

# Predator-Associated Vocalizations in North American Red Squirrels (*Tamiasciurus hudsonicus*): To Whom are Alarm Calls Addressed and How do They Function?

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1 Predator-Associated Vocalizations in North American Red Squirrels (*Tamiasciurus hudsonicus*):  
2 To Whom are Alarm Calls Addressed and How do They Function?

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17 Running headline: Digweed & Rendall: Alarm call function in red squirrels

18 **ABSTRACT:** Alarm vocalizations produced by prey species encountering predators can serve a  
19 variety of functions. North American red squirrels are a small-bodied mammal popularly known  
20 for producing loud, conspicuous alarm calls, but functional accounts of calling in this species are  
21 few and contradictory. We conducted research over a three-year period on a sample of 47 marked  
22 red squirrels in the foothills of the Canadian Rockies. We recorded the production of alarm calls  
23 during encounters with natural predators and in a series of simulated predator experiments. We  
24 tested for variation in call production patterns consistent with three traditional hypotheses  
25 concerning the conspecific warning functions of alarm calling: namely that they serve as  
26 warnings to kin, to potential mates, or to territorial neighbors with which callers have an  
27 established relationship. Patterns of calling did not provide clear support for any of these  
28 hypothesized functions. We consider several possible qualifications to our results. We also  
29 consider the possibility that conspicuous calls given by red squirrels during encounters with  
30 predators are directed at the predators themselves and function to announce their detection and  
31 possibly deter them. This possibility is consistent with additional life-history features of red  
32 squirrels including that they are a relatively solitary and territorial, food-hoarding species that  
33 produces the same conspicuous vocalizations in response to other squirrels intruding on their  
34 territory to steal cones. An important corollary of this account is that red squirrel alarm calls  
35 probably do not entail referentially-specific messages about different types of predator, as  
36 proposed previously.

37 Predation is an important natural threat for many animals, and one common response of prey  
38 species encountering predators is the production of loud, conspicuous vocalizations. Such alarm  
39 vocalizations can serve a variety of functions. They can also provide some insight into how  
40 animals perceive, categorize and communicate about objects and events in the world around  
41 them. For example, research on group-living primates and ground squirrels indicates that alarm  
42 vocalizations can function to warn offspring and collateral kin about impending danger (e.g.,  
43 Sherman 1977; Cheney & Seyfarth 1981). It also shows that prey species sometimes evolve  
44 multiple different alarm calls that communicate different messages to listeners about the type of  
45 predator faced or the imminency of the danger it represents, thereby facilitating even more  
46 specific adaptive responding by listeners (Seyfarth et al. 1980; Owings & Hennessy 1984;  
47 MacWhirter 1992; Evans et al. 1993; Manser 2001).

48 North American red squirrels (*Tamiasciurus hudsonicus*) are also reported to produce  
49 acoustically distinct alarm vocalizations to different types of predators, namely aerial predators  
50 such as goshawks and owls, and terrestrial predators such as coyotes and pine martens (Smith  
51 1968, 1978; Embry 1970; Nodler 1973; Lair 1990; Greene & Meagher 1998). Hence, they are  
52 potentially similar to some other species that produce predator-specific, referential alarm signals  
53 (Macedonia & Evans 1993; Evans & Evans 2007). In red squirrels, however, the same  
54 vocalizations are also produced in non-predator contexts (Smith 1968; Embry 1970; Price et al.  
55 1990), which raises some question about the function of these calls and their referential  
56 specificity.

57 There are also some differences in the socioecology of red squirrels compared to other  
58 species for which alarm calls function as predator-specific, referential alarm messages to  
59 conspecifics. For example, many of these other species are social or group-living species and so  
60 callers are surrounded by various direct and collateral kin that might benefit from such predator

61 warnings. In contrast, red squirrels are solitary and highly territorial. Their social contact with  
62 other squirrels is limited primarily to aggressive interactions with territorial intruders (Smith  
63 1968; Gurnell 1987). As a result, it is not clear that the alarm vocalizations of red squirrels are  
64 even directed at, or for the benefit of, other squirrels and therefore what the value might be of  
65 multiple, predator-specific alarm messages in this species.

