1   **Red squirrels mitigate costs of territory defence through social plasticity**

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18

19   **Abstract**

20   For territorial species, the ability to be behaviourally plastic in response to changes in their social

21   environment may be beneficial by allowing individuals to mitigate conflict with conspecifics and

22   reduce the costs of territoriality. Here we investigated whether North American red squirrels

23   (*Tamiasciurus hudsonicus*) were able to minimize costs of territory defence by adjusting

24   behaviour in response to the familiarity of neighbouring conspecifics. Since red squirrels living

25   in familiar neighbourhoods face reduced intrusion risk, we predicted that increasing familiarity

26   among territorial neighbours would allow squirrels to spend less time on territorial defence and

27   more time in the nest. Long-term behavioural data (1995-2004) collected from the same squirrels

28   across several different social environments indicated that red squirrels reduced rates of

29   territorial vocalizations and increased nest use in response to increasing familiarity with

30   neighbours. In contrast, cross-sectional data (2015-2016), which provided observations from

31   each individual in a single social environment, did not provide evidence of this plasticity. Post-

32   hoc analyses revealed that evidence of social plasticity in this system was primarily due to

33   within-individual changes in behaviour, which we were unable to estimate in the cross-sectional

34   data. Our results demonstrate that red squirrels can reduce the costs of territoriality by

35   appropriately adjusting behaviour in response to changes in their social environment. However,

36   our results also suggest that estimating plasticity by comparing behaviour among individuals (i.e.

37   cross-sectional analyses) may not always be reliable. Our ability to detect these effects may

38   therefore depend on having data with multiple observations from the same individuals across

39   different social environments.

40

41   **Keywords**

42   behavioural plasticity, behavioural time budgets, dear enemy, familiarity, red squirrel, social

43   competence, social environment, territoriality, vocalizations

44

45   **Introduction**

46   Phenotypic plasticity is one way for organisms to adjust their physiology, morphology,

47   and behaviour when the rate of environmental change outpaces the rate of genetic evolutionary

48   change (Piersma & Drent, 2003). Broadly defined, phenotypic plasticity is the ability of a given

49   genotype to express multiple phenotypes in response to different environmental conditions

50   (Pigliucci, 2001). Although classic studies of phenotypic plasticity have focused on changes in

51   non-reversible traits (e.g. morphology) that are expressed within a single genotype (Hebert &

52   Grewe, 1985; Lively, 1986; Greene, 1989), traits that are expressed repeatedly over the course of

53   an organism's lifetime (e.g. timing of reproduction) can be subject to reversible within-individual

54   plasticity (Nussey, Wilson, & Brommer, 2007; Piersma & Drent, 2003). This 'reversible

55   plasticity' (Gabriel, Luttbeg, Sih, & Tollrian, 2005), also referred to as 'phenotypic flexibility'

56   (Piersma & Drent, 2003), or 'responsiveness' (Wolf, Van Doorn, & Weissing, 2008), is a

57   powerful mechanism for adapting to changing and unpredictable environmental conditions.

58   Behavioural traits, in particular, show capacity for substantial phenotypic lability in response to

59   changing environmental conditions within an organism's lifetime and can facilitate an

60   organism's ability to cope with both predictable and unpredictable variation in the environment

61   (Ghalambor, Angeloni, & Carroll, 2010).

62   The social environment is arguably one of the most dynamic and variable realms of an

63 individual's environment, since high levels of unpredictability are inherent when interacting with

64 other agents that can also exhibit plasticity in behaviour. Examples of social plasticity (changes

65 in behaviour in response to changing social conditions; Sih, Chang, & Wey, 2014;1 Montiglio,

66 Wey, Chang, Fogarty, & Sih, 2017) are prevalent. For instance, individuals adjust their level of

67 aggression according to the perceived level of threat imposed by neighbours versus strangers

68 (Temeles, 1994). Interacting individuals change their signaling behaviour in response to

69 bystanders ('audience effect'- Doutrelant, McGregor, & Oliveira, 2001; Pinto, Oates, Grutter, &

70 Bshary, 2011). Behaviour may also be affected by previous social experiences such as 'winner-

71 loser effects' (Hsu, Earley, & Wolf, 2006; Rutte, Taborsky, & Brinkhof, 2006), as well as by

72 'eavesdropping', in which bystanders extract information from interacting individuals (Earley,

73 2010; Mennill, Ratcliffe, & Boag, 2002; Oliveira, McGregor, & Latruffe, 1998).

74   The ability to adjust behaviour in response to social context should allow individuals to

75 avoid costly interactions while appropriately engaging in other social interactions that might

76 enhance fitness (Taborsky & Oliveira, 2012). This ability to show adaptive adjustments in social

77 behaviour has been termed 'social skill' (Sih & Bell, 2008) or 'social competence' (Taborsky &

78 Oliveira, 2012), although few studies have directly demonstrated fitness benefits of social

79 plasticity (Han & Brooks, 2015; Patricelli, Uy, Walsh, & Borgia, 2002; Montiglio et al., 2017).

80 Given the substantial number of social interactions that group-living species must navigate, the

81 benefits of social plasticity are expected to be high in such species (Taborsky, Arnold, Junker, &

82 Tschopp, 2012). However, solitary, territorial species may also benefit from appropriate

83 adjustments in social behaviour, as being socially plastic may allow individuals to mitigate

84 conflict with conspecifics and reduce the costs of territoriality. For example, gladiator frogs

85 (*Hypsiboas rosenbergi*) adjust the timing of vocalizations in response to changing levels of

86 conspecific competition. By reducing calling rates in response to changing social conditions,

87 individuals can minimize an energetically costly behaviour (Höbel, 2015).

88   Solitary, territorial species, like their social counterparts, face variation in their social

89 environments through their interactions with territorial neighbours. A well-described example of

90 this variation is differences in familiarity with neighbours (Bebbington et al., 2017; Beletsky &

91 Orians, 1989; Eason & Hannon, 1994; Grabowska-Zhang, Wilkin, & Sheldon, 2012). Long-term

92 social relationships with neighbours have been presumed to be advantageous by minimizing

93 renegotiation of territory boundaries and therefore reducing aggression as well as time and

94   energy spent on territory defence ('dear-enemy effect'; Fisher, 1954). However, most evidence

95   in support of this cooperative phenomenon comes from experimental studies where individuals

96   are exposed to a familiar and unfamiliar stimulus and a behavioural response is recorded

97   (Temeles, 1994). We know less about how behavioural time budgets are affected by long-term

98   social relationships under natural conditions when individuals may have to navigate territorial

99   dynamics with multiple neighbours (but see Bebbington et al., 2017; Eason & Hannon, 1994).

100   In this study, we used a longitudinal dataset spanning eight years and cross-sectional data

101   from two years to examine whether territorial North American red squirrels (*Tamiasciurus*

102   *hudsonicus*, hereafter 'red squirrels') adjust their behaviour in response to their familiarity with

103   their local social environment. Our long-term dataset contained multiple observations of the

104   same individuals across different social environments, while our cross-sectional data represented

105   an intensive snapshot of a large number of individuals at a single point in time (i.e. a single

106   social environment for each individual), allowing us to compare across individuals to assess

107   differences in behaviour. Although behavioural plasticity is fundamentally a within-individual

108   phenomenon, it can be approximated by comparing among individuals in different environments

109   (Legagneux & Ducatez, 2013; Slabbekoorn & Peet, 2003). While this among-individual

110   approach is a useful tool (particularly where it is challenging or time-consuming to collect data

111   on many individuals over several environments) it relies on the critical assumption that the

112   among-individual relationship is an accurate representation of within-individual changes in

113   behaviour.

