Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency

Kurtis J. Warkentin, Annika T.H. Keeley, and James F. Hare

Abstract: Richardson's ground squirrels, *Spermophilus richardsonii*, produce both repetitive and non-repetitive antipredator calls. While many hypotheses have been advanced to explain non-repetitive calls, the function of repetitive calling has received relatively little attention. We presented juvenile Richardson's ground squirrels with a predator model at distances ranging from 1 to 8 m and recorded the subsequent repetitive calls on digital audiotape. The rate of calling was inversely correlated with the distance between the model and the caller, with distance explaining almost 24% of the variation in call rate. To determine whether call recipients use that information, we manipulated the intersyllable latency of a single repetitive call exemplar to form 3 test stimuli varying only in call rate. Across 16 Richardson's ground squirrel colonies to which these calls were broadcast, the proportion of squirrels assuming the highly vigilant, alert posture increased with the rate of the repetitive call presented. Hence, juvenile Richardson's ground squirrels appear to communicate the proximity and presumably the degree of threat posed by potential predators.

Résumé : Les Spermophiles de Richardson, *Spermophilus richardsonii*, émettent des cris anti-prédateurs répétitifs et non répétitifs. Alors que plusieurs hypothèses ont été avancées pour expliquer les cris non répétitifs, le rôle des cris répétitifs a été peu étudié. Nous avons mis des Spermophiles de Richardson juvéniles en présence d'un modèle de prédateur, à des distances de 1 à 8 m, et avons enregistré les cris répétitifs qui ont suivi sur ruban digital audio. La fréquence des cris était inversement proportionnelle à la distance entre le modèle et le spermophile, et la distance expliquait 24 % de la variation de fréquence des cris. Pour déterminer si les auditeurs des cris utilisent cette information, nous avons manipulé le temps de latence entre les syllabes d'un seul modèle de cri répétitif pour obtenir 3 stimuli expérimentaux ne variant que par la fréquence des cris. Dans 16 colonies de Spermophiles de Richarson auxquelles on a donné à entendre ces cris, la proportion des spermophiles qui ont adopté une posture d'alerte et qui sont restés très vigilants a augmenté en fonction de la fréquence du cri répétitif présenté. Les jeunes Spermophiles de Richardson semblent donc capables de communiquer la proximité et probablement aussi la gravité de la menace que posent les prédateurs potentiels.

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Introduction

Ground-dwelling sciurids (species of *Marmota*, *Cynomys*, and *Spermophilus*) emit vocalizations in response to predators (see Macedonia and Evans 1993). An interesting feature of sciurid vocal communication systems is that many species use both non-repetitive and repetitive call types. In the former, a discrete acoustic element is produced in temporal isolation from other vocalizations, whereas in the latter, that same or similar elements are produced repeatedly, with intervening silences of similar duration to the elements themselves. While non-repetitive calls may serve to warn relatives and neighbours that a potential predator is present (e.g., Sherman 1977), the function of repetitive calls is less certain, since the calls often continue after the predator has departed. Several authors (e.g., Smith et al. 1977; Owings and Hennessey 1984) have suggested that repetitive calling may be a "tonic" form of communication that maintains vigilance in surrounding conspecifics. Limited support for the tonic-communication hypothesis has come from studies of California ground squirrels (*Spermophilus beecheyi*; Loughry and McDonough 1988) and Columbian ground squirrels (*Spermophilus columbianus*; Harris et al. 1983); however, in those studies the vigilance of call recipients eventually declined despite ongoing call production. Thus, while repetitive calling increases the duration of vigilance compared with non-repetitive calling, it does not maintain vigilance over the long term as the tonic-communication hypothesis predicts. Tonic communication may apply in a limited sense, however, if we allow that greater vigilance among call recipients enhances detection at the outset of an encounter but declines over time as the predation risk diminishes.

