Richardson's ground squirrels (*Spermophilus richardsonii*) do not communicate predator movements via changes in call rate

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The call rate of repetitive alarm calls produced by Richardson's ground squirrels conveys the extent of threat during predator encounters. It remains unknown, however, whether changes in call rate communicate predator movements. That is, does an increasing call rate indicate an approaching predator and a decreasing rate the opposite? We presented free-living squirrels with moving predator models and recorded their responses. Vigilant behaviour increased more when predators approached vs. retreated, suggesting that squirrels recognize the changes in threat associated with predator movements. Squirrels rarely produced alarm calls during these encounters, however, suggesting that squirrels do not rely entirely on alarm vocalizations to assess the threat posed by potential predators. Receivers of manipulated calls did not respond differentially to alarm calls containing an increasing or decreasing rate of syllable production. Thus, while rate may encode information about the extent of threat, Richardson's ground squirrels do not communicate predator movements via changes in call rate.

Introduction

Many ground-dwelling sciurids (species of *Marmota, Cynomys and Spermophilus*) produce

alarm calls in response to potential predators (Macedonia and Evans 1993). Vocalizations can

be emitted as single syllables (non-repetitive call), or repeatedly, with intervening silences of

varying lengths (repetitive call). While both call types warn conspecifics of potential danger (e.g.

Sherman 1977; Warkentin et al. 2001), the nature and extent of information encoded within

repeated alarm calls remains unknown. The tonic communication hypothesis predicts that

repetition of syllables serves to prolong residual vigilance in receivers during and after a

predatory threat. Limited support for this hypothesis comes from studies of California (*S.

beecheyi*: Loughry and McDonough 1988) and Columbian (*S. columbianus*: Harris et al. 1983)

ground squirrels, but in these, and recent work on Richardson's ground squirrels (*S.

richardsonii*: Sloan and Hare, in press), repeated calls increased short-term vigilance of receivers

only.

Aspects of call morphology may enrich alarm calls by encoding semantic information

(referential signaling: e.g. Cheney and Seyfarth 1988) or the degree of threat (response

urgency: e.g. Blumstein 1999) associated with a call. Although sciurid signaling systems are

generally considered to be response urgency-based (Marler et al. 1992), Arctic (*S. parryii*),

California, Richardson's and Belding's ground squirrels (*S. beldingi*) are reported to produce

disparate calls in response to different predator types (i.e. terrestrial vs. aerial: see references

in Macedonia and Evans 1993). Rather than denoting specific predator attributes, however,

variation in call type may result from underlying variation in the degree of threat imposed by

certain predator classes. Robinson (1980) showed that Belding's ground squirrels recognize that

aerial and terrestrial predators reliably pose unique levels of threat. Davis' (1984) assertion that

Richardson's ground squirrels emit chirps to aerial threats and long whistles to terrestrial

threats may thus result from differential immediacy of the two types of threat; that is, there

may not be enough time during an aerial attack to complete a long whistle or a prolonged

repetitive call (Warkentin et al. 2001).

Blumstein (1995*a*) demonstrated that the number of syllables emitted by alarm calling

golden marmots (*Marmota caudata aurea*) is inversely correlated with the extent of threat

posed by a potential predator. However, call recipients did not respond in a consistent fashion

to the number of syllables per bout, suggesting that alarm calls are limited to a general alerting

function or that they must be complimented by additional contextual information (Blumstein

1995*b*). Warkentin et al. (2001) demonstrated that Richardson's ground squirrels use the rate

of syllable production within a repetitive call to communicate to conspecifics the proximity and

associated degree of threat imposed by nearby predators. Furthermore, call recipients are able

to integrate information about call rate into their responses and show a greater tendency to

assume the highly vigilant alert posture in response to repeated calls broadcast at a higher rate

(Warkentin et al. 2001). The response-urgency hypothesis suggests that graded signals, such as

the number of notes or call rate, are the result of contextual variation. Thus, variation within

the call rate of a repeated call may stem from the proximity and immediacy of threat (Davis

1984; Warkentin et al. 2001), the type of predator perceived (Robinson 1980) and/or the

motivational state of both the predator and the caller (Marler et al. 1992). However, variation

may simply reflect poor signal quality (Hare and Atkins 2001) or low signal certainty (Sloan and

Hare, in press) on the part of the caller, rather than an additional facet of information that better informs receivers.

