

Are the Alarm Calls of North American Red Squirrels (*Tamiasciurus hudsonicus*) Functionally Referential?

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**Are the alarm calls of North American red squirrels
(*Tamiasciurus hudsonicus*) functionally referential?**

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Summary

North American red squirrels are a small-bodied and solitary-living species that faces a diversity of predators and produces two different variants of alarm calls in response to them. Recent studies have yielded conflicting interpretations of the predator-specific and functionally referential nature of these alarm call variants. We undertook a systematic set of playback experiments to quantify the responses of red squirrels to alarm calls produced by other squirrels during encounters with different predators. The experiment was designed to test a core requirement of functionally referential alarm calls, namely that different alarm call types induce distinct and functionally appropriate escape responses in listeners. Results indicated that squirrels registered and responded to alarm calls produced by others; however, their responses were not differentiated according to the type of alarm call they heard and, thus, did not provide evidence that the different alarm call variants hold any predator-specific, referential value. These outcomes are discussed in light of complementary work on alarm call production in red squirrels and broader aspects of this species' life history in an effort to better understand the necessary and sufficient pressures promoting the evolution of referential call systems in animals.

Keywords: vocal communication, alarm calls, red squirrel, referential signals.

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Introduction

One important focus of research in animal communication concerns the possibility that animal signals might function referentially — that is, signals might refer to objects or events in the external world in a fashion roughly similar to human words (Zuberbühler, 2009). The paradigm case of referential signals in animals concerns the predator alarm calls of vervet monkeys. Vervets are small-bodied primates that face a diversity of predators in the savanna-woodland environments they inhabit in East and southern Africa, including leopards, eagles and other raptors, and snakes such as the python. Seminal research on these monkeys by Struhsaker (1967) and subsequently Seyfarth et al. (1980) showed that vervets produce structurally different alarm calls for each of these major classes of predator. Research also showed that the calls alone are sufficient to induce in other monkeys functionally distinct escape responses appropriate to the different predators (Seyfarth et al., 1980). Because each alarm call is elicited only by a particular predator and because it is sufficient to prompt behaviour similar to that induced by the predator itself, vervet alarm calls seem to refer to the different predators, at least functionally (reviewed in Seyfarth & Cheney, 2003).

Following this landmark work, additional examples of functionally referential vocalizations have been reported in other primate species but they have also been reported in several non-primate species as well including ground squirrels (Hare, 1998; Warkentin et al., 2001; Sloan et al., 2005), marmots (Blumstein, 1995), meerkats (Manser, 2001), ravens (Bugnyar et al., 2001), chickens (Evans & Evans, 2007) and chickadees (Templeton et al., 2005). Many have also involved alarm calls elicited by predators, but referentially specific vocalizations have been reported in other contexts as well (e.g., food discovery: Evans & Evans, 1999; Bugnyar et al., 2001; Di Bitetti, 2003; Kitze-mann & Caine, 2009; social situations: Gouzoules et al., 1984; Gouzoules & Gouzoules, 1998; Slocombe & Zuberbühler, 2005).

Theoretical work in this area now focuses on the variety of selective pressures that might facilitate the evolution of referential communication systems in animals. With respect to alarm calls, in particular, these include basic ecological factors such as the diversity of predators that a species faces and the variety of escape options that are available to it (Macedonia & Evans, 1993). Together, these two factors should influence the variety of different predator messages that would be functional in a given species. At the same time,

1 other social and life-history factors are also proposed to be important, such 1
2 as overall brain size and associated cognitive complexity, and social organi- 2
3 zation (e.g., Marler, 1977; Zuberbühler, 2000, 2001; Snowdon, 2004; Sproul 3
4 et al., 2006; Blumstein, 2007). The potential importance of the latter factors 4
5 is suggested by the fact that many reports of referential communication in- 5
6 involve relatively large-brained and intensely social primate species. They are 6
7 also supported by evidence of broader correlations between species' brain 7
8 size and social complexity (qua group size) and, in turn, between species' 8
9 social complexity and either the size of alarm call repertoires specifically, or 9
10 the size of vocal repertoires more generally. These relationships have been 10
11 documented for primates but they appear also to hold for some non-primate 11
12 taxa (Blumstein & Armitage, 1997; McComb & Semple, 2005; Shultz & 12
13 Dunbar, 2006, 2007; Dunbar, 2009; Le Roux et al., 2009). 13

