1   **Individual variation in the dear enemy phenomenon via territorial vocalizations in red**

2   **squirrels**

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14   **Abstract**

15   Territoriality arises when the benefits of resources exceed the costs of defending them. The dear

16   enemy phenomenon, where familiar territorial neighbours refrain from intruding on one another

17   and mutually reduce their defensive efforts, allows for reduction of these costs but requires

18   discrimination between conspecifics. We hypothesized that territorial vocalizations in red

19   squirrels (*Tamiasciurus hudsonicus*) are used for this discrimination. We performed a speaker

20   replacement experiment where red squirrels (n = 41) were temporarily removed from their

21   territories and replaced with a speaker broadcasting their own call, an unfamiliar call, or silence.

22   Contrary to our prediction, there were no differences in overall intrusion risk among our three

23   playbacks, but the identity of intruders did vary. Existing variation in familiarity within territorial

24   neighbourhoods should be considered, rather than the binary classification of familiar or

25   stranger, when studying dear enemy effects. We also discuss the variable importance of silence

26   in acoustic territorial populations.

27   **Keywords**

28   territorial vocalizations, dear enemy, speaker replacement, red squirrel, individual recognition,

29   familiarity.

30   **Introduction**

31   In populations with intraspecific competition for resources, territoriality as a social

32   structure can arise when individuals benefit from exclusive access to a resource. Resource

33   defense can constitute a substantial portion of a territory owner's time and energy budget

34   (Puckett & Dill, 1985; Heinemann, 1992), but territoriality is only adaptive when the fitness

35   benefit from the defended resource exceeds the costs of defending said resource from

36   conspecifics (Carpenter & MacMillen, 1976). Furthermore, the net benefit to territory owners

37   can be maximized by reducing defensive costs where possible (Rosell, Gundersen, & Le

38   Galliard, 2008).

39   Plasticity in territorial behaviour allows for reduction of unnecessary defensive costs.

40   Territory owners across a broad range of species discriminate between conspecifics based on

41   familiarity, known as the dear enemy phenomenon (Fisher, 1954). The dear enemy phenomenon

42   refers to the tendency of territory owners to respond more antagonistically to unfamiliar

43   individuals than familiar territorial neighbours. There are two main predictions of the dear enemy

44   phenomenon: familiar neighbours refrain from intruding on one another, and also reduce their

45   territory defense (Temeles, 1994). This phenomenon likely arises between neighbours as a form

46   of conditional reciprocity, whereby territory owners form 'agreements' to tolerate one another

47   and both benefit through a decreased defensive effort (Axelrod & Hamilton, 1981). Individuals

48   that break this relationship and intrude on familiar neighbours incur a cost through increased

49   intrusions on their own territory (Akçay et al., 2009). The dear enemy phenomenon has been

50   demonstrated across taxa, in birds (eg. Wei et al. 2011), mammals (Rosell & Bjørkøyli, 2002),

51   amphibians (Jaeger, 1981), fish (Leiser & Itzkowitz, 1999), reptiles (Qualls & Jaeger, 1991), and

52   crustaceans (Booksmythe, Jennions, & Backwell, 2010).

53   Most studies of the dear enemy phenomenon test the central predictions by exposing a

54   territory owner to a cue from a neighbouring individual or a stranger and comparing the intensity

55   of the owner's responses. These experiments are often simple to perform and the pairwise

56   comparison can demonstrate discrimination by the territory owner, but are not directly testing the

57   theory in a territorial context. Such studies also depend on the researchers knowing which

58   identity cue is relevant for their species.

59   *Individual recognition*

60   The dear enemy phenomenon depends on the ability of individuals to recognize the

61   familiarity of conspecifics in some way. For this to occur, there must be a detectable signal of

62   familiarity between individuals. Identity is typically communicated via the dominant sensory

63   modality for that species, so that birds tend to use songs (Briefer et al., 2008) or calls (Hardouin,

64   Tabel, & Bretagnolle, 2006) but not olfactory cues to recognize conspecifics. Most mammals use

65   scent cues, particularly those where vision or hearing are reduced (i.e. subterranean rodents;

66   Zenuto, 2010), but there is evidence of individually unique vocalizations in mammalian species

67   where acoustic communication is important (Koren & Geffen, 2011). Most avian studies of the

68   dear enemy phenomenon use vocalizations as the presumed cue of individual identity (e.g.

69   Briefer, Rybak, & Aubin, 2008), while most studies of territorial mammals use scent cues (e.g.

70   Müller & Manser, 2007). In experimental tests of the dear enemy phenomenon, the choice of cue

71   is based on the researcher's hypothesis of how individuals of that species recognize one another.

72   Positive results provide evidence that individuals can discriminate one another, but a finding of

73   no difference between familiar and unfamiliar cues does not necessarily mean the population

74   does not demonstrate the dear enemy phenomenon. Rather, territory owners might be using

75   different information than that provided during the experiment to adjust their behaviour. Our

76   understanding of the dear enemy phenomenon could be improved by testing multiple or atypical

77   modes of recognition within species to determine whether previous findings are biologically

78   meaningful rather than artifacts of experimental design.

79   *Red squirrels*

80   North American red squirrels (*Tamiasciurus hudsonicus*) are solitary rodents that defend

81   exclusive territories. In the northern boreal forest, these territories are centred on hoards of their

82   primary food source, white spruce (*Picea glauca*) cones, known as middens (Boutin &

83   Schweiger, 1988). A territory with cached resources is required for overwinter survival (Larsen

84   & Boutin, 1995). Juveniles generally acquire a territory before their first winter and remain on

85   the same territory throughout their life. Adult dispersal to new territories is rare, but breeding

86   females may move to another territory and bequeath their own midden to one of their juveniles

87   (Price et al., 1986; Berteaux & Boutin, 2000). Red squirrels primarily defend their territories

88   through vocalizations known as rattles, and direct physical encounters are rare (Smith, 1968;

89   Dantzer et al., 2012). The bioacoustic measures of these calls, such as fundamental frequency

90   and pulse rate, are consistent within individuals (Wilson et al., 2015). Rattles thus provide social

91   information that could be used for individual recognition and discrimination, as red squirrel

92   rattles are individually distinctive (Digweed, Rendall, & Imbeau, 2012; Wilson et al., 2015).

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93   Red squirrel territorial defense is plastic in response to local density (Dantzer et al. 2012),

94   and to the identity of the individuals in their local neighbourhood (Siracusa et al. in review). The

95   dear enemy phenomenon is well demonstrated for this species: squirrels that have been territorial

96   neighbours for longer periods of time are less likely to intrude on each others' territories

97   (Siracusa, Boutin, et al., 2017), and red squirrels increase their territorial defence behaviour

98   toward unfamiliar individuals (Siracusa et al., in review). Increased territorial defense can be

99   costly in this species in both time and energy (Stuart-Smith & Boutin, 1994), so squirrels in

100   relatively familiar neighbourhoods should not expend maximal effort in defending their

101   territories.

