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

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Repetitive alarm vocalizations of Richardson's ground squirrels (*Spermophilus richardsonii*) vary in terms of the acoustic structure of their primary syllables and the inclusion of brief, lower amplitude, frequency-modulated elements trailing those syllables which 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. Further, chuck presence is not independent of primary syllable type: chucks follow primary syllables that have constant frequency and diminishing amplitude producing a "whistle", but do not trail primary syllables with diminishing frequency and non-descending amplitude spectra ("chirps"). Playbacks to free-living squirrels of repeated alarm calls having whistle- or chirp-like primary syllables and factorially combining those 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 both 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 signaler. Multiple acoustic parameters of Richardson's ground squirrel alarm vocalizations thus interact to communicate information regarding several aspects of a predator encounter. Receivers utilize such information to their advantage, affording greater attention to calls that would be more readily located by predators, and hence are more costly for signalers to produce.

Alarm signals warn conspecific and sometimes allospecific individuals of potential danger posed by predators. Considerable diversity exists, however, in the nature of the information conveyed by these signals. 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 signaling: 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 signaling: 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 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 referential signaling is unlikely to be exhibited by ground-dwelling squirrels (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 under-represents 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 Koeppl et al. 1978 Fig. 5H).

While 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 increase the effectiveness of the signal in terms of attracting females (Rand & Ryan 1981) and act as honest indicators 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 signaler. In harbor 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 signaler's risk of predation (Ryan et al. 1982), which in turn would select for honest signaling (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 examine the contextual correlates of their inclusion in repeated calls. Further, we conducted a factorial playback experiment to determine how natural primary syllable attributes and chucks interact in affecting the alarm responses of the squirrels.

METHODS

General Methods

Research involved the characterization of signals and analysis of contextual elements underlying signal production from recordings made in the context of previous alarm communication studies (Hare 1998; Hare & Atkins 2001; Sloan & Hare 2004, Warkentin et al. 2001; Wilson & Hare 2004). 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 x 19.5 cm brim x 13 cm high). The use of models is common in studies of antipredator calling behaviour as models allow greater contextual control than do natural predator encounters (MacWhirter 1992; Hare 1998). All presentations and call recordings were made by JFH 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 to within 15 m. The hat was tossed from hip level with a flip of the wrist to 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. For 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 from 8 April through 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, permanently marked with metal ear tags (National Band & Tag Company #1005) and given unique marks on their dorsal pelage with hair dye (Clairol Hydrience™ 52, Black Pearl). Experimenters 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 Animal Behaviour Society's guidelines for the treatment of animals in behavioural research and teaching.

Spectral Analysis of Call Structure

Preliminary examination of the spectral properties of juvenile Richardson's ground squirrel alarm calls recorded by Hare at sites across southern Manitoba between 1994 and 1998 (see Hare 1998) 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 msec) 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) as 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) in describing chucks, a single syllable/chuck pair was sampled arbitrarily from each calling individual. We used Canary™ 2.04 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 an FFT size of 256 points and Hamming windowing. As 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 employed Fisher's exact tests on contingency tables examining 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, bi-peaked, or multi-peaked, though calls of the latter 3 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, contingency tables were formed considering both the attributes of the preceding syllable relative to chuck presence, and the attributes of the majority of syllables (≥ 75%) relative to chuck presence in the entire call sample.

Further, 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 5 syllables in the call) and the inclusion of chucks within those calls.

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 - total 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 those 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 CST from 5 through 14 July 2004 following a factorial design. Each of 60 subjects received a single 5-syllable playback (3 sec intersyllable latency) of one of four possible call types formed via the manipulation of two syllable attributes: primary syllable type (whistle-like with constant frequency and descending amplitude versus chirps with descending frequency and multi-peaked 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 unique juvenile callers (within the 34 calls above) recorded at sites other than the zoo. Calls having primary syllables with constant frequency, diminishing amplitude and incorporating a chuck were described by Davis (1984) as "whistles", while those having primary syllables with diminishing frequency, multi-peaked amplitude and lacking a chuck fall within the call types Davis described 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 multi-peaked 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 so as 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, including 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. While 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 sec prior to call playback (pre-playback) until 30 sec post-playback. Calls were arbitrarily assigned to subjects, though 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 one hour 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 post-playback periods. In addition, to assess whether certain call parameters facilitate localization of the signaler, 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 (≥75%) of the playback period in 5 degree increments from the speaker, which itself was consistently positioned 9 m to the right of the observers and 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 pre-playback, playback and post-playback 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 call recipients engaged in vigilance during the playback and post-playback 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 and differences were considered significant where *P* £ 0.05.

