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Predator-Associated Vocalizations in North American Red Squirrels (*Tamiasciurus hudsonicus*):
Are Alarm Calls Predator-Specific?

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ABSTRACT: North American red squirrels are a small-bodied, solitary, territorial species that faces a diversity of predators. One report suggested that red squirrels produce two distinct vocalizations to aerial and ground predators: a tonal ‘seet’ and a broadband ‘bark’, respectively. This categorical mapping between alarm call variants and predator classes suggested that red squirrels might manifest a system of predator- specific, referential alarm calls. To test this hypothesis, we undertook a multi-year study of red squirrels in southern Alberta, Canada. We report details of alarm call production by red squirrels during natural predator encounters, in response to a series of predator simulation experiments, and during encounters with non-predatory species, including conspecific territorial intruders. The pattern of alarm call production was consistent across these conditions and involved two main call types, the tonal seet call and a more broadband ‘seet-bark’ call, that corresponded closely to the bark call identified previously. However, there was little evidence that call production was specific to particular predator classes. Instead, the two call types were produced together in mixed bouts to predators of all types as well as to non-predatory species and conspecific intruders. These outcomes contradict the hypothesis that alarm calls in red squirrels are referentially-specific. We suggest instead that calls might be directed primarily at the intruders themselves and function to announce their detection and possibly aid in deterring or repelling them. This possibility is consistent with a variety of other important features of the behavior and life history of red squirrels.

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

Studies of communication are often thought to offer some insight into the way animals perceive the world around them and the proximate internal mechanisms that support adaptive responses to it (Cheney & Seyfarth 1990; Griffin 1992). Alarm calls have been an especially common and productive focus of this kind of research because the calls are often among the most conspicuous in species' repertoires and they can be connected comparatively unambiguously to discrete and dramatic events in the animals' lives, namely encounters with predators (reviewed in Blumstein 2007). One long-standing interpretation is that alarm calls reflect the underlying state of arousal or motivation experienced by callers when they encounter a predator, and that this motivational information is reflected in, and communicated to listeners through, structural details of the calls that are transmitted. Morton elaborated this interpretation of animal experience into a set of motivation-structural rules to account for structural variation in alarm calls and in other kinds of vocalization as well (Morton 1977; 1982). This framework emphasizes an animal's emotional engagement with events in the world both as the mechanistic catalyst to vocal production and as the content of the vocal messages that are thus transmitted to others.

An important shift in interpretations of animal communication was precipitated by landmark studies of the alarm vocalizations of vervet monkeys (Struhsaker 1967; Seyfarth et al. 1980). Vervet monkeys are small terrestrial monkeys subject to heavy predation by large raptors, cats, and snakes. Seyfarth et al. (1980) documented a small repertoire of discrete alarm calls that were produced specifically in response to these different predator classes and the calls alone were sufficient to induce functionally discrete escape responses in listeners. In combination, the predator-specific production of alarm calls and listeners' discrete responses to them suggested a capacity for language-like referential communication. While this framework does not exclude

emotional processes, it does highlight the importance of some additional perceptual or evaluative categorization of predators in both the mechanistic processes that influence signaling and in the content of vocal messages that are then transmitted to listeners (Evans 1997).

Subsequent research has confirmed the potential for categorical classifications of predators in some other primate species as well as some other mammals and birds (e.g., Diana monkeys: Zuberbühler 2000; Tamarins: Kirchlof & Hammerschmidt 2006; Meerkats: Manser 2001; Richardson's ground squirrels: Davis 1984; Chickens: Evans & Marler 1997; Chickadees: Templeton et al. 2005). At the same time, other studies have shown that what is most salient about predator encounters is not always the identity of the predator *per se* but other dimensions of such encounters (e.g., Blumstein 1995; Mateo 1996; Mateo et al. 1997; Le Roux et al. 2001; Fichtel & Kappeler 2002; Randall & Rogovin 2002; Digweed et al. 2005). For example, California ground squirrels (*Spermophilus beecheyi*) generally produce one kind of alarm call (a 'whistle') when they encounter large raptors and a structurally different alarm call (a 'chatter') when they encounter terrestrial predators (Owings & Virginia 1978; Owings & Leger 1980). Production of the two call variants maps closely onto the categorical distinction between aerial and terrestrial predators. However, the apparent predator-specificity of the alarm calls proves to be a coincidence of how squirrels typically encounter aerial versus terrestrial predators because production of the two alarm calls actually tracks variation in the imminence of the threat represented by either class of predator and thus how urgently vulnerable squirrels must respond to them (Owings & Hennessy 1984). Functionally, an alarm call system like this based on a distinction in response urgency, rather than predator class, makes sense for ground-dwelling species with a limited variety of escape options compared to species inhabiting more structurally

89 complex environments (Macedonia & Evans 1993).

90
91 North American red squirrels (*Tamiasciurus hudsonicus*) offer an additional opportunity
92 to examine potential variation in predator perception and response. Red squirrels are exposed to
93 a diversity of predator types (e.g., coyotes, lynx, marten, owls, hawks) and the forest
94 environments they inhabit offer a diversity of possible escape responses. There have been
95 relatively few studies on the vocal communication of red squirrels (Smith 1968; 1978; Embry
96 1970; Lair 1990; Greene & Meagher 1998). However, they are widely known for being
97 extremely vocal and for confronting predators and other intruders with conspicuous
98 vocalizations. One experimental study reported that red squirrels produce one kind of
99 vocalization (a tonal ‘seet’) in response to aerial threats and a structurally distinct vocalization (a
100 broadband ‘bark’) in response to terrestrial threats (Greene & Meagher 1998). This outcome
101 suggests that, like vervet monkeys and some other species, red squirrels might also manifest a
102 system of acoustically distinct, referential alarm calls based on some discrete perception and
103 categorization of different predators. At the same time, other studies of red squirrels have
104 described the production of these same call types in other, non-predatory contexts (Smith 1978;
105 Lair 1990) suggesting that the calls might not be entirely predator-specific.

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107 In this paper, we report results of a multi-year study of red squirrels to address these
108 ambiguities. In part I, we report patterns of behavior and alarm call production during natural
109 encounters with predators. In part II, we report a series of follow-up experiments that probe the
110 predator-specific production of alarm calls more systematically. Finally, in part III, we report
111 patterns of production of the same calls during other, non-predatory disturbances.