Since call rate communicates the distance between a predator and a caller (Warkentin et al. 2001), we predicted that accelerations and decelerations in call rate represent the approach and retreat of predators, respectively. We examined how Richardson's ground squirrels respond to moving predator models and whether changes in call rate are sufficient for receivers to gauge changes in threat *in situ*.

Methods

General Methods

Research was conducted on a 1.5-ha site (50°10.190' N, 98°38.103' W) occupying the northern portion of a 5-ha cattle pasture northwest of Portage La Prairie, Manitoba, from 8 April to 26 July 2002. Squirrels, equipment and observers were located relative to a 10 x 10 m Cartesian coordinate grid that was superimposed onto the site using 0.5-m tall, colour-coded wire pin flags. Observers wore the same outer clothes each day to promote habituation of squirrels to human observers. Adult and juvenile squirrels were trapped upon their initial emergence and permanently marked with numbered metal ear tags (1005 Monel size 1, National Band and Tag Co.). Unique marks were applied to the dorsal pelage with hair dye (Clairol Hydrience, #52 Black Pearl) for identification from afar.

Call Production and Behavioural Responses to Models

Predator tracking was studied in free-living juvenile and adult squirrels by recording their vigilance and vocal responses to moving, taxidermically-prepared predator models. As

part of a broader study addressing referential calling, either a badger, *Taxidea taxus*, or a northern harrier, *Circus cyaneus*, was presented. Models were mounted atop the end of a horizontally oriented 5.5-m camouflaged pole. Two 13-cm diameter wheels on either side of the pole were located 1 m behind the model. To preclude any confounds due to predator approach height, we maintained the models approximately 26 cm above the ground by pivoting the pole on its wheels from the opposite end. From a stationary kneeling position, we manually presented the model at 0.5 m/s for a distance of 2 m towards (approach) or away from (retreat) a focal animal. All treatments were presented to each of 15 adults in a dependent-groups design, while 64 juveniles received presentations of 1 of the 4 treatments in an independent-groups design. One adult and 4 juveniles were excluded from the analysis due to incomplete video coverage of their post-treatment responses. Presentations were randomized with respect to age class, sex and treatment and were spatially separated by 50 m, unless 1 h had passed since a given location was used.

Each trial began by identifying a subject and approaching it to within approximately 15 m. When normal foraging behaviour commenced, the model, which was covered with a white sheet, was revealed and the subject's behaviour was videotaped for 30 s prior to and after the approach or retreat of the predator model. Vocalizations were recorded with a Sony TCD-D8 digital audio recorder and an Audio-Technica AT815b shotgun microphone. Recording sessions were limited to mornings between 07:30 and 11:30 h and evenings between 19:00 and 21:30 h CST when maximum wind speeds did not exceed 10 km/h.

Call Perception

We used manipulated calls in a playback experiment to test how squirrels perceive calls with accelerating and decelerating syllable production. Calling bouts recorded from juvenile Richardson's ground squirrels at spatially remote sites by J.F.H. between 1994 and 1998 (see Hare 1998) were transferred to the program Canary™ on a Macintosh™ computer. Using the syllable of highest quality, we constructed one increasing and one decreasing-rate call per caller and transferred the calls to digital audio tape; each call contained 10 identical syllables. Of the 62 calls constructed, 38 were arranged to have a common 4-syllable prelude with 3 s intersyllable latencies (ISL) and a subsequent increase or decrease in call rate (changing by 0.5 s/syllable). These 38 'fixed initial rate' calls were each broadcast to either one male or one female juvenile squirrel. Although these calls shared a common initial rate, the overall bout length varied considerably (39 +/- 1 s for decreasing rate vs. 18 +/- 1 s for increasing rate). To account for any differential habituation of squirrels to the longer vs. shorter bouts, we constructed an additional 12 increasing (5 to 1 s ILS at 0.5 s/syllable) and 12 decreasing-rate (1 to 5 s ISL at 0.5 s/syllable) calls that shared a common bout length (30 +/- 1 s), but varied in initial call rate. These 'fixed bout length' calls were each broadcast to a maximum of 2 juveniles spatially separated by 50 m, totaling 44 receivers that were distinct from the 38 used above. The responses of 3 individuals to the fixed initial rate calls and of 2 individuals to the fixed bout length calls were excluded from the analysis due to incomplete video coverage of their post-treatment responses.