Disparate call types within an antipredator signaling system may denote predator attributes (referential signaling) or differences in the extent of threat perceived by the caller (response urgency). After reviewing the data on antipredator

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calling in ground squirrels and primates, Macedonia and Evans (1993) suggested that ground squirrels employ response-urgency-based signaling. This contention is consistent with the more recent findings of Blumstein (1995) for golden marmots, *Marmota caudata aurea*, and Blumstein and Arnold (1995) for alpine marmots, *Marmota marmota*, which indicate that repetitive calls communicate the degree of risk experienced by a caller. However, Macedonia and Evans (1993) noted that both arctic (*Spermophilus undulatus*) and Richardson's (*Spermophilus richardsonii*) ground squirrels may be unique among ground squirrels in possessing a referential-calling system. Davis (1984) reported that Richardson's ground squirrels issue higher pitched chirps in response to avian predators and long, lower pitched whistles in response to terrestrial predators. Similarly, in arctic ground squirrels, Melchior (1971) reported that acoustically distinct calls were issued in almost exclusive association with avian versus terrestrial predators.

In contrast with the situation in ground squirrels, the evidence for referential signaling is robust for several primate species, including vervet monkeys, *Cercopithecus aethiops* (Seyfarth et al. 1980; Cheney and Seyfarth 1988), and ring-tailed lemurs, *Lemur catta* (Macedonia 1990). Such unambiguous evidence of referentiality stems from demonstrating not only that calls vary consistently with predator type (the "production component" sensu Marler et al. 1992) but also that the responses of call recipients correlate reliably with the call type broadcast (the "perception component" sensu Marler et al. 1992). The studies on ground squirrel antipredator vocalizations performed by Davis (1984) and Melchior (1971) cannot be regarded as definitive demonstrations of referentiality because only call production was examined. However, given that both Richardson's and arctic ground squirrels potentially represent exceptions to the general pattern of response-urgency calling, further research examining both the production and perception of their alarm calls is warranted.

Richardson's ground squirrels produce both non-repetitive (Davis 1984) and repetitive antipredator calls (Hare 1998). In this study, we investigated the production and perception of repetitive calls of Richardson's ground squirrels. In particular, we examined variation in call rate relative to the spatial proximity of a predator model and the role played by such variation in modulating the vigilance responses of call recipients.

Methods

Call production

To study antipredator-call production, we presented free-living female and male juvenile Richardson's ground squirrels with a predator model and recorded their vocalizations. These recordings were obtained from squirrels occupying sites in cattle pastures within 3 km of Oak Lake Provincial Recreation Park, Manitoba (49°41′N, 100°43′W; elevation ca. 425 m asl), in 1994, 1995, and 1996, and in a cattle pasture ca. 3 km south of Brandon, Manitoba (49°47′N, 99°59′W; elevation ca. 575 m asl), in 1997. Location reference on the sites was facilitated by 10 × 10 m Cartesian coordinate grids of colour-coded wire-pin flags. Human observers on foot were present daily on the sites from before juvenile emergence until after the recording sessions were completed each year. Squirrels on the sites were marked with numbered metal ear tags (Monel No. 1, National Band and Tag Co.) for permanent identification, and a unique number was applied to the dorsal pelage with human hair dye (Clairol Nice 'n Easy No. 124, blue–black) for identification in the course of behavioural observations. Despite the fact that propensity to call, responsiveness to certain call-eliciting stimuli, and behavioural responses to calls may differ between juveniles and adults (Mateo and Holmes 1997; Shriner 1999), we consider only responses of juveniles to presentation of the model predator because a meaningful sample was obtained for that age-class only.

Each juvenile subject was presented with the model predator, a tan Biltmore hat (brim: 19.5 × 32.5 cm, height: 13 cm, as in Hare 1998). The use of models is common in studies of antipredator calling behaviour, as models allow greater contextual control than do natural encounters with predators (MacWhirter 1992; Hare 1998). All presentations and call recordings were made by J.F.H. while wearing the same outer clothing to minimize any confounding effects due to the observer (see Slobodchikoff et al. 1991).

Calls were recorded on digital audiotape (DAT) using a Sony TCD-D7 recorder. In 1994, 1995, and 1996 we used a Dan Gibson P-650 parabolic microphone set to "M" for low-frequency roll-off and fitted with a foam windscreen to reduce noise; in 1997 we used an Audio-Technica AT815b condenser microphone. Wind velocities exceeding ca. 10 km/h produced excessive noise, so recording sessions were limited to relatively calm mornings between 07:30 and 11:30. Calls were recorded between 8 and 27 July in 1994, between 19 July and 3 August in 1995, on 24 June in 1996, and between 11 and 29 June in 1997. Subject juveniles ranged in age from 35–70 days post emergence at the time their calls were recorded.