14 In this paper, we report research addressing the potential referential prop- 14
15 erties of alarm vocalizations produced by North American red squirrels 15
16 (*Tamiasciurus hudsonicus*). Red squirrels are a productive test case for re- 16
17 cent theorizing because they exemplify core ecological factors hypothesized 17
18 to promote the evolution of referential alarm vocalizations (Macedonia & 18
19 Evans, 1993). For example, red squirrels face a diversity of aerial and ter- 19
20 restrial predators (e.g., coyotes, pine martens, weasels, goshawks, owls) and, 20
21 as a semi-arboreal and semi-terrestrial species, they also inhabit a complex 21
22 three-dimensional environment that affords a variety of escape options from 22
23 these different predators. Thus, whereas some ground-dwelling squirrels ef- 23
24 fectively have only a single escape option from the variety of predators they 24
25 face (down a burrow) which selects for alarm call variation that signals the 25
26 imminency of the predatory threat and the urgency of response required (Ow- 26
27 ings & Virginia, 1978; Owings & Leger, 1980); red squirrels move about and 27
28 have refuges in both the trees and underground, and hence might profit from 28
29 alarm call variation that signal these distinct options. 29
30

31 At the same time, however, red squirrels are not so encephalized as many 31
32 of the primate species documented to produce referential vocalizations, nor 32
33 do red squirrels live in cohesive social groups. Instead, red squirrels are com- 33
34 paratively solitary and occupy individual territories that they aggressively 34
35 defend. Apart from during a short spring breeding season, their interactions 35
36 with conspecifics are limited primarily to aggressive confrontations with 36
37 neighbours and territorial intruders. As a result, it is not entirely clear that 37

the alarm calls produced by red squirrels are directed at conspecifics at all (cf., Caro, 1995; Zuberbühler et al., 1999; Rundus et al., 2007).

Taken together, then, red squirrels exemplify several of the ecological factors thought to promote the evolution of referential signals but not either the cognitive or the prosocial factors that are also proposed to be important. Paralleling this mixed picture of the selective factors that might influence referential communication in this species, there is some uncertainty about whether red squirrels actually produce predator-specific, functionally referential alarm calls. Greene & Meagher (1998) reported that red squirrels produce a tonal, high-frequency seet call primarily to aerial predators and a harsher, broadband bark-type call to terrestrial predators. They interpreted this predator-specific pattern of call production as evidence of a system of multiple distinct alarm messages about predators similar to the functionally referential alarm call systems of vervets and other species. Digweed & Rendall (2009a,b) subsequently confirmed the production of these two general call types by red squirrels in encounters with aerial and terrestrial predators. However, they did not find evidence that the call types were produced in a predator-specific fashion. Instead, they found that the two call types were mixed together in protracted bouts of calling to both aerial and terrestrial predators. This pattern of calling was consistent with earlier descriptive studies that noted relatively generalized (not specific) use of calls in this species (e.g., Smith, 1968, 1978; Lair, 1990; Price et al., 1990). As a result, it is currently unclear how closely the production of structurally different alarm vocalizations in red squirrels maps onto categorical distinctions in the types of predators faced.