66 To address these issues, we report results from a multi-year study of alarm call production  
67 by red squirrels. We focus on the possible conspecific warning functions of the calls. If the  
68 different alarm calls that red squirrels produce serve as referentially-specific warnings about  
69 different predators, as has been proposed (Greene & Meagher 1998), then there should be  
70 evidence that the calls are directed at one or more categories of conspecific that could profit from  
71 being informed about different predatory threats. Previous research and theorizing highlights  
72 three possibilities in this regard, namely that alarm calls might function to warn kin, mates, or  
73 other social companions with which an individual has a relationship worth preserving (Kin:  
74 Hamilton 1964; Sherman 1980; Schwagmeyer 1980; Cheney & Seyfarth 1981; Hoogland 1983;  
75 MacWhirter 1992; Da Silva et al. 2002; Blumstein 2007; Wheeler 2008; Mates: Morton &  
76 Shalter 1977; Witkin & Fricken 1979; Krams et al. 2006; Neighbors: Fisher 1954; Ydenberg et  
77 al. 1988; Stoddard 1996; Hare 1998; Hyman 2005).

#### 78 **Potential conspecific warning functions for alarm calls in red squirrels**

79 Red squirrels do not live in cohesive social groups containing a mix of direct and collateral kin.  
80 Instead they occupy individual territories that they defend from conspecifics (Gurnell 1987). As a  
81 result, local kin are limited primarily to a female's dependent offspring prior to their dispersal.  
82 The settlement patterns of dispersing offspring are not well documented but some females have  
83 been reported to bequeath a portion of their territory to offspring (Price & Boutin 1993). As a  
84 result, adult females are likely to have close kin nearby at least seasonally, in the form of young-

85 of-the-year. Some females might also have adult offspring nearby as neighbors.

86       The situation for adult males is different. Mating is polygynous during a short spring  
87 season. Males compete vigorously for mating opportunities and travel relatively long distances  
88 (up to 1km) to seek-out available mates (Gurnell 1987). Although the resulting spatial  
89 distribution of paternity is not fully known, this wandering pattern of males means that they will  
90 not necessarily sire offspring close to the home territory they occupy for the rest of the year as  
91 opposed to farther away.

92       Given these life-history characteristics, the following predictions can be made if alarm calls  
93 function as predator warnings to kin: females should produce alarm calls more than males;  
94 lactating females should call more than non-lactating females; females should call more after pup  
95 emergence when offspring are vulnerable to a more diverse array of predators; and females with  
96 neighbors that include adult offspring should call more than those with neighbors that are not  
97 adult offspring.

98       In red squirrels, males provide no direct investment in offspring care, while females lactate  
99 and provide additional investment during early offspring growth and development (Gurnell  
100 1987). The reproductive success of males post-copulation thus hinges on the short-term survival  
101 and continuing offspring investment of former female mates, while the reproductive success of  
102 females post-copulation does not hinge on the continuing survival of former male mates. As a  
103 result, if alarm calls serve as warnings to mates, then males should produce alarm calls more  
104 often than females; and males that are long-term residents should call more often than recently  
105 immigrated males because resident males will have had more opportunities to mate with local  
106 females.

107       Although red squirrels are generally aggressive towards other adults (that are typically  
108 encountered as territorial intruders), there is some precedent for a degree of tolerance toward

109 established territorial neighbors (Price et al. 1990). Such tolerance might reflect the costs  
110 associated with establishing clear territorial relationships with neighbors to begin with (Healy  
111 1967; Randall 1989). Hence, there might be a benefit to producing alarm calls to warn established  
112 neighbors about predatory threats, thereby preserving an established neighbor relationship and so  
113 avoiding the time, energy, and aggression required to establish a new one with a replacement  
114 neighbor. Both males and females maintain such territorial relationships in red squirrels (Price et  
115 al. 1990). Therefore, if alarm calls function to warn neighbors, then males and females should be  
116 equally likely to produce alarm calls. In addition, individuals with long-term neighbors that  
117 reflect established territorial relationships worth preserving should produce alarm calls more than  
118 those with only short-term neighbors.

119 We examine patterns of alarm call production in a population of wild red squirrels for  
120 evidence of variation in call production aligned with these research predictions.

