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Ontogenic patterns of scent marking in red foxes, *Vulpes vulpes* (Carnivora: Canidae)

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Abstract. Scent marking is widely recognised to have a crucial function in many species. Most research has focussed on adults and very little is known about scent marking patterns during juvenile development. Using video records of juvenile red fox *Vulpes vulpes* across six years, we tested whether scent marking rates varied with age or sex, or whether juveniles remaining on the natal territory (philopatry) marked more frequently than those that disappeared. Our data show that male juvenile red foxes scent marked more than females during early development, but rates rapidly declined as they aged. In contrast, females showed a significantly later and slower rate of decline. Within females, individuals that remained in the natal area had higher scent marking rates than those that disappeared, suggesting that scent marking has a role in social group affiliation within litters. These results demonstrate that scent marking plays an important role in juveniles, including their intra-litter social interactions.

Key words: sociality, sibling rivalry, dominance hierarchy, urine

Introduction

Scent marking may be defined as the deposition of odour by urination, defecation or the release of glandular secretions (Kleiman 1966). In different species and under different ecological conditions, chemical cues found in urine, faeces and scent gland secretions can serve as reliable signals to transmit information about the relative health (Zala et al. 2004), sex (Ferkin & Johnston 1995), social status (Hurst et al. 2001) or reproductive state (Washabaugh & Snowdon 1998) of an individual. In carnivores, scent marking has multiple functions including demarcating territory boundaries, and conveying social and individual information (Gorman & Trowbridge 1998).

There are numerous studies of scent marking among adults within populations (e.g. Sillero-Zubiri & Macdonald 1998, Gould & Overdroff 2002). Urine marking has an important social role in many mammal groups, with sex (e.g. Fawcett et al. 2013) and status differences among adult individuals (e.g. Gese & Ruff 1997, Sillero-Zubiri & Macdonald 1998). In contrast, only a few studies have considered scent marking rates of juvenile individuals (e.g. Gese & Ruff 1997) and even fewer note ontogenic development of marking. Scent marking behaviours begin relatively early during development (Rasa 1973, Roeder 1984, Sliwa

1996, Sharpe et al. 2012). However, it is unknown at what age they develop or whether there are differences according to sex or social status.

Red foxes (*Vulpes vulpes*) are widespread medium-sized (4–7 kg) canids with substantial social and ecological plasticity (Baker & Harris 2004). Scent marking has diverse functions including territorial demarcation and social interactions (Henry 1977, 1980, Macdonald 1979a, Baker et al. 2000, Goszczyński 2002, Arnold et al. 2011). Under some conditions, offspring from previous years remain in the natal territory, leading to the formation of social groups (Macdonald 1979b, Baker et al. 1998, Baker & Harris 2004). Previous work has shown that social behaviour is crucial in determining which cubs remain in the natal territory and which disperse; dispersing individuals had less social interaction (Harris & White 1992) and spent more time away from the home range core areas (Woollard & Harris 1990). Scent marking may be crucial in social interactions among juveniles of red fox groups, possibly relating to social status. Despite this possible importance, there are no empirical data on scent marking patterns in litters of red foxes and what drives variation in frequency. This study had three aims: to test whether patterns of scent marking among cubs (1) varied with

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month; (2) differed between males and females; (3) differed between individuals remaining philopatric or dispersing.

Material and Methods

Study site and video setup

The study site and recording protocols were identical to those described in a previous study (see Fawcett et al. 2013). Briefly, the study site was a largish garden in the New Forest, Hampshire, where foxes regularly attended a feeding station about 15×20 m, mainly comprising rough lawn backed by shrubs. The openness of the lawn facilitated reliable observations. Foxes were filmed with two infra-red/colour video cameras recording continuously from approximately one hour before sunset throughout each night. The study site was illuminated with six infra-red lamps (Fawcett et al. 2013).

Data collection

Foxes were identified by distinctive morphological features and sex was established by observing the genitalia. All urine markings were recorded; though brief (Henry 1977), they were easily observable (Fawcett et al. 2013). Data were documented according to whether an individual was seen to urine mark or completely abstain during attendance that night. We recorded urine marking by juveniles (0–12 months) from first appearance until they disappeared or became adults (> 12 months). We could not ascertain the exact fate of individuals (i.e. whether voluntarily dispersed) but, since most disappearance occurred during the dispersal period (October–March: Soulsbury et al. 2011) and not during peaks of juvenile mortality (e.g. July: Baker et al. 2001), we believe that most disappearances were of dispersing individuals and our categorisation of status as philopatric or dispersed is valid.