An additional uncertainty is that research to date has focused on only one of the two accepted criteria of functionally referential vocalizations, namely the extent to which the production of calls exhibits sufficient ‘stimulus specificity’ (Marler et al., 1992; Macedonia & Evans, 1993; Evans, 1997). The second criterion of functionally referential signals emphasizes the importance of listener responses. Here, the requirement is that the calls alone be sufficient to elicit distinct responses from listeners in the absence of additional contextual information (the criterion of ‘context independent responses’). And it is, arguably, this second criterion that must be the ultimate arbiter of the potential referential value of any calls. That is, despite some previous evidence that red squirrels mix the two basic call types in encounters with all classes of predators, it is possible that squirrels hearing the

calls can nevertheless draw categorical inferences about the different types of predators involved.

To test this possibility, we report the results of a controlled playback experiment using vocalizations produced during natural encounters with aerial and terrestrial predators (Digweed & Rendall, 2009a). If the alarm calls have some referential value, as proposed by Greene & Meagher (1998), then squirrels that hear the different call types should show differentiated responses appropriate to the different predators the calls refer to. For example, in vervet monkeys, listeners that hear the alarm call typically given to leopards run immediately up the nearest tree where they are safe from leopards. In contrast, listeners that hear the alarm call typically elicited by eagles immediately drop down out of the trees where they are more vulnerable to a stooping raptor (Seyfarth et al., 1980). If the alarm calls of red squirrels likewise have some predator-specific, referential value, then listeners should similarly engage appropriately different escape responses. The experiment was also designed to test the possibility that alarm call variation might be associated with variation in response urgency as shown for some other rodent species (Owings & Virginia, 1978; Owings & Leger, 1980).

Materials and methods

Study site and subjects

Research was conducted at the R.B. Miller Field Station in the Sheep River Valley of Kananaskis Provincial Park, AB, Canada (50°39'N, 114°39'W), which is situated in the foothills of the Canadian Rockies. The habitat in the Sheep River Valley is a mix of aspen (*Populus tremuloides*) parkland and montane (sub-alpine) coniferous forest composed primarily of lodgepole pine (*Pinus contorta*) and white-spruce (*Picea glauca*). Red squirrels are more common in the latter forest types in North America where they hoard and feed on the seeds of conifers (Smith, 1968; Hurly & Lourie, 1997). Research focused on a population of 47 individually marked squirrels in a single, contiguous forest patch approximately 60 ha in size. Each squirrel maintained an exclusive territory (approx. 0.5–1.0 ha) containing at least one central midden with a supply of stored cones, which was actively defended against intruders. Territories were distributed virtually uniformly

throughout the forest and individual territories abutted each other with little or no overlap in the territorial boundaries. To facilitate certain individual identification within and across field seasons, each squirrel was captured in its territory using a live-trap baited with peanut butter (Tomahawk Live Trap Company, Tomahawk, WI, USA), and unique dye marks (Clariol #52 Black) and ear tags were applied (Tag no. 1005-1; National Band and Tag Company, Newport, KY, USA). Trapping and handling techniques, and other research protocols, were approved by the Animal Welfare Committee of the University of Lethbridge (Protocol no. 0809) and by Alberta Sustainable Resource Development, Fish and Wildlife Division (Research Permit GP 30031; Collection License CN 30046). Additional details of the forest habitat, predator community, and the sample of squirrels studied are provided in Digweed & Rendall (2009a).

Playback experiment

One core requirement of functionally referential alarm signals is that the calls themselves be sufficient to elicit in listeners responses similar to those elicited by the predators themselves. For example, we would predict that, on hearing the broadband, bark-type alarm call proposed to refer to terrestrial predators, squirrels should move off the ground and higher up into the trees where they are safer from such threats. In contrast, on hearing the tonal, seet alarm call proposed to refer to aerial predators, squirrels should move down out of the treetops where they are more vulnerable to aerial threats. To test this possibility, we conducted a playback experiment using bark and seet alarm vocalizations recorded previously from focal squirrels during natural encounters with aerial and terrestrial predators (see Figure 1). Alarm call recordings were digitally recorded at 44.1 kHz with 16-bit accuracy using a Marantz PMD660 recorder and a Sennheiser ME66 shotgun microphone with a K6 powering module and a Sennheiser MZH60-1 windscreen.