Upon identification of a previously untested squirrel, we approached the prospective subject to within approximately 20 m and set up the playback apparatus, which included a Sony

XM-2025 audio amplifier connected to the digital audio recorder and a Genexxa Pro LX5

loudspeaker, which broadcast calls at a natural sound pressure level (84-91 dB at 1 m from the

speaker). When the subject and nearby conspecifics began foraging, filming commenced and

continued from 1 min pre-playback to 2 min post-playback. We alternated caller sex, the

presentation of increasing/decreasing rate calls and, when possible, the sex of the receiver.

Trials were separated spatially and temporally as in the production component of the study.

Data Coding and Analyses

The dependent variables of interest include the proportion of time that squirrels spent

in low vigilance (standing on 4 feet with the head elevated above the horizontal plane), slouch,

alert (sensu Hare and Atkins 2001) and escape behaviour, including running and entering

burrows. Latencies (as a proportion) to the first vigilant response and the first decrease in

vigilance following the onset of the treatment were also recorded. Insufficient data were

obtained to examine the effect of predator direction on call rate. The variables of interest were

coded from videotape for 30 s immediately prior to and following the treatment presentations

using a using a digital stopwatch and the time-code on the video. For each posture, the post-

pre treatment difference scores produced in response to the approaching vs. retreating

predator models were contrasted among adults using Wilcoxon signed-ranks tests and among

juveniles using Mann-Whitney U-tests. Perception data sets were analyzed with respect to

changes in call rate using Mann-Whitney U-tests. However, this comparison does not consider

instantaneous responses to changes in call rate; conceivably the end of a call indicates that

threat has diminished or that the predator is otherwise occupied. Thus, changes in the

proportionate durations of vigilant postures during the first and last third of the calling bout

were also compared. Given elements of non-independence among dependent variables in the production and perception data analyses, the sequential Bonferroni technique (Rice 1989) was employed to adjust the resultant p-values for the inflation of type I error.

Hare (1998) described the increase in vigilance associated with low vigilance, slouch and alert postures as resulting from the fact that the auditory and visual receptors used for monitoring predators are elevated above the vegetation. Thus as a final, pooled analysis, we weighted the four vigilance postures and escape behaviour with respect to their relative degree of responsiveness by multiplying them by factors 0.25, 0.50, 0.75 and 1.00, respectively. This index was established a priori and treats each ordinal increase in posture as the same relative increase in vigilance, which is the most parsimonious approach. By collapsing the weighted response data into a single score, weighted vigilance (post-pre) was treated as another dependent variable and compared among all treatments with respect to presumptive changes in threat. While this composite score is not independent of the individual postural response tests, and makes only partially substantiated assumptions about the relative meaning of the postures themselves, it was our goal to test exhaustively for any possible effect. Where such violation of independence is committed and no apparent effect is detected, one can be confident that no effect exists (Machlis et al. 1985).

All analyses were one-tailed because our hypotheses provided strong a priori directional predictions of behavioural responses. However, low vigilance was also examined with a two-tailed test to ensure that any associated trends were not overlooked. All research was conducted in accordance with the guidelines set forth by the Canadian Council on Animal Care concerning the ethical treatment of animals in research.