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122

## METHODS

### 123 Study Site and Subjects

124 We conducted research at the R.B. Miller Field Station in the Sheep River Valley of Kananaskis  
125 Provincial Park, Alberta (50°39 N, 114°39 W), which is located in the foothills of the Canadian  
126 Rockies. Research was conducted over three consecutive years (2005-2007) primarily between  
127 May and November representing the late spring, summer, and fall seasons at this latitude. We  
128 focused on a population of 47 individually marked squirrels, each of which maintained an  
129 exclusive territory (0.5 – 1.0 ha) and associated cone caches that were actively defended against  
130 intruders. In order to facilitate certain individual identification within and across field seasons,  
131 each squirrel was captured in its territory using a live-trap baited with peanut butter (Tomahawk  
132 Live Trap Company, Wisconsin), and unique dye marks (Clariol #52 Black) and ear tags were

133 applied (National Band and Tag Company, Kentucky: Tag#1005-1). Trapping and handling  
134 techniques, and the research protocols explained below, were approved by the Animal Welfare  
135 Committee of the University of Lethbridge (Protocol #0809) and by Alberta Sustainable  
136 Resource Development, Fish and Wildlife Division (Research Permit GP 30031; Collection  
137 License CN 30046). Additional details of the forest habitat, predator community, and the sample  
138 of squirrels studied are provided in Digweed & Rendall (2009).

### 139 **General Behavioral and Vocal Responses to Predators**

140 Digweed & Rendall (2009) studied red squirrels' general behavioral responses and production of  
141 alarm calls in natural encounters with predators. In addition, three experiments using simulated  
142 predators were conducted. The first experiment involved presentation of taxidermied models of  
143 three species common in the study area and known to prey on squirrels, namely coyotes (*Canis*  
144 *latrans*), great horned owls (*Bubo virginianus*) and pine martens (*Martes americana*). The second  
145 and third experiments simulated a moving terrestrial and aerial predator, respectively. The  
146 terrestrial predator model was a dog of mixed breed that resembled a coyote in size and pelage.  
147 The dog was presented to squirrels in two conditions representing a predatory threat under  
148 conditions of either low- or high-vulnerability. The aerial predator model was a small, green  
149 Frisbee® that was presented to squirrels by projecting it overhead in two conditions simulating  
150 either a fleeting or a persistent aerial threat (for additional details of experimental design, see  
151 Digweed & Rendall 2009).

152 Squirrels' responses to real and simulated predators were similar. Briefly, squirrels that  
153 spotted a predator, or a predator model, immediately stopped their current activity and either  
154 froze momentarily if they were in a tree, or, if they were on the ground, bolted to the nearest tree  
155 where they climbed to a safe height (5m). They then remained at this safe height staring at the  
156 predator and, after 5-10 seconds, began to stomp their hind feet and flick their tail back-and-forth



157 over their back while producing a steady stream of vocalizations that could last for several  
158 minutes, involve hundreds of calls, and sometimes continue after the predator had left the area.

### 159 **Data Collection and Analysis**

160 Data for use in the present study derived from the record of vocalizations produced by focal  
161 squirrels in response to the real and simulated predators described in Digweed & Rendall (2009).  
162 Only two call-types were produced in these encounters, a relatively soft and tonal ‘seet’ call and a  
163 much louder and harsher ‘seet-bark’ call comprised of a tonal seet concatenated to a broadband  
164 bark.. These two call types matched those reported by others to be produced in encounters with  
165 predators (Smith 1978; Greene & Meagher 1998). All calling bouts to real and simulated  
166 predators involved a mix of both call types. Vocalizations were recorded using a digital Marantz  
167 PMD660 recorder and a Sennheiser ME66 shotgun microphone with Sennheiser MZH60-1  
168 windscreen. In previous analyses, this record of vocalizations was tested for evidence that seets  
169 and seet-barks were produced in predator-specific fashion. In this paper, we examined calling  
170 behavior by individuals belonging to different demographic categories where call production was  
171 predicted to vary under alternative hypotheses of call function.

172         Although squirrels’ behavior in encounters with real and simulated predators was similar,  
173 we nevertheless conducted separate analyses of calling behavior in natural predator encounters  
174 and in experimental predator simulations. We started by analyzing call production for seets and  
175 seet-barks combined. We then conducted separate analyses for the two call types considered  
176 independently. Because the duration of calling bouts varied tremendously, ranging from 30-  
177 seconds up to several minutes, we limited our analyses to the first 30-seconds of calling bouts.  
178 This allowed us to include all recorded calling bouts in tests of the different functional  
179 hypotheses and is consistent with our earlier analyses (Digweed & Rendall 2009). Those analyses  
180 also showed that the general pattern of call production did not differ in longer bouts. The

181 production of seets and seet-barks during the first 30-seconds of calling bouts was tallied and  
182 tested for variation according to a series of demographic distinctions described below.

