

## Red squirrel territorial vocalizations deter intrusions by conspecific rivals

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### Abstract

In many species, territory defense is thought to be one of the primary functions of acoustic communication. North American red squirrels are a territorial species in which ‘rattles’ have long been thought to be the principal signal communicating territory ownership. These vocalizations have been assumed to deter intruders, thus reducing energy costs and the risk of injury associated with direct aggressive interactions. However, this hypothesis has not been directly tested. Here we used a speaker occupation experiment to test whether red squirrel rattles function to deter conspecific rivals. We studied 29 male squirrels and removed each individual from his territory twice in a paired design. During the experimental treatment we simulated the owner’s presence after its removal by broadcasting the owner’s rattle from a loudspeaker at the center of the territory once every seven minutes. During the control treatment the territory was left in silence after the temporary removal of the owner. We found that the presence of a speaker replacement reduced the probability of intrusion by 34% and increased the latency to first intrusion by 7%, providing support for the hypothesis that rattles play an active role in reducing intrusion risk. However, intrusions were not completely averted by the speaker replacement, indicating that vocalizations alone are not sufficient without other cues of the territory owner.

35

## 36 **Keywords**

37 mammalian vocalizations, acoustic communication, territoriality, speaker occupation, red squirrel

38

## 39 **Introduction**

40 Vocal communication is thought to have several principle functions, including territorial  
41 defence (Catchpole, 1982; Catchpole & Slater, 1995; Bradbury & Vehrencamp, 2011). While the  
42 role of vocalizations in repelling conspecific rivals is typically well accepted, this function has  
43 rarely been directly demonstrated. Evidence supporting the functionality of vocalizations as a  
44 deterrent for intruders has come mostly through indirect means, via observational and correlational  
45 studies in the field, rather than direct experimental tests of functionality. For example, vocalizations  
46 commonly observed in association with intrusion events or aggressive interactions among  
47 individuals (Smith, 1978; Catchpole, 1983; Kramer & Lemon, 1983; Sharpe & Goldingay, 2009),  
48 containing characteristics such as low frequency and high intensity (believed to be associated with  
49 aggression; (Morton, 1977; Anderson & Barclay, 1995), or seasonally associated with times of  
50 important territorial defence (Catchpole, 1973; Penteriani, 2002) have typically been ascribed a  
51 territorial function. However, while suggestive, these correlative studies lack the causal evidence to  
52 support the putative defensive functionality of vocalizations.

53 The use of experimental playbacks is one technique that has been employed to study the role  
54 of vocalizations in territory defence. Playbacks have been used to simulate the intrusion of a rival  
55 individual by broadcasting a vocalization from a loudspeaker placed on a focal territory (Weeden &  
56 Falls, 1959). The aggressive reaction of territory owners in response to simulated intrusions has  
57 been used as evidence to support the conclusion that vocalizations play a role in territory defence  
58 against conspecific rivals. This type of aggressive response has been observed in a variety of taxa  
59 including anurans (Wells, 1977; Bastos et al., 2011; Morais et al., 2015), fishes (review: Bass &  
60 McKibben, 2003), birds (Odom & Mennill, 2010; Brumm et al., 2011; Cain & Langmore, 2015)  
61 and mammals (Barlow & Jones, 1997; Reby et al., 1999; Hayes et al., 2004; Darden & Dabelsteen,  
62 2008). By inducing an aggressive reaction in territory owners, the use of playbacks can effectively  
63 demonstrate that vocalizations function in immediate territorial confrontations. However, by  
64 measuring the response of owners, rather than intruders, these studies fail to clarify whether  
65 vocalizations induce avoidance and function to keep conspecifics off the territory, even when  
66 confrontations are not imminent.

