ANIMAL BEHAVIOUR, 2005, **70**, 937–944
doi:10.1016/j.anbehav.2005.01.013

Functional morphology of Richardson's ground squirrel, *Spermophilus richardsonii*, alarm calls: the meaning of chirps, whistles and chucks

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*(Received 24 August 2004; initial acceptance 27 September 2004;
final acceptance 25 January 2005; MS. number: A9980)*

Repetitive alarm vocalizations of Richardson's ground squirrels vary in terms of the acoustic structure of their primary syllables and the inclusion of brief, lower-amplitude, frequency-modulated trailing elements we term 'chucks.' Chucks are included in calls of both males and females and increase in prevalence with the proximity of the caller to the alarm-evoking stimulus. Furthermore, chuck presence is not independent of primary syllable type: chucks follow primary syllables that have constant frequency and diminishing amplitude ('whistle'), but do not trail primary syllables with diminishing frequency and nondescending amplitude spectra ('chirps'). Playbacks to free-living squirrels of repeated alarm calls having whistle- or chirp-like primary syllables factorially combined with chuck presence or absence revealed that chirp-like syllables elicited greater vigilance from call recipients during signal propagation. The addition of chucks to the end of primary syllables of either type, however, increased initial vigilance duration and the proportion of time devoted to vigilance during and after signal reception. Chucks thus promote increased and lasting vigilance on the part of call recipients. Beyond enhancing vigilance, however, the inclusion of frequency-modulated chucks and chirps facilitates the orientation of receivers to the signaller. Multiple acoustic parameters of Richardson's ground squirrel alarm vocalizations thus interact to communicate information regarding several aspects of a predator encounter. Receivers use this information to their advantage, affording greater attention to calls that would be more readily located by predators, and hence are more costly for signallers to produce.

Alarm signals warn conspecific and sometimes allospecific individuals of potential danger posed by predators. However, the nature of the information conveyed by these signals can vary considerably. Specific attributes of predators may be encoded, such that referential information allows signal recipients to respond in a manner that best suits certain predator types or characteristics (referential alarm signalling: Seyfarth et al. 1980; Cheney & Seyfarth 1988; Pereira & Macedonia 1991). Information regarding the situation imposed by the encounter may also supplement or take the place of referential information (situationally specific alarm signalling: Ficken 1989; Blumstein 1995; Blumstein & Arnold 1995) as is the case where signals convey response urgency (Warkentin et al. 2001).

Decoding the information conveyed in a given signal affords insight into the biology of the organism, and into the basic economics by which natural selection operates in refining communication (Marler 1955; Klump & Shalter 1984). Such insights are garnered, however, only via comprehensive consideration of both the circumstances surrounding variation in signal production and documentation of the response to such signals, thereby addressing the perception of the signal by potential receivers (Evans et al. 1993; Macedonia & Evans 1993).

Davis (1984) reported productional specificity in the alarm-calling system of Richardson's ground squirrels, wherein squirrels produced short 'chirps' in response to aerial predators, and longer 'whistles' that were often repeated in response to terrestrial predators. Warkentin et al. (2001) noted, however, that such productional specificity could result from the more imminent threat imposed by faster approaching avian versus terrestrial predator types, and revealed that Richardson's ground squirrels encode the extent of threat imposed by predators

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0003–3472/05/$30.00/0

via variation in the rate of repetitive calling. Differing spectral properties of the syllables underlying repetitive calls may thus act to verify or even refine information regarding response urgency. Indeed, Macedonia & Evans (1993) and Blumstein (1995, 1999) similarly concluded that ground-dwelling squirrels are not likely to use referential signalling (but see Slobodchikoff et al. 1991).

If the spectral variability in Richardson's ground squirrel alarm calls does not provide functional referentiality, why does such pronounced variation exist, and what, if any, information does such variation encode? Davis's dichotomy of whistles and chirps drastically underrepresents the many parameters of Richardson's ground squirrel alarm vocalizations that show spectral variation (Koeppl et al. 1978). Among these, we sought to understand the function of the brief, relatively low-amplitude, frequency-modulated elements, which we termed 'chucks', that often follow the offset of primary syllables in repeated alarm vocalizations (see Figure 5H in Koeppl et al. 1978).

