*) regularly urine mark objects and have been reported to use urine both as a "book keeping system" and potentially as territorial markers (Baker et al.

2000; Henry 1977, 1980; Goszczyński 2002; Macdonald 1979a). However, their nocturnal and cryptic behaviour makes it extremely hard to establish the role of urine marking in foxes. Previous studies in captivity (Blizard and Perry 1979; Macdonald 1979a), occasional field observations (Henry 1980; Goszczyński 1990; Macdonald 1979a) and experimental field studies (Arnold et al. 2011; Whitten et al. 1980) have highlighted the importance of urine in the communication and social systems of foxes. Whilst red foxes are generally regarded as territorial (e.g. Goszczyński 2002; Lloyd 1980; White and Harris 1994) and recent experimental evidence suggests that females are less territorial than males (Arnold et al. 2011), understanding how this translates into variation in urine marking rates is unclear.

We studied urine marking patterns of wild red foxes at a feeding site at an urban–rural interface in Hampshire, UK. Using year-round, night-time video recording, we aimed to assess how urine marking rates varied across the year in relation to key seasonal life history events, and whether these patterns differed between sexes.

Materials and methods

Study site and video setup

The study was conducted within a largish garden in the New Forest, Hampshire. The surrounding habitat was fairly widely spaced detached housing adjacent to open heathland. Foxes regularly attended a feeding site approximately 15 m × 20 m wide of mainly rough lawn backed by shrubs (Fig. 1). Food, mostly left over from domestic use, was placed each evening on a patio. Foxes generally arrived through a gap under a fence, though other routes were sometimes used.

Two infra-red/colour video cameras, with microphones and with focal length set to about 35 mm, recorded the area from approximately 1 h before sunset throughout each night. Cameras were located near the food, so as to maximise detail when foxes were present, but the depth of field allowed observation of distant activity. Six infra-red lamps provided even illumination (Fig. 1). There was continuous recording from the cameras to two DVD-recorders and the results were monitored each following morning. Passages of interest were copied to discs for permanent retention and to facilitate confirmation of fox identities. Cameras and feeding site were used over 1 year before the start of data collection to allow optimisation of methodology and habituation of the foxes to the set-up.

Data collection

Individual foxes usually have a distinctive combination of morphological features such as white tag, ear and facial scarring, ear spots, or black colouration (e.g. Fig 2a–e). Through this method regular attenders are easily identifiable, though those visiting infrequently could be misidentified as new individuals.

Where possible, a fox's sex was established by observing the genitalia or conspicuous nipples (Fig. 2d, e), and this was facilitated by placing the cameras only 25 cm above ground level. Recordings of urination sometimes showed its