102   The territorial function of rattles has been empirically demonstrated with a speaker

103   replacement experiment where broadcasting the owner's rattle reduced the risk of intrusion

104   compared to silence (Siracusa, Morandini, et al., 2017). Behavioural observations of squirrels

105   found that the scale at which the social environment best predicts squirrel behaviour is 150 m

106   around the focal territory (Dantzer et al. 2012), similar to the reported maximum audible distance

107   of a rattle, 130 m (Smith 1978). Red squirrels are sensitive to the acoustic environment around

108   their territory, but rattles may convey more information than just the presence or number of

109   neighbouring conspecifics.

110   Although the dear enemy phenomenon has been clearly shown for this species, the cue

111   used to recognize the familiarity of conspecifics and adjust behaviour accordingly is not known.

112   Tests of the dear enemy phenomenon in mammals commonly use scent cues (Rosell &

113   Bjørkøyli, 2002; Raynaud & Dobson, 2011; Monclús, Saavedra, & de Miguel, 2014), and red

114   squirrels are able to discriminate conspecifics by scent in captivity (Vaché, Ferron, & Gouat,

115   2001).This mode of discrimination would be useful for nearest neighbours, but would require

116   squirrels to venture off territory to obtain social information from distant neighbours. Acoustic

117   signals would allow for red squirrel territorial interactions to occur over long distances while

118   individuals remained on their own territories. Given the importance of rattles in territoriality

119   (Dantzer et al. 2012) and the individual specificity of these calls (Wilson et al. 2015), an acoustic

120   mode of discriminating familiarity in red squirrels seems probable. Directed playback studies

121   have found that red squirrels are more likely to respond to playback of unfamiliar rattles than

122   those of neighbours (Price, Boutin, & Ydenberg, 1990), and less likely to respond to rattles of

123   close kin than of unrelated individuals (Shonfield et al. 2017), but these results have been

124   variable (Wilson et al. 2015) and statistical power is limited by the binomial response. We used a

125   speaker replacement experiment in an attempt to investigate the variation in these findings.

126   *Hypotheses and predictions*

127   Our objective was to investigate whether red squirrels recognize familiarity via

128   vocalizations, facilitating the dear enemy phenomenon in this species. We hypothesized that

129   discrimination between the vocalizations of familiar and unfamiliar conspecifics underlies the

130   dear enemy phenomenon in red squirrels. We tested this hypothesis using a speaker replacement

131   experiment, temporarily removing territory owners and replacing them with a speaker

132   broadcasting their own rattle, the rattle of an unfamiliar individual, or silence. If vocalizations

133   are the cue used to discriminate between conspecifics, then broadcasting an unfamiliar rattle

134   from a given territory should be perceived as a new, unfamiliar owner by neighbouring squirrels.

135   First, we predicted that there would be a higher risk of intrusion by neighbours when

136   broadcasting an unfamiliar rattle compared to the owner's rattle; because squirrels refrain from

137   intruding on familiar individuals, this unfamiliar rattle should be less effective at deterring

138   neighbours from intruding than the territory owner's rattle. Silence should also lead to a higher

139   risk of intrusion by neighbours than the owner's rattle, as shown by Siracusa, Morandini, et al.

140   (2017).

141   Second, as per the dear enemy phenomenon, simulating an unfamiliar territory owner

142   should lead to higher defensive effort by neighbouring squirrels. We predicted that rattling rates

143   in the surrounding acoustic neighbourhood would be higher when broadcasting an unfamiliar

144   rattle than when broadcasting the owner's rattle during our temporary removal experiments.

145   **Methods**

146   *Study system*

147   This study was part of the Kluane Red Squirrel Project, a long term study of a wild

148   population of red squirrels within Champagne and Aishihik First Nations Traditional Territory

149   along the Alaska Highway in the southwest Yukon (61° N, 138° W), which has been running

150   since 1987 (McAdam et al., 2007). The study site is boreal forest dominated by white spruce, the

151   cones of which are cached in middens near the centre of each squirrel's territory.

152   As part of this project, every red squirrel living within several ~40ha study grids was

153   tagged with unique alphanumeric metal ear tags and monitored throughout its life. Coloured

154   wires and pipe cleaners were threaded through the metal ear tags to allow identification of

155   individuals from a distance. Territory ownership was determined through biannual censuses of

156   the population every spring and fall based on live trapping and behavioural observations, so that

157   the location and duration of ownership was known for every individual in the population.

158   We selected a semi-random sample of adult male squirrels (n = 42) from two control

159   study grids (KL and SU) as our focal individuals, each territory separated by > 60m, to reduce

160   confounding effects of neighbours between trials. We did not use female squirrels both due the

161   ethical concerns of removing a mother from her pups during lactation, as well as the potential for

162   maternal protection to affect the intensity of territory defense independent of the social

163   information of interest.

Rattle collection and processing

165   We recorded rattles from each of our focal individuals to use in the speaker replacement

166   trials. Our speaker replacement experiment had a repeated measures design, where each of the 42

167   individuals were temporarily removed from their territory three times, and replaced with a

168   speaker broadcasting their own rattle, an unfamiliar rattle, or silence in a randomized order. Each

169   individual's recorded rattles were used twice, once at their own territory as the owner treatment

170   and once at the territory of an individual on the other study grid as the unfamiliar treatment.

171   We deployed an audio recorder (Zoom Corporation® H2N audio recorder, Tokyo, Japan)

172   on the midden of each of our focal squirrels and recorded for 24 hours. We then went through

173   these recordings and selected the three highest quality recordings of rattles from each individual.

174   Owner rattles were distinguished from neighbours by amplitude, as neighbouring squirrels would

175   not be rattling on the owner's midden. This approach has been previously shown to reliably

176   identify the calls of owners (Siracusa et al. in review). These three rattles were extracted and

177   normalized to the same amplitude for every individual using Avisoft-SAS Pro software (Avisoft

178   Biacoustics), but were otherwise left unmanipulated. We combined these three rattles in a 21-

179   minute audio file with seven minutes of silence separating each rattle; one rattle every seven

180   minutes is the average natural rate for this population (Dantzer et al., 2012).

Speaker replacement experiment

182   We trapped focal individuals using Tomahawk traps (Tomahawk Live Trap, Tomahawk,

183   WI, USA) and temporarily removed them from their midden. Squirrels were placed in a modified

184   box (41 × 17.5 × 19 cm) and provided with a small amount of peanut butter and a slice of apple

8

185   for food and hydration (Donald & Boutin, 2011). The box was placed in a sheltered location

186   away from other squirrel middens, and disinfected with isopropyl alcohol between removals. We

187   conducted all trials during May – August 2017 between 7 am – 12 pm, the main activity period

188   of squirrels during the summer months (Studd et al., 2016), and avoided days with precipitation

189   or high winds, as squirrels tend to be less active during these weather conditions (Williams et al.,

190   2014).