Although lower-amplitude elements in some cases represent echoes of preceding louder components, the elaboration of fine structure within a vocalization may enhance signal transmission or expand information content (Owings & Hennessy 1984; Bradbury & Vehrencamp 1998). Roosters, *Gallus gallus*, often incorporate a relatively brief, but intense broadband pulse of sound immediately before the first syllable of a repeated alarm call, which functions to alert receivers to the subsequent call (Gyger et al. 1987; Bayly & Evans 2003). Similarly, male túngara frogs, *Physalaemus pustulosus*, append one or more broadband 'chucks' to the end of their tonal advertisement call, which increases the effectiveness of the signal in terms of attracting females (Rand & Ryan 1981) and offers an honest indicator of male body size (Ryan 1985).

Both broadband and frequency-modulated sounds are more readily locatable than signals that are restricted to a narrow frequency range (Bradbury & Vehrencamp 1998). Temporally segregated trailing elements may also facilitate localization of the signaller. In harbour seals, *Phoca vitulina*, clicks following grunt vocalizations provide discrete temporal cues that allow localization of the signal source based on interaural differences in their time of arrival (Terhune 1974). The inclusion of such elements in alarm vocalizations may thus increase the signaller's risk of predation (Ryan et al. 1982), which in turn would select for honest signalling (Bradbury & Vehrencamp 1998).

We used Richardson's ground squirrel alarm vocalizations recorded in the context of previous research (Hare 1998) to describe the spectral properties of chucks and to examine the contextual correlates of their inclusion in repeated calls. Furthermore, we conducted a factorial playback experiment to determine how natural primary syllable attributes and chucks interact to affect the alarm responses of the squirrels.

METHODS

General Methods

We used recordings made in the context of previous alarm communication studies (Hare 1998; Hare & Atkins 2001; Warkentin et al. 2001; Wilson & Hare 2003; Sloan & Hare 2004) to characterize signals and to analyse contextual elements underlying signal production. Alarm calls used in those studies were elicited by presenting free-living juvenile Richardson's ground squirrels (Michener & Koeppl 1985) with a model predator: a tan-coloured Biltmore hat (32.5 × 19.5 cm brim × 13 cm high). The use of models is common in studies of antipredator calling behaviour, because models allow greater contextual control than do natural predator encounters (MacWhirter 1992; Hare 1998). Furthermore, the hat has proven to be as effective as a taxidermically prepared badger, *Taxidea taxus*, bobcat, *Felis rufus*, and bird of prey, *Circus cyaneus*, in eliciting calls from Richardson's ground squirrels (unpublished data), and has the advantage of portability in the field. All presentations and call recordings were made by J.F.H. while wearing the same outer clothing to minimize any confounding effects of the observer (see Slobodchikoff et al. 1991). Recording methods followed those described in Hare (1998). Subjects that had not previously been presented with the predator model (hat) were approached within 15 m. The hat was tossed from hip level with a flip of the wrist to land within 1–8 m of the intended subject at an angle of 0–30° relative to a line between the observer and the subject (but never directly over the subject). In all cases, calling did not begin until after the hat landed on the ground. During each recording session, the time of day, position of the recording on the tape, locations of the microphone, predator model and subject at the outset of recording, and the behaviour of the subject coinciding with the presentation of the model (particularly whether the subject faced the model while calling) were recorded. 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.

We conducted additional fieldwork during 8 April–14 July 2004 on free-living Richardson's ground squirrels occupying mowed lawns at the Assiniboine Park Zoo (49°52′N, 97°14′W) in Winnipeg, Manitoba. Juvenile squirrels were live-trapped using National or Tomahawk traps baited with peanut butter, were permanently marked with metal eartags (National Band & Tag Company no. 1005, Newport, Kentucky, U.S.A.), and were given unique marks on their dorsal pelage with hair dye (Clairol Hydrience 52, Black Pearl, Stamford, Connecticut, U.S.A.). We wore the same outer clothing each day to habituate the squirrels to our appearance. All work involving animals conformed to the guidelines for the ethical use of animals in research set forth by the Canadian Council on Animal Care and those outlined under the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching.