### 183 **Demographic Categories**

184 To test the various research predictions, it was necessary to categorize individual squirrels into a  
185 variety of demographic categories. The distinction between males and females was basic. Within  
186 males, residents were distinguished from recent immigrants. Residents were defined as males that  
187 had held their territory for more than one season, while immigrants were males that had arrived  
188 on a territory in the current season. Several distinctions were made among females. First, females  
189 with pups were distinguished from those without pups. This distinction was operationalized in the  
190 field by monitoring female lactational status during routine trapping and inspection. Second, for  
191 females with pups, we further distinguished between those with pups that had not yet emerged  
192 from the nest and those with pups that had emerged and therefore were vulnerable to a wider  
193 range of predators. Third, females that were likely to have kin as neighbors were distinguished  
194 from those with neighbors that were less likely to be kin. Because we could not assess collateral  
195 kinship, or potential kinship extending back several years, this distinction was limited to  
196 offspring from the previous year. Hence, females with neighbors known to include an offspring  
197 from a previous year were distinguished from females for which this was not known to be the  
198 case. Finally, for both sexes, we distinguished between individuals with long-term neighbors and  
199 individuals with only short-term neighbors. Individuals were defined as having long-term  
200 neighbors if the individuals themselves had resided on their territory for more than one season  
201 and one or more of their neighbors had similarly resided on its territory for more than one season.  
202 Otherwise, individuals were defined as having only short-term neighbors, either because they  
203 themselves were recent immigrants or all of their neighbors were.

204

## RESULTS

### A. Call production patterns: seets and seet-barks combined

#### i. Natural disturbances

Focal squirrels were involved in 34 natural disturbances. Of these, 22 involved known predators, either coyotes (*Canis latrans*), great grey owls (*Strix nebulosa*), northern goshawks (*Accipiter gentilis*), or pine martens (*Martes americana*). An additional 12 disturbances involved species that, on the surface, would seem to pose no predatory threat (e.g., ravens, long-tailed weasels, deer). However, squirrels responded to the latter species with the same pattern of behaviors and vocalizations observed in encounters with known predators (Digweed & Rendall 2009). Therefore, disturbances involving both groups were combined for analysis.

Females were involved in just over half of the encounters ( $20/34 = 58\%$ ;  $N = 12$  females, 7 males). Some individuals were involved in more than one encounter; however, where this occurred, the individuals were serving as representatives of different demographic categories in the different encounters and so call production totals could not be averaged within individuals across these encounters. As a result, the data used in statistical testing represented individual disturbances rather than individuals *per se*. Because the call production data were not normally distributed, we used non-parametric, Mann-Whitney tests throughout.

Results of statistical testing of call production patterns are shown in Table 1. There was no significant difference in the rate of calling between males and females (median and interquartile range [IQR] calls per bout = 21 [4-28] males; 20.5 [15-32] females). There was also no tendency for lactating females to call more than non-lactating females (median [IQR] = 20 [6-30] lactating; 29.5 [8-42] non-lactating) or for females to call more after pup emergence than before (median [IQR] = 20 [8-30] after; 26.5 [6-57] before). Females with neighbors known to be offspring from a previous year did not call more than females with neighbors not known to be

229 offspring (median [IQR] = 28 [6-107] offspring neighbors; 20 [14-32] without offspring  
230 neighbors). Among males, there was no difference in call production between resident males that  
231 were more likely to have mated with local females, and immigrant males that were less likely to  
232 have done so (median [IQR] = 20 [3-29] residents; 24 [5-28] immigrants). However, considering  
233 both males and females together, squirrels with at least one long-term neighbor called more than  
234 squirrels with only short-term neighbors (median [IQR] = 25.5 [20-41] long-term; 15 [8-24]  
235 short-term).

## 236 **ii. Simulated predators**

237 In total, 165 trials were conducted across the three predator simulation experiments: 63 trials  
238 involved taxidermied predator models (Experiment I); 47 trials involved simulating a moving  
239 terrestrial predator using a live dog (Experiment II); and 55 involved simulating a moving aerial  
240 predator using a Frisbee® (Experiment III). This experimental sample involved 21 different  
241 female subjects and 18 different male subjects, many of which participated in multiple trials  
242 across the three experiments. In cases where an individual participated in multiple experimental  
243 trials as a representative of one demographic category (e.g., lactating female), we averaged their  
244 calling rates across these multiple trials to arrive at a single score for this individual as a  
245 representative of that particular demographic category. If the same individual was also the subject  
246 of more than one trial as a member of another demographic category (e.g., non-lactating female)  
247 in another season or year, we calculated a separate average of their calling rates across these trials  
248 to arrive at a single score as a representative of this additional demographic category. In this way,  
249 each individual contributed only one data point to any particular demographic category.

