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

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20   **Abstract**

21   Scent marking is widely recognised to have a crucial function in many species. Most

22   research has focussed on adults and very little is known about scent marking patterns

23   during juvenile development. Using video records of juvenile red fox *Vulpes vulpes* across 6

24   years, we tested whether scent marking rates varied with age or sex, or whether juveniles

25   remaining on the natal territory (philopatry) marked more frequently than those that

26   disappeared. Our data show that male juvenile red foxes scent marked more than females

27   during early development, but rates rapidly declined as they aged. In contrast, females

28   showed a significantly later and slower rate of decline. Within females, individuals that

29   remained in the natal area had higher scent marking rates than those that disappeared,

30   suggesting that scent marking has a role in social group affiliation within litters. These

31   results demonstrate that scent marking plays an important role in juveniles, including their

32   intra-litter social interactions.

33

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

35

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 et al. 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 et al. 1998). In contrast, <u>only a few</u> studies have considered scent marking rates of juvenile individuals (<u>e.g.</u> 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-size<u>d</u> (4-7kg) canids with substantial social and ecological plasticity (Baker & Harris 2004). Scent marking has diverse functions including territorial demarcation and social interactions (Henry 1977<u>,</u> 1980, Macdonald 1979a, Baker et al. 2000, Goszczyński 2002, Macdonald 1979a, 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

64 juveniles of red fox groups, possibly relating to social status. Despite this possible

65 importance, there are no empirical data on scent marking patterns in litters of red foxes and

66 what drives variation in frequency. This study had three aims: to test whether patterns of

67 scent marking among cubs (1) varied with month; (2) differed between males and females;

68 (3) differed between individuals remaining philopatric or dispersing.

69

70 **Materials and Methods**

71 Study site and video setup

72 The study site and recording protocols were identical to those described in a previous study

73 (see Fawcett et al. 2013). Briefly, the study site was a largish garden in the New Forest,

74 Hampshire, where foxes regularly attended a feeding station about 15m x 20m, mainly

75 comprising rough lawn backed by shrubs. The openness of the lawn facilitated reliable

76 observations. Foxes were filmed with two infra-red/colour video cameras recording

77 continuously from approximately one hour before sunset throughout each night. The study

78 site was illuminated with six infra-red lamps (Fawcett et al. 2013).

79

80 Data collection

81   Foxes were identified by distinctive morphological features and sex was established

82 by observing the genitalia. All urine markings were recorded; though brief (Henry 1977),

83 they were easily observable (Fawcett et al. 2013). Data were documented according to

84 whether an individual was seen to urine mark or completely abstain during attendance that

85 night. We recorded urine marking by juveniles (0-12 months) from first appearance until they

86 disappeared or became adults (>12 months). We could not ascertain the exact fate of

87 individuals (i.e. whether voluntarily dispersed) but, since most disappearance occurred

88 during the dispersal period (October – March: Soulsbury et al. 2011) and not during peaks of

89 juvenile mortality (e.g. July: Baker et al. 2001), we believe that most disappearances were of

90 dispersing individuals and our categorisation of status as philopatric or dispersed is valid.

91

92   Data analysis

93   Data were collated on a daily basis for each individual observed attending the

94   feeding site, for a total of 6 years (spring 2007 to spring 2013). Urination was categorised as

95   binomial (0= no urination, 1= urination observed) irrespective of the number of urine marks

96   observed during the whole night. To assess monthly, sex- and status-specific patterns of

97   urination in cubs we carried out two binomial general linear mixed-effect models with

98   urination (0, 1) as a dependent variable. In the first model (a), we included month, sex

99   (female/male) and their interaction as fixed factors in the model. In the second model (b), we

100 included month, status (philopatric/dispersed) and their interaction; we had sufficient data to

101 analyse females only. For both models, year and individual were included as random

102 factors. Models were run using the lme4 package (Bates et al. 2014) in R 2.14.1 (R

103 Development Core Team 2012).

104

105 **Results**

106 General

107 We collected data on 14 juvenile foxes (4 males, 10 females), across 6 years, for a total of

108 1676 observations of daily presence/absence of scent marking. For females, 5 were

109 philopatric and 5 disappeared, whereas only 1 male remained philopatric. The peak month

110 for disappearances was October for males (3/3) whereas females disappeared later

111 (October 1/5, December 2/5, February 2/5).

112

113 Sex and ontogenic development of urine marking

114 There was no significant effect of month on overall urine marking rates (Table 1), but the

115 difference between sexes neared significance (P=0.079), whilst the interaction between sex

116 and month was significant (P=0.031; Table 1). Males marked more often than females in

117 June and July when juveniles were fairly young (3-4 months old), but males' marking rates

118 declined rapidly as they aged (Fig. 1a), whereas female marking rates declined later and

119 much more slowly (Fig. 1b).