Spectral Analysis of Call Structure

We examined the spectral properties of juvenile Richardson's ground squirrel alarm calls recorded by Hare (1998) at sites across southern Manitoba between 1994 and 1998. This analysis revealed that, in addition to primary syllable attributes, calls could be categorized according to the presence or absence of a relatively low-amplitude acoustic element that trailed the offset of primary syllables (ca. −20 dB relative to primary) within repetitive calls, after a brief (ca. 10–40 ms) intervening silence (Fig. 1). We refer to these elements as ‘chucks’ (although they lack the overlap in time with the primary syllable, increased amplitude, and abundant and powerful harmonics of túngara frog chucks; Ryan 1985), because their audible effect is to harshen the offset of each syllable, interjecting a pulsatile beat into the end of each utterance.

Of the 34 juvenile Richardson’s ground squirrel repeated calls selected for their high signal-to-noise ratio and used in playback studies by Sloan & Hare (2004) and Wilson & Hare (2003), 14 included at least some syllables accompanied by chucks. To avoid problems associated with pseudoreplication (Machlis et al. 1985), a single syllable–chuck pair was sampled arbitrarily from each calling individual. We used Canary 2.04 (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.) to parameterize the spectral properties of those chucks, measuring their duration, latency and frequency at onset relative to the offset of the preceding primary syllable, frequency at offset, and harmonic structure (Fig. 1). All spectra were generated using a fast Fourier transform size of 256 points and Hamming windowing. Because both males and females issued chucks in some of their calls, we also compared each acoustic parameter of male- versus female-produced chucks using Mann–Whitney *U* tests.

We tested for an association between chuck presence and both the general frequency and amplitude characteristics of the primary syllables contained in 32 of the 34 repeated calls with the highest signal-to-noise ratio. We used Fisher’s exact tests on contingency tables to examine the presence or absence of chucks relative to primary syllable frequency type (categorized from spectra as chirps with frequency descending over time or whistle-like with constant frequency) and amplitude type (categorized from spectra as descending, ascending, dual-peaked, or multi-peaked, although calls of the latter three types were relatively rare and thus pooled into a category called ‘other’ for the purpose of contrasts with descending amplitude calls). To ensure that these association tests were not subject to bias introduced via the arbitrary selection of a single syllable from within each call, we developed contingency tables that considered both the attributes of the preceding syllable relative to chuck presence and the attributes of the majority of syllables ($\geq 75\%$) relative to chuck presence in the entire call sample. Furthermore, we used logistic regression to test for any association between the rate at which syllables were produced (estimated from the time taken to produce the first five syllables in the call) and the inclusion of chucks within those calls.

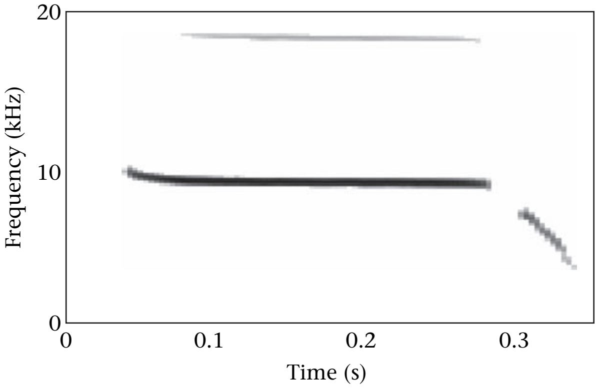

Figure 1. Spectrographic representation of the frequency versus time domain of a Richardson’s ground squirrel ‘whistle’ (sensu Davis 1984) with a ‘chuck’ trailing the primary syllable.

Context of Chuck Production

We reviewed field notes documenting contextual elements associated with the production of the 34 calls used in our studies, including the sex of the caller, distance of the caller from the predator model, distance of the caller from the observer/microphone, date (day within year), time of day, wind speed (an ordinal ranging from 0 = calm, to 3 = very windy) and cloud cover (an ordinal ranging from 0 = clear, to 2 = totally overcast). We subjected data on the sex of the caller versus chuck presence or absence to contingency table analysis using a Fisher’s exact test. The remaining contextual data were analysed using logistic regression to determine whether the environmental parameters measured affected the propensity of individuals to include chucks in their repeated calls.