250       Once again, calling data were not normally distributed and we therefore used non-  
251 parametric, Mann-Whitney tests throughout. Results are shown in Table 1 and largely replicated  
252 patterns observed in encounters with real predators. There was no significant difference in call

253 rates between males and females (median [IQR] calls per bout = 11.07 [6-16] males; 12.75 [8-17]  
254 females). There was also no tendency for lactating females to call more than non-lactating  
255 females (median [IQR] = 9 [7-19] lactating; 14.33 [12-21] non-lactating), or for females to call  
256 more after pup emergence than before (median [IQR] = 15.2 [6-18] after; 5.5 [2-18] before).  
257 Females with neighbors known to be offspring did not call more than females with neighbors not  
258 known to be offspring (median [IQR] = 11.2 [2-27] offspring neighbors; 13.1 [8-17] without  
259 offspring neighbors). Among males, there was no difference in call production between resident  
260 and immigrant males (median [IQR] = 7 [3-16] residents; 15 [4-27] immigrants). Considering  
261 both males and females together, there was again a significant difference in calling rates between  
262 squirrels with at least one long-term neighbor and squirrels with only short-term neighbors.  
263 However, in this case, the pattern was reversed from that observed in natural disturbances:  
264 squirrels with short-term neighbors called more than did squirrels with long-term neighbors  
265 (median [IQR] = 10.1 [6-13] long-term; 18 [11-21] short-term).

266         Squirrels in experimental trials registered and responded to all of the predator models;  
267 however, they did not always produce vocalizations in response to them (35.8% of all trials). To  
268 control for the possibility that these ‘non-calling trials’ might have influenced the result patterns,  
269 we re-ran the previous analyses after excluding these trials. Results paralleled previous analyses  
270 and are shown in Table 1. Once again, there was no difference in call rates between males and  
271 females (median [IQR] calls per bout = 18.8 [10-23] males; 17.6 [13-25] females); between  
272 lactating and non-lactating females (median [IQR] = 17.6 [12-23] lactating; 20 [12-32] non-  
273 lactating); between females after and before pup emergence (median [IQR] = 20 [13-26] after; 18  
274 [3-27] before); between females with offspring as neighbors versus not (median [IQR] = 16.5  
275 [13-36] offspring neighbors; 19 [13-25] without offspring neighbors); or between resident and  
276 immigrant males (median [IQR] = 11.4 [9-24] residents; 19.5 [2-27] immigrants). Again, there

277 was a significant difference in calling rates between squirrels with only short-term neighbors and  
278 those with at least one long-term neighbor (median [IQR] = 16.7 [11-20] long-term; 21.5 [18-23]  
279 short-term): squirrels with short-term neighbors called more than squirrels with long-term  
280 neighbors.

281 The general lack of predicted effects in these analyses could not be attributed to some  
282 broader habituation to experimental protocols. This was examined using regression analyses to  
283 test whether the strength of subjects' calling responses decreased over the course of the study, as  
284 would be predicted if habituation to experimental trials was an issue. Calling rates did not  
285 decrease over time. In fact, they showed a slight increase but the relationship was weak ( $R^2 =$   
286 0.032,  $T=2.31$ ,  $P=0.022$ ).

## 287 **B. Call production patterns: seets and seet-barks independently**

### 288 **i. Natural disturbances and simulated predators**

289 Seet-barks are much louder and more conspicuous than seets. Hence, seet-barks are more likely  
290 to be heard by distant listeners than are seets. Our previous tests that pooled the two call types  
291 might have obscured effects present for one or other call type on their own. Therefore, we re-ran  
292 analyses on the production of each call type independently. Results are shown in Table 2. Result  
293 patterns for seet-barks paralleled the earlier analyses. There was only one significant effect in  
294 both natural disturbances and simulated predator experiments and it involved the distinction  
295 between short- and long-term neighbors. In natural disturbances, individuals with long-term  
296 neighbors produced more seet-barks than those with only short-term neighbors (median [IQR] =  
297 20 [12-25] long-term; 10 [4-16] short-term). As before, this effect was reversed in encounters  
298 with simulated predators (median [IQR] = 10 [6-13] long-term; 14 [10-18] short-term).  
299 Considering the production of seet vocalizations on their own, there were no significant  
300 differences in calling rates among individuals of different demographic categories (Table 2).

301

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## DISCUSSION

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Overall, our analyses of the production of vocalizations by red squirrels during natural

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disturbances and in simulated predator experiments did not provide clear or consistent support for

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any of the traditional conspecific warning functions for alarm calls: the calls did not obviously

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serve as predator warnings to a caller's kin, to their potential mates, or to their territorial

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neighbors. There are, however, some potential qualifications to this conclusion.