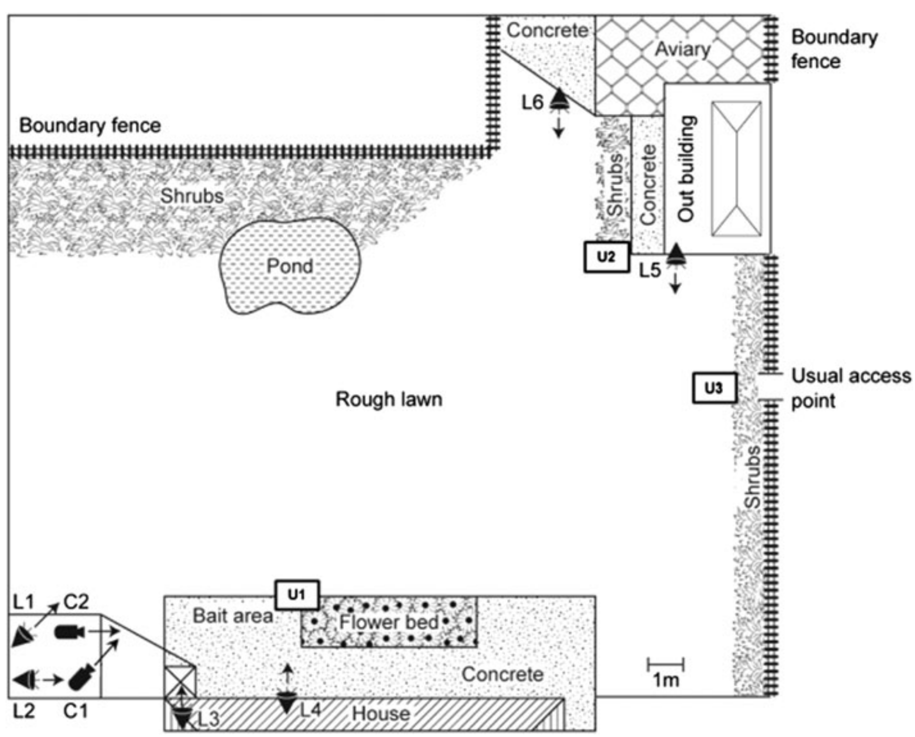

Fig. 1 Schematic representation of the layout, indicating placement and direction of cameras (*C1* and *C2*) and the 6 infrared lamps (*L1-L6*). Foxes usually accessed from a hole under a fence and typically marked near food remains or at three locations: by the feeding site (*U1*), at shrubs near the outbuilding (*U2*), and near the main access (*U3*) usually on departing

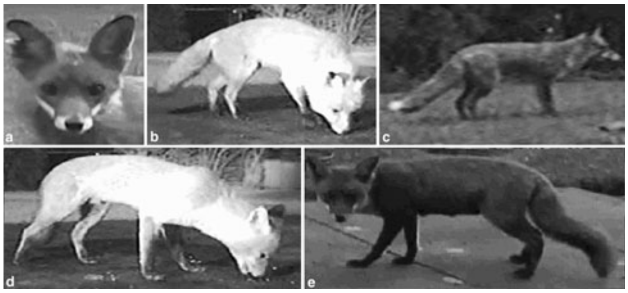

Fig. 2 Illustrations derived from daylight or infra-red video footage, showing different identifiable features: **a** ear damage, **b** short tail without white tag, **c** long tail with white tag, **d** discernible penis and **e** permanently kinked tail and identifiable nipples (i.e. a female)

anatomical origin. Females having bred were identified from clear signs of lactation. General morphology and size of the fox are not dependable as sole criteria of gender. Similarly, posture of urination alone is not an adequate indication because females, as well as males, sometimes "cock" a leg over vegetation and males frequently squat to urinate on the ground, although usually not as low as females (see also Henry 1977, 1980). So a combination of appearance and behaviour was often necessary for reliable identification of gender, which was relatively easy as most individuals attended throughout a substantial sequence of visits. Juveniles (<12 months old) and individuals with unclear gender were excluded from analyses.

From the DVD recordings, we noted when each fox urinated, its physical state (including any injuries) and behavioural or other events (including defaecation, food caching, and intra- and inter-specific interactions). Often, there was a fairly sharp distinction between foxes rigorously abstaining from urination even during prolonged presence and those urinating several times during even brief visits. Urine marking was most often at food remains and at three other sites, shown in Fig. 1. Urinations typically occupied ≤2 s and a range of postures was used (see also Henry 1977). Data were documented according to whether an individual was seen to urine mark or to completely abstain during attendance that night.

Data analysis

Data were collated for each individual observed attending the feeding site on a daily basis. Urination was categorised as binomial (0 = no urination, 1 = urination observed), irrespective of the number of urine marks observed. To assess sex and monthly patterns of urination, we carried out three separate binomial general linear mixed-effect models with urination (0, 1) as a dependent variable. In the first model, we included month (January–December), sex (male, female) and their interaction (sex × month) as fixed factors to assess sexual differences in year-round marking pattern. In the second model, we included fortnightly intervals (0–4) during January and February to cover the peak period of female oestrous (the last 2 weeks of January), sex and their interaction (sex × period) to assess any change in urine marking during the mating period. In the third model, we again assessed urine marking at fortnightly intervals during January and February, but this time included only those females later seen to lactate (so presumed to have mated).

In all models, we included fox and year as random factors. Models were run using the lme4 package (Bates and Maechler 2009) in R 2.14.1 (R Development Core Team 2011). For results and discussion, months are grouped into seasons: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). We assessed repeatability of individual and yearly urine marking rates using the rptR package (Nakagawa and Schielzeth 2010) run in R, and quantified individual heterogeneity (Hamel et al. 2012) in urine marking patterns, from the lme4 package.

Results

Data collection

We collected data across 63 months (1 January 2007–31 March 2012) from 34 foxes (23 females, 11 males) comprising 5,020 observations (3,629 female, 1,391 male) during about 22,000 h of recording (Table 1). Urine marking occurred during 24.6 % of the total observations.