The playback experiment involved three different alarm call stimuli. The first two involved pure bouts of either seets or seet-barks, previously proposed to represent aerial and terrestrial threats, respectively (Greene & Meagher, 1998). The third alarm call stimulus involved a naturalistic mix of both seets and seet-barks. This stimulus type was included specifically because in our own previous work seets and seet-barks were most often produced together in mixed bouts regardless of predator type (Digweed & Rendall, 2009a).

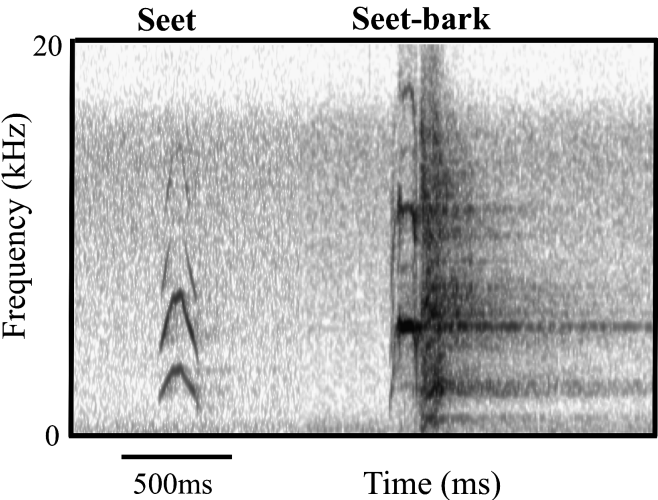


Figure 1. Spectrograms of seet and seet-bark vocalizations. Spectrograms were produced in PRAAT 5.1[®] using a Hanning window and overlapping 220-point fast-Fourier transforms with a 7.5 ms time step and 44.3 Hz frequency step.

In addition, we constructed two different versions of each of these alarm call stimuli, one in which the calls in a bout were concatenated together rapidly (a fast condition) and the other in which the calls were concatenated together more slowly (a slow condition). The fast and slow conditions of each type of alarm call stimulus were designed to test whether the rate of call delivery might also influence squirrels' responses.

The experimental design, thus, entailed six experimental conditions comprised of three different alarm call stimuli (pure bouts of seets, pure bouts of seet-barks, and mixed bouts that combined seets and seet-barks) presented at two different rates of call-delivery (fast and slow).

Stimulus construction and presentation

We constructed stimuli for the six different experimental conditions using seets and seet-barks previously recorded from eight different individuals in the study population. The fast condition for both seets and seet-barks involved a series of four different exemplars of each call type produced by the same caller and concatenated into a continuous bout of calling lasting 60 s. We varied the intervals between adjacent calls within each four-call series to avoid the artificiality that might result from the sound of four calls entirely

evenly spaced and continuously repeated for 60 s. And we created three variants of each four-call series that preserved the interval variation between calls but shuffled its patterning to create a fully balanced set of inter-call variation. Thus, in the first variant of the four-call series, the interval between the first and second call was set at 600 ms, while the intervals between the second and third and between the third and fourth calls was set at 300 ms. In the second variant of the four-call series, the interval between the first and second call was set at 300 ms, the interval between the second and third calls was set at 600 ms, and the interval between the third and fourth calls was set at 300 ms. Finally, in the third variant, the interval between the first and second calls, and between the second and third calls was set at 300 ms, while the interval between the third and fourth calls was set at 600 ms. These three variants of the four-call series were then concatenated together, with a constant interval of 800 ms between each four-call series. And this sequence of three different four-call series was repeated to produce a single continuous stimulus bout lasting 60 s (for additional details, see Figure 2).