114   Red squirrels are territorial rodents that defend year-round exclusive territories (Smith,

115   1968). In the Yukon, red squirrels cache white spruce cones (*Picea glauca*) in a larder hoard

116   called a 'midden' at the center of their territory (Fletcher et al., 2010). This food cache is

117   important for overwinter survival (Kemp & Keith, 1970; LaMontagne et al., 2013) and both

118   sexes heavily defend these resources from conspecifics, primarily through territorial

119   vocalizations called 'rattles' (Smith, 1978). Rattles function to deter intruders (Siracusa,

120   Morandini, et al., 2017b) but are also individually unique (Digweed, Rendall, & Imbeau, 2012;

121   Wilson et al., 2015). Rattles therefore carry important information about the local social

122   environment, such as the identity or density of neighbouring conspecifics. Squirrels have been

123   shown to use this acoustic information to increase rattling rates and vigilance and decrease nest

124   use in response to increasing local density (Dantzer, Boutin, Humphries, & McAdam, 2012).

125   Additionally, familiarity (length of time as neighbours) with territorial neighbours has been

126   shown in this system to have direct effects on territory intrusion risk. Specifically, individuals

127   living in neighbourhoods with higher average familiarity faced reduced intrusion risk (Siracusa,

128   Boutin, et al., 2017a), consistent with the dear enemy phenomenon (Fisher, 1954).

129   Given these previous findings, we predicted that increasing familiarity with territorial

130   neighbours would allow for decreased time spent on territorial defence as evidenced by (1)

131   decreasing rattling rates and (2) reducing time spent vigilant for conspecifics. We also predicted

132   that, as a squirrel's familiarity with its neighbours increased, squirrels would increase the

133   proportion of time spent in nest, as a proxy for time spent on offspring-care or self-maintenance.

134   Changes in behaviour, as predicted above, would allow individuals to minimize aggression and

135   reduce allocation of time and energy to territory defence under social conditions associated with

136   reduced risk of territorial intrusion, and thus would be indicative of social competence in this

137   species.

138

139   **Methods**

140   We studied a natural population of North American red squirrels located in the southwest

141   Yukon near Kluane National Park (61° N, 138° W) that has been monitored continuously since

142   1987 as part of the Kluane Red Squirrel Project (KRSP; McAdam, Boutin, Sykes, & Humphries,

143   2007). To assess social plasticity in red squirrels, we measured behaviour of individuals on three

144   study grids characterized by open boreal forest where white spruce is the dominant tree species

145   (Krebs et al. 2001).

146   Using the longitudinal dataset, we analyzed long-term focal animal observations

147   (Altmann, 1974) of 41 red squirrels across eight years (between 1995 and 2004), collected on

148   one unmanipulated control grid (Sulphur: SU; 40 ha). We also examined a cross-section of data

149   by analyzing focal observations of 108 squirrels in one year (2016) on two unmanipulated

150   control grids (Kloo: KL and SU; 40 ha each) and one food supplemented grid (Agnes: AG; 45

151   ha; see Dantzer et al., 2012 for a description of the food supplementation experiment). In

152   addition to using focal animal observations, we measured the behaviour of squirrels by deploying

153   accelerometers in 2016 and audio recorders in 2015 and 2016. On average, squirrels rattle once

154   every 8.24 min (Dantzer et al., 2012), which makes capturing fine-scale adjustments in

155   behaviour challenging, even with the intensive use of focal observations. Therefore, our intention

156 was to use data from audio recorders and accelerometers as additional measures of social

157 plasticity that might better capture fine-scale adjustments in behaviours such as rattling rates and

158 nest use. This research was approved by the University of Guelph Animal Care Committee (AUP

159 number 1807) and is in compliance with the ASAB/ABS *Guidelines for the Use of Animals in*

160 *Research*. Details on these approaches are provided below.

161

162 *Measuring familiarity*

163 In each year, we enumerated all squirrels living on our study areas and monitored

164 individuals from March until August. We used a combination of live-trapping procedures and

165 behavioural observations to track reproduction, identify territory ownership, and determine

166 offspring recruitment from the previous year (see Berteaux & Boutin, 2000; McAdam et al.,

167 2007 for a complete description of core project protocols). All study grids were staked and

168 flagged at 30 m intervals, which allowed us to record the spatial location of all squirrel territories

169 to the nearest 3 m. In this study system, territory locations were denoted based on the location of

170 an individual's midden, which approximates the center of a squirrel's territory. We did not

171 explicitly map territory boundaries for all individuals.

172 We trapped squirrels using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk,

173 Wisconsin, USA) baited with all natural peanut butter. If previously tagged, the identities of the

174 squirrels were determined from their unique alphanumeric metal ear tags (Monel #1; National

175 Band and Tag, Newport, KY, USA), which they received in their natal nest at around 25 days of

176 age. During the first capture of the season, we marked each squirrel by threading coloured wires

177 through each ear tag, which allowed for individual identification of squirrels during behavioural

178 observations. We censused the population twice annually (in mid-May and mid-August) and

179 determined territory ownership through a combination of consistent live-captures of the same

180 individual at the same midden and behavioural observations of territorial 'rattle' vocalizations

181 (Smith 1978).

182 For each territory owner we defined the social neighbourhood to be all conspecifics

183 whose middens were within a 130 m radius of the owner's midden. One hundred and thirty

184 meters is the furthest distance that red squirrel rattles are known to carry (Smith, 1978) and is

185 similar to the 150 m distance found by (Dantzer et al., 2012) to be most relevant for local density

186 effects of the social environment. We measured pairwise familiarity between the territory owner

187   and each neighbour as the number of days that both individuals were within the same acoustic

188   neighbourhood (i.e. occupied their current neighbouring territories). We then averaged pairwise

189   measures of familiarity between the focal individual and each of the neighbours to provide a

190   measure of the average familiarity of each individual with its entire acoustic neighbourhood

191   (Siracusa, Boutin, et al., 2017a).

192

193   *Focal observations*

194   Red squirrels are an ideal species for behavioural studies because they are diurnal, easy to

195   locate visually or through acoustic cues, and habituate readily to the presence of humans. As part

196   of the KRSP, we have recorded the behaviour of red squirrels through focal sampling of radio-

197   collared individuals (model PD-2C, 4 g, Holohil Systems Ltd., Ontario, Canada) since 1994,

198   although the sampling protocol has varied slightly across this period. For this study, we chose to

199   use a subset of long-term behavioural data where focal observations were collected in a

200   consistent manner by instantaneous sampling at 30-sec intervals for ten continuous minutes

201   (Altmann, 1974) on a single control grid (SU; $N = 487$ 10-min sessions over 41 individuals). We

202   excluded any focals where the squirrel was out of sight for more than half the observation

203   session ($N = 8$). These behavioural observations were available for female squirrels in 1995 ($N = $

204   41), 1996 ($N = 10$), 1997 ($N = 25$), 1999 ($N = 34$), 2001 ($N = 70$), 2002 ($N = 110$), 2003 ($N = $

205   120), and 2004 ($N = 77$) and were recorded by 38 different observers. On average, data were

206   available for two different social environments per individual (range 1-8). We considered any

207   change in average familiarity during the population census to be a change in the social

208   environment. Since the population was censused twice annually (in mid-May and mid-August)

209   individuals could experience up to two different social environments per year.

210   Between 7 May 2016 and 31 August 2016, we used focal animal sampling as described

211   above for seven continuous minutes, rather than ten, to record red squirrel behaviour ($N = 1060$ 7

212   min sessions over 108 individuals). In this cross-sectional data we only had observations from

213   each individual in a single social environment. Since rattling is a rare behaviour and is often

214   missed using instantaneous sampling, in 2016 we recorded all occurrences (Altmann, 1974) of

215   rattle vocalizations emitted by the focal squirrel, including those which fell outside the 30-sec

216   sampling interval (i.e 'critical incidents'). We used all of these data, including critical incidents,

217   to assess how familiarity affected rattling rates in 2016. Four observers collected behavioural

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218   data on both male ($N = 76$) and female ($N = 32$) squirrels across two control grids (KL and SU)

219   and one food-supplemented grid (AG). We monitored each individual for 2-10 days

220   consecutively (barring inclement weather; mean = 4 days) and collected an average of 10 focals

221   per individual (range: 2-29). In instances where multiple focal observations were collected for

222   the same squirrel in a single day, observations were kept 30 minutes apart at minimum. Because

223   an observer was in regular attendance at these territories we could be confident that there was no

224   turnover in the social environment during the sampling period for any of these individuals.