Seasonal and sex differences in urine marking rate

Urine marking varied significantly across months, being lower in June–August (Tables 1, 2; Fig. 3). Also, there was a strong interaction between month and sex (Table 2); marking rates were generally higher for males than females in August–November, but not significantly in the rest of the year (Tables 1, 2), except during March when males urine marked significantly more frequently than females (Tables 1, 2).

We did not find any significant effect of period, sex or their interaction during the period before, during and after the mating season (Table 3; Fig. 4). Even when restricting these data to just females later observed lactating, there was still no evidence of any increase in urine marking rate during the mating period (Table 3).

Heterogeneity and repeatability of urine marking patterns

There was significant repeatability of individual urine marking rates ($R_{\text{logitM}} = 0.42$, SE = 0.07, $P < 0.001$), and significant, but much lower, repeatability of urine marking rates between years ($R_{\mathrm{logitM}} = 0.12$, SE = 0.06, $P < 0.001$). This between-year effect could be largely driven by high between-individual marking rates ($\sigma = 2.89$, SD = 1.70) and therefore which foxes were present in each year would determine how repeatable urine marking was between years.

Discussion

Previous studies on red foxes have not provided a year-round view of red fox urine marking, their results being limited to the winter period (Goszczyński 1990; Henry 1980) or very limited sample sizes ($n = 2$) across the year (Macdonald 1979a). Though our study is limited to a single site, our results provide the first comprehensive overview of red fox urine marking rates for both sexes across the year.

We demonstrated that urine marking rates decline during summer, which supports previous data (Macdonald 1979a). Reduced urine marking in summer does not necessarily mean that foxes reduce territorial defence or reduce responsiveness to scent marks, as red fox territories are stable and mutually exclusive year-round (Henry et al. 2005; White et al. 1996), with little seasonal difference in inter-group interactions (White and Harris 1994). However, it may be predicted that the need to urine mark and demarcate a territory depends on season. For example, during spring, parents and other group members are involved with cub rearing (Robertson et al. 2000). Fox cubs have restricted movement near the den and can be vulnerable to infanticide (Robertson et al. 2000; Vergara 2001), so maintaining urine marking rates in spring may reduce or discourage intruders. Similarly, juveniles (6–12 months) mainly disperse during autumn and winter, and adult males during the mating period (January–February) may make movements away from their resident territories to seek extra-pair copulations (Iossa et al. 2008; Soulsbury et al. 2011; White and Harris 1994). Juvenile dispersal also continues into the spring (Baker et al. 2001; Soulsbury et al. 2011). In consequence, the risks of intrusion and therefore the benefits of urine marking are highest during autumn, winter and spring. It is only during summer that the risk of intrusions into territories declines. During summer, cubs become nutritionally independent from their parents and range increasingly further from the natal den, but still remain in the natal territory (Baker et al. 2001; Robertson et al. 2000; Soulsbury et al. 2008). Additionally, intrusions by non-resident adults are also lowest during summer (Baker et al. 2001). This reduced likelihood of intrusions by either adults or juveniles is probably the primary reason for reduced urine marking during summer.

Table 1 Monthly median (lower quartile/upper quartile) percentage urine marking rates of male and female red foxes *Vulpes vulpes*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Male urine marking rate (%)	19 (0.13/0.4)	17 (0/0.47)	34 (0/0.45)	14 (0.07/0.19)	11 (0/0.36)	0 (0/0.11)	0 (0/0.47)	8 (0/0.16)	28 (0.13/0.75)	20 (0.03/0.38)	22 (0.13/0.39)	10 (0/0.30)
Female urine marking rate (%)	9 (0.02/0.80)	15 (0/0.59)	21 (0/0.46)	4 (0/0.48)	0 (0/0.49)	3 (0/0.46)	0 (0/0.47)	0 (0/0.35)	4 (0/0.36)	0 (0/0.33)	13 (0.03/0.78)	10 (0/0.87)
Significant sex differences	=	=	♂ > ♀	=	=	=	=	♂ > ♀	♂ > ♀	♂ > ♀	♂ > ♀	=
No. observations	♀ = 287	♀ = 282	♀ = 377	♀ = 443	♀ = 435	♀ = 382	♀ = 282	♀ = 231	♀ = 219	♀ = 234	♀ = 212	♀ = 245
	♂ = 149	♂ = 128	♂ = 165	♂ = 106	♂ = 121	♂ = 134	♂ = 116	♂ = 91	♂ = 75	♂ = 67	♂ = 117	♂ = 122