Playback Trials: Call Perception

To determine how alarm call recipients perceive chucks, to ascertain whether chucks exert an effect on receivers independent of the primary syllables they accompany, and to test for any differential effect of the two general primary syllable types, we examined responses of juvenile Richardson’s ground squirrels to playbacks of recorded calls. Playback trials were conducted when both wind and potential public interference were minimal, between 0700 and 2055 hours Central Standard Time (CST) during 5–14 July 2004, following a factorial design. Each of 60 subjects received a single five-syllable playback (3-s intersyllable latency) of one of four possible call types formed via the manipulation of two call attributes: primary syllable type (whistle-like with constant frequency and descending amplitude versus chirps with descending frequency and multipeaked amplitude within each syllable) and chuck presence (present versus absent). Because the rate at which syllables are uttered in repeated calls significantly affects the vigilance responses of call recipients (Warkentin et al. 2001), we held intersyllable latency constant among call types. Thus, calls including chucks and calls composed of whistle-like primary syllables were of longer duration than those without chucks and those composed of chirps. Calls were constructed on Canary 2.04 via the repetition of single syllables derived from the 34 previously recorded calls described earlier. Calls having primary syllables with constant frequency and diminishing amplitude and incorporating a chuck were described by Davis (1984) as 'whistles', whereas those having primary syllables with diminishing frequency, multipeaked amplitude and lacking a chuck fall within the call types described by Davis as 'chirps.' The two artificial call types in our experiment (primary syllables of constant frequency and diminishing amplitude with no chuck, and primary syllables having diminishing frequency but multipeaked amplitude with a chuck) were created by deleting chucks from the whistles used above and appending those chucks to the aforementioned chirps, respectively. Whistles serving as the source of chucks were matched to chirps receiving those chucks to minimize the difference in the onset frequencies of the primary syllables.

Field playbacks of alarm calls followed the general methods described in Hare & Atkins (2001). Upon identification of a previously untested squirrel, we approached the prospective subject to within 15–25 m and set up the playback apparatus, which included a minidisc player (Sony MZ-N707), Sony XM-2025 audio amplifier and a Genexxa Pro LX5 loudspeaker. The playback system collectively reproduced frequencies ranging from 85 Hz to 22 kHz. Although the peak sound pressure level (SPL) of playback exemplars of all four call types diminished with distance from the source, no significant difference in SPL (measured with a Realistic 33-2050 sound-level meter, A weighting, fast response) was detected at either 15 or 25 m from the speaker during a series of SPL measurement trials conducted over similar terrain at a remote site (Table 1). Videotaping (via a tripod-mounted Sony DCR-TRV120 camcorder) commenced when squirrels began to forage and continued from 30 s prior to call playback (preplayback) until 30 s postplayback. Calls were arbitrarily assigned to subjects, but the order in which calls of the four possible types were presented was randomized. Playbacks of different callers within a given day were performed at least 50 m apart from one another, or if within the same general area, were staged at least 1 h apart.

Vigilant Richardson's ground squirrels elevate their head above the horizontal plane. Thus, postural responses to alarm calls provide an assay of vigilance in call recipients (Holmes 1984; Hare 1998; Hare & Atkins 2001). Using a stopwatch and the video record, we quantified responsiveness to alarm calls as the initial vigilance duration of call recipients (the time from the initial expression of vigilance after the first syllable of the playback to any reduction in vigilance posture) and as the total proportion of time spent vigilant (including any posture in which the head is elevated above the horizontal plane; see Hare 1998) during the playback and postplayback periods. In addition, to assess whether certain call parameters facilitate localization of the signaller, we quantified the orientation of call recipients relative to the signal source. We estimated the angular deviation of the subject squirrel's nose over the majority ($\geq 75\%$) of the playback period in 5° increments from the speaker, which itself was consistently positioned 9 m to the right of the observers at roughly the same distance as the observers were to the call recipient. Data were coded from videotape by observers who were blind to the treatment conditions for each trial, but were provided with the time code for the onset and offset of the preplayback, playback and postplayback periods. Data from three trials (one constant-frequency chuck present and two constant-frequency chuck absent) were excluded from the analysis, however, because of loud natural calling during the playback period that could have affected the response of call recipients.