225   Territory turnovers in this system are accompanied by substantial rattling and chasing and are

226   therefore easy to detect. The two squirrels for which we observed a disturbance in the local

227   social environment during the sampling period were excluded from this analysis.

228   For all focal sampling, we recorded and classified red squirrel behaviours in a similar

229   way to previous studies of squirrel behaviour in this system (Anderson & Boutin, 2002; Dantzer

230   et al., 2012; Stuart-Smith & Boutin, 1994). We classified behaviours according to the following

231   categories: vocalizing ("barking" or "rattling"; Smith, 1978), feeding, foraging, traveling,

232   caching food items, interacting with conspecifics, grooming, resting, vigilant, in nest, or out of

233   sight (unknown behaviour). Vigilance could be distinguished from resting by the alert posture of

234   the squirrel; vigilant squirrels typically had their head up and appeared observant, sometimes

235   standing on their hind limbs, while resting squirrels often had their head tucked down or lay

236   stretched out.

237

238   *Audio recording and acoustic analysis*

239   Between 23 June – 25 September 2015 and 8 May – 1 September 2016, we deployed

240   Zoom H2n audio recorders (Zoom Corporation, Tokyo, Japan) to determine rattling rates of

241   squirrels. We attached recorders with windscreens to 1.5 m stakes and placed a single recorder in

242   the center of each squirrel's midden. Since Zoom H2n recorders are not weatherproof, we placed

243   an umbrella approximately 30 cm above each audio recorder to protect it from rain and snow.

244   Each morning, we deployed audio recorders between 0500-0600 h (just before squirrels typically

245   became active). We set audio recorders to record in 44.1kHz/16bit WAVE format, and recorded

246   in 2-channel surround mode with the stereo width set to +6 dB and the mic gain set to 10. We

247   allowed audio recorders to run for a full 24 hours, but in this study we only use data collected

248   between 0700-1300 h, which is the period during which squirrels are typically most active

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249 between early summer and early autumn (Studd, Boutin, McAdam, & Humphries, 2016;

250 Williams et al., 2014). We deployed audio recorders for 137 squirrels ($N = 109$ males and $N = 28$

251 females) and recorded each squirrel for 5 consecutive days on average (range: 1-13 days; $N =$

252 714 days or 4284 hours over 137 individuals). Because we collected audio data over 2 years, we

253 had observations from 2-3 different social environments for 28 of these individuals. Due to the

254 large volume of recordings, we detected rattle vocalizations from recordings automatically using

255 Kaleidoscope software (version 4.3.2; Wildlife Acoustics, Inc., Maynard, MA, USA). Detection

256 settings included a frequency range of 2000–13000 Hz, a signal duration of 0.4–15 s, a

257 maximum intersyllable silence of 0.5 s, a fast Fourier transform size of 512 points

258 (corresponding to a frequency resolution of 86 Hz and a temporal resolution of 6.33 ms), and a

259 distance setting of 2 (this value ensures that all detections are retained).

260   The purpose of using audio recorders was to provide a more accurate estimate of

261 individual rattling rates. A challenge, however, is that the recorders also recorded vocalizations

262 from neighbouring squirrels. Neighbours should be farther away from the recorder. Because

263 sound degrades and attenuates predictably with distance, it should be possible to distinguish

264 between the rattles of focal and neighbour squirrels on the basis of rattle acoustic structure. We

265 tested this by conducting hour-long calibrations on 48 focal individuals between 13 September

266 and 14 October 2015. During these calibrations, audio recorders were set up as described above.

267 A single observer standing near the midden kept the territory owner in sight and recorded

268 whether each rattle belonged to the territory owner or a neighbouring individual.

269   We detected rattle vocalizations from the calibration recordings using Kaleidoscope

270 software (same settings as above). Based on a comparison with the observer's notes, the software

271 detected 100% of the focal squirrel rattles. We then developed a procedure for distinguishing

272 focal squirrel rattles from other types of detections, including neighbour rattles and non-rattles.

273 First, we automatically measured the acoustic structure of every detection using the software

274 package 'Seewave' (version 2.0.5; Sueur, Aubin, & Simonis, 2008) in R (see details of structural

275 measures below). Second, we used the structural measurements in a discriminant function

276 analysis in SPSS (software, version 24; IBM Corporation, Armonk, New York, USA) to develop

277 a predictive model for assigning detections to groups (*i.e.,* focal rattle, neighbour rattle, non-

278 rattle). We developed the model using detections from half of the 1-hour calibration files

279 (selected at random), and then tested it for accuracy by applying it to the detections from the

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280   remaining half. The model correctly assigned 80.6% of the focal rattles to the 'focal rattle' group,

281   meaning we missed 19.4% of focal rattles (i.e. false negatives). Some non-rattle detections were

282   also assigned to the 'focal rattle' group, but we removed these by reviewing the spectrograms of

283   all detections categorized as 'focal rattles'. After removing non-rattle detections, 16.0% of the

284   detections remaining in the 'focal rattle' group were false positives, meaning they were actually

285   from the neighbour instead of the focal squirrel. We then applied the predictive model to the

286   main set of audio files, and reviewed all detections labeled as 'focal rattle' in Kaleidoscope to

287   remove the non-rattle detections.

288   The structural measures included in the discriminant function analysis were: (1) duration,

289   (2) root-mean-square amplitude, (3) pulse rate, (4) duty cycle, and five variables that measured

290   the distribution of energy in the frequency domain, including (5) peak frequency, (6) first energy

291   quartile, (7) skewness, (8) centroid, and (9) and spectral flatness. Duration, root-mean-square

292   amplitude, pulse rate, and duty cycle were measured from a waveform. Pulse rate is the number

293   of pulses in the rattle minus one, divided by the period of time between the beginning of the first

294   pulse and the beginning of the last (as in Wilson et al., 2015). Duty cycle is the proportion of the

295   rattle when a pulse is being produced. For pulse rate and duty cycle, individual pulses were

296   identified using the 'timer' function in seewave (50% amplitude threshold; 200-point smoothing

297   window with 90% overlap). The five energy distribution variables were obtained using the

298   'specprop' function in seewave, and were based on a mean frequency spectrum (512-point fast

299   Fourier transform, hanning window, 0% overlap). Peak frequency is the frequency of maximum

300   amplitude. First energy quartile is the frequency below which 25% of the energy is found.

301   Skewness, centroid, and kurtosis describe the shape of the power spectrum (detailed definitions

302   can be found in Sueur et al., 2008).

303

304   *Accelerometers*

305   Between 4 May and 1 September 2016, we deployed AXY-3 accelerometers

306   (Technosmart Europe srl., Rome, Italy) on 94 squirrels ($N = 66$ males and $N = 28$ females). An

307   accelerometer is an instrument that measures the acceleration of the body along three axes:

308   anterior-posterior (surge), lateral (sway), dorso-ventral (heave) and records temperature,

309   allowing for the characterization of different behavioural patterns. Accelerometers were

310   deployed in combination with radio transmitters (model PD-2C, Holohil Systems Ltd., Ontario,

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311   Canada). Total package weight for collars with both accelerometers and radio transmitters

312   (including battery, packaging, and bonding material) was 9.6 g on average. For a 200-250 g red

313   squirrel (Steele, 1998) this collar weight was less than the recommended 5-10% of the animal's

314   body weight (Wilson, Cole, Nichols, Rudran, & Foster, 1996). We deployed accelerometers on

315   94 individuals for an average of 9 days per individual (range: 4-17; $N = 873$ days over 94

316   individuals) at a sampling rate of 1 Hz. Accelerometers recorded data constantly while deployed,

317   but for this study we only use data between 06:00-21:00 h to estimate time spent in nest during

318   active hours of the day (Williams et al., 2014).