Significant sex differences in monthly rates are shown (see Table 2 for statistical analyses). In addition, the monthly sample sizes for each sex are shown

Table 2 Binomial GLMM results for the relationships between urine marking and month (January–December), sex (male, female) and their interaction

Factor	Estimate	SE	*z* value	*P*
Intercept	−1.66	0.45	−3.69	0.000
Female	0	–	–	–
Male	−0.48	0.71	−0.67	0.501
January	0	–	–	–
February	0.14	0.22	0.61	0.540
March	−0.06	0.22	−0.28	0.779
April	0.06	0.22	0.29	0.775
May	−0.16	0.22	−0.72	0.470
June	−0.60	0.23	−2.60	0.009
July	−1.25	0.26	−4.87	0.000
August	−1.69	0.29	−5.82	0.000
September	−0.75	0.29	−2.59	0.010
October	−0.10	0.28	−0.36	0.716
November	0.11	0.28	0.40	0.690
December	0.23	0.28	0.84	0.401
Male × January	0	–	–	–
Male × February	0.16	0.39	0.41	0.684
Male × March	0.92	0.37	2.47	0.014
Male × April	0.10	0.42	0.23	0.816
Male × May	0.35	0.41	0.85	0.395
Male × June	0.77	0.41	1.87	0.061
Male × July	0.86	0.49	1.76	0.079
Male × August	1.58	0.54	2.90	0.004
Male × September	2.09	0.47	4.48	0.000
Male × October	1.04	0.48	2.16	0.031
Male × November	1.17	0.44	2.68	0.007
Male × December	0.01	0.43	0.02	0.982

Our results also reinforce the view that there are sex differences in territorial behaviour of foxes (Arnold et al. 2011). Urine marking rates by males were generally higher throughout the late summer and autumn in comparison to females, but not significantly during most of winter and spring. Previous sex comparisons have been limited to the winter period when, in line with our results, no sexual differences were found (Goszczyński 1990; Henry 1980). In red foxes, male territory size depends on male body mass and pressure from surrounding males, whereas female territory size depends on the male with which she associates (Iossa et al. 2008). Boundary pressure from competing males, coupled with higher pressure from male dispersers, is probably the main reason for higher urine marking rates in males.

Though males show a seasonal pattern similar to females', their higher urine marking rates probably reflect the greater risk of male intrusions in general, particularly during August–November when male juvenile dispersal is at its highest (Baker et al. 2001; Harris and Trewhella 1988; Soulsbury et al. 2011). Male urine marking was also higher than females' during one month in spring, March, the main period of female parturition. Pre-parturition increases in male urine marking have been observed in

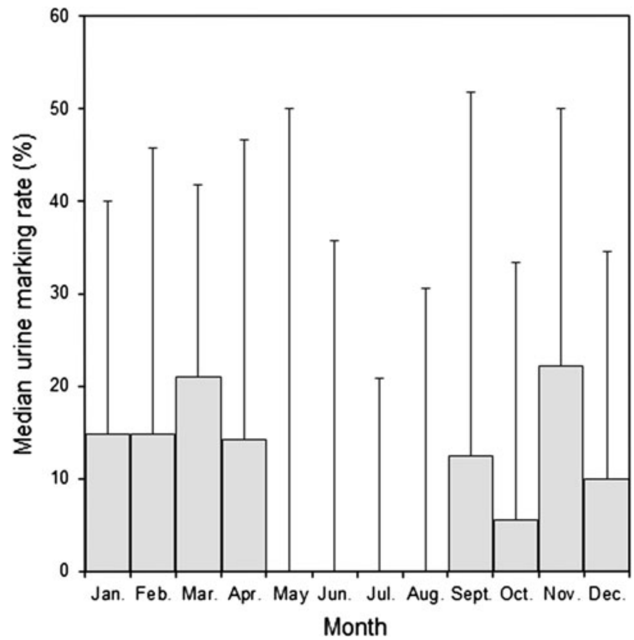

Fig. 3 Median + IQR monthly urine marking rates for both sexes combined. As most of the lower interquartile ranges (like the medians for May–August) are zero, only the upper interquartiles are shown