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I. NATURAL PREDATOR ENCOUNTERS

METHODS

Study Site and Subjects

Research was conducted at the R.B. Miller Field Station in the Sheep River Valley of Kananaskis Provincial Park, Alberta (50°39 N, 114°39 W), which is situated in the foothills of the Canadian Rockies. The habitat 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). Research focused on a population of 47 individually marked squirrels in a single, contiguous forest patch approximately 60 ha in size. Each individual maintained an exclusive territory (0.5 – 1.0 ha) containing at least one central midden with a supply of stored cones that was actively defended against conspecific intruders. In order 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, Wisconsin) and unique dye marks (Clariol #52 Black) and ear tags were applied (National Band and Tag Company, Kentucky: Tag#1005-1). Trapping and handling techniques, and the research protocols explained below, were approved by the Animal Welfare Committee of the University of Lethbridge (Protocol #0809) and by Alberta Sustainable Resource Development, Fish and Wildlife Division (Research Permit GP 30031; Collection License CN 30046).

The Predator Community

Kananaskis Provincial Park is part of a network of protected foothills and mountain habitats extending from Yellowstone National Park, Wyoming (USA) to the Yukon Territory (Canada). In the Kananaskis study area, the predator community contains various raptors that could prey on red squirrels, including large eagles (Golden eagle and Bald-eagle), broad-winged hawks (Red-tailed hawk), forest accipiters (Sharp-shinned hawk, Cooper's Hawk, Northern goshawk), falcons (Prairie falcon) and large owls (Great horned owl, Great gray owl). It also includes several mammals that are frequent or occasional predators on red squirrels including pine martens, long-tailed weasels, coyotes, bobcats, cougars, and grizzly and black bears. During the study, all of these species were confirmed in the study area, although we did not witness squirrels encountering every one of these species during focal observations.

Data Collection and Analyses

Research was conducted in three consecutive years (2005-2007) primarily between May and November, representing the late spring, summer, and fall seasons at this latitude. Data collection focused on all natural encounters with known predators and included the species involved, the squirrel's response, and a continuous record of all vocalizations produced. Vocalizations were recorded using a digital Marantz PMD660 recorder and a Sennheiser ME66 shotgun microphone with a K6 powering module and a Sennheiser MZH60-1 windscreen. The data available for analysis thus consisted of squirrels' behavioral responses to specific classes of predators as well as the number and types of vocalizations they produced.

RESULTS

A. General Responses to Predators

During 536 hours of focal observation, we witnessed 21 cases where a squirrel encountered a known predator (Table 1). This sample involved 16 different squirrels and entailed seven encounters with coyotes (*Canis latrans*), six with Great gray owls (*Strix nebulosa*), four with northern goshawks (*Accipiter gentilis*), and four with pine marten (*Martes americana*). In each case, squirrels who spotted a predator from a position in a tree responded by immediately stopping their current activity and freezing momentarily while oriented toward the predator. They then remained in place staring at the predator and, after a short interval, began to stomp their hind feet and flick their tail back-and-forth over their back while producing a steady stream of vocalizations; or they first scurried a short distance up or down the tree they were in before stopping, orienting again toward the predator, and then stomping their feet, flicking their tail and vocalizing. Alternatively, if the squirrel was on the ground to begin with, it bolted immediately to the nearest tree, climbed to approximately 5m and then commenced foot-stomping, tail-flicking and vocalizing. In each encounter, squirrels produced vocalizations in extended bouts lasting up to 11 minutes ($X = 65.35$ seconds), involving hundreds of calls, and sometimes continuing after the predator had left the area. In all cases, vocal bouts were composed of a mix of two different call types, a tonal 'seet' call and a composite 'seet-bark' call composed of a tonal seet component appended to a broadband 'bark' call. Spectrograms of call types are shown in Figure 1.

We observed an additional 10 cases where squirrels encountered another species that would seem to pose no predatory threat but to which the squirrels showed behavioral and vocal

responses that paralleled their reactions to confirmed predators (Table 1). This sample involved eight different squirrels and entailed six encounters with ravens (*Corvus corax*), three with white-tailed deer (*Odocoileus virginianus*), and one with a short-tailed weasel (*Mustela erminea*). Although none of these species are reported to be predators on squirrels, it is certainly possible that one or more of them (weasel, raven) might represent a threat to infant squirrels or at least that they might be mistaken for a predator in some situations.

B. Predator-Specific Behavioral Responses

The potential association between specific behavioral responses (freeze, move up tree, move down tree) and specific predator types was tested using contingency analyses. Because the sample was small when divided among the different species encountered, we first collapsed the species encountered into two broad predator classes: aerial and terrestrial. The resulting test revealed no significant association between the squirrels' behavioral response and either class of predator (Pearson's Chi-Square: $\chi^2=1.3$, $P=0.51$, $N=31$). Squirrels were as likely to move up or down the tree they were in, or to remain immobile in a tree, after detecting an aerial or terrestrial predator. We then limited the test to encounters with known predators, but the outcome did not change: there was still no association between behavioral response and predator type ($\chi^2=1.55$, $P=0.45$, $N=21$). Finally, we broke the terrestrial predator category into two different categories, one for coyote and one for marten, in case our original lumping of these two predators into a single category blurred important variation in the squirrels' responses to them. Marten are certainly different from coyote in being highly arboreal and capable of pursuing squirrels through the trees as well as on the ground. This re-categorization of predator types did not change the outcome. There were still no significant associations in the squirrels' behavioral

responses to coyote, marten or aerial predators ($\chi^2=6.49$, $P=0.16$, $N=21$).

C. Predator-Specific Vocal Responses

The manifest mixing of both seet and seet-barks within all bouts of calling indicated from the outset that there was no strict association between call type and predator class. Nevertheless, one or other call type might predominate in encounters with particular predators. To test this possibility, the relative production of seets and seet-barks to aerial and terrestrial predators was tested using a Repeated Measures Analysis of Variance (rmANOVA) with both call type and predator type as factors. Because the duration of calling bouts varied tremendously, we focused these and subsequent tests on the squirrels' call production in the first 30-seconds of their encounters with a predator. The first test compared call production in response to aerial and terrestrial categories, where both threatening and non-threatening species were included. Results indicated a main effect for call type (ANOVA: $F_{1,16}=14.9$, $P=0.0014$, $N=31$) with more seet-barks than seets produced overall (partial eta-squared, $h^2=0.167$). However, there was no main effect of predator type ($F_{1,16}=0.90$, $P=0.355$), nor was there a significant interaction term ($F_{1,16}=1.21$, $P=0.288$).

In a follow-up analysis, we again tested for variation in call production to aerial and terrestrial predators but after restricting the sample only to known predators. Results again indicated a main effect for call type ($F_{1,14}=24.61$, $P=0.0002$, $N=21$), with more seet-barks than seets produced overall ($h^2=0.201$). There was no main effect of predator type ($F_{1,14}=0.75$, $P=0.402$) but there was now a significant interaction between call type and predator type ($F_{1,14}=4.84$, $P=0.045$) which reflected greater production of seet-barks to terrestrial predators

($h^2=0.046$).