Data analysis

Data were collated on a daily basis for each individual observed attending the feeding site, for a total of six years (spring 2007 to spring 2013). Urination was categorised as binomial (0 = no urination, 1 = urination observed) irrespective of the number of urine marks observed during the whole night. To assess monthly, sex- and status-specific patterns of urination in cubs we carried out two binomial general linear mixed-effect models with urination (0, 1) as a dependent variable. In the first model (a), we included month, sex (female/male) and their interaction as fixed factors in the model. In the second model (b),

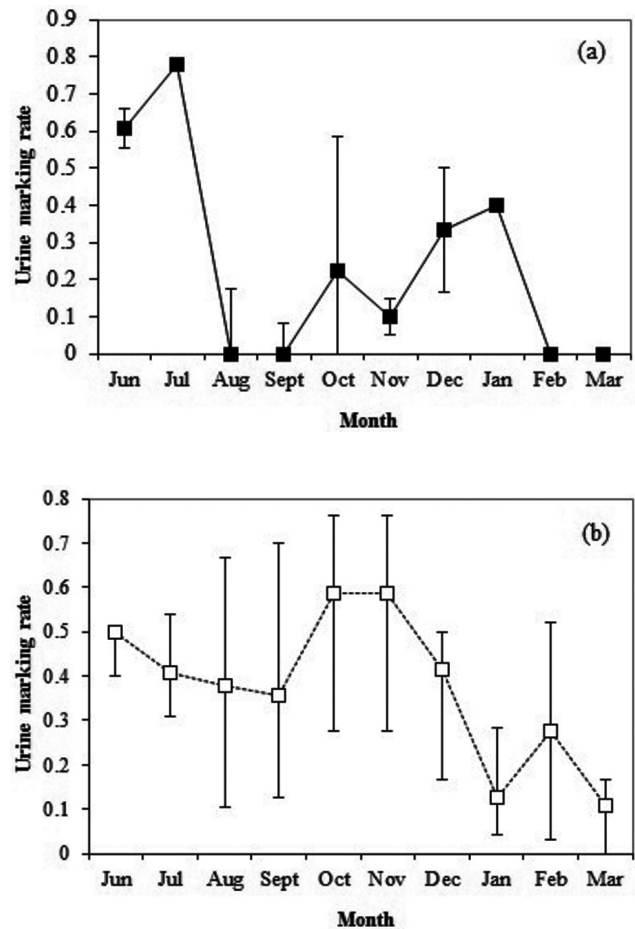


Fig. 1. Median ($\pm$ IQR) proportion of daily visits with urine mark (a) male juvenile red foxes and (b) female juvenile red foxes.

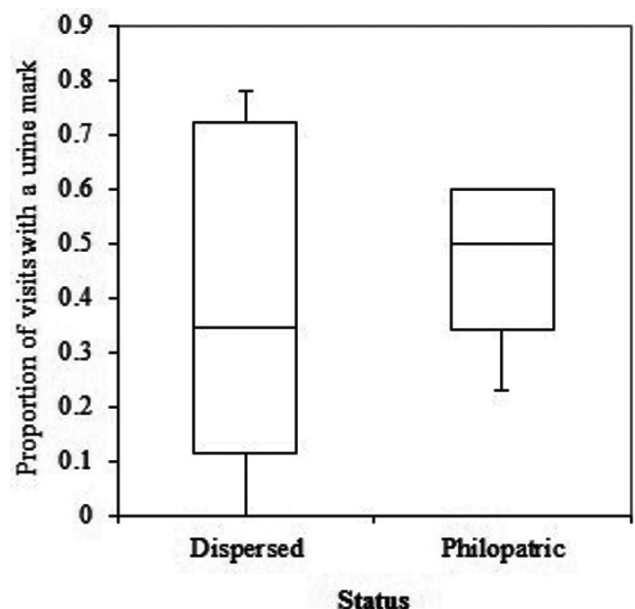


Fig. 2. Boxplot showing the differences in median proportion of daily visits with urine mark between female red foxes that were philopatric and those that dispersed.

Table 1. Binomial GLMM output for (a) daily urine marking rates comparing month, sex and their interaction and (b) female daily urine marking rates comparing month, status (philopatric or dispersed) and their interaction.