We used two-factor analysis of variance (the parametric assumptions of normality and homogeneity of variance were met: all $P > 0.05$) to test for effects of primary syllable type, chuck presence and their interaction on initial vigilance duration, the proportion of time that call recipients engaged in vigilance during the playback and postplayback periods, and orientation relative to the signal source. Miscellaneous grouping factors, including time of trial (0700–2055 hours CST), date (187th–196th day within year), wind speed (0–11.4 kph), temperature (13.1–29.6 °C), relative humidity (35–86%), cloud cover (0–100%), the angle of the speaker relative to the recipient (0–45 °), the distance between the speaker and the call recipient (6.3–24.1 m), the number of natural callers heard during the playback (categorized as none or one, few, or many), and caller sex, were balanced across chuck presence versus absence and primary syllable type (all $P > 0.05$) and thus do not confound the interpretation of receiver responses. Statistical analyses were performed on Statview 5.01 (SAS Institute Inc., Cary, North Carolina, U.S.A.) and differences were considered significant when $P \leq 0.05$.

RESULTS

Spectral Properties of Chucks

A spectrographic representation of a chuck along with its preceding primary syllable is shown in Fig. 1. Thirty-two high-quality calls were initially examined, but all 14 calls recorded in 1994 and 1995 were omitted from further spectral analysis because of potential biases introduced by year, variation among study populations, or the microphone used to record calls in those years. Indeed, chucks were observed in only two of 14 calls (14.3%) recorded in 1994 and 1995 with the parabolic microphone (Dan Gibson P-650), but were present in 12 of 18 calls (66.7%) recorded with the shotgun microphone (Audio-Technica AT815B) in 1997 and 1998. In all of those years, the same experimenter wore the same outer clothing and presented the same call-eliciting model in the same way. In the 12 chuck-containing calling bouts recorded in 1997 and 1998, chucks followed 50–97% of the primary syllables sampled (a mean ± SE proportion of 0.87 ± 0.04 of the syllables), trailed primary syllables by a latency of 10.2–40.7 ms (mean ± SE = 23.2 ± 2.5 ms), and had a duration of 8.7–37.8 ms (mean ± SE = 21.0 ± 2.6 ms). The onset frequency of the chuck was 1.13–5.07 kHz (mean ± SE = 2.84 ± 0.34 kHz) below the offset frequency of the preceding syllable, and chucks themselves were invariably frequency-modulated from a higher frequency at their onset (range 4.48–7.53 kHz, mean ± SE = 6.13 ± 0.23 kHz) to a lower frequency at their offset (range

Table 1. Peak sound pressure level (mean ± SE dB) of the four Richardson's ground squirrel call types ($N = 15$ exemplars/call type) at 15 and 25 m from the loudspeaker

	Call type				
	Whistle-like		Chirp-like		ANOVA
Distance from speaker	With chuck	No chuck	With chuck	No chuck	$F_{3,56}$, P
15 m	62.7±1.0	61.0±0.8	60.3±0.5	60.4±0.8	2.05, 0.12
25 m	58.5±0.8	58.0±0.6	57.8±0.5	58.1±0.6	0.22, 0.88

2.74–4.63 kHz, mean ± SE = 3.52 ± 0.19 kHz). Frequency within chucks thus declined anywhere from 1.33 to 4.67 kHz (mean ± SE = 2.61 ± 0.27 kHz) at a mean ± SE rate of 0.13 ± 0.004 kHz/ms, and all chucks showed a pattern of declining amplitude over their duration. No harmonics or subdominant carriers were detected in any of the chucks recorded in 1997 or 1998.