67 Muting and speaker occupation are two experimental designs that have been used in  
68 songbirds to test the hypothesis that acoustic signals function to deter territory intrusions. In muting

69 experiments, territory owners are rendered silent via devocalizing surgical procedures (Peek, 1972;  
70 Smith, 1979). These experiments have provided empirical evidence for the territorial function of  
71 song by demonstrating that muted males experience higher intrusion rates and increased territory  
72 loss relative to controls whose ability to sing is left intact (Peek, 1972; Smith, 1979; McDonald,  
73 1989; Westcott, 1992). In speaker occupation experiments, territory residents are removed and  
74 replaced by speakers broadcasting the owner's song (Krebs, 1977; Krebs et al., 1978; Yasukawa,  
75 1981; Falls, 1988; Yasukawa, 1990; Nowicki et al., 1998). In most cases, territories with a speaker  
76 replacement remain unoccupied longer and experience lower rates of intrusion than territories that  
77 are left silent, suggesting that song may be important in helping to repel intruders (Krebs, 1977;  
78 Krebs et al., 1978; Falls, 1988; Nowicki et al., 1998).

79 While birdsong is one of the most well-studied phenomena in animal communication, fewer  
80 studies have attempted to experimentally demonstrate the territorial function of vocalizations in  
81 other taxa. Speaker occupation experiments have been used in bicolor damselfish (*Pomacentrus*  
82 *partitus*; Myrberg, 1997) and painted gobies (*Pomatoschistus pictus*; Pereira et al., 2013), and  
83 muting experiments more recently in Lusitanian toadfish (*Halobatrachus didactylus*; Conti et al.,  
84 2015) to show that vocalizations serve as a “keep-out” signal to other conspecifics. Due to the  
85 limitations of finding species amenable to such experimental designs our understanding of the  
86 territorial function of vocalizations in mammals has been limited to observational field studies or  
87 playback experiments that induce an aggressive response in the territory holder (Smith, 1978,  
88 Grinnell et al., 1995, Barlow and Jones, 1997, Reby et al., 1999, Grinnell and McComb, 2001,  
89 Sharpe and Goldingay, 2009). Harrington and Mech (1979) did demonstrate that simulated howling  
90 resulted in retreat or avoidance by neighbouring wolf packs, suggesting that howling serves to deter  
91 intruders and maintain territorial boundaries without direct aggression.

92 To experimentally test the function of vocalizations for territorial defence in a mammalian  
93 species we used a territorial tree squirrel (*Tamiasciurus hudsonicus*). North American red squirrels  
94 are small, arboreal squirrels in which both sexes defend exclusive, individual territories throughout  
95 the year. The core of each territory is a larder hoard of food resources called a “midden”(Smith,  
96 1968). Red squirrels produce several vocalizations, of which the “rattle” is believed to be the most  
97 important for territorial defence (Smith, 1978). Rattles, unlike the vocalizations of songbirds, are  
98 not known to be associated with mating and are used by both sexes. Rattles are known to have a  
99 repeatable acoustic structure that allows for individual identification and discrimination by  
100 conspecifics (Digweed et al., 2012; Wilson et al., 2015). Smith (1978) observed that red squirrels  
101 produce rattles when another squirrel enters its territory, but also periodically when there is no  
102 apparent threat. Rattles were also observed to elicit fleeing behaviour from the intruder (Smith,

103 1978). This suggests that rattles may function as an advertisement of occupancy and help to  
104 maintain the spacing of individuals while minimizing direct aggressive interactions (Smith, 1978;  
105 Lair, 1990). By enabling the avoidance of aggressive interactions such as chases or fights, rattles  
106 may reduce energy costs and risk of injury (Wilson, 1975). The use of playback experiments has  
107 demonstrated that red squirrels can differentiate between neighbours and strangers as well as kin  
108 and non-kin using rattles, and that they respond more aggressively toward simulated intrusions from  
109 strangers (Price et al., 1990) and non-kin (Wilson et al., 2015). In another study, increased  
110 population density was found to increase vigilance and rattling rates in red squirrels (Shonfield et  
111 al., 2012; Dantzer et al., 2012). However, intruder pressure at high densities did not increase, which  
112 suggests that increasing rattling rates may be effective in deterring territorial intrusions (Dantzer et  
113 al., 2012). These observations support the idea that in red squirrels, rattles serve to advertise the  
114 owner's presence to other conspecifics, maintain territory boundaries, and deter intruders. However,  
115 to date there is no direct experimental evidence to support this perceived functionality.