191   Once the owner was removed from its territory, we set up an SME-AFS field speaker

192   (playback range 0.1 – 22.5 kHz, Saul Mineroff Electronics) on the centre of the midden. The

193   speaker played one of the two audio treatments – the owner's rattle or an unfamiliar rattle – or

194   was left inactivated for silent trials. We used a silent control as opposed to a noise control

195   because other sounds in the environment such as bird calls could communicate additional

196   information (Randler, 2006), and we were interested in how neighbouring squirrels would

197   respond to the absence of any acoustic information coming from the focal territory. Rattles were

198   broadcast from this speaker at natural levels of 65–75 dB (Shonfield et al., 2017) measured 2 m

199   from the speaker using a digital sound level metre (RadioShack model 33-2055A). We deployed

200   a Zoom recorder on the focal midden, to record the rattling behaviour of neighbouring

201   individuals throughout the removal. We also manually noted the time and approximate location

202   of any audible neighbour rattles during each trial, as the Zoom recorder could not identify the

203   direction from which each rattle was emitted.

204   Each squirrel was temporarily removed three times, with the treatments performed in

205   randomized order for each individual, separated by 21 - 48 days (median = 28). As dispersal

206   between the two study grids is low, and no squirrels were within 130 m of a squirrel on the other

207   study grid, we paired squirrels so that each playback file was used twice, once at their own

208   territory and once as the unfamiliar treatment at a territory on the other study area. The playback

209   audio files were given 5-digit numerical names so that the identity of the rattle was not known

210   when playing the files and collecting data in the field. The audio treatments during temporary

211   removals were thus partially blind, because the researcher performing the removals did not know

212   if it was the owner or an unfamiliar rattle playing, but the silent trials were identifiable.

213   We observed the focal territory from >10 m away and recorded the time and identity of

214   the first squirrel to step over the edge of the midden, or travel through trees to cross this same

215   threshold. The edge of the midden was defined by the extent of visible cone bracts on the

216   ground. Removals ended after the first intrusion, or if no intrusion occurred, after a maximum

217   latency of two hours. Upon completion of the trial, the owner was returned to the midden and

218   released, and the speaker was removed. This research was approved by the University of Guelph

219   Animal Care Committee (AUP 1807).

220   When performing a temporary removal experiment, the owner is prevented from calling

221   to defend its territory; the treatment is effectively removing their territorial vocalizations from

222   the acoustic environment, and replacing these vocalizations at a hypothesized rate with a

223   speaker. To quantify the difference between our silence and playback treatments, it is important

224   to know actual vocalization rates in the study population during the experiment. To characterize

225   the social context of our population in which we conducted our study, we deployed Zoom

226   recorders on the middens of other squirrels on our study grids (n = 42) as described above in

227   *Rattle collection and processing*. These audio recordings were analyzed as described in Siracusa

228   et al (in review) (modified to include the hours of 08:00 – 13:00 rather than 07:00 – 13:00 due to

229   reduced temporal coverage in 2017) to obtain an average number of rattles per individual

230   throughout the morning active period during which we conducted our speaker replacements.

231   *Long term data*

232   As part of the Kluane Red Squirrel Project, the age, sex, and history of territory

233   ownership for every tagged individual in the population was known. We identified every squirrel

234   living within acoustic range of the focal individuals during the experiment, based on the 130 m

235   range of red squirrel rattles (Smith, 1978). By identifying the earliest census in which the focal

236   squirrel and a neighbour occupied their respective territories, we calculated pairwise familiarity

237   with each neighbour as the number of days that those two squirrels occupied neighbouring

238   territories. Neighbourhood density, age and sex of neighbours, and the distance of each

239   neighbour from the focal midden were also obtained from our existing long-term data.

240   *Statistical analysis*

241   We tested the effect of the rattle playback on the risk of intrusion using a Cox

242   proportional hazard mixed effects model. This model works well with censored data, where the

243   time to an event is recorded but in some trials the event never occurs. The binary response (did

244   an intrusion occur?), and the latency to the event (how long did it take for the intruder to

245   appear?), which has a maximum value of 120 min, were incorporated together as a single

246   response known as a hazard function. We included audio treatment as a three-level categorical

247   predictor, and because there were repeated measures for the same individual, we also included a

248   random effect of owner ID to account for variation in intrusion risk among neighbourhoods.

249   We analyzed neighbourhood rattling rate (number of rattles/min from all neighbours)

250   during each removal using a linear mixed effects model, testing for an effect of audio treatment

251   while also incorporating day of year, local neighbourhood density and familiarity, and a random

252   effect of owner ID.

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253   As neighbourhood-level analyses found no evidence of rattle identity on intrusion risk

254   (see *Overall intrusion risk* results below), we performed two sets of post hoc analyses. First, we

255   added several other neighbourhood covariates that are known to affect intrusion probability and

256   intensity of defense (Siracusa, Boutin, et al., 2017) to the models of hazard of intrusion and

257   rattling rate. We included local neighbourhood density, average neighbourhood familiarity, study

258   grid, and day of year in each model, and we interacted audio treatment with each of these in turn

259   to test whether responses to different playback types were dependent on one of these other

260   factors.

261   Next, based on Siracusa, Boutin, et al. (2017) which found that unfamiliar neighbours

262   were more likely to intrude than familiar neighbours within the same neighbourhood, we

263   modelled the individual hazard of intrusion of each neighbour intruding at each temporary

264   removal. For each speaker replacement trial, all squirrels living within 130 m of the removal

265   territory were considered potential intruders and coded as intruding (1) or not intruding (0) for

266   each temporary removal. We used a Cox proportional hazard model as for the neighbourhood-

267   level model above, but now testing which of the neighbours intruded, rather than whether any

268   intrusion occurred at the focal territory. As we ended removals after the first intruder appeared,

269   when one neighbour intruded it prevented us from detecting intrusions by other neighbours. The

270   Cox proportional hazard model tests whether an event occurs within a given maximum possible

271   timespan; when an intrusion occurred, this maximum latency was less than 120 minutes for the

272   other neighbours. Thus, if no squirrel intruded, we scored all neighbours as 0 and 120 min was

273   the maximum latency; if a neighbour intruded after 45 min, we scored this neighbour as a 1

274   while all other neighbours were 0, and all squirrels had the same maximum latency of 45 min.

275   For trials where a non-neighbouring squirrel intruded, the maximum latency for all neighbours

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276   was the time to this intrusion, but we scored all individuals as 0 (not intruding) because the

277   intruder was not a member of this neighbourhood.