120

121 Status and ontogenic variation in scent marking

122 Using data from only females, there was no effect of month or the interaction between

123 month and status (philopatric or dispersing) on urine marking rates (Table 1). In contrast,

124 status was highly significant (Table 1). Individuals that remained philopatric had significantly

125 higher urine marking rates than individuals that dispersed (Fig. 2).

126

127 **Discussion**

128 The effects of sex and ontogeny on scent marking

129 Our results demonstrated complicated patterns of scent marking in red fox cubs. Male cubs

130 marked more frequently than females during early development (3-4 months old), but this

131 difference disappeared as juvenile foxes became older. This contrasts with other social

132 species: studies of spotted hyaenas during the pre-puberty failed to report sex differences

133 either in the wild (Mills & Gorman 1987) or in captivity (Woodmansee et al. 1991). In

134 sexually dimorphic species with different adult social roles one expects sex differences in

135 scent marking during development (Whitworth & Southwick 1984). However, in

136 behaviourally and physically monomorphic carnivores, like aardwolves *Proteles cristatus*,

137 one would predict minimal sex differences in early development (Sliwa 1996). Red fox cubs

138 show low, but clear, sexual dimorphism in body size at an early age (Soulsbury et al. 2008).

139 Hence it is likely that that the higher rate of scent marking by male juvenile foxes during

140 June and July reflects some aspect of social relationships possibly including dominance.

141 Red foxes establish a dominance hierarchy when very young (Meyer & Weber 1996)

142 and, like other carnivores, they scent mark when fairly young (Rasa 1973, Roeder 1984,

143 Sliwa 1996). Our results showed that for male juveniles there was a rapid decline in scent

144 marking rates as they aged. In contrast, females showed a later and slower decline. Many

145 social species show a decline in scent marking as they reach maturity, possibly avoiding

146 conflict with adult territory holders (Sliwa 1996). Our data may support this hypothesis for

147 males at least. Male red foxes disperse earlier than females (Soulsbury et al. 2011) and

148 conflict with dominant males in social groups may occur earlier for males. Evidence also

149 suggests that the factors linked to dispersal occur earlier in males than in females (Harris &

150 White 1992). Our evidence indicates that this earlier lowering of social group affiliation, or

151 increased within-group conflict among males, leads to earlier reductions in urine marking

152 rates, compared to females.

153

154 Status and scent marking rates in juvenile red foxes

155 In this study, females that disappeared/dispersed had lower rates of scent marking than

156 philopatric individuals. Previous studies have noted that individuals scent mark less during

157 dispersal (Gese and Ruff 1997); this is the first study to report differences in scent marking

158 rates pre-dispersal. In many species, more dominant adults show higher scent marking

159 rates (e.g. Sillero-Zubiri & Macdonald 1998), but there has been little previous study of

160 marking rates within juvenile groups. The only scent marking study comparing differences

161 dependent on social status occurred in a captive spotted hyena colony (Woodmansee et al.

162 1991). Here too, dominant individuals marked more frequently than subordinates

163 (Woodmansee et al. 1991). In red foxes, offspring of subordinate females usually disperse

164 (Whiteside et al. 2010) and dispersing individuals in fox groups are usually subordinate and

165 less socially-bonded pre-dispersal (Woollard & Harris 1990, Harris & White 1992). Our

166 evidence suggests that the social relationships within litters of red foxes already manifests

167 itself in patterns of scent marking.

168   In conclusion, we found the interaction between month and sex affected the

169 frequency of urine marking by juvenile red foxes. Males scent-marked more frequently than

170 females during early development but the frequency quickly declined as they aged. Marking

171 rates decreased later and more gradually in females than in males. Marking rates were

172 significantly higher among females remaining philopatric than among those

173 disappeared/dispersing. Overall, these results highlight the importance of scent marking

174 during ontogeny.

175

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262

263 **Table 1.** Binomial GLMM output for (a) <u>daily</u> urine marking rates comparing month, sex and

264 their interaction and (b) female <u>daily urine</u> marking rates comparing month, status

265 (philopatric or dispersed) and their interaction

266

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 x 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 x Status	-0.12	0.10	-1.26	0.206

267

268

269   Figure legends

270   **Fig. 1.** Median (± IQR) <u>proportion of daily visits with urine mark</u> (a) male juvenile red foxes