The slow condition for both seets and seet-barks was constructed in exactly the same fashion, except that the intervals between calls within a four-call series and between concatenated series was doubled (i.e., 1200 ms, 600 ms and 1600 ms, respectively). The entire duration of such stimuli was also, therefore, doubled (to 120 s) in order to hold constant the total number of individual calls that subjects heard across the fast and slow experimental conditions. The only difference between the two conditions was the rate of call

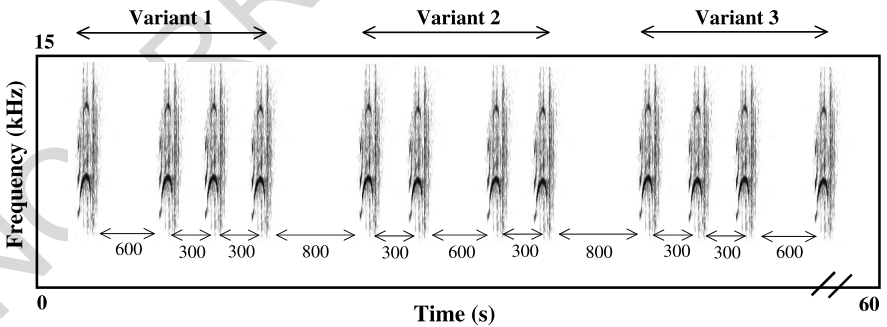


Figure 2. Graphic illustrating the construction of playback stimuli. Three different variants of a four-call series, each one varying the internal spacing of calls within a series, were concatenated together and the pattern repeated to produce a total stimulus lasting either 60 or 120 s. The example illustrated is for seets constructed in the fast condition. The same procedure was used for seet-barks.

1 delivery and, ultimately, the time period over which the calls were delivered 1
2 (60 versus 120 s). 2

3 We constructed three different sets of fast and slow versions of the seet and 3
4 seet-bark stimuli, with each set constructed of calls produced by a different 4
5 squirrel but matched for caller within a particular set (i.e., a fast seet stimulus 5
6 and a slow seet stimulus from each of three different callers; and a fast seet- 6
7 bark stimulus and a slow seet-bark stimulus from each of three different 7
8 callers; Total = 12 different experimental stimuli). 8

9 The combination-call stimuli were constructed from naturally occurring 9
10 mixed bouts of seets and seet-barks produced during predator encounters. 10
11 They involved no modification of the internal sub-structuring of call series. 11
12 Instead, they simply preserved mixed call sequences whose rate of call delivery 12
13 varied and approximately matched that used in our fast and slow condi- 13
14 tions of pure bouts of seets and seet-barks. These naturally mixed-bouts were 14
15 then truncated either at 60 ms or 120 ms to match the length of the other stim- 15
16 uli. Six such bouts were used as experimental stimuli, three each in the fast 16
17 and slow experimental conditions. Each bout came from a different caller. 17

18 All experimental stimuli were assembled into individual stimulus files using 18
19 PRAAT[®] 4.6.3 (Boersma, 2001). Playback stimuli were then stored on 19
20 and played from a Panasonic CF-P1 handheld computer. They were played 20
21 back through a Mineroff SME-AFS portable speaker (frequency response 21
22 110–12 000 Hz). Standardized amplitudes were used for each stimulus and 22
23 were established during a pre-testing period in a similar area of forest 1 km 23
24 away from the study site and out of the hearing range of squirrels who would 24
25 subsequently serve as experimental subjects. In this pre-testing period, stim- 25
26 uli were played from a distance of 50 m at a variety of different amplitudes 26
27 to establish realistic levels for the different call types at this distance and in 27
28 this type of forest. Thereafter, amplitude settings were held constant for each 28
29 stimulus type in experimental trials. 29
30

31 *Playback trials* 31
32

33 Experimental trials were conducted during the course of daily observations 33
34 of focal squirrels only as appropriate conditions arose. These included the 34
35 following requirements: that the focal squirrel had not encountered a preda- 35
36 tor that day; that it had been in its territory for the previous 15 min; that it had 36
37 not had a territorial interaction with another squirrel during this period; that 37

it had not itself vocalized in this period; and that no vocalizations (including
seets or seet-barks) had been heard from neighbouring squirrels during this
period.