Table 3 Binomial GLMM results for the relationships between urine marking and (*A*) sex (male, female), period (period 1: 1–14 January, period 2: 15–31 January; period 3: 1–14 February, period 4: 15–28 February) and their interaction and (*B*) period for females later observed lactating

Model	Factor	Estimate	SE	*z* value	*P*
A	Intercept	−1.53	0.62	−2.45	0.014
	Female	0			
	Male	−0.44	0.35	−1.24	0.216
	Period 1	0			
	Period 2	−0.10	0.36	−0.28	0.778
	Period 3	−0.17	0.36	−0.47	0.636
	Period 4	−0.10	0.92	−0.11	0.909
	Period 1 × Male	0			
	Period 2 × Male	0.30	0.57	0.52	0.600
	Period 3 × Male	−0.43	0.64	−0.68	0.496
	Period 4 × Male	1.02	0.58	1.76	0.079
B	Intercept	−0.52	0.89	−0.59	0.559
	Period 1	0			
	Period 2	−0.23	0.39	−0.59	0.555
	Period 3	−0.09	0.40	−0.23	0.822
	Period 4	−0.16	0.40	−0.40	0.692

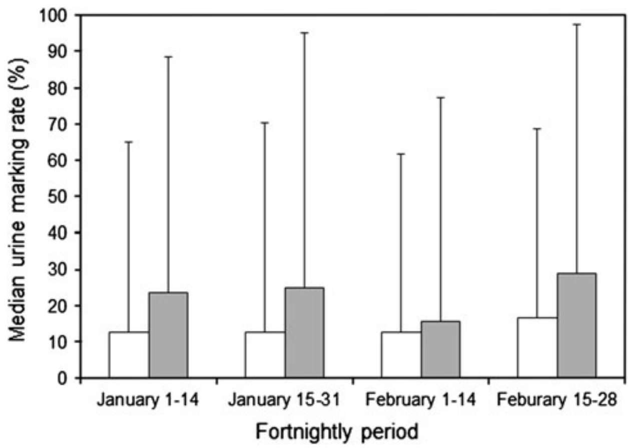

Fig. 4 Median + IQR individual urine marking rates at fortnightly intervals during January and February. Females (*white*) and males (*grey*) are shown separately. As most of the lower interquartiles are zero, only the upper interquartiles are shown

other species, such as arctic foxes *Vulpes alopex* (Kullberg and Angerbjörn 1992). Females are generally restricted to near the den site during the period of parturition (Doncaster and Macdonald 1997; Iossa 2005), so it is possible that males increase their own marking to reinforce territory boundaries when cubs are very vulnerable.

There is mixed evidence for increased urine marking during the mating period in red foxes. Henry (1980) found no temporal or sexual differences in urine marking rates before, during and after the mating period, whereas Goszczyński (1990) found differences in urine marking rates in open but not forested habitat. More detailed counts of a single female's urine marking rates showed a sudden decline after mating, though mean monthly rates showed little evidence of change (Macdonald 1979a). We did not find any evidence of increased urine marking during the mating period (late January to early February) or any differences between sexes. As foxes urine mark frequently, perhaps there is no value in further increasing already high marking rates. Instead, additional forms of communication, such as increased vocalisations, may be important during the winter to communicate reproductive activity (Newton-Fisher et al. 1993). Also, urine marking rates may be directed at specific areas of the territory (e.g. Goszczyński 1990). Our method examines urine marking as present/absent on a daily basis, but this may mask changes in frequency of urine marking within days (Macdonald 1979a). Hence, a more detailed investigation is needed into urine marking rates during the mating period.

Urine marking rates by individuals showed a moderate level of repeatability, but there was also considerable variation in urine marking rates between individuals. Several factors may alter individual urine marking rates, such as dominance status; dominants in many species mark more than subordinates (Asa et al. 1990; Gese and Ruff 1997; Sillero-Zubiri and Macdonald 1998). Red foxes have a flexible social system with group sizes that vary from 2 to 10 individuals (Baker and Harris 2004; Cavallini 1996). A group is usually an extended family comprising a dominant pair and non-dispersing offspring (Iossa et al. 2009). These non-dispersing offspring can be of either sex but are most commonly female (Baker and Harris 2004; Macdonald 1979b). In our study, we have limited information on social group size, composition or dominance status, and nor is it generally known whether dominance status influences urine marking rates in red foxes, though it has been suggested (Macdonald 1979a). Whether dominance status among red foxes plays an important role in driving between-individual differences in marking rates and whether this may be related to sex and seasonal patterns is a key topic for future study.