116 The aim of our study was to experimentally test whether red squirrel rattling functions to  
117 deter intruders. To assess this we employed a speaker occupation experiment and temporarily  
118 removed 29 squirrels from their territories in a paired design. During the control treatment the  
119 territory was left in silence, while during the experimental treatment we simulated the owner's  
120 presence by broadcasting the owner's rattle from a loudspeaker at the centre of the territory. We  
121 predicted that if rattles function to deter intruders in the absence of the territory owner then,  
122 compared to territories left in silence, territories with a speaker replacement would have: 1) a lower  
123 probability of intrusion and, 2) a longer latency to intrusion.

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## 125 **Material and methods**

### 126 *Population and Study Area*

127 We studied a wild population of North American red squirrels (*Tamiasciurus hudsonicus*) in  
128 the southwest Yukon, Canada (61° N, 138° W), near Kluane National Park. The habitat of the study  
129 area is open boreal forest dominated by white spruce (*Picea glauca*; Berteaux & Boutin 2000;  
130 Humphries & Boutin, 2000; Krebs et al., 2001). This population has been monitored continuously  
131 since 1987 as part of the Kluane Red Squirrel Project (McAdam et al., 2007), on up to six study  
132 sites. We conducted our experiment on two study sites; one site was maintained as a control (40 ha)  
133 while the other study site (45 ha) was an experimental food-add site that has been supplemented  
134 with peanut butter between October and May every year since 2004 as part of a larger on-going  
135 study (Dantzer et al., 2013).

136 Each year in May and August we enumerated all individuals in the population and  
137 determined territory ownership using live-trapping methods and behavioural observations. We  
138 permanently tagged squirrels with uniquely numbered metal ear tags (National Band and Tag,  
139 Newport, KY, U.S.A) around 25 days old in their natal nest. Each squirrel was also given a unique  
140 combination of coloured wires that were threaded through the ear tags to allow individuals to be  
141 identified from a distance (see Berteaux & Boutin, 2000; McAdam et al., 2007 for a detailed  
142 description of study sites and project protocols).

143

#### 144 *Rattle Recordings*

145 Between June and August 2015 we recorded 240 rattles from 29 male squirrels (minimum 4-  
146 5 rattles each squirrel) using a Marantz® Professional Solid State Recorder (model PMD660; 44.1  
147 kHz sampling rate; 16-bit accuracy; WAVE format) with a Sennheiser® shotgun microphone  
148 (model ME66 with K6 power supply; 40-20000 Hz frequency response ( $\pm 2.5$  dB); super-cardioid  
149 polar pattern; Wilson et al., 2015, Shonfield et al., 2016). We collected all rattles opportunistically  
150 in the morning, between 0730 and 1100 hours. Squirrels were followed at a distance when  
151 attempting to collect a rattle and were not stimulated with a playback or otherwise provoked during  
152 rattle collection (Wilson et al., 2015). Although we cannot exclude the possibility that the  
153 observer's presence elicited the rattles, squirrels on our study sites were well habituated to human  
154 observers. We edited the recorded rattles using Avisoft-SASLab Pro (Avisoft Bioacustics). To  
155 preserve rattle characteristics, we imported the recorded calls into Avisoft as uncompressed 16-bit  
156 .wav files. For each squirrel, we chose three rattles with minimum background noise. We adjusted  
157 rattles to ensure that all recordings had similar power (dB). We stored the three rattles, interspersed  
158 with 7-minute intervals of silence, as .wav files.

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#### 160 *Speaker Occupation Experiment*

161 Between August and September 2015, we conducted temporary removals of 29 male  
162 squirrels from their territories, 15 from the control site and 14 from the experimental food addition  
163 site ( $n = 29$ ). We trapped squirrels with Tomahawk live traps (Tomahawk Live Trap Co.,  
164 Tomahawk, Wisconsin), and removed each squirrel from his territory twice, once as a treatment and  
165 once as a control (order of treatment and control was randomly assigned). Treatments were  
166 conducted no less than 3 days apart (range: 4-41 days). Once trapped, we placed the squirrel in a  
167 modified box (41 cm x 17.5 cm x 19 cm) to help keep the squirrel quiet and calm for the duration of  
168 the removal (Donald & Boutin, 2011). A small amount of peanut butter and some spruce cones  
169 were also provided in the modified box. We then moved the squirrel 20-30 m away from his

170 midden, and placed the individual in a shady location. Care was taken not to place the removed  
171 individual on another squirrel's territory.

