

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

3

4 Carl D. Soulsbury¹ and John K. Fawcett²

5 ¹ *School of Life Sciences, University of Lincoln, Brayford Pool, Lincoln LN6 7TS*

6 ² *14 Forest Glade Close, Brockenhurst, Hampshire SO42 7QY*

7

8

9

10

11

12 Corresponding author: Carl Soulsbury

13 Email: csoulsbury@lincoln.ac.uk

14 *Address: School of Life Sciences*

15 *University of Lincoln*

16 *Brayford Pool*

17 *Lincoln*

18 *LN6 7TS*

19

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

36 **Introduction**

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

45 There are numerous studies of scent marking among adults within populations (e.g.
46 Sillero-Zubiri et al. 1998, Gould & Overdroff 2002). Urine marking has an important social
47 role in many mammal groups, with sex (e.g. Fawcett et al. 2013) and status differences
48 among adult individuals (e.g. Gese & Ruff 1997; Sillero-Zubiri et al. 1998). In contrast, only a
49 few studies have considered scent marking rates of juvenile individuals (e.g. Gese & Ruff
50 1997) and even fewer note ontogenic development of marking. Scent marking behaviours
51 begin relatively early during development (Rasa 1973, Roeder 1984, Sliwa 1996, Sharpe et
52 al. 2012). However, it is unknown at what age they develop or whether there are differences
53 according to sex or social status.

54 Red foxes (*Vulpes vulpes*) are widespread medium-sized (4-7kg) canids with
55 substantial social and ecological plasticity (Baker & Harris 2004). Scent marking has diverse
56 functions including territorial demarcation and social interactions (Henry 1977, 1980,
57 Macdonald 1979a, Baker et al. 2000, Goszczyński 2002, Macdonald 1979a, Arnold et al.
58 2011). Under some conditions, offspring from previous years remain in the natal territory,
59 leading to the formation of social groups (Macdonald 1979b, Baker et al. 1998, Baker &
60 Harris 2004). Previous work has shown that social behaviour is crucial in determining which
61 cubs remain in the natal territory and which disperse; dispersing individuals had less social
62 interaction (Harris & White 1992) and spent more time away from the home range core
63 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

176 **Acknowledgements**

177 We are extremely grateful to Jeanne Fawcett whose help in recording, watching and
178 interpreting the videos was of fundamental importance to this paper.

179

180 **References**

181 Arnold J., Soulsbury C.D. & Harris S. 2011: Spatial and behavioral changes by red foxes
182 (*Vulpes vulpes*) in response to artificial territory intrusion. *Can. J. Zool.* 89: 808-815.

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

186 Baker P.J., Funk S.M., Harris S. & White PCL 2000: Flexible spatial organization of urban
187 foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Anim. Behav.*
188 59: 127-146.

189 Baker P.J., Harris S., Robertson C.P.J., Saunders G. & White P.C.L. 2001: Differences in
190 the capture rate of cage-trapped red foxes *Vulpes vulpes* and an evaluation of rabies
191 control measures in Britain. *J. Appl. Ecol.* 38: 823–835.

192 Baker P.J., Robertson C.P., Funk S.M. & Harris S. 1998: Potential fitness benefits of group
193 living in the red fox, *Vulpes vulpes*. *Anim. Behav.* 56: 1411-1424.

194 Bates, D., Maechler, M. & Bolker, B. 2012: lme4: Linear mixed-effects models using S4
195 classes. R package version 0.999999-0. *Computer software*]. Retrieved from
196 <http://CRAN.R-project.org/package=lme4>.

197 Fawcett J.K., Fawcett J.M. & Soulsbury C.D. 2013: Seasonal and sex differences in urine
198 marking rates of wild red foxes *Vulpes vulpes*. *J. Ethol.* 31: 41-47.

199 Ferkin M.H. & Johnston R.E. 1995: Meadow voles, *Microtus pennsylvanicus*, use multiple
200 sources of scent for sex recognition. *Anim. Behav.* 49: 37-44.

201 Gese E.M. & Ruff EL 1997: Scent-marking by coyotes, *Canis latrans*: the influence of social
202 and ecological factors. *Anim. Behav.* 54: 1155-1166.

203 Gorman M.L. & Trowbridge B.J. 1989: The role of odor in the social lives of carnivores. In
204 Gittleman, J.L (ed). *Carnivore behavior, ecology, and evolution Vol. 1*, Cornell University
205 Press, USA, pp. 57-88.

206 Goszczyński J. 2002: Home ranges in red fox: territoriality diminishes with increasing area.
207 *Acta. Theriol. 47*: 103-114.

208 Gould L. & Overdorff D.J. 2002: Adult male scent-marking in *Lemur catta* and *Eulemur*
209 *fulvus rufus*. *Int. J. Primat. 23*: 575-586.