More generally, our results are similar to those for studies in other canids. For example, feral dogs *Canis familiaris* show a similar seasonal pattern of urine marking, with males marking more frequently than females and with lower marking rates during summer (Pal 2003). However, in contrast to our results for the red fox, urine marking rates are typically higher in the mating season in other canid species (wolf: Asa et al. 1990; coyote *Canis latrans*: Gese and Ruff 1997; arctic fox: Korhonen and Alasuutari 1995; feral dog *Canis familiaris*: Pal 2003). Our results demonstrate that red fox urine marking rates show patterns similar to other canid species', and provide a basis for further examination of urine marking and its role in this species.

Conclusions

We show that urine marking rates decline during summer and that male foxes urine mark more frequently than females during summer and autumn. We did not find any increase in urine marking during the mating season.

We have also shown that the use of video cameras can be valuable in analysing hard-to-observe behaviours such as urine marking, and has provided useful data on urine marking patterns that will aid further elucidation of the role of scent in the territorial and communication systems of red foxes. Future work will need to expand monitoring across multiple sites within territories to test whether the patterns we observe at one site are found across the whole territory.

References

Arnold J, Soulsbury CD, Harris S (2011) Spatial and behavioral changes by red foxes (*Vulpes vulpes* L., 1758) in response to artificial territory intrusion. Can J Zool 89:808–815

Asa CS, Mech LD, Seal US, Plotka ED (1990) The influence of social and endocrine factors on urine-marking by captive wolves (*Canis lupus*). Horm Behav 24:497–509

Baker PJ, Harris S (2004) Red foxes: the behavioural ecology of red foxes in urban Bristol, pp 207–216. In: Macdonald DW, Sillero-Zubiri C (eds) The biology and conservation of wild canids. Oxford University Press, Oxford

Baker PJ, Funk SM, Harris S, White PCL (2000) Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. Anim Behav 59:127–146

Baker PJ, Harris S, Robertson CPJ, Saunders G, White PCL (2001) Differences in the capture rate of cage-trapped red foxes *Vulpes vulpes* and an evaluation of rabies control measures in Britain. J Appl Ecol 38:823–835

Barja I, de Miguel FJ, Bárcena F (2005) Faecal marking behaviour of Iberian wolf in different zones of their territory. Folia Zool 54:21–29

Bates D, Maechler M (2009) lme4: linear mixed-effects models using S4 classes, R package version 0.999375-31. (http://lme4.r-forge.r-project.org/)

Begg CM, Begg KS, Du Toit JT, Mills MBL (2003) Scent-marking behaviour of the honey badger, *Mellivora capensis* (Mustelidae), in the southern Kalahari. Anim Behav 66:917–929

Blizard RA, Perry GC (1979) Response of captive male red foxes (*Vulpes vulpes* L.) to some conspecific odors. J Chem Ecol 5:869–880

Cavallini P (1996) Variation in the social system of the red fox. Ethol Ecol Evol 8:323–342

Doncaster CP, Macdonald DW (1997) Activity patterns and interactions of red foxes (*Vulpes vulpes*) in Oxford city. J Zool 241:73–87

Eisenberg JF, Kleiman DG (1972) Olfactory communication in mammals. Ann Rev Ecol Syst 3:1–32

Gese EM, Ruff EL (1997) Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors. Anim Behav 54:1155–1166

Goszczyński J (1990) Scent marking by red foxes in central Poland during the winter season. Acta Theriol 35:7–16

Goszczyński J (2002) Home ranges in red fox: territoriality diminishes with increasing area. Acta Theriol 47(Suppl. 1):103–114

Hamel S, Yoccoz NG, Gaillard J-M (2012) Statistical evaluation of parameters estimating autocorrelation and individual heterogeneity in longitudinal studies. Methods Ecol Evol 3:731–742

Harris S, Trewhella WJ (1988) An analysis of some of the factors affecting dispersal in an urban fox (*Vulpes vulpes*) population. J Appl Ecol 25:409–422

Henry JD (1977) The use of urine marking in the scavenging behavior of the red fox (*Vulpes vulpes*). Behaviour 61:82–106

Henry JD (1980) The urine marking behavior and movement patterns of red foxes (*Vulpes vulpes*) during a breeding and post-breeding period. In: Müller-Schwarze D, Silverstein RM (eds) Chemical signals: vertebrates and aquatic invertebrates. Plenum Press, New York, pp 11–27