Contextual Correlates of Chuck Production

Signaller attributes

Female and male juveniles showed an equal propensity to include chucks in their repeated calls (seven females produced repeated calls with chucks and four produced calls without chucks whereas five males produced repeated calls with chucks and two produced calls without chucks: Fisher's exact test: $P = 1.0$). Females and males also incorporated chucks into a similar proportion of their syllables (Mann–Whitney U test: $U = 14.5$, $N_1 = 5$, $N_2 = 7$, $P = 0.62$; Table 2). Furthermore, no significant differences were detected between male- and female-produced chucks in terms of their maximum frequency, minimum frequency, change in frequency from onset to offset, the rate of change in frequency, the difference in their onset frequency relative to the offset frequency of the preceding syllable, the latency from the primary syllable to chuck onset, or chuck duration (all $P \geq 0.22$; see Table 2). The statistical power of these contrasts was limited, however, by the small samples of male- and female-produced calls.

Influence of primary syllables

The presence of chucks was significantly correlated with both the general amplitude and frequency attributes of the primary syllables found within repeated calls. Chucks were more likely to be present when either the preceding syllable (Fisher's exact test: $P = 0.01$) or the majority of syllables in the call (Fisher's exact test: $P = 0.00$) decreased in amplitude from onset to offset (Table 3). Chucks were also more likely to be present when either the preceding syllable (Fisher's exact test: $P = 0.00$) or the majority of syllables in the call (Fisher's exact test: $P = 0.00$) had constant as opposed to a descending fundamental frequency from their onset to offset (Table 4). The rate at which syllables were produced had no effect, however, on the likelihood of chucks accompanying those syllables ($\text{logit}(P) = 0.95 - 1.0x$, $\chi^2_1=0.02$, $P = 0.89$, $R^2 = 0.001$).

Environmental factors

Only the distance between the predator model and the signaller had a significant influence on whether repeated calls included chucks (Table 5). The likelihood of calls incorporating chucks increased as the model was positioned in closer proximity to the caller.

Table 2. Comparison of chuck parameters (mean ± SE) in male- versus female-produced Richardson's ground squirrel alarm calls

	Sex of caller			
Call attribute	Male (N=5)	Female (N=7)	U	P
Proportion of syllables with a chuck	0.85±0.09	0.90±0.02	14.5	0.62
Chuck duration (ms)	22.5±4.4	19.9±3.5	13.5	0.52
Latency to chuck (ms)	20.9±3.4	24.8±3.6	13.0	0.46
Minimum frequency (kHz)	3.18±0.15	3.76±0.29	10.0	0.22
Maximum frequency (kHz)	5.86±0.41	6.31±0.28	12.0	0.37
Frequency change (kHz)	2.68±0.35	2.56±0.42	14.0	0.57
Frequency rate change (kHz/ms)	0.13±0.01	0.13±0.01	15.0	0.68
Frequency drop from primary offset to chuck onset (kHz)	3.40±0.64	2.45±0.32	11.0	0.29

Table 3. Amplitude type of preceding primary syllables and majority (≥75%) of primary syllables in calls with and without an accompanying chuck in Richardson's ground squirrel alarm calls; 'other' includes dual-peaked, multipeaked and ascending

	Preceding syllable amplitude type		Majority amplitude type	
	Descending	Other	Descending	Other
Chuck present	8	4	12	0
Chuck absent	0	6	0	6

Playback Trials: Chuck versus Primary Syllable Effects

The inclusion of chucks in repeated calls significantly increased the initial vigilance duration of call recipients and the total proportion of time devoted to vigilance during and immediately after the playback (Table 6). Whereas the proportion of time devoted to vigilance was significantly greater for chirp-like (decreasing frequency and multipeaked amplitude) primary syllables during the playback, and squirrels tended to prolong initial vigilance in response to chirp-like syllables, primary syllable type did not affect the proportion of time devoted to vigilance after the playback (Table 6). Furthermore, primary syllable type did not interact with chuck presence for any of the vigilance response measures (Table 6).

Unlike vigilance proper, orientation of call recipients to the signal source was unaffected by either chuck presence or primary syllable type alone. However, chuck presence increased orientation to the source when paired with whistle-like primary syllables but not chirp-like syllables (Table 6). Orientation of the head to the signal source was most pronounced for chirp-like primary syllables without chucks (chirps sensu Davis 1984) and decreasingly pronounced for whistle-like syllables with chucks (whistles sensu Davis 1984), chirp-like syllables with chucks, and whistle-like syllables without chucks, in that order (Table 6).