Finally, we again sub-divided the terrestrial predator category into separate categories for coyote and marten. Results were similar in that there was again a main effect for call type ($F_{1,13}=32.27$, $P=0.000075$, $N=21$), with more seet-barks than seets produced overall ($h^2=0.182$) but still no main effect of predator type ($F_{2,13}=0.35$, $P=0.709$). There was again a significant interaction between call type and predator type ($F_{2,13}=7.40$, $P=0.0071$), which appeared to be driven by the fact that coyotes elicited more seet-barks and fewer seets by comparison to the other predators ($h^2=0.092$; Figure 2).

D. Call Patterning within Encounters

To examine the additional possibility that the mixed bouts of seets and seet-barks produced in all predator encounters might nevertheless show some predator-specific patterns of internal structuring, we divided the initial 30-seconds of each calling bout into three successive time bins (i.e., 0-10 seconds; 10-20 seconds; and 20-30 seconds). We then tallied the production of seets and seet-barks within each time bin, and used a rmANOVA to test these tallies for variation as a function of predator type after limiting the data to encounters with known predators. Results indicated a main effect of call type (ANOVA: $F_{1,13}=34.21$, $P=0.000057$, $N=21$), with more seet-barks than seets produced overall ($h^2=0.147$). There was no main effect of predator type ($F_{2,13}=0.33$, $P=0.726$), but there was a significant interaction between call type and predator type ($F_{2,13}=8.04$, $P=0.0053$), with the coyote eliciting more seet-barks and fewer seets compared to the other predators ($h^2=0.075$). There was no main effect of time bin ($F_{2,26}=0.18$, $P=0.998$), but there was an interaction between call type and time bin ($F_{2,26}=7.39$, $P=0.00288$) with seet calls

produced more in the first time bin and seet-barks produced more in the later time bins ($h^2=0.114$; Figure 3a).

DISCUSSION

Squirrels in our study population were exposed to a full complement of predators and their behavioral and vocal responses to them agreed well with previous descriptions (Smith 1968; 1978; Lair 1990; Embry 1970). Thus, squirrels displayed the two broad patterns of response commonly described: the first being to remain silent and immobile initially and to monitor the predator from a safe location; and the other being conversely to confront predators with a stream of loud vocalizations, while stomping their hind feet and flicking their tail over their back.

The more detailed pattern of call production we observed also agreed in broad outline with that described more recently by Greene & Meagher (1998). In that study, squirrels tended to produce two different calls in encounters with predators, a relatively low amplitude, high-frequency and tonal seet call that resembled in structure the ventriloquial seet alarm vocalizations of many passerine birds; and a broadband bark call that resembled the more localizable calls used by passerine birds when mobbing a predator (Marler 1955). Squirrels in our study likewise produced the same tonal seet call as well as a more broadband call variant that combined a tonal seet note appended to a broadband bark, yielding a composite ‘seet-bark’ call. Greene & Meagher (1998) also reported use of this combination seet-bark call in predator encounters but it was produced less frequently than either the seet or the bark calls alone. In contrast, although squirrels in our study population also occasionally produced bark calls by themselves, they did not do so in encounters with predators.

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272 This variation in call usage might reflect a real difference in call production by squirrels
273 in the two study populations. However, it is also possible that the differences are largely
274 definitional. While seets are structurally distinct and are easily discriminated from the other two
275 call types spectrographically, the delineation of barks and seet-barks is less straightforward
276 because the structure of these call variants grades continuously. Hence, some of the differences
277 in call production might be attributed simply to a difference in the criteria used to label the
278 broadband call variants (i.e., barks and seet-barks) in the two studies.

279
280 At the same time, Greene & Meagher (1998) reported that seets were produced primarily
281 in response to aerial threats and barks were produced primarily in response to terrestrial threats.
282 They proposed that this categorical mapping of call types and predator classes was the basis for a
283 system of referential communication about predators. Our results were again similar in as much
284 as terrestrial threats (coyotes) also elicited more of the broadband type of call (seet-bark);
285 however, we did not find anything like exclusive use of either the tonal or the broadband call
286 types in encounters with particular predators. Instead, squirrels used the tonal and broadband call
287 types in a far more mixed fashion: both types of call were produced in mixed bouts to each of the
288 different classes of predator, with the tonal seet call predominating in the early stages of a calling
289 bout and giving way to the more broadband seet-bark call as a calling bout continued. Greene &
290 Meagher do not say whether this kind of mixing of tonal and broadband call types occurred
291 within single calling bouts in their study. However, they do report some mixing of both tonal and
292 broadband calls to predators of the same type. For example, they found that both tonal seets and
293 the more broadband seet-bark calls were produced to aerial threats, and that, although terrestrial

threats elicited primarily bark calls, they also elicited a small number of seet calls as well (see Figure 2 in Greene & Meagher 1998).

It is also possible that some of the remaining differences between the studies reflect qualitative differences in research design and predator sampling. Whereas the results that we report, and that form the basis of earlier descriptive studies, are based on naturalistic predator encounters, the results reported by Greene & Meagher (1998) are from an experimental study involving simulated predators. This difference in predator exposure might have influenced squirrels' vocal responses. To address this possibility, we also conducted a set of experiments using simulated predators.

II. EXPERIMENTS USING SIMULATED PREDATORS

We conducted a series of three experiments involving simulated predators. The first involved using taxidermied models of known predators. The second and third experiments incorporated movement into the predator simulations and replicated as closely as possible the experimental treatments used previously by Greene & Meagher (1998).

METHODS

A. Taxidermied Predators

This experiment involved taxidermied models of known predators that were also present in the study area and encountered by squirrels during our research: coyote, marten, and great horned owl. Focal squirrels were the subject of one trial with each of the three models with presentation order randomized across subjects. The experimental protocol was designed to standardize as

much as possible the way each squirrel encountered the predator mount. To this end, a focal squirrel was first trapped in its territory. The cage was then covered with a canvas cloth and moved to the central midden in the territory, while the predator model was set-up on or next to the midden approximately 5m from the trapped squirrel. The canvas cover was left in place for 60 seconds, after which it was lifted to expose the squirrel to the model from within the trap. The squirrel was then released in the direction of the predator model and its behavioral and vocal responses in the 10-minutes following release were audio- and video-recorded for later scoring.

Using this trapping protocol, we could control in our experiment for variation in many aspects of a squirrel's recent experience that might otherwise affect its detection of, or response to, the different predator models. We could also standardize how squirrels encountered each predator and where in their territory they encountered it, which could otherwise introduce additional uncontrolled variability into squirrels' responses. These squirrels were regularly trapped, handled and released in the course of other aspects of this research such as to accommodate routine animal assessment, weighing and marking, or to facilitate other research protocols. As a result, they were accustomed to the trapping regimen and readily entered traps.

