

Red squirrels mitigate costs of territory defence through social plasticity

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Abstract

For territorial species, the ability to be behaviourally plastic in response to changes in their social environment may be beneficial by allowing individuals to mitigate conflict with conspecifics and reduce the costs of territoriality. Here we investigated whether North American red squirrels (*Tamiasciurus hudsonicus*) were able to minimize costs of territory defence by adjusting behaviour in response to the familiarity of neighbouring conspecifics. Since red squirrels living in familiar neighbourhoods face reduced intrusion risk, we predicted that increasing familiarity among territorial neighbours would allow squirrels to spend less time on territorial defence and more time in the nest. Long-term behavioural data (1995-2004) collected from the same squirrels across several different social environments indicated that red squirrels reduced rates of territorial vocalizations and increased nest use in response to increasing familiarity with neighbours. In contrast, cross-sectional data (2015-2016), which provided observations from 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

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

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

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) 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,

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

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

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 \pm 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

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 ($\beta = -0.29 \pm 0.12$, $z = -2.48$, $P = 0.01$; 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 ($\beta = -0.20 \pm 0.11$, $z = -1.85$, $P = 0.06$; Table 1). On average, squirrels
444 spent $6.0 \pm 0.7\%$ of their time vigilant, but did not show changes in vigilance behaviour in
445 response to changing familiarity with neighbours ($\beta = 0.02 \pm 0.13$, $z = 0.15$, $P = 0.88$; Table 1).

446 *Nest use*

447 Based on the long-term data, red squirrels spent, on average, $31.0 \pm 2.0\%$ of their time in
448 nest. Red squirrels responded to changing social conditions by increasing nest use in response to
449 increasing familiarity ($\beta = 0.26 \pm 0.12$, $z = 2.31$, $P = 0.02$; 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 $7.0\% \pm 0.5\%$ of their time vigilant, on average, but did not
465 adjust vigilance behaviour in response to changing familiarity with neighbours ($\beta = 0.05 \pm 0.07$,

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 $36.0\% \pm 1.0\%$ 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 ($36.0\% \pm 0.4\%$). 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).

473

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 $0.18 \pm 0.12, z = -1.50, P = 0.13$; 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 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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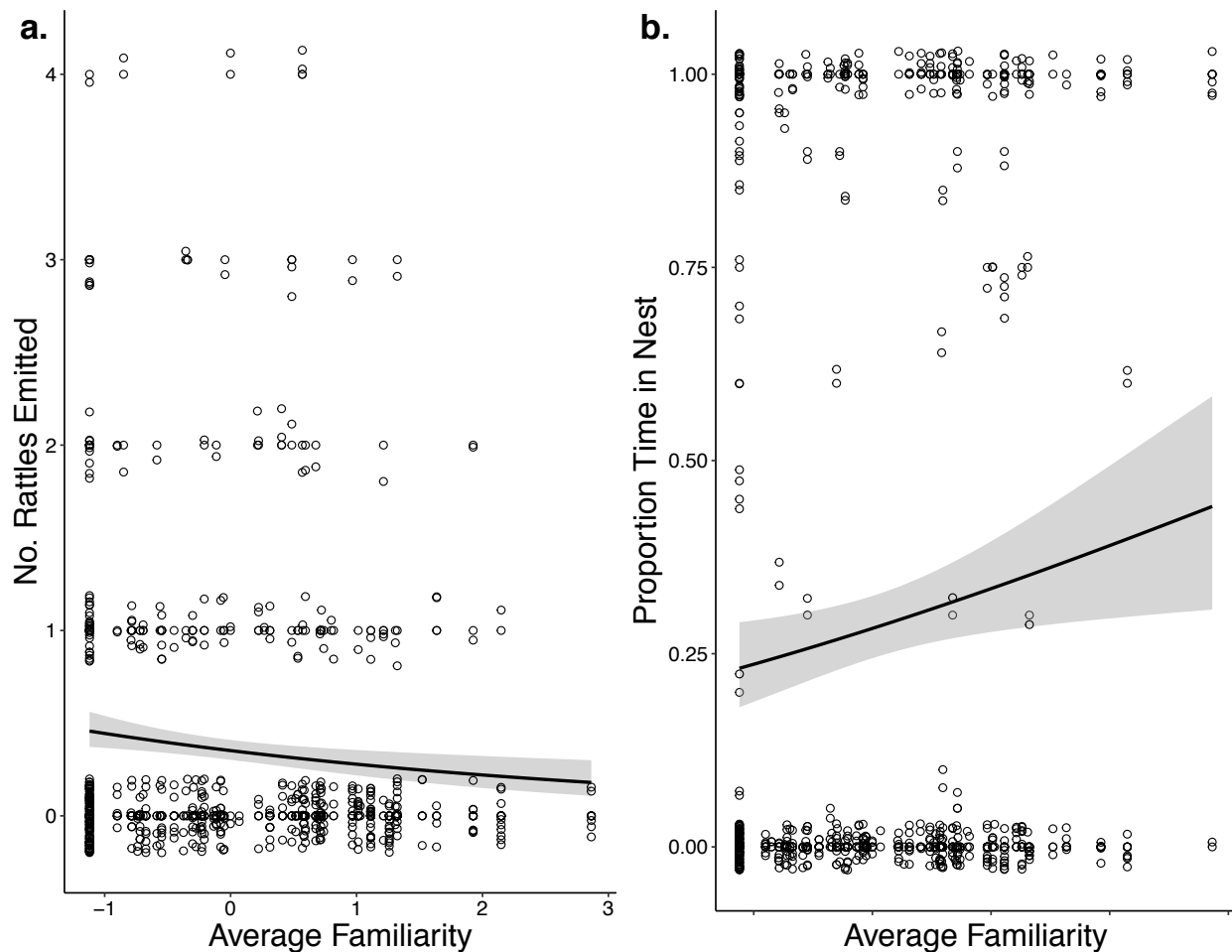
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495 **Figure 1.** Red squirrels adjust a) rattling rate and b) proportion of time spent in nest in response
496 to the average familiarity of their social neighbourhood ($N = 487$). Results are based on 10-min
497 behavioural observations of squirrels between 1995-2004. Values on x-axis are standardized
498 measures of average familiarity. Points indicate raw data with a small amount of jitter introduced
499 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	<i>N</i>	Model	Fixed effect	Parameter +/- SE	<i>z</i>	<i>P</i>
Longitudinal focals	1995-2004	487					
			Rattle rate (<i>GLMM</i>)	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 (<i>BB</i>)	Familiarity	0.02 ± 0.13	0.15	0.88
				Density	0.05 ± 0.26	0.19	0.85
			Nest Use (<i>BB</i>)	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 (<i>GLMM</i>)	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 (<i>BB</i>)	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 (<i>BB</i>)	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 (<i>GLMM</i>)	Familiarity	-0.05 ± 0.04	-1.24	0.21
				Age	-0.09 ± 0.05	-1.86	0.06