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First, we did find some evidence that alarm calls might function to warn territorial

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neighbors. Specifically, we found that males and females, that are equally likely to have such

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neighbors, called at equivalent rates. However, the absence of an effect, even if predicted *a*

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*priori*, is only very weak support for a hypothesis. We also found a difference in calling rates

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between squirrels with at least one long-term neighbor and those with only short-term neighbors,

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but the direction of this effect was not consistent. In encounters with real predators, squirrels with

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long-term neighbors called more than those with only short-term neighbors as predicted. But, in

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encounters with simulated predators, the pattern was reversed. It is possible that this shifting

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pattern reflects a real difference in squirrels' behavior in encounters with real versus simulated

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predators. However, it is not obvious what sorts of factors might create such a shift that would

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not also create other differences in the squirrels' behavior and calling in the two situations, which

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otherwise were shown to be very similar (Digweed & Rendall 2009). As a result, although the

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potential for neighbor-effects might be fruitfully pursued in future, the weak and inconsistent

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effects are, for now, parsimoniously interpreted as unreliable support for a neighbor-warning

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function.

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It is also the case that our tests of the potential function of alarm calls in warning kin were

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limited to direct offspring because we lacked more complete information on the possible

325 collateral relatedness of individuals in our study population. Hence, we cannot exclude the  
326 possibility that alarm calls might serve as predator warnings to more distantly related kin. At the  
327 same time, we found no evidence that adult females were calling to warn their own offspring  
328 regardless of whether those offspring were very young and still dependent on their mother, or  
329 they were adults that had settled on an adjacent territory and hence had become one of their  
330 mother's neighbors. If calling by mothers is not an attempt to warn their own offspring, then it  
331 seems unlikely that it would be an attempt to warn more distantly related kin instead.

332       Finally, our failure to find support for a function of alarm calls in warning mates must also  
333 be qualified by the fact that we lacked data on actual mating activity between adult males and  
334 females in the study population. As a result, although we found no support for the prediction that  
335 resident males should call more than recently immigrated males (with fewer mating  
336 opportunities, all else equal), we cannot be certain that resident males, in fact, mated with local  
337 females more than did recently immigrated males. However, we found no support for a second  
338 prediction of the mate-warning hypothesis namely that males in general should call more than  
339 females because male reproductive success should depend on the continued survival and  
340 offspring investment of female mates more than the reverse.

341       Taken together, although we cannot conclude definitively that red squirrel alarm calls can  
342 play no role in warning conspecifics about predatory threats, our results suggest that these  
343 functions are not primary in the operation and evolution of alarm calling in this species and that  
344 additional alternatives might be considered.

#### 345 **Vocal deterrence of predators and other intruders**

346 One plausible alternative is that the calls are directed primarily at the predators themselves and  
347 function to announce that they have been detected (Hasson 1991;Caro 1995). Such predator-  
348 directed signals have been described in other species (Tilson & Norton 1981; Hersek & Owings



1993; Zuberbühler et al. 1999; Blumstein 2007). Indeed, a broad precedent for this phenomenon was described originally for passerine birds by Marler (1955). Many passerine species produce two, structurally distinct types of alarm calls. One type is a loud, harsh (i.e., broadband) call, often termed a ‘chit’ or ‘chirt’, that is accompanied by close approach, inspection and mobbing of a predator. The structural features of this call make it conspicuous and easy to localize and thus well-suited to recruiting additional mobbers to harass predators. In contrast, a second call type, commonly referred to as a seet, is comparatively soft, high-frequency and tonal, which gives it a ventriloquial quality that is difficult for predators to localize. Seets are also typically accompanied in callers by hiding or immediate withdrawal from the area.

It is possible that the alarm calls of red squirrels might function similarly. We have no data with which to test this possibility directly and so it must remain speculative. However, various indirect lines of evidence are consistent with it. For example, like passerine birds, red squirrel alarm calls include both a relatively soft, high-frequency and tonal seet variant and a much louder, harsh, broadband variant, either a bark, or a seet-bark (Greene & Meagher 1998; Digweed & Rendall 2009). The soft, high-frequency qualities of the seet mean that it transmits poorly in forest habitats and is unlikely even to be heard by other squirrels on neighboring territories. However, these same properties make red squirrel seets structurally similar to the seet calls of passerines (Greene & Meagher 1988) and thus give them a similar ventriloquial quality. Red squirrels produce seet calls disproportionately at the start of calling bouts in response to predators (Digweed & Rendall 2009) and this temporal pattern might be functional if it is important to remain inconspicuous in the initial stages of predator encounters until the more specific nature of the predatory threat can be established.