B. Moving Terrestrial Predator

In their simulation of a terrestrial predator, Greene & Meagher (1998) used three dogs of different breeds. In experimental trials, one of the dogs was released toward a squirrel that was "foraging on the ground, collecting cones in trees, or resting on a branch." The latter conditions included obvious variation in the squirrel's vulnerability, but this was not controlled or analyzed systematically. In our experiment, we attempted to replicate this protocol but also to control for

variation in how squirrels encountered the terrestrial predator. We selected one dog (Billy) who was ideally suited for this experiment. Billy was of mixed breed and similar in size and coat-color to a coyote.

Experimental trials were conducted only after a focal squirrel had been followed for 10 minutes during which time it remained in its own territory and had not encountered a neighboring squirrel or any other disturbance. Trials were conducted in two different conditions. The first condition was designed to simulate a threat in a context of high vulnerability. In this condition, the focal squirrel was followed until it was located on or near the ground, and Billy was held on-leash and maintained out of sight. On instruction, Billy was moved into the area and allowed to locate the squirrel on his own, at which point the leash-control was relaxed and Billy was allowed to pursue the squirrel naturally. However, we maintained control of the leash at all times to ensure that no harm could come to the squirrel, and to stop the trial if necessary.

The second condition was designed to simulate a threat in a context of low vulnerability. The protocol in this condition was the same except that the focal squirrel was followed until it was located in a tree a safe distance off the ground ($>5\text{m}$), at which point, Billy was moved into the area and to the base of the tree containing the squirrel. Thereafter, he was permitted to react naturally but retained on-leash. In both conditions, Billy remained in the territory for 5-min after which he was led away and out of sight. We continued to follow the focal squirrel and record its behavioral and vocal responses for an additional 10-minutes.

C. Moving Aerial Predator

The simulated aerial predator used by Greene & Meagher (1998) was a small model bird ('Amazing TIM': De Ruymbeke Co. Marseille, France). The model had an approximate wingspan of 30 cm and was described as similar in body size to a Cooper's Hawk (*Accipter cooperii*). The main body of the model was clear plastic and the wings were multi-colored with portions of blue, green, red and yellow. The model was made to fly by means of a wind-up rubber band that resulted in a sustained flapping flight. In an attempt to replicate this experiment, we obtained the same bird model. In initial efforts to use this model, we found it difficult to control its flapping flight pattern and trajectory, which was not at all natural for a stooping raptor. In flight, the unwinding elastic band also made considerable noise, as did the flapping of the plastic wings. Both noises were conspicuous and unnatural. As a result, we abandoned the use of this model. In its place, we used a small Frisbee®, which has become a standard protocol for simulating a low-flying aerial predator and has been used successfully in previous studies on ground squirrels (e.g. MacWhirter 1992; Sloan et al. 2005; Wilson & Hare 2006).

Experimental trials followed the same precautions outlined previously. In addition, trials in this experiment were conducted only when the squirrel subject was stationary or moving slowly across the ground, and thus in a vulnerable position. Trials were conducted in two different conditions. The first condition was designed to simulate a fleeting predator threat. In this condition, the Frisbee® was projected over the squirrel's head at a height of approximately 1.5m to mimic the low-flight of a stooping raptor and landing out of sight. The Frisbee® was small (25 cm in diameter) and forest-green in color to limit the squirrel's ability to localize it after it passed over-head. The second condition was designed to simulate a more persistent aerial

threat. In this condition, the Frisbee® was projected over the squirrel's head and in the direction of, and landing near, the taxidermied model of a great-horned owl. This combination was designed to simulate both the rapid movement of an aerial predator followed by its persistence in the area. In both conditions, data were collected on the squirrel's behavioral and vocal responses in the 10-min following stimulus presentation.

RESULTS

A. Taxidermied Predators

Eleven different squirrels were tested, each one receiving one trial with each of the three predator types. The squirrels' responses in these trials were similar to those observed in natural encounters with predators. After release from the trap, squirrels tended to bolt immediately to the nearest tree and retreat to a safe height, where they then either remained silent and immobile while focused on the predator, or began foot-stomping, tail-flicking and vocalizing. In five trials, they bolted directly to their central midden instead, and disappeared into one of its burrows, or they bolted across the ground and out of sight. These behavioral responses were not differentiated by predator type (Pearson's Chi-square: $\chi^2=4.38$, $P=0.35$, $N=84$).

Squirrels vocalized in 20 of the 33 trials, in each case in bouts containing both seets and seet-barks. As in the natural predator encounters, there was a main effect of call type (ANOVA: $F_{1,10}=11.4$, $P=0.0070$), with more seet-barks than seets produced overall ($h^2=0.06$). There was some indication that predator type affected the number of calls given, with more calls produced to the coyote mount than to other mounts, however this effect was not statistically significant ($F_{2,10}=2.72$, $P=0.090$). There was no interaction of call type and predator type ($F_{2,20}=1.11$,

$P=0.349$). There was also no main effect of time bin ($F_{2,10}=0.17$, $P=0.842$) but there was a significant interaction between call type and time bin ($F_{2,10}=16.53$, $P=0.000058$) with seets produced more in the first time bin and seet-barks more in the latter two time bins ($h^2=0.07$; Figure 3b). There was also some indication of a three-way interaction between call type, predator type and time bin, with more seet-barks produced to the coyote mount in later time bins, however this interaction term was not statistically significant ($F_{4,40}=2.46$, $P=0.060$).

B. Moving Terrestrial Predator

A total of 12 different squirrels were tested in both experimental conditions (Table 1). In all trials in the high vulnerability context and most of those in the low vulnerability context, Billy easily detected the squirrel and ran after it. Billy was remarkably silent throughout, never growling or barking at the squirrel. However, he did remain fixated on it throughout each trial until led away, in many cases shifting position to get a better look at the squirrel when it moved and often lunging toward the squirrel or stretching up the base of the tree in an attempt to reach it. In the low vulnerability trials, when squirrels started from a safe location in a tree, their initial response was to freeze and remain in the same position, while monitoring the dog. If Billy subsequently moved quickly or attempted to stretch up the tree, the squirrel typically retreated further up the tree. In the high vulnerability trials, when squirrels started on or near the ground, they bolted to and up the nearest tree. If Billy remained motionless for a time at the base of the tree, squirrels would then often move down the tree to inspect Billy more closely. If he moved again, squirrels retreated back up the tree. There was a greater tendency for squirrels to retreat further up the tree in high vulnerability trials (32.1%) and to remain in the same position in low vulnerability trials (21.4%). However, analyses of the more protracted responses in the two experimental conditions

indicated that these differences were not statistically significant (Pearson's Chi-square: $\chi^2=6.72$, $P=0.081$, $N=24$).