319   Raw accelerometer data were classified into 5 behavioural categories using threshold

320   values of summary statistics according to the decision tree developed for red squirrel

321   accelerometers and temperature data loggers by Studd et al. (in review). Following methods

322   proposed by Collins et al. (2015), the decision tree was created using 83.8 hours of direct

323   behavioural observations on 67 free-ranging squirrels and had an overall accuracy of correctly

324   classifying known behaviours of 94.9% (Studd et al. in review). Briefly, warm stable

325   temperatures were used to identify when the animal was in the nest with the additional constraint

326   that the individual must not be moving for the majority of each nest bout. Low acceleration

327   values were associated with not moving, moderate acceleration values denoted feeding, and high

328   acceleration corresponded to travelling. Travelling was further categorized as running when the

329   peak acceleration value of the surge axis was above a threshold of 1.15 G.

330

331   *Statistical analyses*

332   Given that previous work in this study system (Dantzer et al., 2012) allowed us to make

333   specific predictions about how squirrels should adjust rattling rates, vigilance and nest use in

334   response to their social environment, here we used univariate models to test for the effects of

335   familiarity on each of these behaviours explicitly. For all models we included local density,

336   measured as the number of squirrels per hectare within 130 m, as a continuous predictor, to

337   account for the fact that previous work in the study system has found local density to be an

338   important predictor of behavioural time budgets (Dantzer et al., 2012). We also included age as a

339   fixed effect in all rattling rate models since we expected that the vigor of territory defence might

340   decline with physical deterioration, but we did not have specific predictions as to how age might

341   affect nest use or vigilance. However, it is important to note that since young squirrels are

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342   inherently unfamiliar with their neighbours and familiarity increases with age, age and

343   familiarity were strongly correlated (Pearson's correlation coefficient ranged between 0.42 and

344   0.58 for these analyses) although variance inflation factors were low (< 3; Zuur, Ieno, & Elphick,

345   2009). Fixed effects and random effects of all models are summarized in Tables 1 and 2,

346   respectively.

347   *Focal data*

348   To account for the structural differences in our data sets, multiple observations of the

349   same individuals across different social environments (longitudinal data) versus observations

350   from different individuals, each in a single social environment (cross-sectional data), we

351   analyzed the longitudinal ($N = 487$ 10-min sessions) and cross-sectional ($N = 1060$ 7-min

352   sessions) focal data separately. In the long-term data, there was a single data point where the

353   number of rattles recorded was 25 times greater than the mean. This outlier was likely an error in

354   data entry and was removed (see Figure S1). We analyzed the effects of neighbourhood

355   familiarity on (1) the frequency of territorial vocalizations (rattles), (2) the proportion of time

356   spent vigilant, and (3) the proportion of time spent in nest. We modeled the frequency of

357   territorial vocalizations using a generalized linear mixed-effect model (GLMM) with a bobyqa

358   optimizer and a Poisson error distribution (log-link) where the response variable was the number

359   of rattles emitted during the 10-min focal session. For both the proportion of time spent in nest

360   and the proportion of time spent vigilant, we fitted a Beta-Binomial model to account for

361   overdispersion in the data (Harrison, 2015). Using the 'cbind' function, we defined the response

362   variable as a 2-column matrix composed of the number of observations of the given behaviour

363   (in nest or vigilant) and the number of observations of all other behaviours (not including

364   observations when the squirrel was out of sight). In all models we included average familiarity

365   and local density as continuous predictors, and for the rattling rate models we included age as a

366   continuous fixed effect. We included grid, sex and observer identity as categorical fixed effects

367   for the 2016 focal data (it was not necessary to include grid or sex for the long-term data as all

368   data were collected on females on a single grid). For both datasets, we included a random

369   intercept term for squirrel identity (squirrel ID) to account for repeated observations of the same

370   squirrels. We also included a random effect of year and observer identity for the long-term

371   dataset to account for inter-individual differences in behavioural scoring.

372   *Audio recorder data*

373   To assess the effects of familiarity on rattling rates derived from the audio recorder data,

374   we fitted a GLMM with a Poisson error distribution (log-link). Our response variable was the

375   number of rattles emitted between 0700 – 13:00 h (i.e. number of 'focal rattles', unadjusted for

376   false positive or false negative error rates; $N = 714$ days of recordings). We included average

377   familiarity, local density, age, grid, and sex as covariates in the model, as well as a random

378   intercept term for squirrel ID, and an observation-level random effect (OLRE) to account for

379   overdispersion in the model.

380   *Accelerometer data*

381   Using accelerometer data, we assessed the effect of neighbourhood familiarity on the

382   proportion of time spent in nest between 06:00 – 21:00 h using a Beta-Binomial model ($N = 873$

383   days). Our response variable was defined as above, using a two-column matrix that included the

384   number of nest observations and the number of observations of all other behaviours. We

385   included average familiarity, local density, grid, and sex as fixed effects in the model, and

386   included a random effect for squirrel ID and accelerometer collar.

387   *Exploratory post-hoc analysis*

388   Upon finding evidence of behavioural plasticity in the long-term data but not the cross-

389   sectional data (see results below), we conducted an exploratory post-hoc analysis in an attempt to

390   understand the inconsistencies in our results. While the longitudinal data provided multiple

391   measures of the same individuals across different social environments, allowing us to estimate

392   within-individual relationships, we could only estimate among-individual relationships in the

393   cross-sectional data. To assess whether our results might be driven by a within-individual effect,

394   thus limiting our ability to detect behavioural plasticity in the cross-sectional data, we re-fit our

395   rattling rate and nest use models from the long-term data using a within-subject mean centering

396   approach. Following the methodology of van de Pol & Wright (2009), we split our familiarity

397   term into an among-individual effect of familiarity (i.e. the mean familiarity score for an

398   individual across all observations) and a within-individual effect of familiarity (i.e. the deviation

399   in each familiarity observation for each individual from their mean score). We applied the same

400   approach to the 2015 and 2016 audio recorder data for which we had observations from

401   individuals across multiple social environments (Table 3).

402   We conducted analyses using R version 3.4.1 (R Core Team, 2017) and fitted all

403   GLMMs using the lme4 package (version 1.1-13; Bates, Maechler, Bolker, & Walker, 2015). For

13

404   all analyses, we fitted generalized additive models to confirm that there were no significant non-

405   linearities between our predictor and response variables. We checked for overdispersion by

406   comparing the ratio of the sum of the squared Pearson residuals to the residual degrees of

407   freedom in each model (Zuur et al., 2009) and assessing whether the sum of squared Pearson

408   residuals approximated a Chi-squared distribution with n-p degrees of freedom (Bolker et al.,

409   2009). As stated above, we accounted for overdispersion in Poisson models by including an

410   observation-level random effect (OLRE; Harrison, 2014). For models with binomial data, we

411   accounted for overdispersion using Beta-Binomial models, which have been demonstrated to

412   better cope with overdispersion in binomial data (Harrison, 2015). We fitted all Beta-Binomial

413   models using the package glmmADMB (version 0.8.3.3; Harrison, 2015; Skaug, Fournier,

414   Nielsen, Magnusson, & Bolker, 2018). We standardized all continuous fixed effects to a mean of

415   zero and unit variance. For the following results we present all means ± SE, unless otherwise

416   stated, and consider differences statistically significant at P < 0.05.

417

418   **Results**

419   Among the years in which we analyzed long-term focal data (1995-2004), variation in

420   average neighbourhood familiarity ranged from 0 (corresponding to when a squirrel first

421   established its territory) to 813 days (mean: 229 ± 9 days) and variation in local density ranged

422   from 0.57 to 5.84 squirrels/hectare (mean: 1.93 ± 0.05 squirrels/hectare). In our 2015 and 2016

423   data, there was a nearly equivalent amount of variation in average neighbourhood familiarity and

424   local density. Neighbourhood familiarity ranged from 0 to 855 days (mean: 296 ± 5 days) and

425   local density ranged from 1.13 to 6.03 (mean: 3.34 ± 0.03 squirrels/hectare). Below we discuss

426   the effects of familiarity and age on behavioural patterns. Results for other fixed effects in the

427   models can be found in Table 1.