When these conditions were met, a playback trial involved playing calls
from one of the six experimental conditions from a speaker hung approxi-
mately two-meters up a tree located next to the central midden of an adja-
cent territory (approx. 50 m away). Playing calls from an adjacent territory
allowed us to simulate a predator nearby without introducing the additional
possible confound that the calls would be interpreted as representing a terri-
torial intrusion by a neighbouring squirrel were they heard emanating from
a location within the subject's territory.

The focal squirrel was observed for 10-min post-playback to record its im-
mediate reactions to the playback stimulus. During this time, vocalizations
and behaviours were recorded in an all-occurrences fashion. An extended
15-min follow was then conducted on the focal squirrel to catalogue any
more protracted vigilance response squirrels might have had to the experi-
mental stimulus. To test any such protracted responses, we compared sub-
jects' vigilance rates (head-up scanning behaviour) during these 15-minute
post-playback intervals to baseline rates of vigilance recorded for the same
individuals. Baseline vigilance rates were calculated for each experimental
subject from exactly the same kind of 15-min follows conducted on days
prior to playback trials. Three such matched control periods were used to
calculate baseline vigilance rates for each experimental subject.

Results

General responses to alarm calls

A fully balanced set of 60 playback trials was conducted on ten squirrels,
each individual serving as a subject in all six experimental conditions. In
response to hearing alarm calls played back to them, focal squirrels stopped
their current activity and at least looked briefly in the direction of the speaker
(96.7%). In many trials, they also oriented their entire body (68.3%) so as to
face directly towards the speaker. Beyond such orienting movements, squir-
rels tended to remain motionless until the calls stopped. Occasionally, they
moved a short distance up or down the tree or across the ground (18.4%).
In no case did focal squirrels produce vocalizations themselves in response

to hearing the alarm calls of others played to them. Squirrels resumed their original activity (feeding or foraging) shortly after the alarm calls stopped but they also remained vigilant for an extended period, frequently interrupting their activity to scan the area.

Call-type specific responses

Focal squirrels' responses to alarm calls were not differentiated by experimental condition. Squirrels were equally likely to look immediately in the direction of the speaker whether the alarm calls played were seets, seet-barks or the combination variant in either their fast or slow versions (Fast: $\chi_2 = 2.07$, $p = 0.36$, $N = 30$; Slow: $\chi_2 = 1.79$, $p = 0.41$, $N = 30$). Similarly, they were equally likely to orient their entire body and to stare toward the speaker whether the alarm calls were seets, seet-barks or the combination variant in either the fast or slow versions (Fast: $\chi_2 = 0.67$, $p = 0.72$, $N = 30$; Slow: $\chi_2 = 1.58$, $p = 0.46$, $N = 30$). Squirrels' tendency to move a short distance up or down the tree in response to hearing alarm calls was not significantly different as a function of the type of call heard (Fast: $\chi_6 = 4.13$, $p = 0.39$, $N = 30$; Slow: $\chi_6 = 5.99$, $p = 0.42$, $N = 30$).

Protracted vigilance responses

Focal squirrels' vigilance rates following playback of alarm calls differed significantly from those observed during baseline observations ($F_{1,9} = 16.93$, $p = 0.0026$, $N = 90$). Rates of vigilance following alarm calls were, on average, five times higher than they were during matched control periods (Figure 3a). However, there was little evidence that squirrels' vigilance rates following alarm call playbacks differed significantly as a function of the particular alarm call stimulus they heard. Squirrels tended to be more vigilant following playback of either the naturalistic combination of seets and seet-barks or the pure bouts of seet-barks compared to the pure bouts of seets (Figure 3b). However, these outcomes were not statistically significant ($F_{2,9} = 2.82$, $p = 0.086$, $N = 60$). Differences in the rate of call delivery in the various stimulus types did not affect vigilance rates ($F_{1,9} = 0.2$, $p = 0.89$, $N = 60$).