In contrast, when predators persist in the area, squirrels switch to producing the loud, harsh call variant, which they then produce repeatedly for up to 10-minutes (Digweed & Rendall

373 2009). The loud, broadband structure of this call type and its protracted repetition make it  
374 extremely conspicuous. These characteristics are consistent with a function in conspicuously  
375 announcing to predators that they have been detected but only after a squirrel has identified the  
376 nature of the threat and retreated up a tree.

377         Several other aspects of squirrels' responses to predators are also consistent with this  
378 possibility. For example, when predators persist in the area, red squirrels, like passerine birds,  
379 often approach toward and inspect the predator rather than retreating. At the same time, they  
380 produce additional conspicuous foot-stomping and tail-flagging behaviors (Smith 1968; Gurnell  
381 1987; Digweed & Rendall 2009). Such foot-stomping and tail-flagging is unlikely to be visible to  
382 other squirrels in neighboring territories that are, on average, 100-m away through dense  
383 coniferous forest. Hence, they are unlikely to serve as a signal to conspecifics. However, they  
384 could be visible to predators at close range, and, indeed additional conspicuous behaviors like  
385 these have been reported to accompany vocalizing in other squirrel species (Tamura & Yong  
386 1993; Owings et al. 2001). In some cases, tail-flagging behavior by itself seems to serve a  
387 deterrent function for at least some types of predator (Hersek & Owings 1993; Rundus et al.  
388 2007).

389         It is also notable that red squirrels vocalize conspicuously in encounters with non-  
390 predators as well (Lair 1990; Price et al. 1990; Digweed & Rendall 2009). These include humans  
391 and other forest interlopers but also conspecific squirrels that frequently trespass to steal cones  
392 stored in central middens and distributed caches. Squirrels produce the same seet and seet-bark  
393 calls in encounters with conspecific intruders as they do during encounters with predators, and  
394 with the very same temporal patterns (Digweed & Rendall 2009). This convergence might  
395 underscore a functional similarity that is addressed by calling in these two contexts. That is, it is  
396 possible that conspecific intruders and predators both represent an important threat to individual

397 survival. Trespassing and cone pilfering is ubiquitous in red squirrels (Rusch & Reeder 1978;  
398 Price et al. 1990). Cone losses to theft by neighbors can account for up to 84% of the stored food  
399 supply that individuals rely on for overwinter survival (Gerhardt 2005). Given the energetic  
400 constraints facing a small-bodied, non-hibernating mammal overwintering in boreal forests, cone  
401 loss might therefore represent as serious a threat to survival as do many forms of predation.  
402 Hence, the common use of seets and seet-barks in both predator encounters and territorial  
403 intrusions might reflect a common attempt to announce detection of intruders of various kinds in  
404 an effort to deter them. In the case of conspecific intruders, squirrels take additional steps by  
405 aggressively confronting and chasing them out of the territory (Nodler 1973; Lair 1990; Price et  
406 al. 1990).

407         An important corollary of this account is that the vocalizations produced by red squirrels  
408 during encounters with predators are probably not best interpreted as predator-specific,  
409 referential warnings similar to the referentially-specific alarm calls of some other animal species,  
410 as proposed by Greene & Meagher (1998). Rather, the alarm calls of red squirrels might be more  
411 conservatively interpreted as reflecting the salience of disturbances of various kinds that threaten  
412 territory integrity and individual survival.

413         By extension, continuing research and theoretical consideration of the evolution of  
414 functionally referential vocal signals in animals (e.g., Evans 1997; Evans & Evans 2007; Furrer  
415 & Manser 2009) might profit from considering an even broader variety of influencing factors.  
416 Previous work has emphasized the importance of species' social systems and specific ecological  
417 factors such as the variety of predators a species faces and the variety of escape options that are  
418 available to it (Macedonia & Evans 1993). However, it could be important to consider even  
419 broader aspects of a species' life-history because the problems posed by predators might not  
420 always be unique but rather might overlap with problems faced in other domains. As a result,

421 some species might develop adaptive communicative solutions that are common across  
422 seemingly disparate problem domains, which, in turn, might limit the utility of vocal signals with  
423 referentially-specific messages particular to any one of them.