428

429   *Longitudinal data*

430   *Territorial defence*

431   During the long-term focal observations, red squirrels emitted an average of 0.37 ± 0.04

432   rattles per 10-min observation session (range: 0-4), which is equivalent to one rattle every 27.06

433   minutes. (Rattling rates were much lower than in the cross-sectional data (see below) due to

434   differences in behavioural sampling protocol. In 2016, all occurrences of rattling were recorded

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435   as 'critical incidents', while in the long-term data rattles were only recorded if they fell on a 30-

436   second sampling interval. When critical incidents of rattling were removed from the 2016 data,

437   rattling rates dropped to one rattle every 40.55 minutes.) Red squirrels in the longitudinal dataset

438   adjusted their behaviour in response to increasing average neighbourhood familiarity by emitting

439   significantly fewer rattles (β = -0.29 ± 0.12, z = -2.48, P = 0.01; Figure 1). This corresponds to a

440   predicted three-fold decrease in rattling rates: in neighbourhoods with the lowest familiarity,

441   squirrels were predicted to rattle once every 24.76 minutes and in neighbourhoods with the

442   highest familiarity, only once every 79.75 minutes. The effect of age on rattling rates was

443   marginally non-significant (β = -0.20 ± 0.11, z = -1.85, P = 0.06; Table 1). On average, squirrels

444   spent 6.0 ± 0.7% of their time vigilant, but did not show changes in vigilance behaviour in

445   response to changing familiarity with neighbours (β = 0.02 ± 0.13, z = 0.15, P = 0.88; Table 1).

446   *Nest use*

447   Based on the long-term data, red squirrels spent, on average, 31.0 ± 2.0% of their time in

448   nest. Red squirrels responded to changing social conditions by increasing nest use in response to

449   increasing familiarity (β = 0.26 ± 0.12, z = 2.31, P = 0.02; Figure 1). This is equivalent to a

450   predicted 24% increase in nest use: squirrels in neighbourhoods with the lowest familiarity were

451   predicted to spend only 19% of their time in nest compared to 43% in neighbourhoods with the

452   highest familiarity.

453

454   *Cross-sectional data*

455   *Territorial defence*

456   During focal observations in 2016, red squirrels emitted 0.71 ± 0.03 rattles per 7-min

457   observation session (range: 0-6), which equates to approximately one rattle every 9.80 minutes.

458   Data from audio recorders in 2015 and 2016 provided very similar estimates of rattling rates. We

459   captured, on average, 33.96 ± 0.72 rattles per 6-hours of recording (range: 3-123), which, after

460   correcting for the error rates in our discriminant function analysis, is equivalent to one rattle

461   every 9.81 minutes. Based on both cross-sectional focal observations and audio recorder data,

462   neither average familiarity of the social neighbourhood (all |z| < 1.25, all P > 0.21) nor age (all |z|

463   < 1.87, all $P \geq$ 0.06) were significant predictors of rattling rate (Table 1). Focal observations

464   indicated that red squirrels spent 7.0% ± 0.5% of their time vigilant, on average, but did not

465   adjust vigilance behaviour in response to changing familiarity with neighbours (β = 0.05 ± 0.07,

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466    $z = 0.69$, $P = 0.49$; Table 1).

467   *Nest use*

468   Based on focal observations in 2016, red squirrels spent an average of 36.0% ± 1.0% of

469   their time in nest. Accelerometer data from 2016 provided similar estimates of average

470   proportion of time spent in nest during daylight hours (36.0% ± 0.4%). Both focal observations

471   and accelerometer data indicated that squirrels did not adjust their nest use in response to

472   familiarity with neighbours (all $|z| < 1.22$, all $P > 0.22$; Table 1).

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474   *Exploratory post-hoc analysis*

475   In our post-hoc analyses we found evidence to suggest that effects of familiarity on

476   rattling rates were primarily due to within-individual changes in behaviour rather than among-

477   individual differences. In the long-term data, increasing familiarity led to a significant decrease

478   in rattling rates within ($\beta = -0.21 \pm 0.08$, $z = -2.51$, $P = 0.01$), but not among individuals ($\beta = -$

479   0.18 ± 0.12, $z = -1.50$, $P = 0.13$; Table 3). There was a positive within and among-individual

480   effect of familiarity on nest use, but neither of these effects were significant (all $|z| < 1.69$, all $P >$

481   0.08; Table 3). Audio recorder data from 2015 and 2016 also a revealed a significant negative

482   within-individual effect ($\beta = -0.03 \pm 0.01$, $z = -2.55$, $P = 0.01$), but not among-individual effect

483   of familiarity on rattling rates ($\beta = 0.02 \pm 0.05$, $z = 0.34$, $P = 0.74$; Table 3). Results from the

484   audio data should be interpreted with caution as the inclusion of year in the model affected these

485   results (see Table S1).

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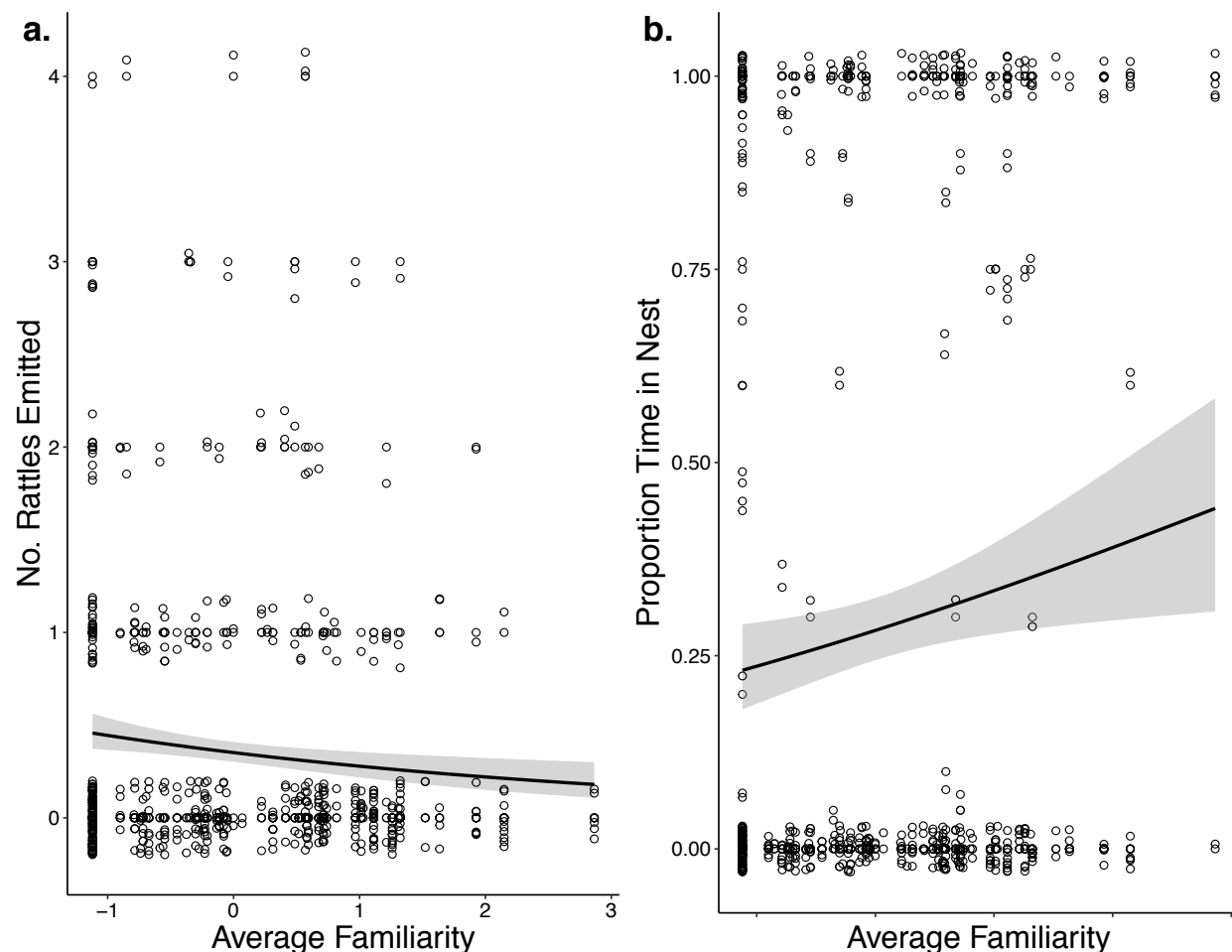
Figure 1. Red squirrels adjust a) rattling rate and b) proportion of time spent in nest in response to the average familiarity of their social neighbourhood (*N* = 487). Results are based on 10-min behavioural observations of squirrels between 1995-2004. Values on x-axis are standardized measures of average familiarity. Points indicate raw data with a small amount of jitter introduced to show overlapping points.