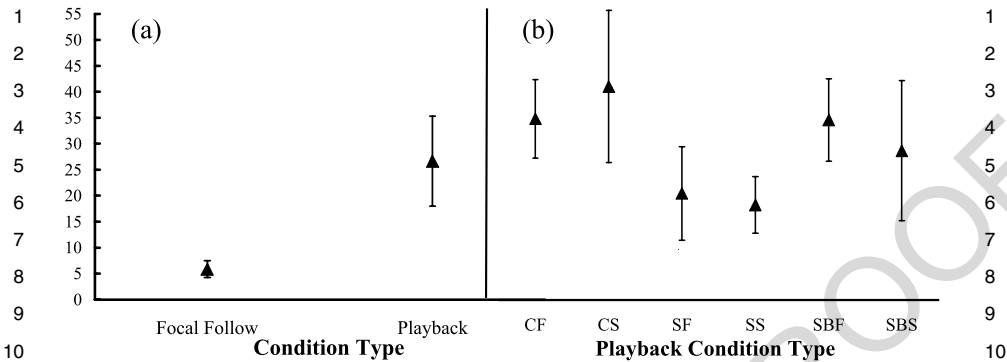


Figure 3. Comparisons of the percent of time (mean \pm SE) squirrels were vigilant during 15-min focal follows conducted under baseline conditions versus across all playback experimental conditions combined (a) and in each of the different playback experimental conditions (b). CF = combination fast; CS = combination slow; SF = seet fast; SS = seet slow; SBF = seet-bark fast; SBS = seet-bark slow.

Discussion

Red squirrels hearing their own species' alarm calls played to them from neighbouring territories responded immediately by interrupting their current activity and looking and sometimes orienting fully toward the source of the calls. At times, they also moved a short distance up or down the tree they were in. Squirrels also showed a more protracted change in their general vigilance, showing an increase in head-up scanning of their surroundings after hearing alarm calls. These responses indicate that squirrels registered alarm calls produced by others and found them salient, perhaps inducing some change in their general sensitivity to risk. However, there was little in the squirrels' responses to indicate that the different types of alarm call held any predator-specific, referential value for them. Thus, squirrels' tendency to attend and respond to alarm calls was not different for seets and seet-barks that have previously been proposed to reflect a referential distinction between aerial and terrestrial predators. Nor was there a difference in squirrels' tendency to move up or down the trees they were in to reduce the specific risks commonly associated with terrestrial and aerial predators, respectively (Macedonia & Evans, 1993).

There was a non-significant trend toward greater vigilance after hearing seet-barks than seets. This quantitative difference in vigilance behaviour might be interpreted as being consistent with a categorical distinction in the

types of predator signalled by the two call types and, thus, with a referential function of the calls. However, it is just as possible that the observed quantitative differences in vigilance reflects quantitative variation in some other non-referential dimensions associated with the two call types such as in their variable perceptual salience or the variable arousal induced by them, or in the variable imminence of the threat entailed (Owings & Hennessy, 1984; Owren & Rendall, 2001). At the same time, squirrels' vigilance responses were actually strongest to the combination call stimuli, which mixed seets and seet-barks together in the same bouts, and this outcome tends to muddy any straightforward categorical distinction in predator type signified by seets and seet-barks independently. More importantly, none of these quantitative differences in vigilance were actually statistically significant in our experiments. Hence, the pattern of non-significant variation does not really warrant specific inferences of any kind at this stage.

Overall, then, squirrels' responses were not sufficiently distinct or specific to the different alarm call types to support the proposal that the different alarm calls have predator-specific, referential value (Greene & Meagher, 1998). This outcome dovetails with complementary findings related to call production. Thus, Digweed & Rendall (2009a,b) reported that seets and seet-barks were produced together in mixed bouts of calling in response to predators of all major types. Indeed, they reported that the same two call types were also produced in similarly mixed vocal bouts during aggressive encounters with other squirrels intruding on a resident's territory (Digweed & Rendall, 2009b). Moreover, they reported that one of the call types (seets) was produced in an even wider range of contexts that involved no interaction with conspecifics, predators, or other individuals of any kind. For example, when moving entirely on their own, red squirrels often produce seets when making large leaps between trees and when descending the trunk of a tree toward the ground. The function of call production in the latter contexts remains enigmatic. However, it contributes to the species' relatively unspecific patterns of call production, which were noted as well in early descriptive and experimental studies (Smith, 1978; Lair, 1990; Price et al., 1990).