278   To investigate which characteristics might predict how neighbours responded to the audio

279   treatments, we included day of year, neighbour sex, and within-neighbourhood standardized

280   measures of neighbour age, pairwise familiarity with the removed owner, and distance from

281   focal midden as fixed effects, and a random effect of trial ID. We tested for significant

282   interactions with playback type for each of these in turn.

283   All statistical analyses were conducted using R version 3.3.3 (R Core Team 2017), using

284   the packages coxme (version 2.2-5, Therneau, 2015), lmerTest (version 2.0-33, Kuznetsova,

285   Brockhoff, & Christensen, 2016), and visreg (version 2.4-1, Breheny & Burchett, 2017).

286   Reported estimates are means ± SE.

287   **Results**

288   We performed a total of 126 temporary removals among 42 male squirrels. Some trials

289   had to be discarded due to weather (rain during the trial) or speaker malfunctions; excluding

290   these, there were 115 removals across the three playback types among 41 male squirrels. Of

291   these 115 trials, there were four (one silent, one owner playback, two unfamiliar playback) in

292   which an intruder appeared within three minutes of the removal starting. In all stimulus tracks,

293   the first rattle in the audio track played after three minutes of silence, so in these removals an

294   intrusion occurred prior to the first possible rattle in the recording. These trials cannot be

295   considered as either playback, and rather than reclassifying them as silent trials – which would

296   substantially increase the overall risk of intrusion for the silent treatment – they were removed

297   from the analysis. Thus, the models described below include 111 temporary removals among 41

298   individuals: 35 owner playback, 34 unfamiliar playback, and 42 silent trials.

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299   There were 19 trials of these 111 in which an intrusion occurred, but the intruding

300   individual was identified as a squirrel living outside the 130 m radius around the removal

301   territory. These squirrels cannot be considered to have experienced the speaker treatment

302   equivalently to neighbouring squirrels to the removal territory. The dear enemy phenomenon

303   would only predict differing risks of intrusion when playing an owner's call compared to an

304   unfamiliar call if all individuals hearing these rattles broadcast were familiar with the territory

305   owner. For squirrels outside the social acoustic neighbourhood, there is no reason to predict

306   discrimination between these rattles because both calls are unfamiliar. Additionally, it is unclear

307   to what extent these squirrels would have heard any rattles being broadcast as their territories lie

308   outside the acoustic range of the speaker. Thus, all results presented below include these 19 trials

309   redefined as not having an intrusion but with a maximum latency of when the non-neighbour

310   intrusion occurred.

311   Local density for our focal squirrels was 2.65 ± 0.12 squirrels/ha and familiarity was 495

312   ± 31 days. Local densities on KL (3.11 ± 0.15 squirrels/ha) were higher than those on SU ($2.22 \pm$

313   0.11; $t = 4.72$, df = 39, $p < 0.0001$), but neighbourhood familiarity did not differ ($t = 0.54$, df =

314   39, $p = 0.59$). Squirrels on KL rattled more than those on SU during a five-hour period in the

315   morning (32.1 ± 9.2 vs. 13.5 ± 2.1 rattles; $t = 2.25$, df = 40, $p = 0.03$). The overall average was

316   21.5 rattles over five hours, corresponding to one rattle every 14 minutes.

317   *Overall intrusion risk*

318   There was no overall effect of the playback type on the risk of intrusion by neighbours

319   (Figure 1). The overall probability of intrusion was 24 %, and the proportion of trials with an

320   intrusion did not vary between treatments (Figure 2), nor did the average latency to an intruder

321   (owner = 43.7 ± 7.7 min, silence = 46.1 ± 7.7 min, unfamiliar = 59.5 ± 7.9 min; overall = $49.1 \pm$

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322   4.6 min). Including all intrusions, or only those from within the social neighbourhood, did not

323   change the interpretation of the playback effect.
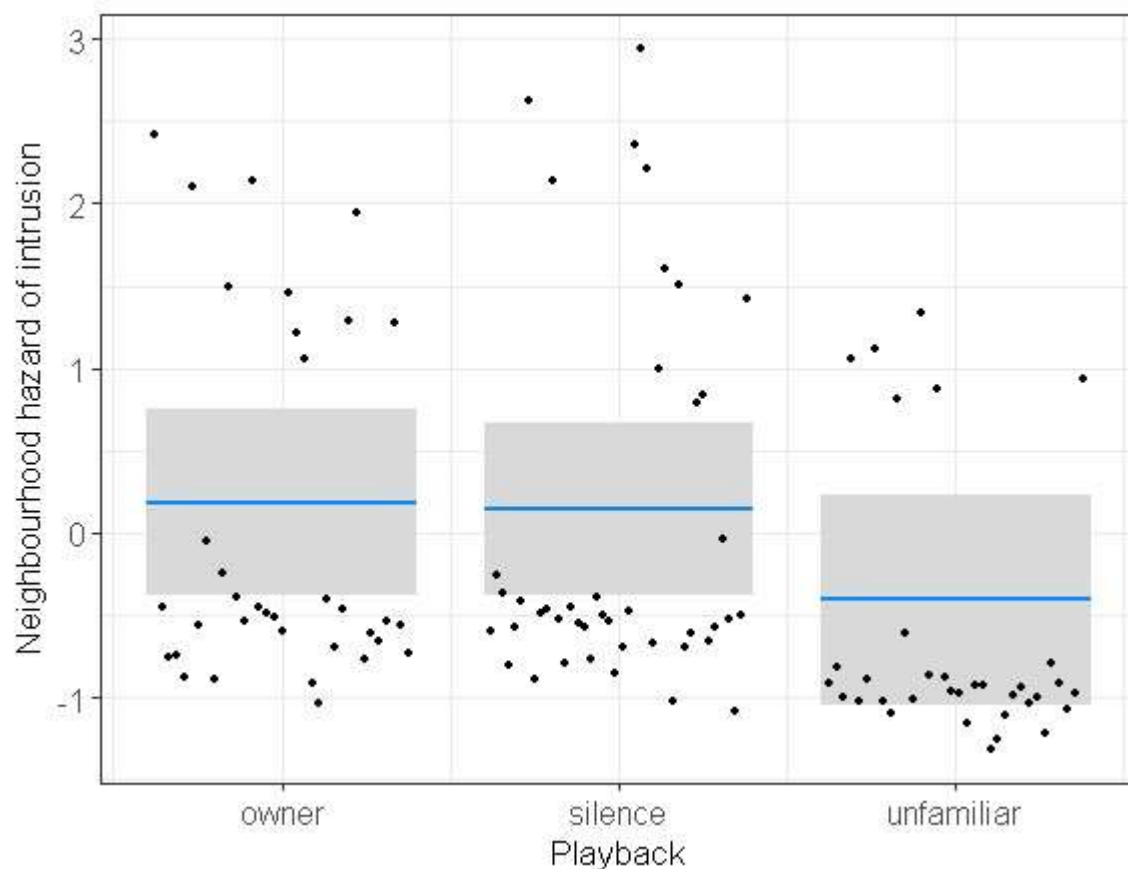
324

325   **Figure 1.** Cox proportional hazard model of intrusion by neighbours, incorporating whether or

326   not an intrusion occurred with the latency to that intrusion event. There were no differences in

327   intrusion hazard between owner playback and silence ($z = -0.15$, $p = 0.88$) or owner and

328   unfamiliar playbacks ($z = -1.48$, $p = 0.14$).