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506 **Table 1.** Fixed effects from all generalized linear mixed-effects (*GLMM*) and Beta-Binomial

507 (*BB*) models, showing effects of average neighbourhood familiarity, local density, and focal

508 squirrel's age on rattling rate, nest use and vigilance behaviour. Regression coefficients for

509 familiarity, age and density are standardized. Significant effects are indicated in bold.

510

Method of data collection	Years	*N*	Model	Fixed effect	Parameter +/- SE	*z*	*P*
Longitudinal focals	1995-2004	487					
			Rattle rate *(GLMM)*	**Familiarity**	**-0.29 ± 0.12**	**-2.48**	**0.01**
				Age	-0.20 ± 0.11	-1.85	0.06
				Density	-0.17 ± 0.13	-1.38	0.17
			Vigilance *(BB)*	Familiarity	0.02 ± 0.13	0.15	0.88
				Density	0.05 ± 0.26	0.19	0.85
			Nest Use *(BB)*	**Familiarity**	**0.26 ± 0.12**	**2.31**	**0.02**
				Density	**-0.37 ± 0.15**	**-2.53**	**0.01**
Cross-sectional focals	2016	1060					
			Rattle rate *(GLMM)*	Familiarity	0.07 ± 0.07	1.09	0.27
				Age	-0.02 ± 0.07	-0.25	0.80
				Density	**-0.12 ± 0.06**	**-2.01**	**0.04**
				Sex-M [+]	-0.13 ± 0.13	-1.02	0.31
				Grid-KL [*]	-0.15 ± 0.13	-1.11	0.27
				Grid-SU [*]	**-0.52 ± 0.17**	**-3.09**	**0.002**
				Obs- JR [†]	0.14 ± 0.25	0.58	0.56
				Obs- MT [†]	**-0.34 ± 0.09**	**-3.87**	**<0.001**
				Obs- YS [†]	**-0.47 ± 0.10**	**-4.92**	**<0.001**
			Vigilance *(BB)*	Familiarity	0.05 ± 0.07	0.69	0.49
				Density	-0.01 ± 0.09	-0.07	0.95
				Sex-M [+]	0.26 ± 0.18	1.48	0.14
				Grid-KL [*]	**-0.42 ± 0.17**	**-2.48**	**0.01**
				Grid-SU [*]	-0.36 ± 0.22	-1.63	0.10
				Obs- JR [†]	0.66 ± 0.38	1.73	0.08
				Obs- MT [†]	**-0.86 ± 0.16**	**-5.44**	**<0.001**
				Obs- YS [†]	**0.44 ± 0.14**	**3.24**	**0.001**
			Nest Use *(BB)*	Familiarity	-0.11 ± 0.09	-1.21	0.23
				Density	0.08 ± 0.10	0.79	0.43
				Sex-M [+]	0.11 ± 0.21	0.52	0.60
				Grid-KL [*]	0.15 ± 0.22	0.70	0.48
				Grid-SU [*]	0.50 ± 0.27	1.85	0.06
				Obs- JR [†]	-0.59 ± 0.57	-1.02	0.31
				Obs- MT [†]	**0.41 ± 0.16**	**2.62**	**0.009**
				Obs- YS [†]	**0.37 ± 0.16**	**2.24**	**0.02**
Audio recordings	2015-2016	714					
			Rattle rate *(GLMM)*	Familiarity	-0.05 ± 0.04	-1.24	0.21
				Age	-0.09 ± 0.05	-1.86	0.06

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					Density	0.003 ± 0.04	0.08	0.94
					Sex-M [+]	0.01 ± 0.10	0.13	0.90
					Grid-KL [*]	**-0.28 ± 0.09**	**-3.13**	**0.001**
					Grid-SU [*]	**-0.73 ± 0.12**	**-6.10**	**<0.001**
Accelerometers	2016	873						
			Nest Use *(BB)*	Familiarity	-0.0005 ± 0.04	-0.01	0.99	
				Density	-0.07 ± 0.04	-1.51	0.13	
				Sex-M [+]	0.04 ± 0.08	0.53	0.60	
				Grid-KL [*]	0.13 ± 0.09	1.36	0.17	
				Grid-SU [*]	0.01 ± 0.11	0.11	0.91	

511   + Female taken as the reference

512   * AG (food supplemented grid) taken as the reference

513   † Observer ES taken as the reference

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530 **Table 2.** Random effects from all generalized linear mixed-effects (*GLMM*) and Beta-Binomial

531 (*BB*) models. Significance assessed using a log-likelihood ratio test (LRT) with one degree of

532 freedom to compare models with and without the listed random effect. Significant effects are

533 indicated in bold.

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Method of data collection	Years	Model	Random effect	Variance	χ^2	df	*P*
Longitudinal focals	1995-2004						
		Rattle rate *(GLMM)*	Squirrel ID	0.09	2.19	1	0.14
			Year	<0.01	<0.01	1	>0.999
			Observer	**0.48**	**18.55**	**1**	**<0.001**
		Vigilance *(BB)*	Squirrel ID	0.08	0.56	1	0.45
			Year	**1.11**	**5.03**	**1**	**0.02**
			Observer	**0.62**	**10.53**	**1**	**0.001**
		Nest Use *(BB)*	Squirrel ID	<0.01	<0.01	1	>0.999
			Year	0.10	1.20	1	0.27
			Observer	0.10	1.80	1	0.18
Cross-sectional focals	2016						
		Rattle rate *(GLMM)*	**Squirrel ID**	**0.14**	**37.53**	**1**	**<0.001**
		Vigilance *(BB)*	**Squirrel ID**	**0.14**	**8.16**	**1**	**0.004**
		Nest Use *(BB)*	**Squirrel ID**	**0.32**	**19.20**	**1**	**<0.001**
Audio recordings	2015-2016						
		Rattle rate *(GLMM)*	**Squirrel ID**	**0.18**	**422.38**	**1**	**<0.001**
			OLRE	**0.06**	**558.11**	**1**	**<0.001**
Accelerometers	2016						
		Nest Use *(BB)*	**Squirrel ID**	**0.10**	**157.58**	**1**	**<0.001**
			AXY No.	<0.01	<0.01	1	>0.999

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541 **Table 3.** Fixed effects from exploratory post-hoc models including a within-individual

542 (Familiarity$_W$) and among-individual (Familiarity$_A$) effect of familiarity. Regression coefficients

543 for familiarity, age and density are standardized. Significant effects are indicated in bold.