Recording methods followed those described in Hare (1998). Subjects that had not previously been presented with the predator model (hat) were approached to within 15 m. The hat was tossed from hip level with a flip of the wrist to a distance of 1–8 m from the subject and at an angle of 0°–30° relative to a line between the observer and the subject (but never directly over the subject). All vocalizations produced by the subject in the 5 min following presentation of the predator model were recorded. For each recording session the following information was documented: time, position of recording on the tape, locations of the microphone, predator model, and subject at the onset of recording, and behaviour of the subject coinciding with the presentation of the model (particularly whether the subject faced the model while calling). Only sessions in which juveniles faced the predator model while calling were used in subsequent analysis and playbacks, thus decreasing the probability of spurious responses to the experimenter or other elements in the squirrels' environment. In all cases, calling did not begin until after the hat had landed on the ground.

To quantify repetitive calling we used a stopwatch to measure the time (in seconds) that elapsed while the first 10 syllables (utterances separated by silence) of each subject's call were played from the tapes. We divided 10 (syllables) by the time elapsed to give us the call rate in syllables per second. By limiting calculation of call rate to this early segment of the calls we reduced the probability of the call rate being confounded by other events in the caller's environment, including the influence of other alarm callers. The distance (in metres) from the subject to the predator model (on the ground) was calculated using the Cartesian coordinates derived from the recording session. A linear-regression model of call rate versus distance between the caller and the predator model was computed using Statview™ on a Macintosh™ computer.

Call perception

To study how antipredator calls made at different rates are perceived by Richardson's ground squirrels, we played manipulated calls to ground squirrel colonies and measured the squirrels' responses. We used 16 colonies of free-living ground squirrels inhabiting roadside cattle pastures within 20 km of Oak Lake Provincial Recreation Park. Unlike the sites used in the production

Fig. 1. Rates of repetitive calling by 36 juvenile squirrels at various distances from a predator model ($y = 0.423 - 3.146e^{-2}x$, $R^2 = 0.238$, $P = 0.003$).

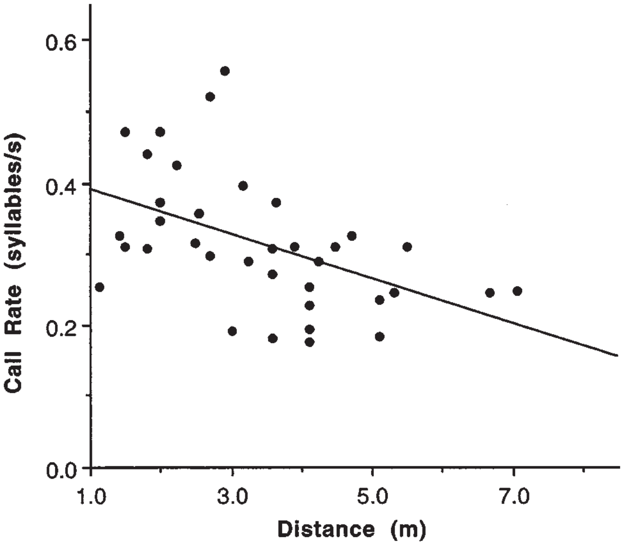
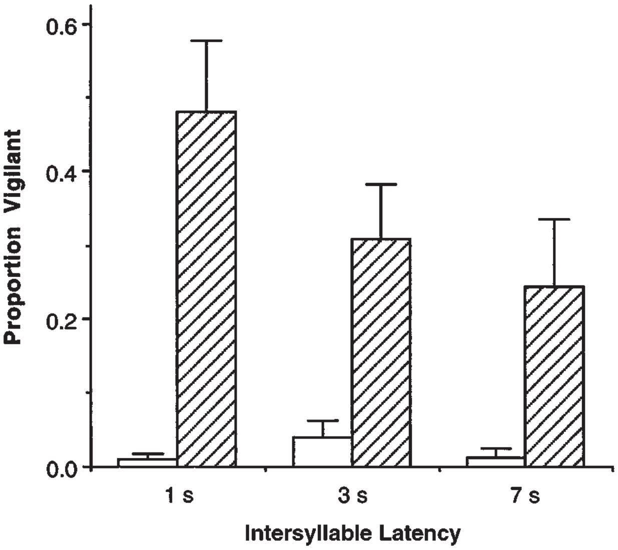