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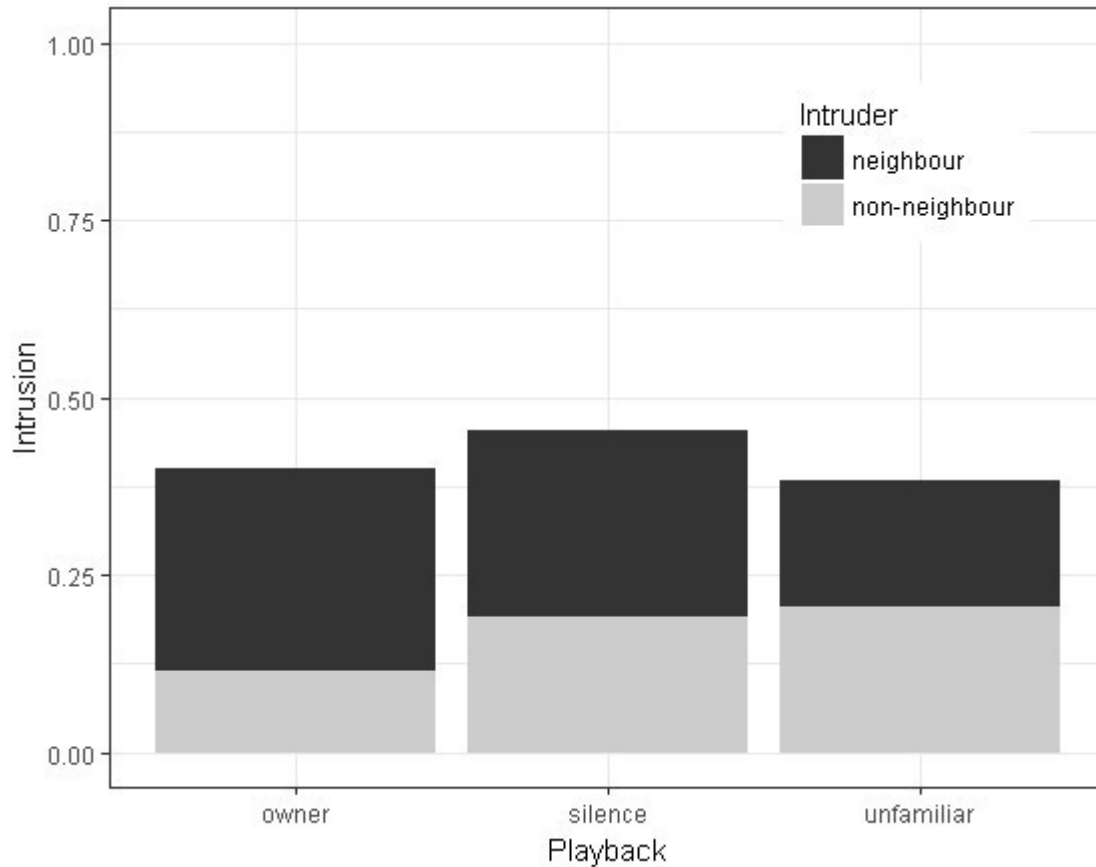
Figure 2. Proportion of trials across three playback treatments where a neighbour (black) or non-neighbouring (grey) squirrel intruded during a 2-hour temporary removal. There were no significant differences between playbacks when considering all trials, only neighbour intrusions, or only non-neighbour intrusions.

It is unlikely that censoring trials upon the first intrusion affected these relationships. If either non-neighbour intrusions or those from within the social neighbourhood happened earlier, it is possible that detecting intruders from a different source was prevented by ending the trial upon seeing the first squirrel. However, in about 60% of all trials, there were no intruders at all; if there was some sort of masking effect preventing detection of both types of intruders at a given territory, there should be fewer removals with no intruder at all. Additionally, there was no difference between the average latencies of intrusions coming from within the neighbourhood

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342   (45.9 ± 5.8 min) and those from non-neighbours (53.8 ± 7.4 min) ($t = 0.85$, df $= 44$, $p = 0.40$), so

343   it is unlikely that censoring trials when the first intruder appeared prevented detection of a later

344   intrusion.

345   *Neighbourhood rattling rates*

346   The number of rattles/min heard by observers during the removals was highly right

347   skewed (mean $= 0.54$, median $= 0.46$, range $= 0 – 2.49$ rattles/min). This response was, therefore,

348    $\log_{10}(x + 0.1)$ adjusted prior to analysis ($+ 0.1$ as three trials had zero rattles heard). Contrary to

349   our second prediction, rattling rate in the neighbourhood did not vary among the three treatments

350   ($F_{2,76} = 0.267$, $p = 0.77$). Although trials varied in length when intrusions occurred, the duration

351   of the trial did not affect the observed rattling rate ($t = -0.27$, df $= 109$, $p = 0.79$).

352   *Post hoc analyses*

353   In the Cox proportional hazard model of neighbourhood intrusion risk, none of the other

354   neighbourhood factors had a significant effect on the risk of intrusion (familiarity: $z = 1.15$, $p =$

355   0.25; date: $z = 0.55$, $p = 0.66$; grid: $z = 1.16$, $p = 0.25$; density: $z = 0.54$, $p = 0.59$). Interacting

356   playback type with each of these covariates in turn, also provided no evidence that the effect of

357   the speaker on intrusion hazard was dependent on any of these factors.

358   Although these neighbourhood characteristics did not predict the risk of intrusion, some

359   did have an effect on rattling rates during the temporary removals. Unsurprisingly, local density

360   had a positive effect on neighbourhood rattling rate; with more neighbours around the removal

361   midden, there were more audible neighbour rattles ($t = 2.46$, df $= 109$, $p = 0.01$). When

362   accounting for the effect of local density, there were also more rattles on KL grid than on SU ($t =$

363   2.93, df $= 109$, $p = 0.004$), suggesting that there are underlying differences in the behaviour of

364   the squirrels in these areas beyond the differences in population density. Neighbourhood rattling

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365   rate also increased with day of year, with more rattles later in the summer (t = 2.71, df = 109, p =

366   0.007). Average familiarity around the removal territory did not affect neighbourhood rattling

367   rates (t = 1.03, df = 109, p = 0.31). As squirrels adjust their rattling behaviour in response to their

368   local familiarity and density (Siracusa et al, in review), we calculated familiarity and density for

369   the 130m radius around each individual neighbour squirrel and included these values in our

370   model. The average of the familiarity and density values for every neighbour around each

371   removal also did not affect the neighbourhood rattling rate observed during the speaker

372   replacements (familiarity: t = 0.67, df = 109, p = 0.50; density: t = 0.68, df = 109, p = 0.50).