In all 12 of the high vulnerability trials, but only five of the 12 low vulnerability trials, squirrels also vocalized. Once again, calling involved mixed bouts of both seet and seet-bark vocalizations and was accompanied by foot-stomping and tail-flicking. Results revealed no main effect of call type (ANOVA: $F_{1,11}=0.25$, $P=0.623$, $N=24$) but a main effect of experimental condition ($F_{1,11}=8.57$, $P=0.013$), with more calls of either type being produced in the high vulnerability condition ($h^2=0.131$). There was no main effect of time bin ($F_{2,11}=0.25$, $P=0.782$), but there was a significant interaction of call type and time bin ($F_{2,11}=6.29$, $P=0.006$). This interaction showed the same pattern observed in the natural predator encounters and the two previous experiments, with seet calls predominating early in calling bouts and giving way to seet-barks as calling bouts continued ($h^2=0.063$; Fig. 3d).

C. Moving Aerial Predator

A total of 13 different squirrels were tested in both experimental conditions (Table 1). In all cases, squirrels were on or near the ground when tested and their initial responses to the Frisbee® passing over-head were the same in both experimental conditions: they bolted to and up the nearest tree and then oriented in the direction of the Frisbee's® flight path. In one trial, a squirrel froze momentarily on the ground as the Frisbee® passed overhead before bolting for the nearest tree. In none of these trials did squirrels run to their midden or for any extended distance across the ground and out of sight. In the fleeting condition, and once in a tree, they remained focused on the Frisbee® if it remained in sight, or scanned the area if it did not. In the persistent

condition, and once in a tree, they tended to remain fixated on the owl mount for an extended period. Their more protracted responses in the two conditions involved either remaining in place or moving some distance up or down the tree while scanning the area or fixating on the visible Frisbee® or the owl mount. These more protracted behavioral responses were not differentiated by experimental condition (Pearson's Chi-square: $\chi^2_1=0.722$, $P=0.395$, $N=26$).

In 11 of 13 trials in the fleeting condition, and 12 of 13 trials in the persistent condition, squirrels produced vocalizations upon reaching the tree. Once again, calling involved mixed bouts of both seet and seet-bark vocalizations and was accompanied by foot-stomping and tail-flicking. Results revealed no main effect of call type (ANOVA: $F_{1,12}=0.53$, $P=0.480$, $N=26$) but a main effect of experimental condition ($F_{1,12}=5.09$, $P=0.043$), with more calls of either type being produced in the persistent condition ($h^2=0.050$). There was no main effect of time bin ($F_{2,12}=2.08$, $P=0.146$). The interaction of call type and time bin showed the same pattern as observed in the still mount experiment and natural predator encounters with more seet-barks than seets being produced in later time bins, but this pattern was not actually significant in this case ($F_{1,12}=2.8$, $P=0.08$, $N=26$).

In this experiment, the nature of the threat represented by the Frisbee® passing overhead might have been ambiguous to squirrels initially and so we re-ran this analysis after extending the response window beyond the initial 30-second period to include two additional time bins. These two additional time bins were constructed by dividing the remaining portion of each calling bout into middle and end time bins of equal length. Because the absolute duration of these additional time bins could vary across individuals and calling bouts, we adjusted the call tallies

in these time bins to generate a rate of calling expressed per 10-second interval, making the values in these time bins equivalent to those for the initial three time bins and our previous tests.

Results of these more protracted calling patterns confirmed the former main effect of experimental condition (ANOVA: $F_{1,12}=10.73$, $P=0.0066$), with more calls of either type being produced in the persistent condition ($h^2=0.042$). They also revealed a main effect of call type ($F_{1,12}=7.82$, $P=0.016$, $N=26$), with more seet-barks than seets produced overall ($h^2=0.043$), and a main effect of time bin ($F_{4,48}=2.80$, $P=0.036$) with more calls produced in the final time bin ($h^2=0.18$). The interaction of call type and time bin was now significant ($F_{4,48}=5.10$, $P=0.0016$; Figure 3c) with more seet-barks being produced in the later time bins ($h^2=0.047$). Finally, there was also a significant three-way interaction between call type, time bin and experimental condition ($F_{4,48}=2.65$, $P=0.044$), with more seet-barks produced in the later time bins particularly in the persistent predator condition ($h^2=0.021$).

DISCUSSION

Squirrels appeared to treat the taxidermied predator models and the simulated moving predators similarly to natural predators. They showed similar behavioral responses to the various predator models, including retreating to a safe distance or freezing and remaining immobile in a safe position while monitoring the predator initially. They then confronted the models with a stream of vocalizations while foot-stomping and tail-flicking, thereafter periodically shifting up or down the tree in order to retreat further away, or to approach and inspect the model. The specific patterns of call production to the predator models also mirrored those observed in response to real predators. Thus, the squirrels produced protracted bouts of calling which were again

composed of a mix of both seet and seet-bark vocalizations. Seet-bark calls were produced in greater numbers overall, as was true in natural predator encounters as well. There was also some indication that seet-bark calls were produced more in response to the taxidermied coyote model. This association was not statistically significant, but it did parallel the pattern observed in response to real coyotes in part I and matched the strongest call-type association reported by Greene & Meagher (1988). However, there were actually no significant predator-type effects on patterns of alarm call production, and thus little additional evidence that alarm calls were used in a predator-specific fashion.

At the same time, there were a number of additional illuminating patterns. First, in experimental trials with Billy, there was a clear effect of a squirrel's initial vulnerability on their call production: squirrels called at much higher rates when they detected Billy from a relatively vulnerable position on the ground compared to when they detected Billy from a relatively safe location in a tree. This outcome suggests that relative vulnerability and perhaps the naturally associated dimensions of relative risk, threat and response urgency are additional salient dimensions of predator encounters which can affecting calling behavior in red squirrels, just as they do in some other species (Owings & Hennessy 1984; Blumstein 1995; Warkentin et al. 2001).

Notably, the mixing of seet and seet-bark calls within call bouts did not change in high-vulnerability conditions, only overall vocal output. Indeed, this pattern of mixed bouts of seets and seet-barks was consistent across the three experiments as well as the natural predator encounters and showed an additional consistent temporal pattern: low-amplitude seet calls were

523 produced early in a calling bout and gave way to louder, broadband seet-barks as calling bouts
524 continued. The consistency in this calling pattern across all predator classes strongly suggests
525 that predator identity by itself is not the most salient dimension of predator encounters
526 influencing call production. Rather, it suggests that there might be something specifically about
527 the temporal patterning of such encounters that is more salient. Indeed, that possibility is
528 supported by results of the simulated aerial predator experiment. Squirrels' vocal responses in
529 that experiment showed the same mixing of seet and seet-bark calls within calling bouts. They
530 also showed higher overall levels of call production specifically in the persistent condition,
531 which simulated an aerial predator remaining in the area after passing overhead. Furthermore,
532 this increase in overall call production in the persistent condition was driven by greater
533 production of seet-barks in the later time bins as calling bouts became more protracted.