DISCUSSION

We investigated the function of the chucks, chirps and whistles that constitute the audible alarm vocalizations of Richardson's ground squirrels. The likelihood of chucks being incorporated into repeated alarm calls increased with proximity to the call-eliciting stimulus. Furthermore, the broadcast of chucks both increased the initial vigilance duration and exerted a tonic effect (Schleidt 1973; Owings et al. 1986), prompting squirrels to devote a greater proportion of their time to vigilance once the alarm signal had ceased. Thus, chucks appear to heighten the perception of threat by call recipients. Because a caller producing chucks may be more easily detected by a predator, chucks lend credence to the message conveyed by the preceding primary syllables. For that reason, calls incorporating chucks are treated as more reliable indicators of threat, and are afforded greater attention by signal recipients, just as juvenile Richardson's ground squirrels attend more to reliable signallers (Hare & Atkins 2001) and signals that temporally convey the extent of threat with greater certainty (Sloan & Hare 2004).

Table 4. Frequency type of preceding primary syllables and the majority (≥75%) of syllables in calls with and without an accompanying chuck in Richardson's ground squirrel alarm calls

	Preceding syllable frequency type		Majority frequency type	
	Descending	Constant	Descending	Constant
Chuck present	0	12	0	12
Chuck absent	6	0	6	0

Our playback results also reveal, however, that the two primary syllable types differed in their salience to receivers over the short term. Chirp-like primary syllables elicited greater vigilance responses than whistle-like primary syllables during their broadcast, but that difference did not persist into the postplayback period. The observed difference in response to chirps versus whistles may be explained by Davis's (1984) finding that chirps tend to be produced in response to avian predators whereas whistles tend to be produced in response to terrestrial predators. Avian predators typically appear suddenly, stoop on prospective prey, and retreat to cover. Thus, they present an immediate but transitory threat that requires an immediate and pronounced response.

Consistent with that interpretation, we found that in natural calls, chucks trailed whistle-like, but not chirp-like, primary syllables. Chucks may be incorporated into whistles in cases where predators present an immediate threat, but omitted where the caller perceives a lesser threat. In our playback experiment, receivers oriented more directly to the source when chucks were left in whistles than when chucks were appended to chirps. Because squirrels can enhance their safety in the face of terrestrial predators by monitoring the location of the predator (Lima & Dill 1990), the inclusion of chucks in calls issued to terrestrial predators may result from selection favouring localization of the signaller, whose calls may serve in part as a pronouncement of vigilance, but ultimately benefit the signaller by warning others of the predator's presence (Sherman 1977). Indeed, by discriminating among individual callers (Hare 1998), and estimating the distance of the predator from the signaller via perception of the rate of repetitive calling (Warkentin et al. 2001), receivers that can locate the signaller in space could infer their distance from the predator based on alarm vocalizations alone. Moreover, they could potentially integrate information from multiple signallers to pinpoint the position of the presumptive predator within the colony. The persistence of vigilance beyond the end of the repeated call where chucks are present most likely reflects receivers' attempts to visually locate the predator that elicited the signal.

The retention of chucks where primary syllables had constant frequency enhanced orientation towards the signal source, but the most direct orientation to the source

Table 5. Summary of contextual influences on chuck production in Richardson's ground squirrel alarm calls

Variable	Logistic likelihood			% Correct predictions	Effect size (R^2)
	Logit(P)=	χ^2	P		
Date	$15.07-0.08x$	2.18	0.14	70	0.08
Time	$4.45-0.39x$	0.75	0.39	60	0.03
Cloud cover	$0.91-0.39x$	0.43	0.51	65	0.02
Wind speed	$0.67-0.13x$	0.03	0.87	65	0.00
Caller–observer distance	$4.79-0.68x$	2.95	0.09	68	0.12
Caller–hat distance	$5.90-2.50x$	11.40	0.00	85	0.44

was observed for chirps that lacked chucks altogether (Table 6). It is likely that the highly frequency-modulated nature of the chirps, along with the high response urgency such syllables convey, promote this pronounced orientation to the signal source. Monitoring positional changes of a predator imposing an imminent threat may not be practical, but it would prove selectively advantageous if alarm signals given in that context provided information that allowed receivers to orient their evasive responses accordingly. Diminution of the orientation response when chucks are appended to the chirps, or when chucks are deleted from whistles, may reflect potentially conflicting or incomplete information in those two artificial call types.