373   There was no significant effect of playback with the inclusion of these covariates in the model

374   ($F_{2,104}$ = 0.37, p = 0.69). Interactions between the playback type and each of these factors were

375   tested, but no combinations were significant.

376   *Individual hazard of intrusion*

377   The second stage of post hoc analyses considered which individual squirrels within the

378   acoustic neighbourhood were more likely to intrude during a given trial. Red squirrel

379   neighbourhoods are not homogenous, and neighbours have varying degrees of familiarity with

380   each focal individual. Our original prediction that there would be more intrusions during

381   unfamiliar rattle playbacks presumed that all neighbours were uniformly familiar with the

382   removed squirrel and would all exhibit dear enemy relationships. However, new neighbours or

383   squirrels that have just joined the social neighbourhood would not have as much familiarity with

384   the focal squirrel being removed, and so might not be expected to discriminate as strongly

385   between the two playback types, leading to less difference between the audio treatments.

386   Overall, closer neighbours had a higher hazard of intrusion (β = - 0.02, z = -3.50, p =

387   0.0005) and younger neighbours tended to intrude more (β = -0.31, z = -1.39, p = 0.16).

18

388   Neighbour sex did not affect intrusion hazard ($z = -0.55$, $p = 0.58$). Interacting the standardized

389   familiarity of neighbours with the playback type, the discrimination between owner and

390   unfamiliar playbacks varied depending on how familiar the neighbour was with the focal squirrel

391   (Figure 3). Relative familiarity within the neighbourhood had no effect on individual hazard of

392   intrusion during silence (slope = -0.16 ± 0.34, $p = 0.63$) or unfamiliar playback (slope = $-0.07 \pm$

393   0.49, $p = 0.88$). However, when broadcasting the owner's call, unfamiliar neighbours were more

394   likely to intrude, while familiar neighbours refrained from intruding (slope = -1.12 ± 0.39, $p =$

395   0.004).
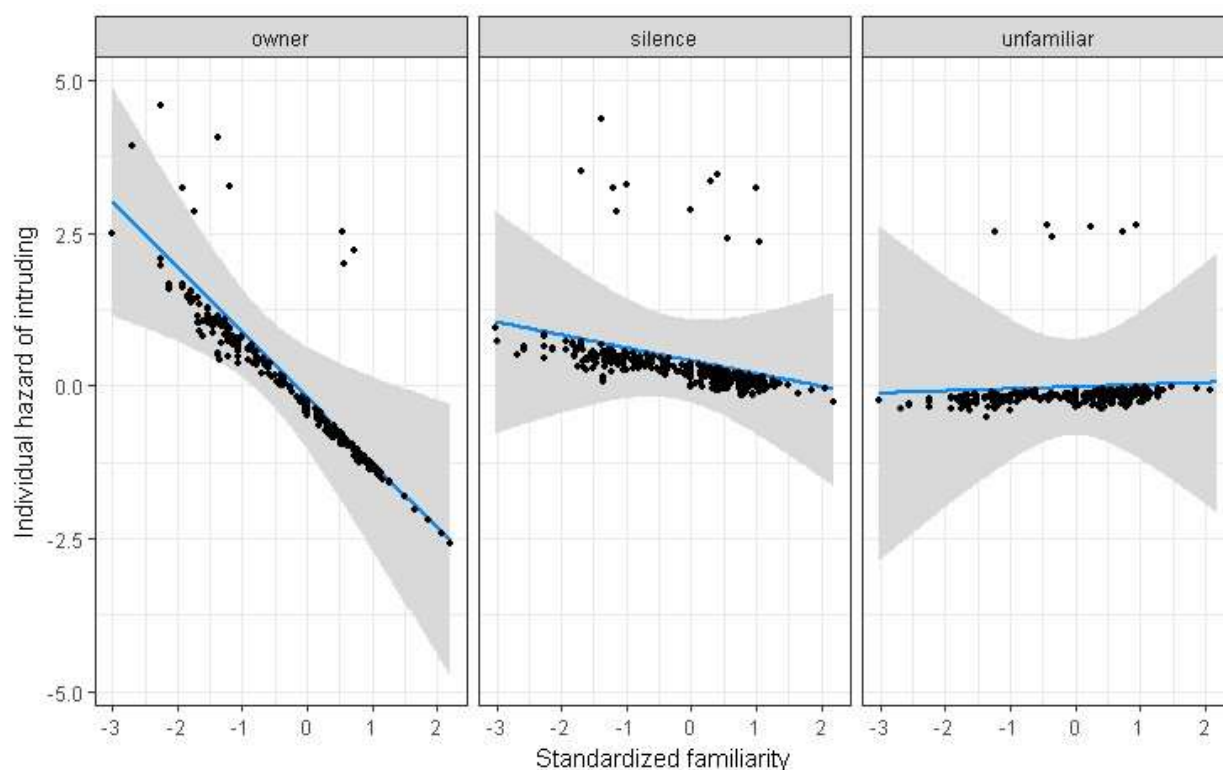
396

397   **Figure 3**. Relative hazard of intrusion by individual neighbouring squirrels during a temporary

398   removal, under three audio treatments. Intrusion hazard is modelled using a mixed effects Cox

399   proportional hazard model, accounting for the latency to an intrusion event and whether or not

400   one occurred within the two-hour temporary removal; a high hazard corresponds to a shorter

401   latency and higher probability of intrusion. There was a higher hazard of intrusion from

402   relatively unfamiliar neighbours when broadcasting the owner's rattle ($\beta = -1.05$, $z = -2.82$, $p =$

19

403   0.005), whereas relative familiarity did not affect the hazard of intrusion during silence ($\beta = -$

404   0.16, $z = 0.49$, $p = 0.63$) or unfamiliar rattle playbacks ($\beta = 0.07$, $z = 0.15$, $p = 0.88$).