Results

For the 60 juveniles in the production experiment, the changes in the proportionate durations of each of the vigilant and non-vigilant postures did not differ with predator direction (responses to harrier and badger models are pooled: all p > 0.1; table 1). Pooled vigilance, latency to respond and duration of pronounced vigilance were not significantly different when predators approached relative to when they retreated, though non-significant trends (p < 0.1) did follow our predictions (table 1). Among adults, direction of the moving models had no effect on non-vigilant behaviour, though the duration of low vigilance was significantly reduced in response to the approaching vs. retreating harrier model (two-tailed: Z = 2.668, p = 0.0380; Tables 2a and b). Total weighted vigilance was also higher in response to the approaching vs. retreating harrier (Z = -1.712, p = 0.0435; Table 2a). The latency and duration of vigilance among adults, as well as the durations of slouch, alert and escape behaviour, were unaffected by the direction of the moving predator models (all p >= 0.1; Tables 2a and b). Neither juvenile nor adult squirrels showed significantly different responses to the badger and harrier models in any component of the production study (all p > 0.1), although no differences were detected for any variable in response to the badger model (Table 2b). In response to the 124 model presentations, only 3 juveniles and 4 adults produced calls that spanned the movement of the predator model.

The duration of non-vigilant and vigilant postures among 35 juveniles was not higher after 'fixed initial rate' calls with decreasing vs. increasing call rate, though total weighted vigilance did become higher after increasing rate calls (Z = -1.749, p = 0.0401; Table 3a).

Further, the change in the proportionate durations of all non-vigilant and vigilant behaviours within the call (first vs. last third), including total weighted vigilance, did not differ between bouts of increasing and decreasing call rate (all p > 0.1; Table 3b). The latency to the first increase in vigilant behaviour after the first syllable was produced did not vary between treatments, though the duration of that increased vigilance was significantly higher when call rate was increasing (Z = -2.005, p = 0.0225; Table 3a). The 42 juveniles subjected to the 'fixed bout length' playbacks showed no differences in any postural response, including total weighted vigilance, to calls of increasing vs. decreasing call rate (all p > 0.1; Tables 4a and b). The latency to the first increase in vigilant behaviour after the first syllable was produced, and the duration of that increased vigilance, did not differ between increasing and decreasing rate calls where bout length was held constant (Table 4a).

Discussion

Increasing vigilance permits squirrels to better detect and monitor predators above the grass (Hare 1998). Adult squirrels exhibited greater and more prolonged vigilance behaviour in response to approaching vs. retreating predator models, indicating that adults do, indeed, distinguish between and react appropriately to predator movements *in situ*. As threat diminished, however, high vigilance was not replaced by complete non-vigilance, but rather, by low vigilance, suggesting that adults exercise extended caution after predator attacks and that low vigilance is the minimum "safeguard" behaviour displayed in the presence of predators. The absence of significant trends among juveniles may be due to poor perception and/or responsiveness, or may simply reflect the greater resolving power of the dependent-groups

design used with adults. While evidence of productional changes cannot be gleaned from this study, it is apparent from the paucity of vocal responses to the models presented that squirrels cannot rely solely on alarm vocalizations to assess the threat posed by potential predators.

Squirrels responded as predicted to playbacks with fixed initial call rates; vigilance increased more in response to increasing vs. decreasing rate calls. The complete absence of such a trend, however, in response to playbacks with a fixed bout length suggests that those trends are more likely an artifact of differential call length (39 +/- 1 s vs. 18 +/- 1 s). Calls with a fixed initial call rate and a subsequent increasing rate have a higher average rate and associated vigilance response than similar calls with a decreasing rate, and thus communicate a higher average level of threat. Indeed, the absence of different responses to increasing vs. decreasing rate calls when bout length is held constant clearly refutes an effect of changing call rate per se. The lack of response to changes in call rate despite squirrels' ability to perceive predator movements and to convey the extent of threat (Warkentin 2001) parallels the lack of response by golden marmots to changes in call number (Blumstein 1995*b*), despite their ability to perceive the degree of risk present (Blumstein 1995*a*).

Variation in call rate reflects either perceived changes in threat caused by predator movements or ambiguities concerning the true location of the predator. Sloan and Hare (in press) suggested that signal certainty is higher in monotonous vs. variable calls because they better indicate the caller's certainty about the proximity of predators and the extent of threat posed (Warkentin et al. 2001). Variable calls convey uncertain information about predator location, making those calls unreliable indicators of threat. Koops and Abrahams (1998) concluded that as the fitness consequences of vigilance behaviour increase with respect to time

lost from foraging, resting, or caring for young, animals should become less tolerant of imperfect information. Receiving squirrels discriminate among individual callers according to their past reliability and show reduced responsiveness to callers deemed unreliable (Hare and Atkins 2001), suggesting that the costs associated with time spent vigilant outweigh the potential benefits of responding to unreliable callers (Koops and Abrahams 1998). Thus, receivers should eventually habituate to an unreliable calling bout, such as those with either an increasing or decreasing call rate, unless that pattern of variation is otherwise beneficial (Hare and Atkins 2001). This notion is supported by our observation that receivers habituated more and assumed less vigilant postures by the end of the longer call.