534
535 Taken together, these patterns suggest that the more salient dimension of predator
536 encounters, at least as they affect the production of alarm calls, might be the persistence of the
537 threat that it represents rather than the specific type of predator involved. In the initial stages of
538 an encounter with any predator, red squirrels produce the low-amplitude tonal seet call. These
539 calls give way to louder broadband calls if the predator persists in the area. This patterned vocal
540 response could sometimes create an incidental association between call type and predator class,
541 if aerial predators often present themselves fleetingly (and thus elicit only seets), whereas
542 terrestrial predators tend to remain in the area longer (and thus elicit seet-barks as well). And this
543 account might help to explain the statistical association between seet-barks and coyotes observed
544 in the natural predator encounters we report because that association emerged in the later stages
545 of calling bouts. It might also explain why we did not find the same association in the subsequent

experiment using taxidermied predator models. In that experiment, we controlled and standardized how long squirrels saw each of the different predator models and thereby removed any natural occurring variation in predator persistence among them. This account might also help to explain the apparent predator-specificity of seets and barks reported by Greene & Meagher (1998) if there was some difference in how long the bird model and live dogs were presented to squirrels in their experiment.

Of course, it could still be argued that, although predator persistence might be the more salient dimension of predator encounters to the squirrels, the incidental association between predator persistence and predator identity nevertheless yields an alarm call system that is functionally referential in the sense that the calls will often effectively serve to pick out the predator class distinction between aerial versus terrestrial threats. We acknowledge this possibility but it is weakened substantially by the observation that red squirrels also produce the same calls to non-predators, a phenomenon that others have described (Smith 1978; Embry 1970; Price et al. 1990; Price 1994) and that we also observed and reported in part I. It is possible, as noted earlier, that some of these other non-predatory species elicit calling because they are mistaken for predators. However, among the non-predators that elicit these same calls are other, conspecific squirrels, and it is doubtful that they too are routinely mistaken for predators. It is not clear, though, whether call usage in encounters with other squirrels is similar to that observed in predator encounters, and so to address this issue, we report in the next section on squirrels' behavioral and vocal responses in encounters with other squirrels.

III. ENCOUNTERS WITH OTHER SQUIRRELS

METHODS

Data Collection and Analysis

Instances in which a focal squirrel encountered and engaged another squirrel intruding on its territory were recorded during the course of behavioral sampling in the same way that encounters with predators were recorded.

RESULTS

A. General Responses to Squirrel Intruders

We observed 36 cases where the focal squirrel being sampled actively engaged a conspecific intruder detected on its territory. This sample involved 18 different focal squirrels and at least 11 different intruders. In these interactions, focal squirrels (the residents) were typically in a tree (80.6%) when they detected the intruder moving along the ground across the resident's territory. Residents stopped their current activity and oriented toward the intruder. They then vocalized and flicked their tail over their head (but tended not to foot-stomp). They then either remained in place while continuing to vocalize and tail-flick, or they bolted down the tree and gave chase while the intruders retreated. Chases sometimes involved physical contact if residents overtook intruders. Encounters sometimes also involved repeated cycles of calling and chasing if intruders remained within or near the territory, or returned to it again shortly after being chased away. As a result, some encounters were relatively short, while others were quite protracted lasting up to 15.6 minutes and involving hundreds of calls.

In 29 of the encounters, residents produced seets, seet-barks, or more typically a

combination of the two call types in protracted bouts like those produced in response to predators. In 10 of these encounters they also produced one or more ‘rattle’ calls. In an additional seven cases, they produced only rattle calls. In some encounters, intruders also vocalized. Although it was not possible to collect systematic data on the calls produced by the intruder at the same time that these data were being collected for the resident, intruders did not produce rattles, seets or seet-barks but rather only ‘squeak’ calls.

B. Call Patterning within Squirrel Encounters

Because rattles were produced in only a fraction of encounters, our analysis of call patterning during encounters with other squirrels focused on their production of seets and seet-barks and was conducted in exactly the same way as our tests of calling patterns in response to predators. rmANOVA tests revealed a main effect of call type (ANOVA: $F_{1,17}=15.15$, $P=0.0011$, $N=29$), with more seet-barks than seets being produced overall ($h^2=0.57$). There was also an effect of time bin ($F_{2,17}=3.40$, $P=0.045$), with the number of calls produced increasing over time ($h^2=0.15$). There was also an interaction between call type and time bin ($F_{2,17}=10.64$, $P=0.00025$) which paralleled the pattern observed in natural and simulated predator encounters: seets were produced more in the first 10-seconds of encounters with other squirrels and then decreased in frequency, while the production of seet-barks increased over time and predominated in the 20 and 30 second time bins ($h^2=0.36$; Figure 3e).

DISCUSSION

Squirrels’ responses to conspecific intruders were both similar to, and different from, their responses to predators. The principal difference was that squirrels aggressively chased intruders,

typically across the ground, which is something they never did to predators. In contrast, their vocal responses to intruding squirrels closely paralleled their vocal responses to predators. When confronting intruders, resident squirrels sometimes produced one or more ‘rattle’ calls, which are often also produced spontaneously throughout the day when no intruders are present and are regarded as general territorial announcements (Smith 1978; Lair 1990; Price et al. 1990; Price 1994). However, the preponderance of their vocal responses were protracted and mixed bouts of seet and seet-bark calls paralleling those produced in encounters with predators. Once again, seet-bark calls were produced in greater numbers than were seet calls, and calling bouts showed the same internal structuring as observed in calling bouts to predators: seets were produced primarily in the initial stages of calling bouts and gave way to seet-barks as calling bouts continued.

This combination of responses indicates that the squirrels clearly do discriminate in important ways between conspecific intruders, who they call at and chase, and predators, who they call at but do not chase. As a result, the fact that their calling patterns to the two groups are so similar strongly suggests that the calls themselves are not ‘about predators’ *per se* but rather reflect the broader importance of disturbances of any kind.