405

406   The differences in intruders between the three treatments can be elucidated by comparing

407   the relative familiarity of intruders under the three playback types (Figure 4). When the owner's

408   rattle was broadcast, intruders ($n = 9$, mean familiarity z-score $= -1.04 \pm 0.44$) were less familiar

409   than other neighbours ($t = -2.85$, df $= 23$, $p = 0.009$), while intruders during silent trials ($n = 14$,

410   z-score $= -0.22 \pm 0.27$) and trials playing an unfamiliar call ($n = 6$, z-score $= -0.02 \pm 0.33$) were

411   not different from the average familiarity within the neighbourhood (silence $t = -0.84$, df $= 23$, p

412     $= 0.41$; unfamiliar $t = -0.03$, df $= 23$, $p = 0.97$). Squirrels intruding when the owner's rattle was

413   broadcast were marginally less familiar than intruders during the unfamiliar playback ($t = -1.8$, df

414     $= 23$, $p = 0.08$).
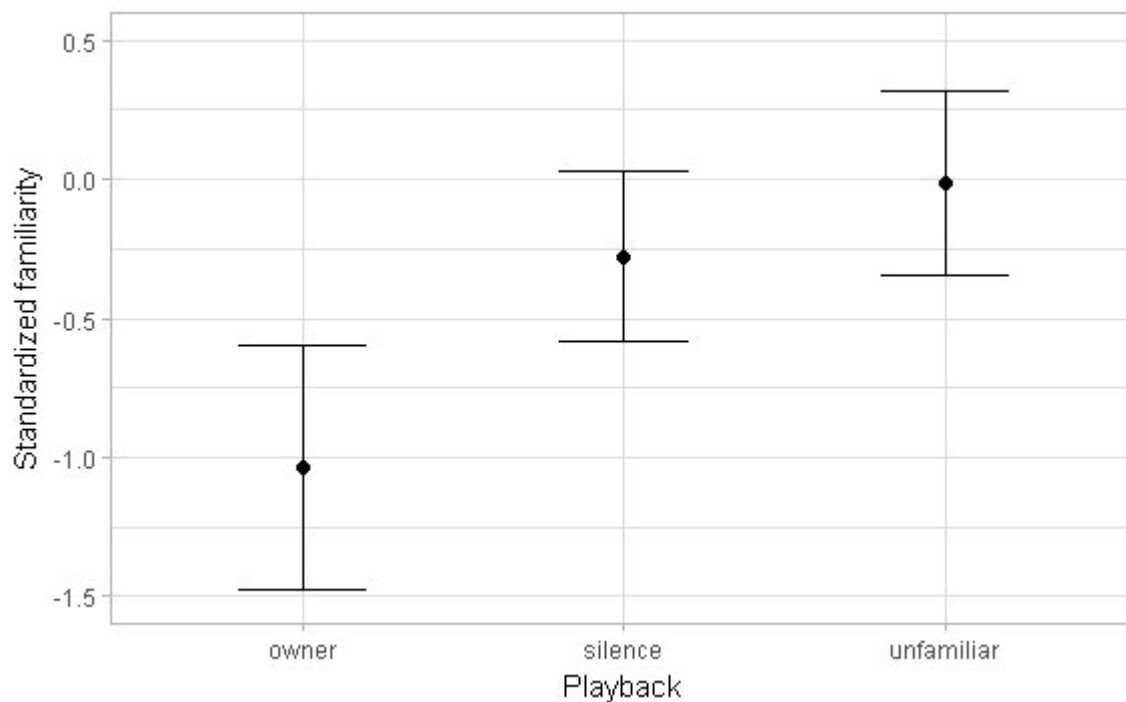
415

416   **Figure 4.** Standardized familiarity (z-scores, relative to neighbourhood) of intruding neighbours

417   during temporary removals when broadcasting the owner's call (n = 9), silence (n = 14), or an

20

418 unfamiliar call (n = 6). Standardized familiarity for intruders on the owner's rattle was different

419 from zero (t = -2.85, df = 23, p = 0.009), but this was not the case for either of the other two

420 groups (silence: t = -0.84, df = 23, p = 0.41; unfamiliar: t = -0.03, df = 23, p = 0.97).

421

Discussion

423   Our a priori prediction that neighbouring red squirrels would intrude less when the

424 territory owner's rattle was broadcast from its territory as opposed to a broadcast of an

425 unfamiliar rattle was not supported by this study, nor did we find that either rattle reduced the

426 risk of intrusion relative to silence. Similarly, rattling rate from surrounding territories was

427 unaffected by the identity of the rattle played. However, post hoc analyses revealed that

428 neighbouring squirrels had differing responses to the owner and unfamiliar rattles based on pre-

429 existing familiarity with the owner: familiar neighbours refrained from intruding during owner

430 playback but did intrude when broadcasting the stranger rattle, whereas unfamiliar neighbours

431 did not discriminate rattle identity as strongly. Differing responses of familiar and unfamiliar

432 neighbours masked any differences in intrusion risk overall at the neighbourhood level, but the

433 identity of intruders differed between playback types (Figure 4). The difference in familiarity of

434 intruders between owner and unfamiliar speaker replacements supports the ability of red

435 squirrels to recognize familiarity in the rattles of conspecifics, but the behavioural responses did

436 not differ as initially predicted.

437   Most tests of the dear enemy phenomenon define familiarity as a binary of neighbours

438 and strangers. However, familiarity with territorial neighbours is a continuum, and in longer-

439 lived year-round territorial species familiarity can accrue substantially. Average lifespan of red

440 squirrels in this area that recruit into the population as adults is 3.5 years (McAdam et al., 2007),

441 but the highest pairwise familiarity between two red squirrels in this study was 6.2 years. Other

21

442   squirrels had been neighbours for less than a week prior to the temporary removal: these

443   situations are evidently not equivalent, but both would be categorized as neighbours in a binary

444   model. The lack of overall difference in intrusion risk between the familiar and unfamiliar rattle

445   playback, but the clear difference in response to these treatments based on pre-existing

446   familiarity, corroborates the necessity of considering familiarity in territorial populations as a

447   continuous measure. The available data for territory occupancy from this long-term project

448   allowed us to identify these individually variable responses that were masked when averaging

449   across neighbourhoods. These more nuanced effects of individual familiarity in response to cues

450   from neighbours might similarly obscure dear enemy relationships in other systems where

451   familiarity has been classified as neighbour or non-neighbour. Further studies of the dear enemy

452   phenomenon would benefit from considering individual variation within territorial populations,

453   and the effects this variation can have on observed overall trends.

454   At first our results appeared to be contrary to previous studies documenting the territorial

455   defense function of rattles (Siracusa, Morandini, et al., 2017) and the effects of familiarity on

456   intrusion risk (Siracusa, Boutin, et al., 2017), but this is not surprising given the natural inter-

457   annual fluctuations in food, density, and predators in this population (Boutin et al., 2006; Dantzer

458   et al., 2013; Studd et al., 2015). Overall, intrusion rates in this study were lower than those

459   observed in a previous speaker replacement study (Siracusa, Morandini, et al., 2017). This

460   previous study was conducted in fall 2015, a year immediately following a white spruce masting

461   event in our study area. In a mast year, trees coordinate their production of cones to create a

462   superabundance of resources, followed by several years of very low or zero cones produced so

463   that cone availability varies by several orders of magnitude (Lamontagne & Boutin, 2007).