172 Each trial commenced immediately following the removal of the territory owner. When  
173 removed as a control, we left the territory owner's midden silent. When removed as a treatment, we  
174 placed a Saul Mineroff SME-AFS field speaker with a playback range of 0.1-22.5 kHz face-up on  
175 the ground at the centre of the squirrel's midden. We then broadcast the owner's rattle from this  
176 speaker at a level between 65-75 dB (Shonfield et al., 2016) at 7-minute intervals (Dantzer et al.,  
177 2012) for the duration of the removal. We checked the power of each recording in the field, prior to  
178 the start of the speaker replacement, using a digital sound level meter measured 2 m from the  
179 upwards-facing speaker.

180 During each removal an observer monitored the midden from a distance of no less than 5 m  
181 away from the midden center. If an intrusion was witnessed the observer recorded the time of  
182 intrusion and the identity of the intruding squirrel. An intrusion was defined as occurring when a  
183 squirrel moved onto the pile of cone scales, which is considered to define the edges of a squirrel's  
184 midden. Each removal lasted 120 minutes or until an intruder arrived, whichever came first, after  
185 which point we released the captive squirrel at the site of capture. This research was approved by  
186 the University of Guelph Animal Care Committee.

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### 188 *Statistical analysis*

189 To assess whether the presence of a speaker replacement reduced the probability of a  
190 squirrel intruding and the latency to intrusion we used a Cox proportional hazard mixed effects  
191 model (PHMM) in the R package *coxme* (version 2.2-5: Therneau, 2015). We used a survival  
192 analysis approach because removals in which no intruder was observed in the 120 min time-period  
193 had censored values for time to intrusion. The response variable for Cox proportional hazard  
194 models is a single measure called the hazard of intrusion. This response variable takes into account  
195 both the probability of intrusion (1 = yes there was an intrusion, 0 = no intrusion observed) as well  
196 as the time to intrusion (measured in minutes). For the purposes of interpretability, hereafter we will  
197 refer to the outcome of this model as the 'risk of intrusion'. In all cases, a high risk of intrusion is  
198 equivalent to a high probability of intrusion and a fast time to intrusion.

199 Our model included speaker treatment (speaker or no speaker) and study site as categorical  
200 predictors. We also included squirrel identity as a random intercept term to account for our matched  
201 pairs design. Our PHMM was found to sufficiently meet the proportional hazards assumption. We  
202 examined *dfbeta* residuals to ensure that there were no influential observations. All analysis were



203 performed using R software 3.3.2 (R Core Team, 2016). For the following results, we considered  
204 differences statistically significant at  $\alpha=0.05$  and report all means  $\pm$  SE, unless otherwise stated.

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## 206 **Results**

207 Our Cox proportional hazards model revealed that the risk of intrusion was significantly  
208 lower in the presence of the speaker replacement, meaning that playbacks of the owner's rattle  
209 reduced the overall probability of intrusion and also delayed the time to intrusion by a neighbouring  
210 squirrel ( $\beta = -0.92 \pm 0.33$ ,  $z = -2.77$ ,  $P = 0.01$ ). There were no differences in the risk of intrusion  
211 between the two study sites ( $\beta = -0.24 \pm 0.32$ ,  $z = -0.75$ ,  $P = 0.45$ ). For each treatment we conducted  
212 29 temporary removals of territory owners. Twenty-five intrusions occurred when no speaker  
213 replacement was present (86% of removals) and only 15 intrusions were observed when a speaker  
214 was used to broadcast the rattle of the territory owner (52% of removals). The proportion of  
215 intrusions with the speaker replacement was significantly lower than when the territory was left  
216 silent (McNemar's Chi-squared test;  $\chi^2 = 5.79$ ,  $df = 1$ ,  $P = 0.02$ ; Figure 1). However, the average  
217 time to first intrusion on empty territories was 52.20 minutes (SD:  $\pm 36.84$  min; range: 0-120 min)  
218 and on speaker occupied territories was 60.13 minutes (SD:  $\pm 38.62$  min; range: 15-120 min), which  
219 were not significantly different (Welch Two Sample t-test;  $t = -0.64$ ,  $df = 28.50$ ,  $P = 0.74$ ; Figure  
220 2). Thus, over a 120-minute period the presence of a rattle vocalization reduced the probability of  
221 intrusion by 34% but only reduced the time to intrusion by 7%, suggesting that the reduced risk of  
222 intrusion was primarily due to a reduced probability of intrusion.