In fact, this broader emphasis on the importance of disturbances of various kinds dovetails well with the general ecology and life-history of red squirrels. Red squirrels are solitary throughout the year, except during the short mating season. They actively defend a small territory year-round in which they harvest cones that are their principal food supply (Boutin & Schweiger 1988). They spend considerable time and energy caching these cones in a central

637 midden and additional distributed cache sites in anticipation of winter (Hurly & Lourie 1997;
638 Hurly & Robertson 1987) and this stored supply of cones is critical to a squirrel's overwinter
639 survival (Gurnell 1984). These cone caches are also subject to intense pilfering from neighboring
640 squirrels and other cone-eating species (e.g., chipmunks, mice and jays). Gerhardt (2005) found
641 that, in any given year, 97% of all red squirrels stole cones from neighboring caches and 92% of
642 all squirrels lost some portion of their cache to pilferage. Losses for individual squirrels ran as
643 high as 84% of their cone supply. On average, squirrels lost 25% of their cache to pilferage.
644 Given the energetic constraints facing a small-bodied, non-hibernating mammal overwintering in
645 boreal forests, cone loss might therefore represent as serious a threat to red squirrel survival as
646 do many forms of predation.

647

648 These life-history factors might help to explain why red squirrels seem to call vigorously
649 and relatively indiscriminately at a wide variety of predatory and non-predatory species,
650 including conspecific intruders: as a small-bodied, territorial, food-caching species, disturbances
651 of many kinds are salient and threatening. The obvious corollary is that this vigorous calling
652 might not be an attempt to communicate about either predators or intruders to other distant or
653 neighboring squirrels. Rather, the calls might be directed primarily at the intruders themselves –
654 whether predators or cone-pilfering intruders – and function as part of a common attempt to deter
655 or repel those intruders by conspicuously announcing their detection, and, in the case of cone-
656 pilfering intruders, vigorously chasing them (Digweed & Rendall 2009). There is certainly a
657 precedent for similar predator-directed signals in other prey species that appear to serve a
658 deterrent function (Caro 1986, 1995; Zuberbühler et al. 1999; Rundus et al. 2007). In such cases,
659 the value of multiple, informationally-specific and functionally referential vocal messages might

be quite limited.

This possibility bears importantly on theoretical considerations related to the evolution of functionally referential vocal signals in different species (Evans & Evans 2007; Furrer & Manser 2009). It supports the recent point that, in addition to the variety of predators faced and escape options available (Macedonia & Evans 1993), a species' social system can either facilitate or constrain the functional value of a repertoire of multiple, informationally-specific signals (Furrer & Manser 2009). Furthermore, it suggests that, for any given species, a full understanding of the design and function of vocalizations used specifically in the context of predators might not be possible by studying the predation context in isolation of other aspects of that species behavior and ecology. Familiarity with these broader aspects of the species' behavior and life history might yield a wider sense of the communicative problems faced and the extent to which adaptive solutions developed for predator-related challenges overlap with those related to challenges faced in other domains.

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844 Table 1. The sample of squirrels involved in natural disturbance encounters (a), encounters with
845 intruder squirrels (e), or who served as subjects in the predator simulation experiments (b-d).

Individual	(a) Natural Disturbances*	(b) Taxidermied Predator Models	(c) Moving Aerial Predator	(d) Moving Terrestrial Predator	(e) Intruder Squirrels
Ajax		X	X		X
Aphrodite	G, C	X			
Ares			X	X	
Artemis	D, W, M		X	X	X
Arthur			X	X	
Athena	C, O	X			
Calpurnia					X
Cassie	G				
Dionysus					X
Eros	D, M, R	X			X
Hades		X			
Hermes	O, R			X	
Holmes			X	X	X
Homer					X
Hudson					X
Isadora					X
Lestrade		X			
Moriarty	R				X
Mortimer	O				X
Mycroft				X	X
Negra	M, G				X
Nibbles		X			
Persaus	C				
Rip					X
Rowdy			X	X	
Russel	C, D				
Scar	C, R	X			
Scratch	R		X		X
Slip			X		
Snap	O, C	X			
Triton	G		X	X	
Vesper			X	X	X
Watson	C, O	X	X		X
Winter	O, R		X	X	
Zap				X	
Zip	M	X	X	X	X

846 * Natural disturbances: G=goshawk, O=owl, R=raven, C=coyote, M=marten, D=deer,

847 W=weasel.

848

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

852

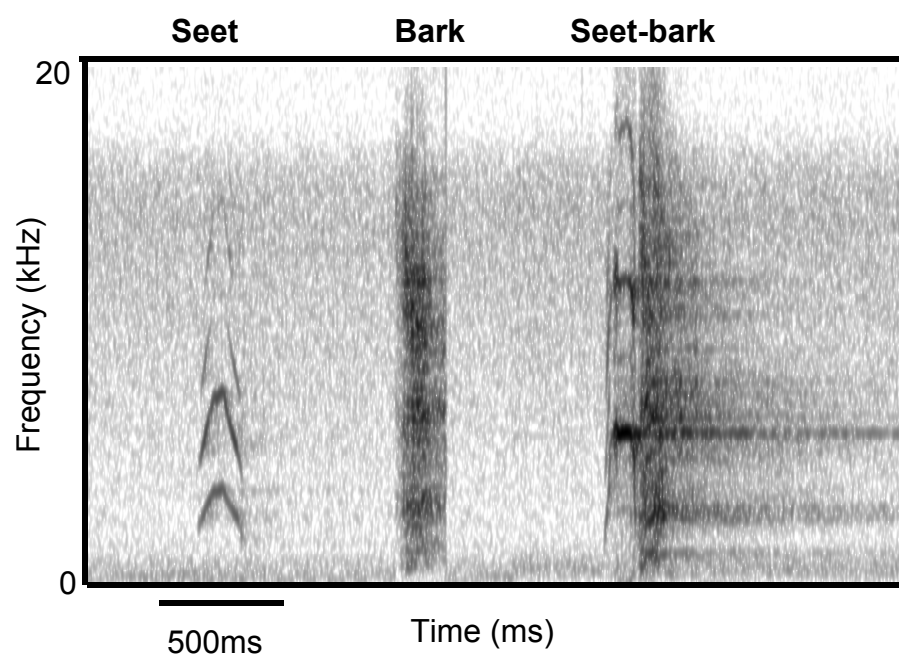
853 Figure 2. Variation in the production of seets and seet-barks in the first 30-seconds of calling
854 bouts during natural encounters with coyote, marten and owl predators.