464   Squirrel populations track this variation, with densities ranging from 0.4 – 3.0 squirrels/ha

22

465   (Dantzer et al., 2013). Recruitment of juvenile red squirrels is much higher than usual following

466   a mast year (McAdam & Boutin, 2003), resulting in high densities and low familiarities in the

467   subsequent year. With minimal juvenile recruitment in subsequent low cone crop years, density

468   typically declines and average familiarity increases in the years following a mast event. The

469   average local density and familiarity in this study were significantly lower ($t = -8.41$, df $= 94$, $p <$

470   0.0001) and higher ($t = 8.48$, df $= 94$, $p < 0.0001$) respectively than those in 2015 (Figure 5).

471   Although these inter-annual differences could explain the reduction in overall intrusion risk

472   between years, they should not affect the discrimination between familiar and unfamiliar calls,

473   nor the effectiveness of rattle playbacks.

474
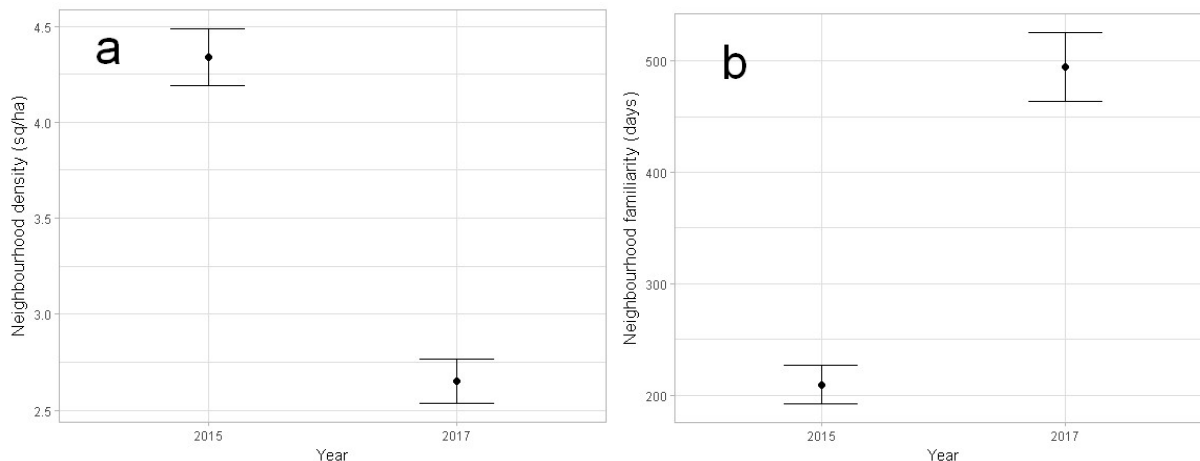
475

476   **Figure 5.** Comparison of (a) local density and (b) familiarity within 130m of focal squirrels used

477   for temporary removal experiments in 2015 (n = 55) and 2017 (n = 41). With two further years

478   of very low cone production since the 2014 mast event, population density has fallen with the

479   lack of new food resources while average familiarity in 2017 has accrued as there was minimal

480   recruitment of juveniles during this period.

481

482   The central anomalous finding of this study, in light of the results from Siracusa, Boutin,

483   et al. (2017), is that unfamiliar neighbours failed to intrude during silent trials, but did intrude on

23

484   the owner's rattle. Why these unfamiliar squirrels refrained from intruding during silence, but

485   were seemingly attracted by the owner's rattle, is unclear. Potentially, in a social environment

486   with scarce acoustic information, the presence of the owner rattle attracted these unfamiliar

487   neighbours to intrude, but the lack of information during silence created uncertainty that

488   discouraged these squirrels from intruding. This raises questions of the importance of silence in

489   populations where the primary territorial defense is acoustic.

490   Siracusa, Morandini, et al. (2017) documented a strong effect of broadcasting the owner's

491   rattle relative to silence, reducing the risk of intrusion at the same territory by 2.5 times. This is a

492   much stronger effect than that observed in this study, and this discrepancy can likely be

493   explained by year to year variation in both intrusion pressure and ambient rattling rate. Siracusa,

494   Morandini, et al. (2017) conducted their trials in the fall, when neighbourhood rattling rates

495   during removals in this study were highest ($t = 2.71$, df $= 109$, $p = 0.007$). Under conditions

496   where ambient rattling rate is high, such as low familiarity and high density (as in 2015), the

497   absence of rattles from a territory becomes a meaningful source of information to neighbours that

498   the owner is not actively defending their midden. However, squirrels on the same study grid

499   (KL) rattled 45% less in 2017 than they did in 2015: 46.44 ± 1.8 (n $= 85$) rattles per morning in

500   2015 vs. 32.1 ± 9.2 (n $= 18$) in 2017 ($t = 2.52$, df $= 101$, $p = 0.013$). Our speaker replacement

501   used the previously reported average rattling rate of 1 call per 7 minutes (Dantzer et al., 2012),

502   whereas the average time between rattles across both grids in 2017 was 14 minutes. A silent 2-

503   hour removal thus corresponds to only 8 or 9 missing rattles, rather than 17 rattles based on the

504   playback rate of one call every seven minutes. This drastically reduces the value of silence,

505   relative to either owner or unfamiliar rattle playback, in determining whether a territory is being

506   defended.

24

507   Speaker replacement or targeted playback experiments are often used to test the dear

508 enemy phenomenon or the value of territorial vocalizations more generally. An important

509 component of these studies is the temporal rate at which calls are broadcast from the speaker;

510 this is generally based on reported average vocalization rates for the study species, but as

511 demonstrated in this study, these rates are not fixed values and the speaker may not be simulating

512 typical defensive behaviour in that population. Comparisons of defensive calls relative to silence

513 on a territory are implicitly testing the value of silence as information, which is dependent on the

514 expected amount of acoustic information present in the environment.

515   Our speaker replacement experiment demonstrated that red squirrels are capable of

516 discriminating familiarity in vocalizations, but did not respond behaviourally as we had initially

517 predicted. Our results differed from previous temporary removal and speaker replacement studies

518 in the population, likely due to interannual differences in social composition and defensive

519 effort. The extensive within-neighbourhood variation in familiarity documented in this system,

520 and the individually variable responses of neighbours to familiar and unfamiliar vocalizations,

521 reinforces the need to consider territorial familiarity as a continuously variable trait within

522 populations, rather than as a binary of neighbours and strangers. We also highlight the

523 importance of silence as information in acoustically territorial populations, and how the relative

524 value of silence depends on expected rates of vocalization.

525 **Acknowledgements**

25

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