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 (<i>BB</i>)	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.

534

Method of data collection	Years	Model	Random effect	Variance	χ^2	df	<i>P</i>
Longitudinal focals	1995-2004	Rattle rate (<i>GLMM</i>)	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 (<i>BB</i>)	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 (<i>BB</i>)	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 (<i>GLMM</i>)	Squirrel ID	0.14	37.53	1	<0.001
			Vigilance (<i>BB</i>)	Squirrel ID	0.14	8.16	1
		Nest Use (<i>BB</i>)	Squirrel ID	0.32	19.20	1	<0.001
			Audio recordings	2015-2016	Rattle rate (<i>GLMM</i>)	Squirrel ID	0.18
			OLRE	0.06	558.11	1	<0.001
Accelerometers	2016	Nest Use (<i>BB</i>)	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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556 **Discussion**

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.

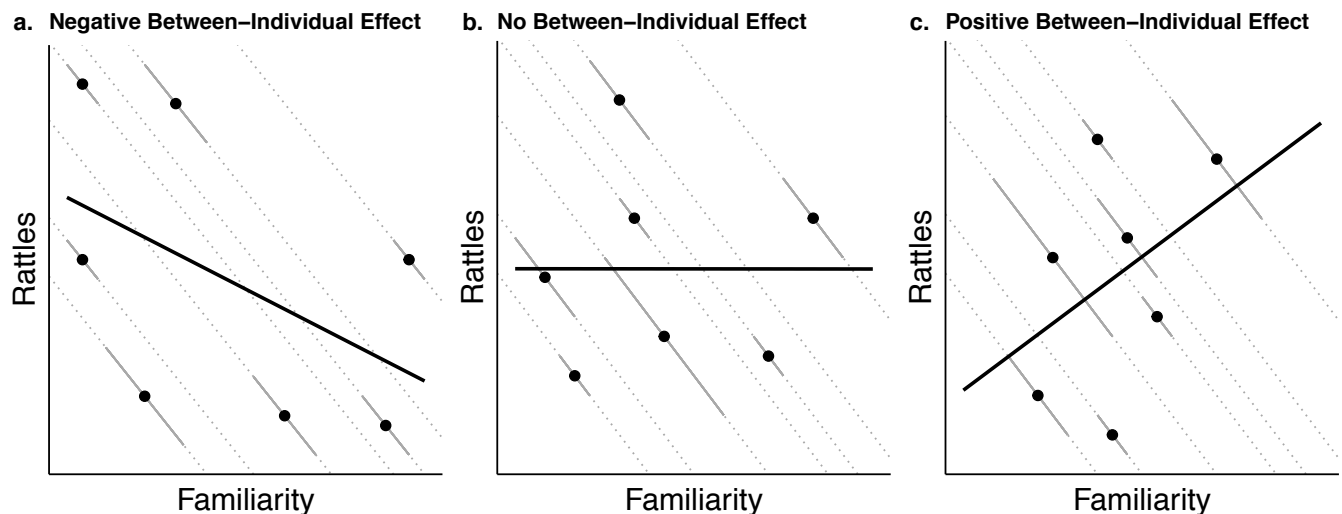
580 We did not, however, find effects of neighbourhood familiarity on vigilance behaviour.
581 This could be due to vigilance for conspecifics being easily confounded with vigilance for
582 predators. In contrast, Dantzer et al. (2012) found significant effects of local density on vigilance
583 using 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

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

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 rattling 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.



632

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.

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.

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

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.

716

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731 **References**

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