Method of data collection	Years	N	Model	Fixed effect	Parameter +/- SE	z	P
Longitudinal focals	1995-2004	487					
			Rattle rate *(GLMM)*	**Familiarity$_W$**	**-0.21 ± 0.08**	**-2.51**	**0.01**
				Familiarity$_A$	-0.18 ± 0.12	-1.50	0.13
				Age	**-0.22 ± 0.11**	**-2.02**	**0.04**
				Density	-0.18 ± 0.13	-1.42	0.15
			Nest Use *(BB)*	Familiarity$_W$	0.17 ± 0.10	1.68	0.09
				Familiarity$_A$	0.19 ± 0.13	1.53	0.13
				Density	**-0.37 ± 0.15**	**-2.50**	**0.01**
Audio recordings	2015-2016	714					
			Rattle rate *(GLMM)*	**Familiarity$_W$**	**-0.03 ± 0.01**	**-2.55**	**0.01**
				Familiarity$_A$	0.02 ± 0.05	0.34	0.74
				Age	**-0.10 ± 0.05**	**-2.09**	**0.04**
				Density	-0.02 ± 0.04	-0.56	0.58
				Sex-M [+]	0.01 ± 0.10	0.12	0.90
				Grid-KL [*]	**-0.28 ± 0.09**	**-3.16**	**0.002**
				Grid-SU [*]	**-0.81 ± 0.12**	**-6.58**	**<0.001**

544 + Female taken as the reference

545 * AG (food supplemented grid) taken as the reference

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Discussion

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557   For territorial species, the ability to be responsive to changes in the social environment

558   may convey a fitness advantage by allowing individuals to reduce time and energy investment in

559   costly behaviours (Höbel, 2015; Krobath, Römer, & Hartbauer, 2017; Ydenberg, Giraldeau, &

560   Falls, 1988). In this study, we used multiple types of behavioural data, as well as a longitudinal

561   and cross-sectional dataset, to test a single overarching hypothesis: that red squirrels show

562   behavioural plasticity in response to the familiarity of their social neighbourhood. Our results

563   provide evidence that an 'asocial' species, the North American red squirrel, can respond to

564   changes in the composition of its social environment, and that red squirrels do so under natural

565   conditions and in a manner that is consistent with our expectations for adaptive behavioural

566   change in this species.

567   Previous work in this study system has demonstrated that red squirrels face reduced

568   intrusion risk in social neighbourhoods with high average familiarity (Siracusa, Boutin, et al.,

569   2017a). As such, we predicted that red squirrels would show appropriate social plasticity by

570   reducing territorial defence behaviours and increasing time and energy spent on self-maintenance

571   behaviours when familiar with neighbouring conspecifics. Results from behavioural observations

572   across eight years provided support for these predictions, indicating that red squirrels

573   demonstrated social plasticity by reducing rattling rates and increasing the proportion of time

574   spent in nest in social neighbourhoods with high average familiarity (Figure 1). Such changes in

575   behaviour not only minimize the time spent on territory defence but might also reduce associated

576   costs of territoriality. Territorial vocalizations may attract the attention of predators (Abbey-Lee,

577   Kaiser, Mouchet, & Dingemanse, 2016) and rattles are loud, broadband signals which should be

578   easy to localize (Marler 1955). By reducing rattling rates under less risky social conditions,

579   squirrels may also benefit from reduced predation risk.

580   We did not, however, find effects of neighbourhood familiarity on vigilance behaviour.

581   This could be due to vigilance for conspecifics being easily confounded with vigilance for

582   predators. In contrast, Dantzer et al. (2012) found significant effects of local density on vigilance

583   using behavioural data collected over a similar time frame, indicating that conspecific rather than

584   heterospecific effects on vigilance are detectable in this system. While we included local density

585   as a covariate in all of our models to account for the potential effects of density on behaviour

586   (Dantzer et al., 2012), our goal was not to directly estimate effects of density, and our results

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587   therefore are not a clean representation of density effects. In several cases density was correlated

588   with other variables in the model, such as grid, leading to substantial changes in the parameter

589   estimates for density. As a result, the effects of density on behaviour that we have reported here

590   cannot be compared directly to previous studies of these effects in this population (e.g. Dantzer

591   et al., 2012; Shonfield, Taylor, Boutin, Humphries, & McAdam, 2012) and we do not discuss the

592   effects of density further.

593   Results from the cross-sectional data in 2015 and 2016 did not corroborate our long-term

594   results showing behavioural responses to familiarity. Findings from the behavioural observations,

595   audio recorders, and accelerometers indicated that when using among-individual relationships to

596   estimate the effects of the social environment on behaviour, there was no effect of familiarity on

597   territorial behaviours (rattling rates, vigilance) or self-maintenance (nest use; Table 1). In light of

598   this inconsistency with the longitudinal data, we conducted an exploratory post-hoc analysis to

599   assess whether using longitudinal data (where we can estimate within-individual changes in

600   behaviour) rather than cross-sectional data (where the analysis is largely among individuals)

601   might account for our different findings. Since behavioural plasticity is functionally a within-

602   individual phenomenon, using among-individual differences in behaviour to estimate these

603   effects relies on the assumption that the among-individual relationship is an accurate

604   representation of the within-individual relationship. Here we used a within-subject centering

605   approach (van de Pol & Wright, 2009) and found that the within and among-individual effects

606   were not equivalent. In the long-term data, we found that individuals adjusted rattling rates in

607   response to changes within their own social environment (i.e. a significant within-individual

608   effect) but did not observe significant differences in rattling rates when comparing among

609   individuals (Table 3). Similarly, for the audio recorder data (the only cross-sectional data for

610   which we had observations of individuals across multiple social environments) we found

611   evidence of a significant within-individual, but not among-individual, effect (Table 3). Thus,

612   while we clearly see evidence of plasticity when considering changes in individual behaviour

613   across different social environments, in this study system it appears that we cannot estimate these

614   effects by comparing behaviour among individuals.

615   One potential explanation for this discrepancy is that the among-individual effect is

616   masked by individual variation in plasticity, whereby substantially different individual 'slopes'

617   result in a 'mean slope' of zero (i.e. the absence of a significant population-level response to the

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618   environment; Nussey et al., 2007). We were unable to test this hypothesis as we lacked the

619   statistical power to include a random slope term in our models (Martin, Nussey, Wilson, & Réale,

620   2011). Furthermore, even if all individuals demonstrate negative reaction norms (i.e. reduced

621   rattling rate in response to increasing familiarity), there are still several reasons we might fail to

622   detect differences among individuals. First, it seems unlikely that squirrels can assess their

623   absolute familiarity, meaning that behavioural adjustments are dependent on the relative social

624   environments individuals experience rather than absolute changes in familiarity. Additionally,

625   variation in individual mean ratting rates (i.e. random intercepts) due to differences in sex, age,

626   personality, stress, among other possibilities, might mask an among-individual effect. These

627   factors, combined with variation in the range of social environments sampled for a given

628   individual, mean that, even when all individuals show negative reaction norms, it is possible to

629   measure a lack of (Figure 2b), or even a positive among-individual effect (Figure 2c). Additional

630   individual data, spanning a range of social environments, is necessary to better understand the

631   patterns leading to within versus among-individual effects in this system.