Sullivan (1994) explained that the time required to produce and assess a signal increases with the complexity of that signal. Encoding predator movements requires multiple assessments of a predator's location, while discerning changes in call rate requires integration of several syllables. The unpredictability and immediacy of a predator encounter places potential time constraints on the production and assessment of alarm calls, which may limit calls to those that are rapidly assessable and call content to the general extent of threat (Sullivan 1994). The absence of different responses to increasing vs. decreasing call rate in this study suggests that variation surrounding the average call rate during a predator encounter is most likely an artifact of imperfect information, rather than a reflection of predator movements.

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Table 1. Results of Mann-Whitney U-tests (one-tailed) comparing vigilance responses of 60

juveniles to the approaching vs. retreating predator model (responses to the badger and harrier

models are pooled) presentations. Mean proportions (+/- SE) are given for all difference scores

and latencies. Significance values (p) and Z-values are given for all dependent variables of

interest and are corrected for ties and inflation of type I error. Statistically significant

differences (at α = 0.05) are denoted by an asterisk (*).

Dependent variable	Approach mean (SE)	Retreat mean (SE)	Z	p
non-vigilance	0.131 (0.066)	-0.043 (0.058)	-1.183	0.4740
low vigilance	0.063 (0.057)	-0.046 (0.077)	-1.058	0.4740
slouch	0.012 (0.038)	0.049 (0.053)	-0.247	0.7584
alert	0.073 (0.048)	-0.044 (0.056)	-1.512	0.3265
escape	0.001 (0.006)	-0.003 (0.007)	-0.308	0.7584
pooled score	0.077 (0.037)	-0.023 (0.034)	-1.465	0.0715
pre-vigilant latency	0.043 (0.019)	0.138 (0.054)	-1.580	0.0571
duration of response	0.711 (0.065)	0.567 (0.073)	-1.451	0.0735

Table 2. Results of Wilcoxon signed-rank tests (s4hu is two-tailed, all others are one-tailed) comparing vigilance responses of 14 adults to the approaching vs. retreating predator models. Mean proportions (+/- SE) are given for all difference scores and latencies. Significance values (p) and Z-values are given for all dependent variables of interest and are corrected for ties and inflation of type I error. Statistically significant differences (at α = 0.05) are denoted by an asterisk (*).

a) Harrier model

Dependent variable	Approach mean (SE)	Retreat mean (SE)	Z	p
non-vigilance	0.084 (0.074)	0.078 (0.035)	-0.153	0.4392
low vigilance	-0.234 (0.089)	0.054 (0.089)	2.668	0.0380*
slouch	0.251 (0.101)	0.023 (0.090)	-1.961	0.1000
alert	0.054 (0.035)	0.004 (0.004)	-1.219	0.2228
escape	0.014 (0.010)	-0.002 (0.003)	-1.625	0.1563
pooled score	0.483 (0.148)	0.102 (0.103)	-1.712	0.0435*
pre-vigilant latency	0.024 (0.013)	0.009 (0.006)	-1.214	0.2249
duration of response	0.712 (0.107)	0.789 (0.094)	-0.652	0.5147

b) Badger model

Dependent variable	Approach mean (SE)	Retreat mean (SE)	Z	p
non-vigilance	0.022 (0.074)	0.044 (0.073)	0.000	1.0000
low vigilance	-1.126 (0.054)	0.089 (0.078)	1.957	0.2012
slouch	0.110 (0.093)	-0.056 (0.051)	-1.296	0.2925
alert	0.009 (0.009)	0.013 (0.034)	0.000	1.0000
escape	0.006 (0.004)	-0.002 (0.003)	-1.807	0.1770
pooled score	0.147 (0.166)	0.006 (0.117)	-0.384	0.3504
pre-vigilant latency	0.010 (0.010)	0.124 (0.071)	-1.483	0.1380
duration of response	0.594 (0.113)	0.604 (0.096)	-0.533	0.5937