Model	Variable	Estimate	SE	z	P
(a)	(Intercept)	−0.84	0.95		
	Month	−0.03	0.04	−0.86	0.391
	Sex	2.64	1.51	1.76	0.079
	Month × sex	−0.36	0.17	−2.16	0.031
(b)	(Intercept)	−2.26	1.37		
	Month	0.05	0.08	0.57	0.566
	Status	2.84	0.96	2.97	0.003
	Month × status	−0.12	0.10	−1.26	0.206

we included month, status (philopatric/dispersed) and their interaction; we had sufficient data to analyse females only. For both models, year and individual were included as random factors. Models were run using the lme4 package (Bates et al. 2012) in R 2.14.1 (R Development Core Team 2012).

Results

General

We collected data on 14 juvenile foxes (4 males, 10 females), across six years, for a total of 1676 observations of daily presence/absence of scent marking. For females, five were philopatric and five disappeared, whereas only one male remained philopatric. The peak month for disappearances was October for males (3/3) whereas females disappeared later (October 1/5, December 2/5, February 2/5).

Sex and ontogenic development of urine marking

There was no significant effect of month on overall urine marking rates (Table 1), but the difference between sexes neared significance (P = 0.079), whilst the interaction between sex and month was significant (P = 0.031, Table 1). Males marked more often than females in June and July when juveniles were fairly young (3–4 months old), but males’ marking rates declined rapidly as they aged (Fig. 1a), whereas female marking rates declined later and much more slowly (Fig. 1b).

Status and ontogenic variation in scent marking

Using data from only females, there was no effect of month or the interaction between month and status (philopatric or dispersing) on urine marking rates (Table 1). In contrast, status was highly significant (Table 1). Individuals that remained philopatric had significantly higher urine marking rates than individuals that dispersed (Fig. 2).

Discussion

The effects of sex and ontogeny on scent marking

Our results demonstrated complicated patterns of scent marking in red fox cubs. Male cubs marked more frequently than females during early development (3–4 months old), but this difference disappeared as juvenile foxes became older. This contrasts with other social species: studies of spotted hyaenas during the pre-puberty failed to report sex differences either in the wild (Mills & Gorman 1987) or in captivity (Woodmansee et al. 1991). In sexually dimorphic species with different adult social roles one expects sex differences in scent marking during development (Whitworth & Southwick 1984). However, in behaviourally and physically monomorphic carnivores, like aardwolves *Proteles cristatus*, one would predict minimal sex differences in early development (Sliwa 1996). Red fox cubs show low, but clear, sexual dimorphism in body size at an early age (Soulsbury et al. 2008). Hence it is likely that the higher rate of scent marking by male juvenile foxes during June and July reflects some aspect of social relationships possibly including dominance.

Red foxes establish a dominance hierarchy when very young (Meyer & Weber 1996) and, like other carnivores, they scent mark when fairly young (Rasa 1973, Roeder 1984, Sliwa 1996). Our results showed that for male juveniles there was a rapid decline in scent marking rates as they aged. In contrast, females showed a later and slower decline. Many social species show a decline in scent marking as they reach maturity, possibly avoiding conflict with adult territory holders (Sliwa 1996). Our data may support this hypothesis for males at least. Male red foxes disperse earlier than females (Soulsbury et al. 2011) and conflict with dominant males in social groups may occur earlier for males. Evidence also suggests that the factors linked to dispersal occur earlier in males than in females

(Harris & White 1992). Our evidence indicates that this earlier lowering of social group affiliation, or increased within-group conflict among males, leads to earlier reductions in urine marking rates, compared to females.

Status and scent marking rates in juvenile red foxes

In this study, females that disappeared/dispersed had lower rates of scent marking than philopatric individuals. Previous studies have noted that individuals scent mark less during dispersal (Gese & Ruff 1997); this is the first study to report differences in scent marking rates pre-dispersal. In many species, more dominant adults show higher scent marking rates (e.g. Sillero-Zubiri & Macdonald 1998), but there has been little previous study of marking rates within juvenile groups. The only scent marking study comparing differences dependent on social status occurred in a captive spotted hyena colony (Woodmansee et al. 1991). Here too, dominant individuals marked more frequently than subordinates (Woodmansee et al. 1991). In red foxes, offspring of

subordinate females usually disperse (Whiteside et al. 2011) and dispersing individuals in fox groups are usually subordinate and less socially-bonded pre-dispersal (Woollard & Harris 1990, Harris & White 1992). Our evidence suggests that the social relationships within litters of red foxes already manifests itself in patterns of scent marking.

In conclusion, we found the interaction between month and sex affected the frequency of urine marking by juvenile red foxes. Males scent-marked more frequently than females during early development but the frequency quickly declined as they aged. Marking rates decreased later and more gradually in females than in males. Marking rates were significantly higher among females remaining philopatric than among those disappeared/dispersed. Overall, these results highlight the importance of scent marking during ontogeny.

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