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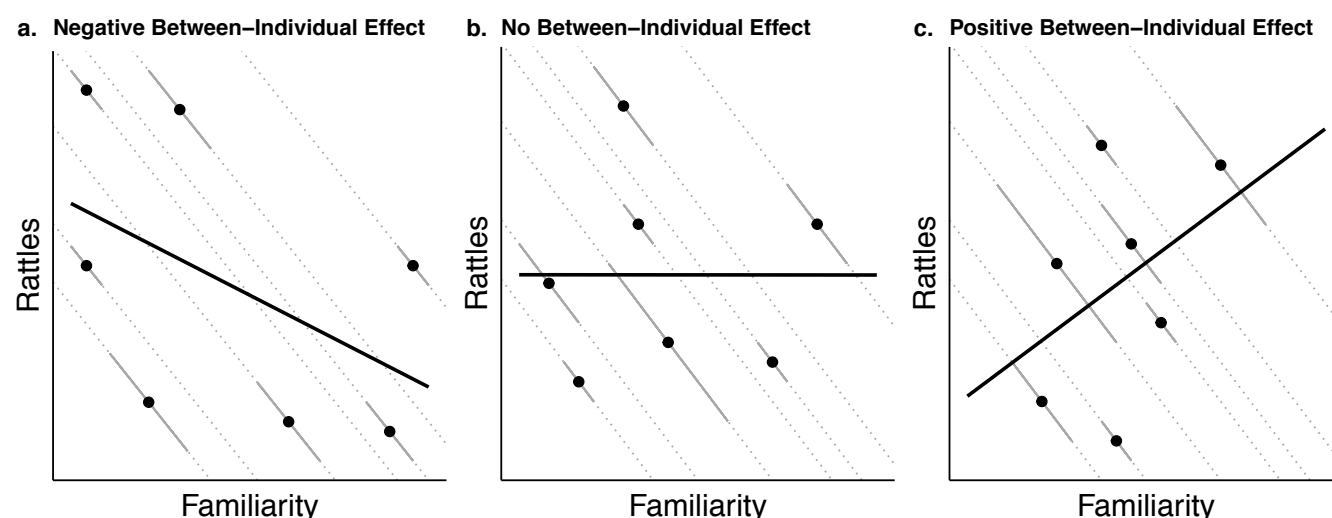
633   **Figure 2.** Three different scenarios for how variation in mean rattling rate (random intercepts) in

634   combination with variation in data sampling structure might change our ability to detect among-

635   individual effects when individuals have the same slope. We schematically depict the within-

636   individual slopes (solid grey lines) of seven subjects ($j = 1$ to $j = 7$). The solid grey lines indicate

637   the range over which each individual was sampled. Dotted lines provide an extension of these

638   slopes to the edge of the figure. The among-subject slope (solid black line) is based on the

639   association between $\bar{x}_j$ and $\bar{y}_j$ as denoted by the filled black circles.

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640   Although we have provided an explanation for the differences in our long-term and cross-

641 sectional findings, there are a couple reasons why it is important to interpret our results with

642 caution. First, there is potential for changes in rattling rates to be driven by effects of age rather

643 than familiarity if the strength of territory defence declines with physical deterioration. We have

644 done our best to account for this possibility in our analyses, but given that these variables are

645 strongly correlated an experimental approach would prove useful in disentangling these effects

646 as they are difficult to tease apart statistically. Second, it is worth addressing our use of multiple

647 univariate analyses to test a single overarching hypothesis. Previous research in this study system

648 has detected effects of the social environment on vigilance and nest use using a multivariate

649 analysis (Dantzer et al., 2012), allowing us to make specific predictions about how squirrels

650 should adjust patterns of nest use and vigilance in response to neighbourhood familiarity. Given

651 this, we felt that analyzing the effects of familiarity on each of these behaviours individually

652 provided a more elegant test of our hypothesis. However, it is important to be aware that our use

653 of univariate analyses increases our chances of committing a Type I error by attributing variance

654 as unique to a single response variable when it may in fact be shared (Huberty & Morris, 1989).

655   Despite these limitations, we believe that the results from our study, in particular the data

656 for which we can estimate within-individual changes in behaviour, provide evidence that red

657 squirrels are socially plastic. Furthermore, although we have not directly tested the fitness

658 consequences of social plasticity, red squirrels reduced rattling rates, thereby spending less time

659 on territory defence and potentially minimizing risk of detection by predators, under social

660 conditions where intrusion risk was low (Siracusa, Boutin, et al., 2017a). This suggests that

661 'asocial' species can not only be socially responsive but also socially competent in their

662 behaviour (Taborsky & Oliveira, 2013; 2012). Familiarity with conspecifics has long been

663 assumed to be beneficial by allowing individuals to minimize energy expended on territory

664 contests and increase time devoted to reproduction and growth (Getty, 1987; Temeles, 1994;

665 Ydenberg et al., 1988). Evidence for reduced aggression toward familiar conspecifics is

666 taxonomically widespread (reviewed in Temeles, 1994). However, these studies have typically

667 been focused on documenting behavioural changes on short timescales through exposure to an

668 experimental stimulus. Our study is one of few to demonstrate that natural variation in

669 neighbourhood familiarity has direct consequences for behavioural time budgets by allowing

670 individuals with familiar neighbours to reduce territory defence and increase time spent in nest.

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671   A handful of previous studies have demonstrated similar patterns in wild populations under

672   natural social conditions. Willow ptarmigan (*Lagopus lagopus*) males were found to spend

673   significantly more time engaged in territorial border disputes when they had more new

674   neighbours (Eason & Hannon, 1994). In Seychelles warblers (*Acrocephalus sechellensis*), living

675   near familiar individuals provided important benefits by reducing immediate energetic costs

676   through fewer physical fights (Bebbington et al., 2017).

677   Additionally, recent research has increasingly noted the importance of group composition

678   in shaping individual behaviour (Farine, Montiglio, & Spiegel, 2015). For example, nutmeg

679   mannikins (*Lonchura punctulata*) have been shown to forego consistent individual differences in

680   scrounger-forager tactics when flock composition changes, and to adjust their social strategy

681   according to frequency-dependent pay-offs (Morand-Ferron, Wu, & Giraldeau, 2011). Water

682   striders (*Aquarius remigis*) also show plasticity in aggression and activity in response to the

683   presence of hyperaggressive individuals in the group (Sih et al., 2014) or changes in male-male

684   competition (Montiglio et al., 2017). Although territorial species do not act in clearly defined,

685   discrete units, we have demonstrated that red squirrels show similar social plasticity in response

686   to the composition of neighbouring territory holders at the scale of the acoustic social

687   environment (i.e. 130 m radius). Our results emphasize that the composition of neighbouring

688   conspecifics, in addition to quantity of individuals in the social environment (Dantzer et al.,

689   2012), can shape the behaviour of territorial species.

690

691   *Conclusion*

692   The advantage of territoriality is contingent on the benefits of resource acquisition

693   outweighing the costs of defending those resources from competitors (Brown, 1964; Schoener,

694   1987). Although the dear-enemy effect has been a well-recognized phenomenon in territorial

695   species for several decades (Temeles, 1994), the relative importance of social interactions for

696   maintaining this cost-benefit ratio under natural conditions has rarely been explored. Here we

697   show that red squirrels adjust their behaviour in response to the familiarity of their social

698   environment and that squirrels living in unfamiliar social neighbourhoods pay a cost in time by

699   increasing rattling rates three-fold and reducing nest use by approximately 25% in order maintain

700   their territory under conditions of high intrusion risk. Importantly, our results suggest that

701   behavioural plasticity in this species cannot be estimated by comparing differences in behaviour

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702   among-individuals, emphasizing the need to have observations from the same individuals across

703   multiple social environments in order to detect these behavioural patterns.

704   Taken altogether, these results provide evidence that territorial species have the capacity

705   to assess and respond to nuanced changes in their social environment, despite not typically being

706   considered to engage in important social interactions. Social relationships may therefore be more

707   important than previously appreciated for apparently 'asocial' species. Several studies have

708   demonstrated that familiarity with territory neighbours can have fitness benefits, including

709   increased growth rate and survival (Höjesjö, Johnsson, Petersson, & Järvi, 1998; Seppä, Laurila,

710   Peuhkuri, Piironen, & Lower, 2001), reduced telomere attrition (Bebbington et al., 2017) and

711   increased reproductive success (Beletsky & Orians, 1989; Grabowska-Zhang et al., 2012). Given

712   that these long-term social relationships have been demonstrated to affect both intrusion risk

713   (Siracusa, Boutin, et al., 2017a) and behavioural time budgets (this study) in red squirrels, it

714   seems likely that familiarity with territory neighbours could also have important fitness

715   consequences for this species, but this has yet to be explored.

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