

**Ultrasonic alarm signals of Richardson's ground squirrels
(*Spermophilus richardsonii*).**

by

David R. Wilson

A thesis submitted to the Faculty of Graduate Studies in
partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Zoology

University of Manitoba

Winnipeg, Manitoba

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THE UNIVERSITY OF MANITOBA
FACULTY OF GRADUATE STUDIES

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ABSTRACT

The evolution and maintenance of anti-predator alarm calling are subject to tradeoffs between warning conspecifics and minimizing the risk of predation. Although ultrasonic alarm signals (frequencies > 15 kHz) have not previously been detected in any animal group, their rapid attenuation and highly directional nature could allow callers to warn nearby conspecifics without attracting distant predator attention. I recorded ultrasonic signals from free-living Richardson's ground squirrels (*Spermophilus richardsonii*); these 'whisper calls' were of short duration (225 ± 8 ms, mean \pm SE), loud (66.8 ± 2.1 dB SPL at 1 m from source), and had a dominant frequency of 48.0 ± 2.3 kHz (mean \pm SE). In response to playback of whisper calls, squirrels exhibited more vigilant behaviours than they did in response to playback of background noise, demonstrating unambiguously that whisper calls warn conspecifics of danger.

Squirrels' responses to whisper calls and to pure tones matching the dominant frequency of those calls were not significantly different, suggesting that much of the communicatory value of whisper calls is contained in the dominant frequency. To further elucidate their perceptual capacity, I used a classical conditioning paradigm to train captive squirrels to respond to tones of increasing frequency. Though several problems precluded extensive testing at higher frequencies, it was clear that squirrels could hear up to at least 40 kHz. As cues for localizing sound are greater at higher frequencies, the ability to detect 40 kHz may prove advantageous by allowing recipients to accurately locate the signaler.

Whisper calls elicited less overt behavioural responses from squirrels than did audible calls, suggesting either that whisper calls convey less urgency, or, consistent with the furtive nature of ultrasound, that recipients respond to whisper calls in a less conspicuous fashion. In support of that 'covert signaling hypothesis,' data gleaned from previous alarm calling studies revealed that squirrels produce whisper calls most often when predators are located farther away. Given the short range of ultrasound, however, it is also possible that whisper calls serve to warn nearby kin. Indeed, one of the two contexts in which I confirmed that whisper calls function is during juvenile emergence, when kin are abundant, spatially clustered, and vulnerable to predation.

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Chapter 1: General introduction

Many group-living species produce and respond to alarm signals in threatening situations (Macedonia & Evans 1993). By attending to alarm signals, recipients benefit from the enhanced detection of predators afforded by a group (Pulliam 1973; Bertram 1978; Hoogland 1979) and can replace time spent vigilant with time spent foraging, resting, or caring for young (Siegfried & Underhill 1975; Caraco et al. 1980; Abrams 1983). Callers may ultimately benefit through reciprocity (Trivers 1971; Axelrod & Hamilton 1981; Hare 1998a) and/or kinship (Hamilton 1964; Maynard Smith 1965; Dunford 1977), but are immediately burdened with the energetic costs (Eberhardt 1994; Bradbury & Vehrencamp 1998) and increased risk of predation (Sherman 1977; Yasukawa 1989) associated with calling. Selection is thus expected to enhance a caller's fitness by refining the structure (Marler 1955; Klump & Shalter 1984) and efficacy (Marler et al. 1992; Macedonia & Evans 1993; Bradbury & Vehrencamp 1998) of alarm calls.

The ability of a receiver to respond appropriately to an alarm call during a predator encounter depends greatly upon the information content (Marler et al. 1992; Macedonia & Evans 1993; Bradbury & Vehrencamp 1998) and the reliability (Cheney & Seyfarth 1988; Koops & Abrahams 1998; Hare & Atkins 2001; Blumstein et al. 2004) of the signal. Variation in alarm calls may encode semantic information (referential signaling: Seyfarth et al. 1980; Cheney & Seyfarth 1988; Pereira & Macedonia 1991) or the degree of urgency (response

urgency: Blumstein 1995; Blumstein 1999; Warkentin et al. 2001) associated with a threat. Vervet monkeys (*Cercopithecus aethiops*) and ring-tailed lemurs (*Lemur catta*) issue disparate alarm calls to aerial and terrestrial predators, and recipients of these two call-types respond appropriately by hiding in thick bush or climbing high into the trees, respectively (Seyfarth et al. 1980; Pereira & Macedonia 1991). These alarm calls are referential in nature because they communicate specific information about a potential threat with little ambiguity, allowing receivers to respond appropriately to calls even when a predator is not visible.