Taken together, the evidence on call production and on listener responses to calls suggests that the alarm calls that red squirrels produce in encounters with predators, as well as in other contexts, do not meet either functional criteria established for referential signals (Marler et al., 1992; Macedonia & Evans, 1993; Evans, 1997). This outcome for red squirrels bears on recent

1 theorizing about the range of factors that might facilitate or constrain the 1
2 evolution of referential communication systems in animals (Macedonia & 2
3 Evans, 1993; Blumstein, 2007; Furrer & Manser, 2009; Zuberbühler, 2009). 3
4 It suggests that, while the diversity of predators faced and the range of escape 4
5 options available might be important, and even necessary, conditions 5
6 for the development of referentially specific predator messages, they are not 6
7 by themselves sufficient. Red squirrels face a predator complement as diverse 7
8 as that faced by many primate and non-primate species reported to 8
9 produce referentially-specific predator vocalizations; and they inhabit forest 9
10 environments that offer equally (or more) diverse predator escape options. 10
11 Yet these conditions have not yielded informationally-specific vocalizations 11
12 about predators in red squirrels. 12

13 It is possible that this result reflects important social and life-history differences 13
14 between red squirrels and the primate and other taxa that are reported 14
15 to produce referential alarm calls (Blumstein & Armitage, 1997; Mc- 15
16 Comb & Semple, 2005; Sproul et al., 2006). The latter taxa are relatively 16
17 gregarious, group-living species surrounded by offspring and collateral kin. 17
18 These social conditions create the context in which referentially-specific 18
19 messages about predators might be functional to other group members and 19
20 where the costs associated with producing conspicuous alarm calls are more 20
21 than compensated by benefits accruing through kin selection, group augmentation 21
22 or other social processes (Sherman, 1977; Kokko et al., 2001; Da 22
23 Silva et al., 2002; Blumstein & Daniel, 2004; Blumstein, 2007; Wheeler, 23
24 2008). In contrast, red squirrels are largely solitary and assiduously territorial. 24
25 Their interactions with others are limited primarily to competitive interactions 25
26 over territories and the caches of stored cones they contain (Smith, 26
27 1968, 1978; Lair, 1990). The broader social networks of red squirrels are 27
28 not entirely known because settlement patterns of dispersing offspring are 28
29 not well documented, and long-term studies of individual social relationships 29
30 are lacking. Nevertheless, the generally solitary and competitive food- 30
31 hoarding and pilfering lifestyle of red squirrels as we currently understand it 31
32 suggests that they lack the social preconditions that favour the development 32
33 of referentially-specific predator warnings in more gregarious species. 33

34 Of course, this explanation then begs the question of why red squirrels 34
35 actually produce conspicuous alarm calls at all in encounters with predators 35
36 and in other situations? Elsewhere, we have suggested that this apparent 36
37 paradox might be resolved if the calls that red squirrels produce are not 37

actually targeted towards conspecifics as warnings about predators but rather are targeted directly at the predators (and other intruders) themselves as announcements that they have been detected (Digweed & Rendall, 2009b). Although not formally considered before for red squirrels, such predator-directed signals have been reported for a variety of other species (e.g., Tilson & Norton, 1981; Caro, 1995; Zuberbühler et al., 1999; Shelley & Blumstein, 2004; Fichtel, 2007; Rundus et al., 2007). Future research to evaluate this possibility in red squirrels will contribute further to our understanding of the evolution of alarm communication in animals.

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