210 Harris S. & White P.C.L. 1992: Is reduced affiliative rather than increased agonistic
211 behaviour associated with dispersal in red foxes? *Anim. Behav. 44*: 1085-1089.

212 Henry J.D. 1977: The use of urine marking in the scavenging behavior of the red fox (*Vulpes*
213 *vulpes*). *Behav. 61*: 82-106.

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

218 Hurst J.L., Beynon R.J., Humphries R.E., Malone N., Nevison C.M., Payne C.E., Robertson
219 D.H.L. & Veggerby C. 2001 Information in scent signals of competitive social status: the
220 interface between behaviour and chemistry. In Marchelewska-Koj A, Muller-Schwarze D,
221 Lepri J (eds) *Chemical Signals in Vertebrates 9*, Plenum Press, New York, pp. 43-52.

222 Kleiman D. 1966 Scent marking in the Canidae. *Symp. Zool. Soc. Lond. 18*: 167-177.

223 Macdonald D.W. 1979a: Some observations and field experiments on the urine marking
224 behaviour of the red fox, *Vulpes vulpes* L. *Z. Tierpsych. 51*: 1-22.

225 Macdonald D.W. 1979b. 'Helpers' in fox society. *Nature 282*: 69-71.

226 Meyer S. & Weber J.M. 1996: Ontogeny of dominance in free-living red foxes. *Ethol. 102*:
227 1008-1019.

228 Mills M.G.L. & Gorman M.L. 1987: The scent-marking behaviour of the spotted hyaena
229 *Crocuta crocuta* in the southern Kalahari. *J. Zool. 212*: 483-497.

230 Rasa O.A.E. 1973: Marking behaviour and its social significance in the African dwarf
 231 mongoose, *Helogale undulata rufula*. *Z. Tierpsych.* 32: 293-318.

232 Roeder J.J. 1984: Ontogenese des systemes de communication chez la genette (*Genetta*
 233 *genetta* L.). *Behav.* 90: 259-301.

234 Sharpe L.L., Jooste M.M. & Cherry M.I. 2012: Handstand scent marking in the dwarf
 235 mongoose (*Helogale parvula*). *Ethol.* 118: 575-583.

236 Sillero-Zubiri C. & Macdonald D.W. 1998: Scent-marking and territorial behaviour of
 237 Ethiopian wolves *Canis simensis*. *J. Zool.* 245: 351–361

238 Sliwa A. 1996: A functional analysis of scent marking and mating behaviour in the aardwolf.
 239 PhD Thesis, University of Pretoria.

240 Soulsbury C.D., Iossa G., Baker P.J. & Harris S. 2008: Environmental variation at the onset
 241 of independent foraging affects full-grown body mass in the red fox. *Proc R Soc B* 275:
 242 2411-2418.

243 Soulsbury C.D., Iossa G., Baker P.J., White P.C.L. & Harris S. 2011: Behavioral and spatial
 244 analysis of extraterritorial movements in red foxes (*Vulpes vulpes*). *J. Mammal.* 92: 190-
 245 199.

246 Washabaugh, K. & Snowdon, C.T. 1998: Chemical communication of reproductive status in
 247 female cotton-top tamarins (*Saguinus oedipusoedipus*). *Am. J. Primat.* 45: 337-349.

248 Whiteside H.M., Dawson D.A., Soulsbury C.D. & Harris S. 2011: Mother knows best:
 249 dominant females determine offspring dispersal in red foxes (*Vulpes vulpes*). *PloS One*
 250 6: e22145.

251 Whitworth M.R. & Southwick C.H. 1984: Sex differences in the ontogeny of social behavior
 252 in pikas: possible relationships to dispersal and territoriality. *Behav. Ecol. Sociobiol.* 15:
 253 175-182.

254 Woodmansee K.B., Zabel C.J., Glickman S.E., Frank L.G. & Keppel G. 1991: Scent marking
 255 (pasting) in a colony of immature spotted hyenas (*Crocuta crocuta*): A developmental
 256 study. *J. Comp. Psych.* 105: 10-14.

257 Woollard T. & Harris S. 1990: A behavioural comparison of dispersing and non-dispersing
258 foxes (*Vulpes vulpes*) and an evaluation of some dispersal hypotheses. *J. Anim. Ecol.*
259 59: 709-722.

260 Zala S.M., Potts W.K. & Penn D.J. 2004: Scent-marking displays provide honest signals of
261 health and infection. *Behav. Ecol.* 15: 338-344.

262

263 **Table 1.** Binomial GLMM output for (a) daily urine marking rates comparing month, sex and
 264 their interaction and (b) female daily urine 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 (\pm IQR) proportion of daily visits with urine mark (a) male juvenile red foxes
271 and (b) female juvenile red foxes.