Macedonia & Evans (1993) and Pereira & Macedonia (1991) noted that, in contrast to vervets and ring-tails, most ground-dwelling animals flee from all types of predator in a similar fashion (e.g. entering burrows). Thus, information regarding the immediacy of a threat (e.g. approach speed or proximity of predator) is potentially more valuable to ground-dwellers than is information pertaining to predator type and/or how to flee (Macedonia & Evans 1993). Warkentin et al. (2001) demonstrated that the rate of repetitive calling by Richardson's ground squirrels (*Spermophilus richardsonii*) varies directly with the degree of risk perceived by the caller. Further, call recipients are more likely to assume the highly vigilant alert posture in response to calls broadcast at a higher call rate, indicating that call rate can be graded to convey the extent of threat imposed by a predator (Marler et al. 1992; Warkentin et al. 2001). Although most studies of ground squirrel communication tend to support only the response urgency hypothesis (Macedonia & Evans 1993; Blumstein 1995, 1999; Warkentin

et al. 2001), it remains possible that a single alarm signaling system may convey both response urgency and reference to external stimuli (Marler et al. 1992).

The reliability of a signal can also affect a receiver's response, as responding to unreliable signals can result in time lost from foraging, resting, or caring for young (Ydenberg & Dill 1986; Koops & Abrahams 1998; Hare & Atkins 2001). Consequently, several species recognize the vocalizations of unreliable individuals and show reduced responsiveness to those callers (Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004). Among Richardson's ground squirrels, receivers can further discriminate among different calls issued by the same caller, showing enhanced responsiveness to calls that encode the proximity of a predator with greater certainty (Sloan & Hare 2004). By integrating information about the spatial locations of the caller (e.g. neighbour vs. non-neighbour: Hare 1998b) and predator (e.g. via call rate, Warkentin et al. 2001), a receiver could potentially assess a risk in relation to the location and identity of the caller and tailor its response according to the expected costs and benefits of the situation (Hare 1998a; Koops & Abrahams 1998; Hare & Atkins 2001).

In addition to the benefits provided by enhanced signal information content, aspects of signal structure may also enrich alarm calls by reducing the costs of predation associated with calling. Signals that are short in duration, contain few frequency bands, and lack frequency modulation are difficult for predators to localize (Marler 1955; Brown et al. 1978a and b; Klump & Shalter 1984). Such 'ventriloquial' signals remain highly detectable by conspecifics,

however, because their energy is concentrated in the frequency domain, which maximizes the sound pressure level and overall detectability of the signal to conspecifics (Klump & Shalter 1984). Furthermore, alarm calls are often repeated, which facilitates signal detection in the face of fluctuating environmental noise (Endler 1993; Bradbury & Vehrencamp 1998).

Although callers may be capable of producing ventriloquial alarm signals that reduce their risk of predation by nearby predators, the high detectability of such signals may actually attract more distant predators that would not otherwise have noticed the group, placing the entire group at greater risk of predation (Klump & Shalter 1984; Endler 1993). Furthermore, the intended receivers share with predators the difficulty of locating ventriloquial alarm signals, which may compromise their ability to extract and integrate information regarding spatial relationships with and between the predator and caller (Marler 1955; Klump & Shalter 1984). It is therefore reasonable to assume that the refinement of a species' alarm signals is constrained by the tradeoffs between the degree of conspecific and predator dependence on signal detection and localization. An exception to this evolutionary constraint, however, is when predators are incapable of detecting the signal altogether, either because they lack the physiological capacity or because signalers only signal when the predator is beyond the signal's active space (Endler 1993).

Many small passerine birds are more sensitive to their own alarm calls than are the large birds of prey that feed upon them (Marler 1955). The great tit (*Parus major*) produces an 8 kHz pure tone 'seet' call that warns the entire tit

flock of its primary predator, the European sparrowhawk (*Accipiter nisus*, Latimer 1977). Because the tit is more sensitive than the sparrowhawk to high frequencies (31 vs. 7 m perceptual range at 8 kHz, respectively), and because a tit will only alarm call if a sparrowhawk is over 7 m away, a tit can alert the entire tit flock without drawing the sparrowhawk's attention (Klump & Shalter 1984). However, mammalian predators are generally more sensitive than predatory birds to high-frequency sounds and are thus more likely to detect alarm signals (Masterton et al. 1969; Brown & Pye 1974). Among prey species with mammalian predators then, selection should favour highly specialized signaling systems that prevent eavesdropping by sensitive mammalian predators (Endler 1993).