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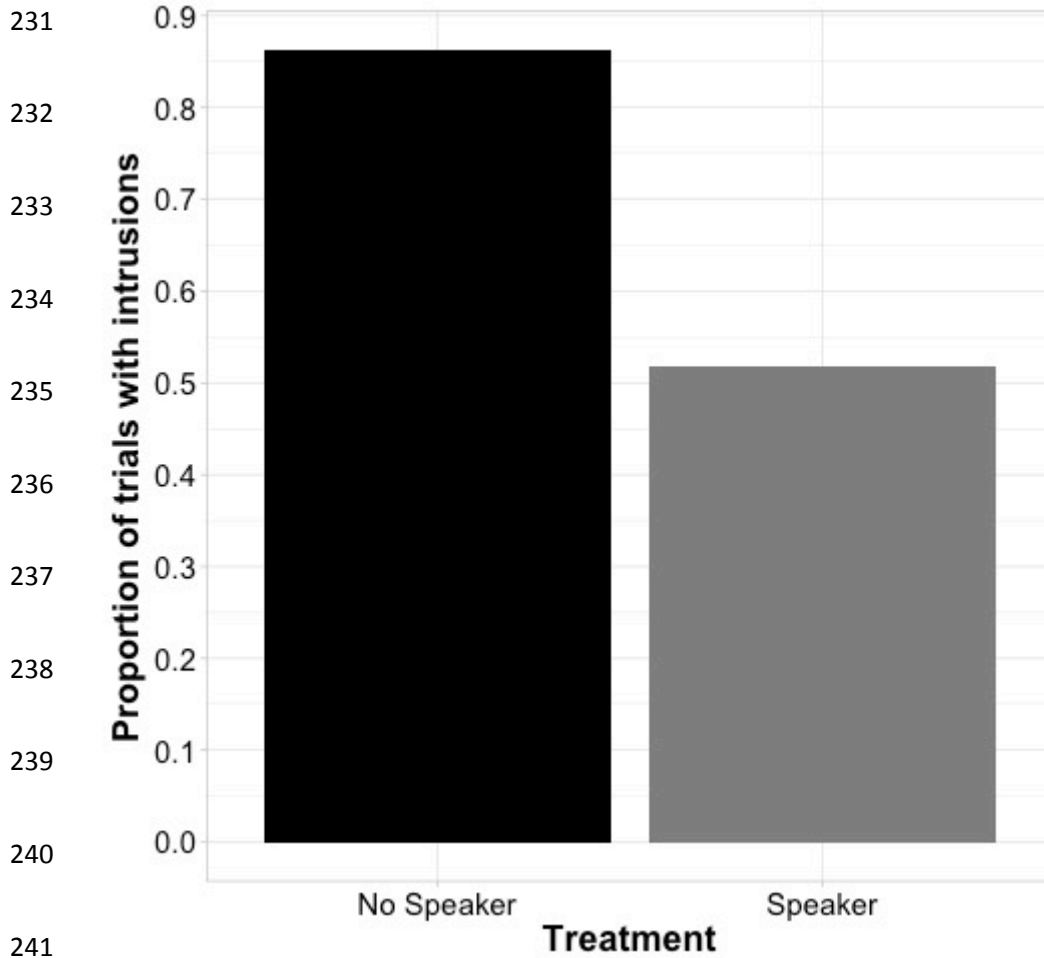
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242 **Figure 1.** The effect of a speaker replacement following the temporary removal of a territory owner  
243 on the proportion of trials with intrusions (McNemar's Chi-squared test;  $\chi^2 = 5.79$ ,  $df = 1$ ,  $P = 0.02$ ;  
244  $n = 29$ ).