Henry C, Poulle M-L, Roeder J-J (2005) Effect of sex and female reproductive status on seasonal home range size and stability in rural red foxes (*Vulpes vulpes*). Ecoscience 12:203–209

Hutchings MR, Service KM, Harris S (2001) Defecation and urination patterns of badgers *Meles meles* at low density in south west England. Acta Theriol 46:87–96

Iossa G (2005) The reproductive behaviour of an urban red fox (*Vulpes vulpes*) population. Ph.D. dissertation, University of Bristol, Bristol, UK

Iossa G, Soulsbury CD, Baker PJ, Harris S (2008) Body mass, territory size, and life-history tactics in a socially monogamous canid, the red fox *Vulpes vulpes*. J Mammal 89:1481–1490

Iossa G, Soulsbury CD, Baker PJ, Edwards KJ, Harris S (2009) Behavioral changes associated with a population density decline in the facultatively social red fox. Behav Ecol 20:385–395

Johansson BG, Jones TM (2007) The role of chemical communication in mate choice. Biol Rev 82:265–289

Jordan NR (2007) Scent-marking investment is determined by sex and breeding status in meerkats. Anim Behav 74:531–540

Korhonen H, Alasuutari S (1995) Dominance relations in captive groups of adult and juvenile arctic blue foxes *Alopex lagopus*. Polar Biol 15:353–358

Kullberg C, Angerbjörn A (1992) Social behavior and cooperative breeding in arctic foxes in a semi-natural environment. Ethology 90:321–335

Lloyd HG (1980) The red fox. Batsford, London

Macdonald DW (1979a) Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes* L. Z Tierpsychl 51:1–22

Macdonald DW (1979b) 'Helpers' in fox society. Nature 282:69–71

Macdonald DW, Buesching CD, Stopka P, Henderson J, Ellwood SA, Baker SE (2004) Encounters between two sympatric carnivores: red foxes (*Vulpes vulpes*) and European badgers (*Meles meles*). J Zool 263:385–392

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev 85:935–956

Newton-Fisher N, Harris S, White P, Jones G (1993) Structure and function of red fox *Vulpes vulpes* vocalizations. Bioacoustics 5:1–31

Pal SK (2003) Urine marking by free-ranging dogs (*Canis familiaris*) in relation to sex, season, place and posture. Appl Anim Behav Sci 80:45–59

R Development Core Team (2011) R A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http://www.r-project.org/)

Ralls K (1971) Mammalian scent marking. Science 171:443–449

Robertson CPJ, Baker PJ, Harris S (2000) Ranging behaviour of juvenile red foxes and its implications for management. Acta Theriol 45:525–535

Roper TJ, Shepherdson DJ, Davies JM (1986) Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. Behaviour 97:94–117

Sillero-Zubiri C, Macdonald DW (1998) Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. J Zool 245:351–361

Smith JLD, McDougal C, Miquelle D (1989) Scent marking in free ranging tigers, *Panthera tigris*. Anim Behav 37:1–10

Soulsbury CD, Iossa G, Baker PJ, Harris S (2008) Environmental variation at the onset of independent foraging affects full-grown body mass in the red fox. Proc R Soc Lond B Biol Sci 275:2411–2418

Soulsbury CD, Iossa G, Baker PJ, White PCL, Harris S (2011) Behavioral and spatial analysis of extraterritorial movements in red foxes (*Vulpes vulpes*). J Mammal 92:190–199

Vergara V (2001) Two cases of infanticide in a red fox,*Vulpes vulpes*, family in southern Ontario. Can FieldNat 115:170–172

White PCL, Harris S (1994) Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, social cohesion and dispersal. J Anim Ecol 63:315–327

White PCL, Saunders G, Harris S (1996) Spatio-temporal patterns of home range use by foxes (*Vulpes vulpes*) in urban environments. J Anim Ecol 65:121–125

Whitten WK, Wilson MC, Wilson SR, Jorgenson JW, Novotny M, Carmack M (1980) Induction of marking behavior in wild red foxes (*Vulpes vulpes* L.) by synthetic urinary constituents. J Chem Ecol 6:49–55

Wyatt TD (2003) Pheromones and animal behaviour: communication by smell and taste. Cambridge University Press, Cambridge