Very little is known about the use of ultrasound (frequencies > 15 kHz) for alarm communication, though its unique properties - high directionality and rapid environmental attenuation (Sales & Pye 1974; Pye & Langbauer 1998) - have been well studied in the context of echolocation and the pursuit of prey by chiropteran bats and odontocete whales (Norris 1969; Simmons et al. 1979). An alarm signal could presumably exploit these same properties, limiting the audible range of alarm calls to nearby conspecifics (Smith 1979) and allowing callers to direct calls away from predators or at specific intended receivers (Witkin 1977). Sales & Pye (1974) argue that ultrasonic signals did not evolve because they exceed the frequency response of predators, however, as many animals, including several carnivores, can detect ultrasound (Brown & Pye 1974). Many predatory birds, however, are unable to detect ultrasound (Marler 1955; Sales &

Pye 1974; Klump & Shalter 1984) and, thus, it remains possible that ultrasonic signals do function in this capacity among prey with avian predators.

Richardson's ground squirrels are semi-fossorial Sciurid rodents that live in large colonies on the open prairies (Michener & Koepl 1985). In response to predators, squirrels warn conspecifics by producing single or repeated alarm calls that consist of 'chirps,' 'churrs,' 'whistles,' or 'squeals' (Koepl et al. 1978; Davis 1984; Sloan et al. in press). Syllables are short in duration (< 0.5 s), have a fundamental frequency near 8 kHz, are narrow-band or pure tone, and generally lack frequency modulation (see Koepl et al. 1978; Davis 1984); they are loud (84 - 91 dB SPL at 1 m from source: Hare 1998a), easily detected over long distances, and are difficult for humans to localize.

Hare (unpublished data) observed an adult squirrel performing motions consistent with alarm calling (suddenly expanding the thoracic cavity and opening the mouth widely), but without the production of an audible sound. He obtained a preliminary recording of this behaviour with an ultrasound recorder, which revealed that this undocumented 'whisper call' contained ultrasonic frequencies near 50 kHz. Although the production of ultrasound has not been detected in any Sciurid rodent in any context and, although whisper calling is relatively rare, numerous squirrels from every population we have subsequently studied have been observed whisper calling. The whisper call thus constitutes an undescribed vocalization of Richardson's ground squirrels.

No previous study has successfully described whisper calls, established the context in which they are produced, or addressed the possible functions of

these potentially valuable calls. This study thus had four goals: to 1) record and parameterize several whisper calls produced by free-living juvenile and adult Richardson's ground squirrels (production component), 2) determine the maximum auditory frequency response of squirrels (detection component), 3) broadcast whisper calls back to free-living squirrels to test if calls elicit an anti-predator response and thus serve as alarm signals (perception, or functional component), and 4) describe the natural context surrounding this potentially valuable signaling system. I discuss the ecological and evolutionary significance of my results in the context of the unique opportunities that ultrasound provides and the selective pressures that drive alarm communication.

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Chapter 2: Richardson's ground squirrels (*Spermophilus richardsonii*) use ultrasonic alarm signals.¹

The use of ultrasound is well understood in the context of echolocation and the pursuit of prey by chiropteran bats and odontocete whales (Norris 1969; Simmons et al. 1979), but its function in other animal groups, such as rodents, remains unclear (Smith 1979). Among rodents, purely ultrasonic signals have been described only for the family Muridae (Sales & Pye 1974; Nowak 1999), though ultrasonic harmonic components are present in the audible calls of other rodent taxa (Eiler & Banack 2004). The context for ultrasound production in Murids is highly variable, ranging from infant isolation and distress (Sewell 1968; Sewell 1970) to sexual (Pierce et al. 1989) and predator encounters (Blanchard et al. 1991) in adults. Few studies have focused on how, or if, rodents respond to ultrasound, but those that have suggest that it plays a role in maternal retrieval of infants (Sewell 1970) and prolonging lordosis (Cherry 1989). Most studies of ultrasonic communication, however, have been conducted in a laboratory where normal social behaviour could be compromised and signal function obfuscated (Smith 1979).

Ultrasound includes frequencies that exceed the normal hearing range of humans (Pye & Langbauer 1998: > 15 kHz) and most avian predators (Sales & Pye 1974). Owing to their high frequencies, ultrasonic signals attenuate far more rapidly in the atmosphere than audible signals of the same initial intensity,

¹ A version of this manuscript has been published (see appendix B). **Wilson, D.R. & Hare, J.F.** 2004. Ground squirrel uses ultrasonic alarms. *Nature*, **430**, 523.