Table 3. Results from Mann-Whitney U-tests comparing vigilance responses of 35 juveniles to playback of fixed initial rate calls with increasing vs. decreasing call rate. Mean proportions (+/-SE) are given for all difference scores and latencies. Significance values (p) and Z-values are given for all dependent variables of interest and are corrected for ties and inflation of type I error. Statistically significant differences (at $\alpha = 0.05$) are denoted by an asterisk (*).

a) Pre vs. post call

Dependent variable	Increasing mean (SE)	Decreasing mean (SE)	Z	p
non-vigilance	0.402 (0.081)	0.117 (0.098)	-2.047	0.1018
low vigilance	0.041 (0.088)	-0.081 (0.079)	-0.792	0.4848
slouch	0.263 (0.100)	0.177 (0.070)	-0.516	0.4848
alert	0.094 (0.052)	0.021 (0.034)	-0.988	0.4848
escape	0.004 (0.002)	-0.001 (0.009)	-1.247	0.4246
pooled score	0.864 (0.185)	0.334 (0.157)	-1.749	0.0401*
pre-vigilant latency	0.020 (0.020)	0.008 (0.006)	-0.578	0.2818
duration of latency	0.612 (0.088)	0.385 (0.049)	-2.005	0.0225*

b) First vs. last third

Dependent variable	Increasing mean (SE)	Decreasing mean (SE)	Z	p
non-vigilance	-0.048 (0.064)	-0.193 (0.069)	-1.802	0.1788
low vigilance	-0.070 (0.076)	-0.155 (0.072)	-1.357	0.3498
slouch	-0.009 (0.073)	-0.058 (0.098)	0.070	0.9734
alert	0.009 (0.064)	0.037 (0.051)	-0.124	0.9734
escape	-0.014 (0.013)	-0.013 (0.007)	-0.455	0.9734
pooled score	-0.120 (0.211)	-0.209 (0.177)	-0.759	0.2239

Table 4. Results from Mann-Whitney U-tests comparing vigilance responses of 42 juveniles to playback of fixed bout length calls with increasing vs. decreasing call rate. Mean proportions (+/- SE) are given for all difference scores and latencies. Significance values (p) and Z-values are given for all dependent variables of interest and are corrected for ties and inflation of type I error. Statistically significant differences (at α = 0.05) are denoted by an asterisk (*).

a) Pre vs. post call

Dependent variable	Increasing mean (SE)	Decreasing mean (SE)	Z	p
non-vigilance	0.205 (0.065)	0.356 (0.069)	-1.196	0.5790
low vigilance	0.047 (0.069)	0.129 (0.060)	-0.428	0.9513
slouch	0.061 (0.052)	0.153 (0.058)	-0.938	0.6964
alert	0.098 (0.054)	0.074 (0.041)	-0.221	0.9513
escape	-0.001 (0.008)	0.000 (0.010)	-0.476	0.9513
pooled score	0.460 (0.163)	0.657 (0.162)	-0.705	0.2404
pre-vigilant latency	0.001 (0.001)	0.008 (0.004)	-1.280	0.1002
duration of latency	0.513 (0.078)	0.438 (0.064)	-0.757	0.2245

b) First vs. last third

Dependent variable	Increasing mean (SE)	Decreasing mean (SE)	Z	p
non-vigilance	-0.106 (0.060)	-0.154 (0.067)	-0.335	1.0000
low vigilance	-0.115 (0.078)	-0.120 (0.088)	-0.454	1.0000
slouch	-0.025 (0.068)	0.016 (0.088)	-0.162	1.0000
alert	0.061 (0.081)	0.057 (0.084)	-0.213	1.0000
escape	-0.042 (0.013)	0.002 (0.044)	-0.640	1.0000
pooled score	-0.151 (0.170)	0.089 (0.440)	-0.126	0.4999