Fig. 2. Proportion of squirrels (mean + SE) observed in the alert posture in pre-playback (open bars) and post-playback (hatched bars) scans for calls with intersyllable latencies of 1, 3, and 7 s (n = 16 colonies).



component of this study, these sites were not regularly visited by humans on foot (with the exception of two sites in a recreation area), had no wire-pin grids, and the squirrels had not, to our knowledge, been handled by humans. Using such sites for playback precluded the identification of individual squirrels, their sex, and their age-class, though it did allow response data to be collected for groups in manner that minimized any habituation to calls.

We arbitrarily chose one call from the recordings made in 1994 that we deemed to be of high quality (i.e., clearly audible with little background noise) for playbacks. Using SoundEdit 16™ software, we created 3 repetitive calls from that single exemplar, each with 5 syllables but differing in the length of time between syllables. The calls created had an intersyllable latency of 1, 3, or 7 s, corresponding to call rates of 0.5, 0.3, and 0.2 syllables/s, respectively. This range of rates approximates that observed in recording sessions (0.18–0.56 syllables/s) about an observed mean rate of 0.32 syllables/s. The manipulated calls were transferred from the computer onto DAT for subsequent playback.

The playback apparatus consisted of the DAT player connected to a Sony XM-2025 amplifier and Realistic Minimus-77 loudspeaker. Playbacks were accomplished by parking a car (used as a blind) on the roadside next to a colony and placing the loudspeaker 5 m from the car facing the subject colony. Each playback session began at least 10 min after the loudspeaker had been placed in position, when the majority of squirrels visible in the colony were engaged in relatively low-vigilance postures with all four feet on the ground.

Playback sessions took place over a 17-day period (18 June – 4 July 1995). Each of the 3 calls was played to each colony once in random order, with at least 1 day separating the playbacks to a particular colony. At the beginning of each session the distance between the loudspeaker and the nearest visible squirrel ranged from 5 to 30 m.

During each playback session, A.T.H.K. scanned the colony immediately before (pre-playback) and immediately after the call was played (post-playback). For each scan, the posture of every visible squirrel was recorded as either alert or non-alert. Alert was defined as standing on the hind legs with the back erect and this is deemed to be the highest degree of vigilance (Hare 1998); non-alert encompassed all other postures and behaviours.

For calls emitted at each rate, the proportion of visible squirrels in the alert posture in the prescan was compared with the proportion in the alert posture in the postscan, using Wilcoxon's signed-ranks test. The influence of call rate on the proportion of squirrels alert was determined for the post-playback sample, using Friedman's test. Further, the proportion of squirrels alert in the high-call-rate treatment was contrasted with that in the low-call-rate treatment using Wilcoxon's signed-ranks test. All work was conducted in accordance with the policies established by the Canadian Council on Animal Care and the Animal Behavior Society for the ethical treatment of animals in research.

Results

Call production

Thirty-three of the 36 callers produced whistles in their initial utterance, while only 3 of the callers began their repeated call with chirps (sensu Davis 1984). All repeated calls, however, ultimately became a series of whistles. The distance of the calling squirrel from the predator model significantly influenced the call rate, explaining nearly 24% of the variation in that variable ($p = 0.0023$, $R^2 = 0.238$; Fig. 1). For the 36 individuals' calls used to generate this model, the call rate was 0.32 ± 0.02 syllables/s (mean ± SE), which translates to an intersyllable latency of approximately 3 s at a distance from predator model of 3.42 ± 0.25 m (mean ± SE). The sex and age of the caller, time of day, ordinal number of the model presentation within a day, and distance of the caller from the observer had no detectable relationship with the call rate.