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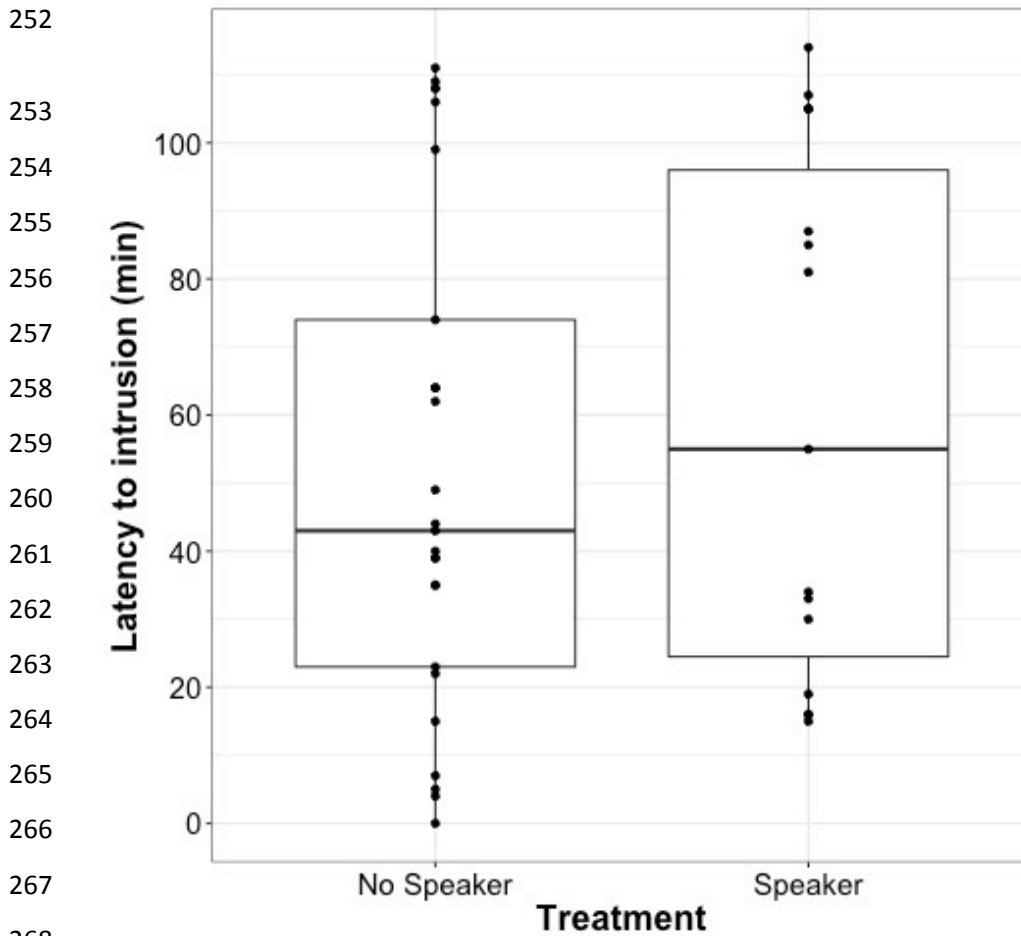
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269 **Figure 2.** The effect of a speaker replacement following the temporary removal of a territory owner  
270 on the latency to intrusion (Welch Two Sample t-test;  $t = -0.64$ ,  $df = 28.50$ ,  $P = 0.74$ ;  $n = 29$ ).

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## 285 **Discussion**

286 In this study we investigated the territorial function of vocalizations in the North American  
287 red squirrel. Specifically, we tested the role of rattles in discouraging conspecific intruders. The  
288 results from this study confirmed our hypothesis that red squirrel rattles reduce intrusion risk by  
289 demonstrating that territories occupied by a speaker replacement had a significantly lower  
290 probability of intrusion and a delayed time to first intrusion compared to territories that were left  
291 empty.