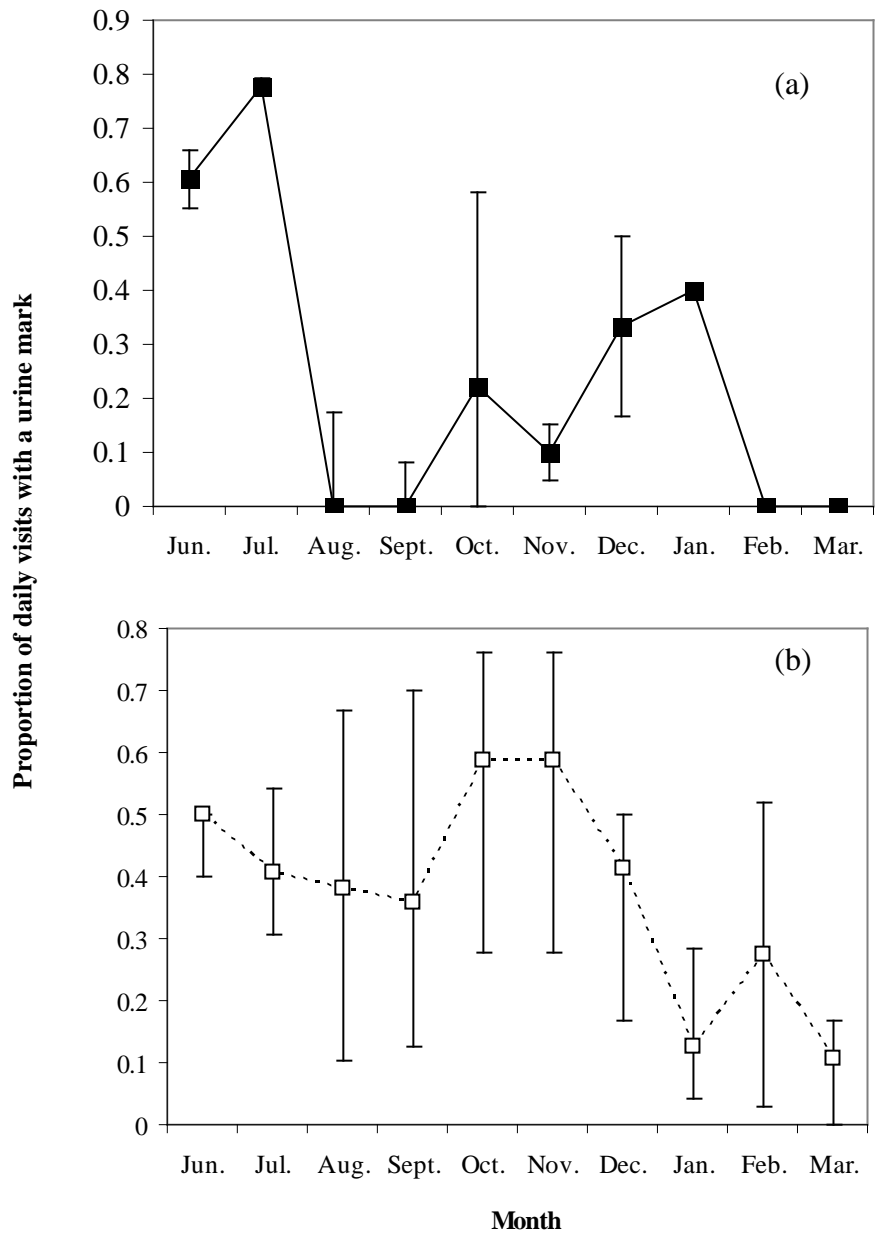
272

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

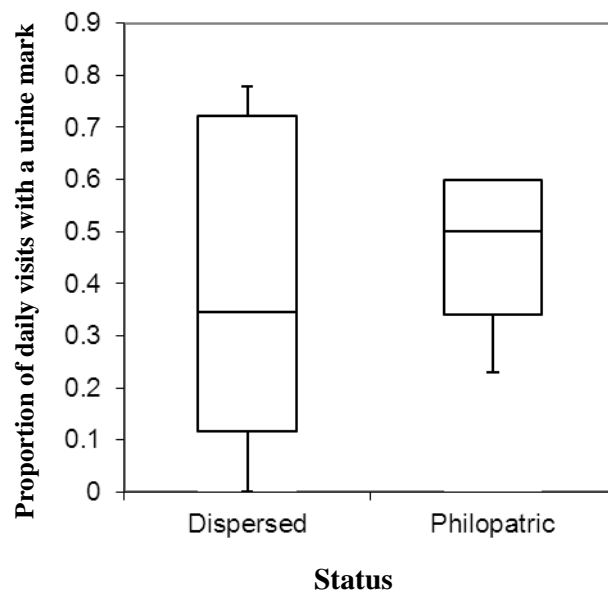
275

276

277
278
279
280



281



282

283

284

Figure 2