Call perception

All three call rates (intersyllable latencies of 1, 3, and 7 s) produced significant increases in the proportion of alert squirrels between the pre- and post-playback scans (Fig. 2). The magnitude of that effect increased with call rate (Wilcoxon's signed-ranks test, intersyllable latency 7 s, $Z = -2.21$, $p = 0.027$; 3 s, $Z = -2.66$, $p = 0.008$; 1 s, $Z = -2.94$, $p = 0.003$) though the overall trend in the proportion of squirrels becoming vigilant did not differ significantly among treatments (Friedman's test, df = 2, χ_r^2 (corrected for ties) = 3.82, $p = 0.15$; Fig. 2). A significantly greater proportion of squirrels became alert, however, in response to the high- versus low-call-rate treatment ($Z = -2.20$, $p = 0.028$; Fig. 2).

Discussion

Call rates decreased with increasing distance between the caller and the predator model. Further, a higher proportion of call recipients became alert in response to the high- versus the low-call-rate presentation. Thus, the call rate communicates response urgency in juvenile Richardson's ground squirrels. This finding is consistent with Macedonia and Evans' (1993) generalization that ground-dwelling squirrels use alarm call systems based upon response urgency and corresponds to reports of other rodents that vary the call rate according to the extent of threat (e.g., yellow-bellied marmots, *Marmota flaviventris*, Waring 1966; golden marmots, Blumstein 1995; alpine marmots, Blumstein and Arnold 1995; eastern chipmunks, *Tamias striatus*, Burke da Silva et al. 1994; Columbian ground squirrels, Harris et al. 1983). The near ubiquitous use of call rate to modulate information about extent of threat may stem from the reliability of that acoustic parameter in conveying information in a noise-ridden environment. Wind noise itself may make perceived amplitude an unreliable signal parameter (Larom et al. 1997), while call rate can be determined by receivers with little ambiguity. Increasing rates of signal production in the context of increasing threat may also relate to the underlying motivational state, or level of arousal, of the signaler (Jürgens 1979), which may have provided the evolutionary impetus for call-rate assessment on the part of call recipients.

The distinct call types produced by Richardson's ground squirrels in response to avian and terrestrial predators (Davis 1984) are compatible with the response-urgency hypothesis and are not necessarily indicators of referential calling. The short chirp call issued in response to avian predators, as described by Davis (1984), may be a product of the extreme urgency of the situation, as avian predators arrive suddenly and usually attack quickly after arriving in the vicinity of the caller. Terrestrial predators, on the other hand, approach more slowly, allowing squirrels time to produce the longer whistle call (Davis 1984) or extended repetitive calls (Owings and Hennessy 1984). Squirrels responded almost invariably with whistles rather than chirps in the present study, suggesting either that the hat was considered by most individuals to be a terrestrial predator (referentiality hypothesis) despite its initial approach through the air, or that it posed a low degree of threat (response-urgency hypothesis) to the majority of callers. The present data cannot discern between these hypotheses, however, as callers typically retreated into a burrow as the hat was launched toward them, and vocalized only upon reemergence when the hat was stationary on the ground. In that context, the hat represents at best an unknown potential predator on the ground, though we are ultimately uncertain how the model was perceived.

Response-urgency and referential-signaling systems are not mutually exclusive (Marler et al. 1992), so Richardson's ground squirrels may use a combination of the two, or combinations of other systems. Indeed, Richardson's ground squirrels' alarm calls contain sufficient semantic information to allow call recipients to discriminate among callers at the level of individuals (Hare 1998), and thus calls can be regarded as multidimensional. While Davis' (1984) study satisfied the production component of a referential-signaling system, the perception component has yet to be investigated. To establish external reference, playback experiments must reveal that distinct call types elicit distinct responses in the absence of other predator stimuli (Marler et al. 1992; Macedonia and Evans 1993).

Altering the call rate may also function in predator deterrence. To evaluate the probability of a successful attack, predators must assess the alertness of potential prey (Hasson 1991). The results of the production component of this study are consistent with the predator-deterrence hypothesis. Higher call rates would make the caller more conspicuous to predators, presumably indicating that the caller is highly vigilant and aware of the predator's presence. This notion is supported by our observation that callers almost always faced the predator model when calling.

Since juvenile Richardson's ground squirrels can discriminate between individual callers (Hare 1998), and call rate provides a reliable indicator of the caller's proximity to a potential predator (this study), call recipients may also be able to integrate information from multiple callers to locate and track the movements of a predator through a colony.

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