855

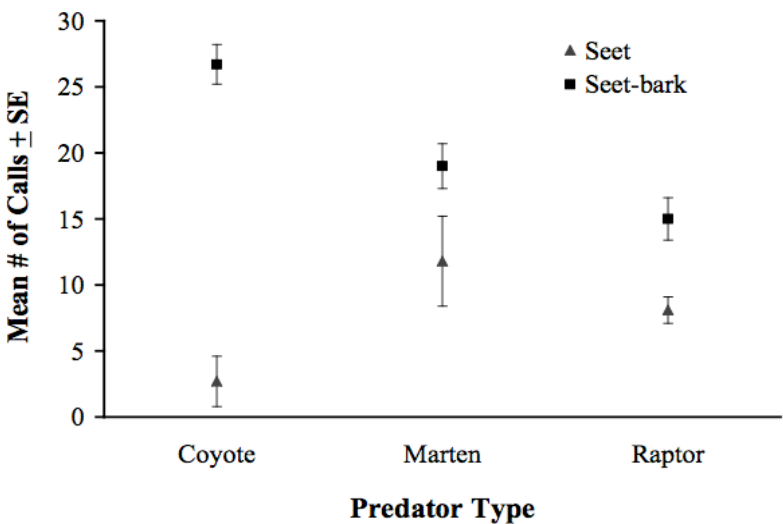
856 Figure 3a-e. The time-course of seets and seet-barks produced during the first 30-seconds of
857 mixed calling bouts to natural predators (a), to taxidermied predator models (b), to a moving
858 aerial predator (c), to a moving terrestrial predator (d) and to other squirrels intruding on a
859 resident's territory (e).

860 Figure 1

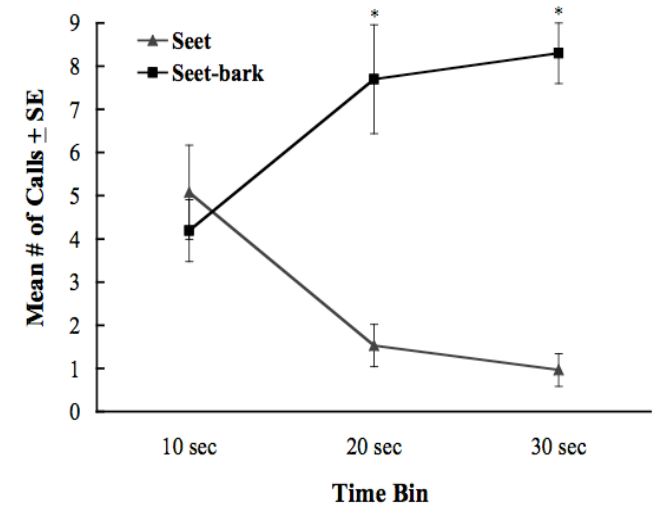
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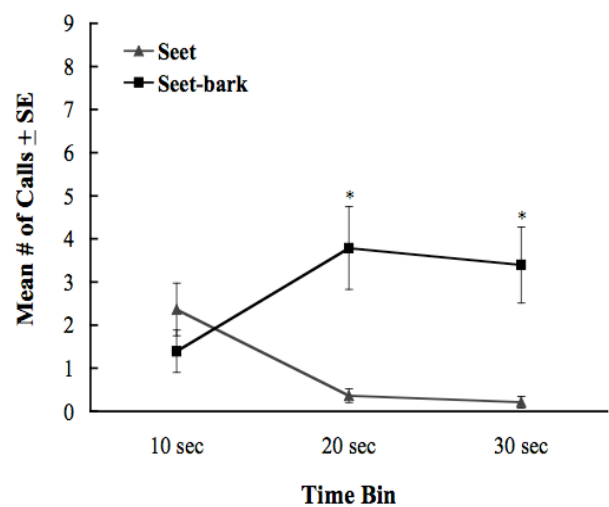
862 Figure 2



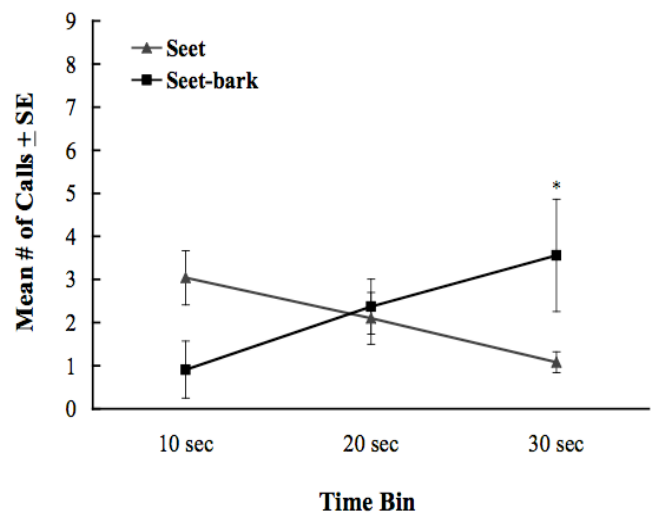
863
864 Figure 3a



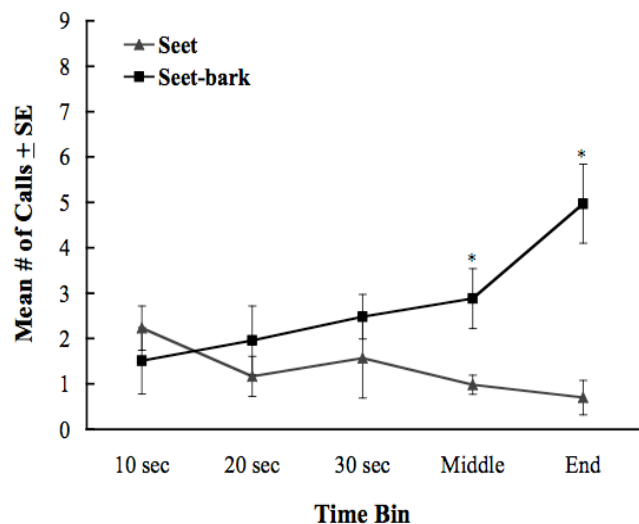
868 Figure 3b



869
870 Figure 3c

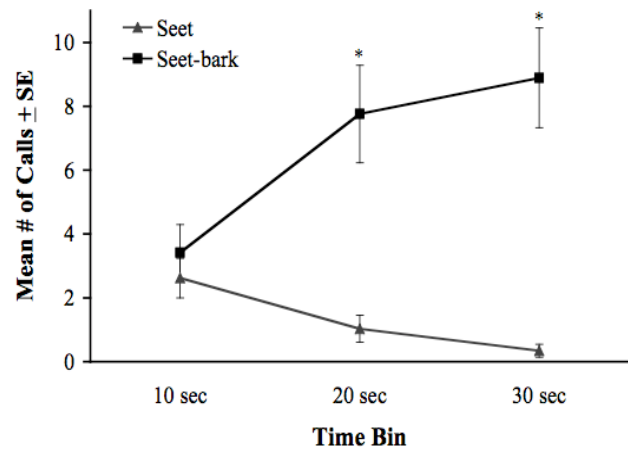


873 Figure 3d



874

875 Figure 3e



876