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Predator-associated vocalizations in North American red squirrels, *Tamiasciurus hudsonicus*: are alarm calls predator specific?

Shannon M. Digweed*, Drew Rendall [1]

Behaviour and Evolution Research Group, University of Lethbridge

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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 nonpredatory 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, which 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 nonpredatory 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 behaviour and life history of red squirrels.

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 the structural details of transmitted calls. Morton (1977, 1982) 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 vocalizations as well. 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, *Cercopithecus aethiops* (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 signalling 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

* Correspondence and present address: S. M. Digweed, Department of Psychology, Grant MacEwan College, Edmonton, AB T5J 2P2, Canada.
E-mail address: shannon.digweed@uleth.ca (S.M. Digweed).
[1] D. Rendall is at the Department of Psychology, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada

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some other mammals and birds (e.g. Diana monkeys, *Cercopithecus diana*: Zuberbühler 2000; tamarins, *Saguinus fuscicollis* and *Saguinus mystax*: Kirchlof & Hammerschmidt 2006; meerkats, *Suricata suricatta*: Manser 2001; Richardson's ground squirrels, *Spermophilus richardsonii*: Davis 1984; chickens, *Gallus gallus domesticus*: Evans et al. 1993; chickadees, *Poecile articapillus*: 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 & Holmes, 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 another 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 complex environments (Macedonia & Evans 1993).

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

Here we report results of a multi-year study of red squirrels to address these ambiguities. First, we report patterns of behaviour and alarm call production during natural encounters with predators. Then, we report a series of follow-up experiments that probe the predator-specific production of alarm calls more systematically. Finally, we report patterns of production of the same calls during other, nonpredatory disturbances.

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°39N, 114°39W), which is situated in the foothills of the Canadian Rockies. The habitat is a mix of aspen (*Populus tremuloides*) parkland and montane (subalpine) 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 of approximately 60 ha. 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. 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 Co., Tomahawk, WI, U.S.A.) and unique dye marks (Clariol no. 52 Black) and eartags were applied (National Band and Tag Co., Newport, KY, U.S.A.: tag no. 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 no. 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 (U.S.A.) 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, *Aquila chrysaetos* and bald eagle, *Haliaeetus leucocephalus*), broad-winged hawks (red-tailed hawk, *Buteo jamaicensis*), forest accipiters (sharp-shinned hawk, *Accipiter striatus*, Cooper's hawk, *Accipter cooperii*, northern goshawk, *Accipiter gentilis*), falcons (prairie falcon, *Falco mexicanus*) and large owls (great horned owl, *Bubo virginianus*, great grey owl, *Strix nebulosa*). It also includes several mammals that are frequent or occasional predators on red squirrels including pine martens, *Martes americana*, long-tailed weasels, *Mustela frenata*, coyotes, *Canis latrans*, bobcats, *Lynx rufus*, cougars, *Puma concolor*, grizzly bears, *Ursus arctos horribilis*, and black bears, *Ursus americanus*. 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 3 consecutive years (2005–2007) primarily between May and November, representing the late spring, summer and autumn 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' behavioural responses to specific classes of predators as well as the number and types of vocalizations they produced.

Results

General responses to predators

During 536 h 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, six encounters with great grey owls, four encounters with northern goshawks and four encounters with pine martens. In each