Whistles containing chucks may be beneficial not only in situations involving terrestrial predators, but may sometimes be useful in response to avian predators, which perch, or even land on the ground, within or in close proximity to a colony, and may resume their attack from those positions. It is not surprising then that the level of productional specificity reported by Davis (1984) is not absolute: whistles are sometimes given in response to aerial predators and chirps are sometimes produced in response to terrestrial predators. Indeed, both the chirps and the whistles used in our study were elicited by tossing the same tan-coloured hat towards squirrels in the field (see Hare 1998). Contrary to Davis, Richardson's ground squirrels appear to use spectrally distinct calls to communicate different information (chirps for immediate threats and whistles incorporating chucks for more tonic threats that should be tracked independent of taxonomic affiliation) rather than to represent different predator classes per se. Further experimentation using live, or at least life-like models of terrestrial and avian predators is necessary, however, to address the extent to which information regarding predator type, or specific predator attributes, may also be communicated in Richardson's ground squirrel alarm signals.

Because chucks are temporally segregated from the primary syllables they accompany, they provide a discrete temporal cue that may facilitate localization of the signal's source (Terhune 1974). Like chirps themselves, however, the frequency-modulated nature of chucks would also promote such localization (Bradbury & Vehrencamp 1998). Whereas locating the signal source may prove advantageous to conspecifics, individuals producing such localizable calls would incur an increased cost given that eavesdropping predators could more readily locate the caller (Sherman 1977; Ryan 1985). That such signalling is costly, however, provides further reason why call recipients can rely on those signals and show enhanced responsiveness to repeated calls containing frequency-modulated elements such as chirps and chucks. The inclusion of frequency-modulated components within Richardson's ground squirrel repeated calls expands their information content and communicates underlying signal veracity.

Table 6. The influence of primary syllable type, chuck presence and their interaction on the vigilance responses (in seconds) of Richardson's ground squirrel call recipients; results are shown as mean ± SE (N)

Dependent variable	Call type				Significance tests		
	Whistle-like		Chirp-like		Primary syllable	Chuck	Interaction
	With chuck	No chuck	With chuck	No chuck	$F_{1,53}$, P	$F_{1,53}$, P	$F_{1,53}$, P
Initial vigilance duration	7.4±3.1 (14)	2.2±0.6 (13)	12.9±3.7 (15)	6.6±1.7 (15)	3.4, 0.07	4.6, 0.04	0.0, 0.83
Total vigilance (playback)	0.6±0.1 (14)	0.4±0.1 (13)	0.7±0.1 (15)	0.6±0.1 (15)	6.5, 0.01	7.2, 0.01	0.0, 0.89
Total vigilance (postplayback)	0.5±0.1 (14)	0.5±0.1 (13)	0.7±0.1 (15)	0.4±0.1 (15)	0.2, 0.68	4.5, 0.04	3.7, 0.06
Orientation to source (*$F_{1,54}$)	74.3±12.1 (15)	100.0±17.3 (14)	84.3±14.3 (14)	54.0±9.0 (10)	1.8*, 0.18	0.0*, 0.86	4.4*, 0.04

Acknowledgments

We are grateful to the Rousson family of Oak Lake, MB, the Brown family of Brandon, MB, the Gray family of Delta Marsh, MB, and Dr Bob Wrigley of the Assiniboine Park Zoo for providing access to ground squirrel colonies. We thank Jack Terhune for drawing our attention to the possible role of chucks in localizing the signal source, and Carl Gerhardt, Kris Bruner and two anonymous referees whose comments significantly improved our manuscript. Our research was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Undergraduate Summer Research Awards and NSERC Postgraduate Scholarships awarded to J.L.S. and D.R.W., and by NSERC Discovery Grants awarded to J.F.H. This is paper 310 of the Delta Marsh Field Station.

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