271   and (b) female juvenile red foxes.
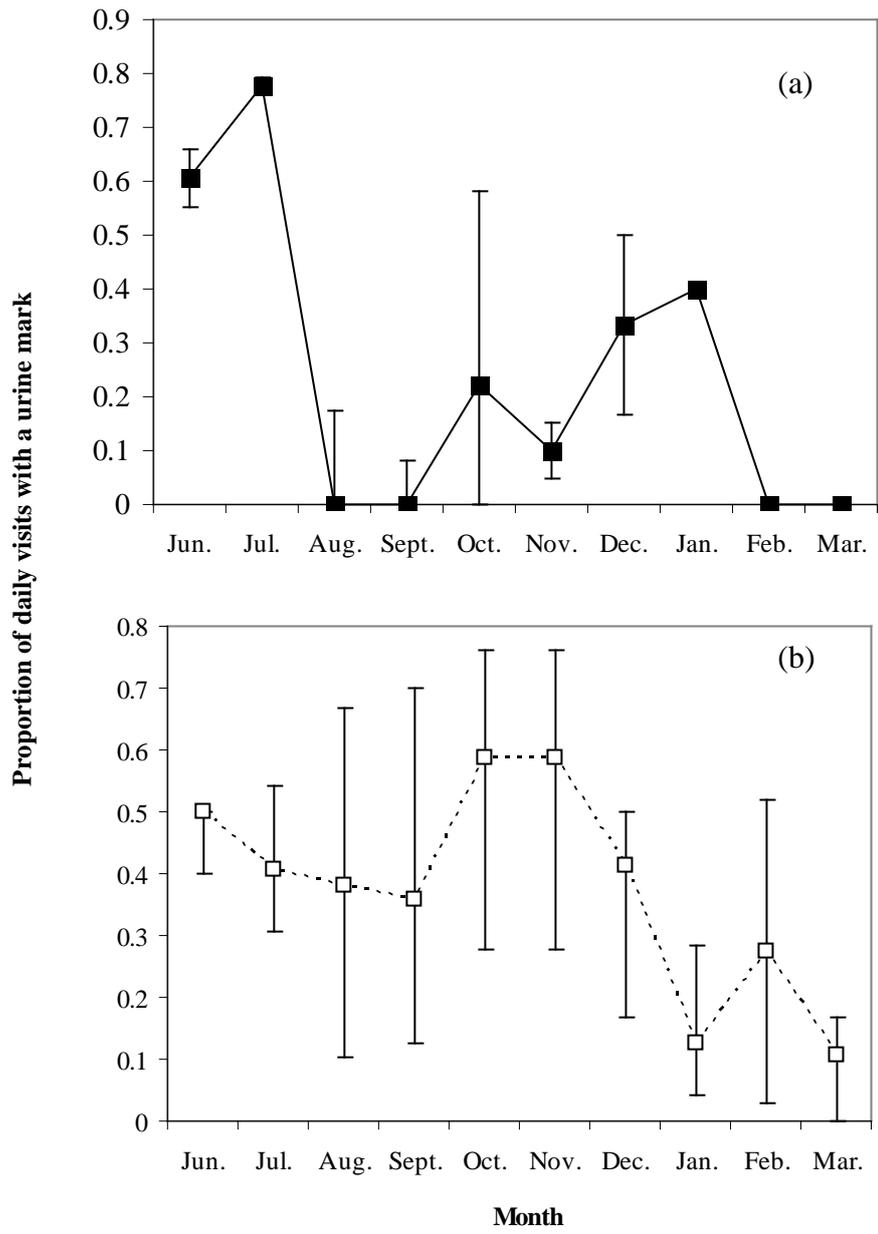
272

273   **Fig. 2.** Boxplot showing the differences in median <u>proportion of daily visits with urine mark</u>

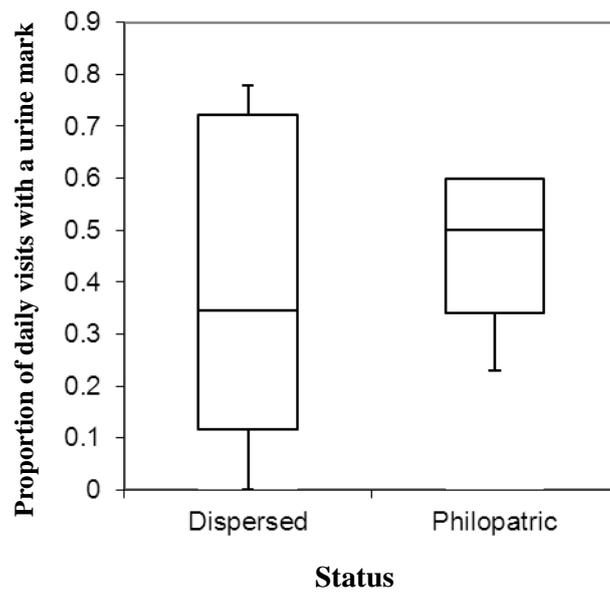274   between female red foxes that were philopatric and those that dispersed.

275

276

Figure 2

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