292 Our results, obtained using a speaker occupation design, are the first to experimentally  
293 demonstrate the territorial function of vocalizations in a mammal. Moreover, our findings support  
294 the conclusions of previous speaker occupation studies in both songbirds and territorial fishes that  
295 have demonstrated the importance of acoustic signalling for territory defence and retention (Krebs,  
296 1977; Krebs et al., 1978; Falls, 1988; Myrberg, 1997; Nowicki et al., 1998; Pereira et al., 2013).  
297 However, while in red squirrels the number of intrusions was clearly reduced by the rattle playback,  
298 the presence of the speaker replacement alone was not 100% effective in deterring intrusions. Of the  
299 29 territories which received a speaker playback, 15 experienced a territorial intrusion, which is just  
300 over half of the territories (52%), suggesting that visual cues, or other stimuli from the territory  
301 owner, are also an important component of territory defence. This is consistent with previous  
302 speaker occupation studies which demonstrate lower intrusion rates or delayed intrusions in the  
303 presence of playbacks, but do not preclude intrusions altogether (Falls, 1988; Myrberg, 1997;  
304 Nowicki et al., 1998). Falls (1988) suggested that the effectiveness of the speaker occupation design  
305 may depend in part on the conspicuousness of the territorial species that is being studied. Speaker  
306 replacement should be most effective in species that are visually inconspicuous because it allows  
307 the façade of occupancy to be maintained for a longer period of time. Red squirrels are usually  
308 fairly visible to their neighbours as they are diurnal and spend a significant portion of their time  
309 foraging and feeding on or around their territory. Red squirrels will also actively chase intruders off  
310 their midden if necessary, although such direct acts of aggression are usually rare (Gorrell et al.,  
311 2010; Dantzer et al., 2012).

312 Given the potential importance of the physical presence of the territory owner, it is not  
313 surprising that the speaker replacement experiments were not wholly effective in deterring red  
314 squirrel intruders. In fact, in some studies, speaker replacements initially induced avoidance of  
315 ‘occupied territories’, but had unexpected effects on intrusion rates. For example, in red-winged  
316 blackbirds there were reduced rates of fly-through, but not neighbour trespass, on speaker  
317 replacement territories, suggesting that visual displays may be crucial for territory retention  
318 (Yasukawa, 1981). In painted gobies the presence of a playback ultimately led to higher rates of

319 territory intrusion than in territories that were left silent. Painted gobies approached ‘occupied’ nests  
320 more frequently than silent nests but then demonstrated avoidance after approaching the agonistic  
321 calls. However, when the gobies were unable to associate the sound with the physical presence of a  
322 territory holder they proceeded to intrude on the ‘occupied’ territory (Pereira et al., 2013).  
323 Anecdotally, we observed similar patterns of behaviour in red squirrels. Potential intruders that  
324 appeared at the edge of the territory initially appeared to be deterred by the broadcast rattle,  
325 however, after remaining on the territory for several minutes without sighting the territory owner,  
326 these loitering individuals entered the midden and, when not chased off by a resident squirrel,  
327 proceeded to pilfer food resources. Without the visual presence of the territory owner, potential  
328 intruders appear to become habituated to a repetitive acoustic stimulus. While we have confirmed  
329 the significance of rattles in red squirrel territory defence, altogether these results suggest that,  
330 similar to other acoustic signals, rattles only serve as a temporary deterrent to territorial intrusions  
331 until the absence of the territory owner is confirmed. This underscores the importance of the  
332 combined effects of visual and acoustic cues for deterring conspecific rivals.

333 A more precise understanding of how rattles function in territory defence is still lacking.  
334 Red squirrel rattles are known to have unique signatures that allow for individual identification by  
335 other conspecifics (Wilson et al., 2015), but it is unclear if rattles will indiscriminately discourage  
336 intruders regardless of whether that rattle is from a resident or non-resident conspecific. Yasukawa  
337 (1981) suggested that one reason the speaker replacement did not deter neighbour trespass in red-  
338 winged blackbirds is because song types were used which were unfamiliar to neighbouring  
339 conspecifics. Yasukawa speculated that neighbouring males interpreted this as an attempted  
340 territory establishment by a new individual and therefore responded by either attempting to re-  
341 negotiate boundaries or claim the abandoned territory before the new male had time to fully settle  
342 (Yasukawa, 1981). Here we used only the calls of the territory owners in our speaker replacements.  
343 Future studies should employ the use of speaker occupation experiments using calls from different  
344 signallers to better understand if red squirrels are able gather and respond to more complex  
345 information about their social environment.

346

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