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585 Table 1. Results of pooled analyses of the production of seet and seet-bark vocalizations elicited  
 586 by natural and simulated predators. Significant results are bolded and marked with an asterisk (\*)  
 587 and measures of effect size are provided as partial eta-squared values ( $h^2$ ).  
 588  
 589  
 590

|                           | Natural Predator Encounters                        | Simulated Predator Experiments                     | Simulated Predator Experiments (Callers Only)     |
|---------------------------|--|--|---|
| <b>Warning Kin:</b>       |  |  |   |
| F > M                     | $Z=-1.02, P=0.309$                                 | $Z=-0.31, P=0.757$                                 | $Z=-0.53, P=0.599$                                |
| F/L > F/NL                | $Z=0.95, P=0.341$                                  | $Z=0.94, P=0.345$                                  | $Z=0.68, P=0.497$                                 |
| F/A > F/B                 | $Z=0.58, P=0.562$                                  | $Z=1.38, P=0.167$                                  | $Z=0.68, P=0.496$                                 |
| F/O > F/WO                | $Z=0.79, P=0.429$                                  | $Z=0.27, P=0.784$                                  | $Z=0.14, P=0.887$                                 |
| <b>Warning Mates:</b>     |  |  |   |
| M > F                     | $Z=-1.02, P=0.309$                                 | $Z=-0.31, P=0.757$                                 | $Z=-0.53, P=0.599$                                |
| M/R > M/I                 | $Z=0.16, P=0.875$                                  | $Z=1.19, P=0.232$                                  | $Z=0.94, P=0.346$                                 |
| <b>Warning Neighbors:</b> |  |  |   |
| F = M                     | $Z=-1.02, P=0.309$                                 | $Z=-0.31, P=0.757$                                 | $Z=-0.53, P=0.599$                                |
| *LT/N > ST/N              | <b><math>Z=-2.17, P=0.029</math></b><br>$h^2=0.15$ |  |   |
| *ST/N > LT/N              |  | <b><math>Z=2.87, P=0.0039</math></b><br>$h^2=0.19$ | <b><math>Z=2.39, P=0.016</math></b><br>$h^2=0.10$ |

591 Table 2. Results of separate analyses conducted on the production of seet and seet-bark  
 592 vocalizations elicited by natural and simulated predators.  
 593

|                           | Natural<br>Predator<br>Encounters<br>(Seets) | Simulated<br>Predator<br>Experiments<br>(Seets) | Natural<br>Predator<br>Encounters<br>(Seet-barks)  | Simulated<br>Predator<br>Experiments<br>(Seet-barks) |
|---------------------------|--|---|--|--|
| <b>Warning Kin:</b>       |  |   |  |  |
| F > M                     | $Z=-0.23, P=0.407$                           | $Z=-0.31, P=0.364$                              | $Z=-1.61, P=0.106$                                 | $Z=0.02, P=0.977$                                    |
| F/L > F/NL                | $Z=1.46, P=0.142$                            | $Z=0.93, P=0.350$                               | $Z=1.23, P=0.216$                                  | $Z=1.21, P=0.225$                                    |
| F/A > F/B                 | $Z=0.18, P=0.572$                            | $Z=1.12, P=0.187$                               | $Z=-0.22, P=0.819$                                 | $Z=-1.48, P=0.135$                                   |
| F/O > F/WO                | $Z=1.41, P=0.874$                            | $Z=1.27, P=0.230$                               | $Z=0.28, P=0.772$                                  | $Z=-0.31, P=0.761$                                   |
| <b>Warning Mates:</b>     |  |   |  |  |
| M > F                     | $Z=-0.23, P=0.407$                           | $Z=-0.31, P=0.364$                              | $Z=-1.61, P=0.106$                                 | $Z=0.02, P=0.977$                                    |
| M/R > M/I                 | $Z=-0.74, P=0.771$                           | $Z=1.17, P=0.230$                               | $Z=0.15, P=0.875$                                  | $Z=1.23, P=0.217$                                    |
| <b>Warning Neighbors:</b> |  |   |  |  |
| F = M                     | $Z=-0.23, P=0.407$                           | $Z=-0.31, P=0.364$                              | $Z=-1.61, P=0.106$                                 | $Z=0.02, P=0.977$                                    |
| *LT/N > ST/N              | $Z=-0.45, P=0.323$                           |   | <b><math>Z=-2.24, P=0.024</math></b><br>$h^2=0.13$ |  |
| *ST/N > LT/N              |  | $Z=-1.08, P=0.316$                              |  | <b><math>Z=2.32, P=0.019</math></b><br>$h^2=0.12$    |

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