RESULTS

Spectral Properties of Chucks

A spectrographic representation of a chuck along with its preceding primary syllable is shown in Fig. 1. While thirty-two high-quality calls were initially examined, 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 2 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 despite the fact that the same experimenter, wearing the same outer clothing, presented the same call-eliciting model in the same way in all of those years. In the 12 chuck-containing calling bouts recorded in 1997 and 1998, chucks followed 50 to 97% of the primary syllables sampled (a proportion of 0.87 ± 0.04 of the syllables, mean ± SE), trailed primary syllables by a latency of 10.2 to 40.7 msec (23.2 ± 2.5 msec), and had a duration of 8.7 to 37.8 msec (21.0 ± 2.6 msec). The onset frequency of the chuck was 1.13 to 5.07 KHz (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 to 7.53 KHz, mean ± SE: 6.13 ± 0.23 KHz) to a lower frequency at their offset (range: 2.74 to 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 rate of 0.13 ± 0.004 KHz/msec (mean ± SE), and all chucks exhibited a pattern of declining amplitude over their duration. No harmonics or sub-dominant carriers were detected in any of the chucks recorded in 1997 or 1998.

Contextual Correlates of Chuck Production

Signaler attributes

Female and male juveniles had 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 (Table 2: $Z_c = 0.49$, $P = 0.62$). Further, 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 is 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 uttered had no effect, however, on the likelihood of chucks accompanying those syllables (Logit(P) = 0.95 -1.0x, $X^2_1 = 0.02$, $P = 0.89$, $R^2 = 0.001$).

Environmental factors

Only the distance between the predator model and the signaler 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.

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 multi-peaked 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). Further, 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, though a significant interaction was apparent such that 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 less so 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 chucks, chirps and whistles that comprise 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. Further, the broadcast of chucks increased both 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, lending credence to the message conveyed by their preceding primary syllables. In that sense, 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 to more reliable signalers (Hare & Atkins 2001) and signals that temporally convey the extent of threat with greater certainty (Sloan & Hare 2004).

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, though that difference did not persist into the post-playback 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 and whistles 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, which would require immediate and pronounced response.

Consistent with that interpretation, we found that in natural calls, chucks trailed syllables with constant frequency and descending amplitude, producing whistles, but not primary syllables uttered as chirps. Chucks then, 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 favoring localization of the signaler, whose calls may serve in part as a pronouncement of vigilance, but ultimately benefit the signaler 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 signaler via perception of the rate of repetitive calling (Warkentin et al. 2001), receivers that could locate the signaler in space could infer their distance from the predator based on alarm vocalizations alone, perhaps even integrating information from multiple signalers 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 likely reflects receiver's attempts to visually locate the predator that elicited the signal.

Whereas the retention of chucks where primary syllables had constant frequency enhanced orientation toward the signal source, the most direct orientation to the source was observed for chirps which 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, though it would prove selectively advantageous if alarm signals given in that context provided information allowing receivers to orient their evasive response 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 respectively.

Whereas uttering whistles containing chucks would serve squirrels encountering terrestrial predators, avian predators sometimes perch, or even land on the ground, within or in close proximity to a colony, resuming 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 to aerial predators and chirps to terrestrial predators. Indeed both the chirps and the whistles used in our study were elicited by tossing the same tan-coloured hat toward squirrels in the field (see Hare 1998). Contrary to Davis then, Richardson's ground squirrels appear to use chirps and whistles to communicate different information - chirps for immediate threat and whistles incorporating chucks for more tonic threats that should be tracked independent of taxonomic affiliation - rather than using spectrally distinct calls to represent different predator classes per se. Further experimentation employing 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 signaling 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.

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References

Bayly, K. L. & Evans, C. S. 2003. Dynamic changes in alarm call structure: a strategy for reducing conspicuousness to avian predators? *Behaviour*, **140**, 353-369.

Blumstein, D. T. 1995. Golden marmot alarm calls: I. The production of situationally-specific vocalizations. *Ethology*, **100**, 113-125.

Blumstein, D. T. 1999. Alarm calling in three species of marmots. *Behaviour*, **136**, 731-757.

Blumstein, D. T. & Arnold, W. 1995. Situational specificity in alpine marmot alarm communication. *Ethology*, **100**, 1-13.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sinauer Associates Inc., Sunderland, MA.

Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, **36**, 477-486.

Davis, L. S. 1984. Alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*). *Zeitschrift für Tierpsychologie*, **66**, 152-164.

Evans, C. S., Evans, L. & Marler, P. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, **46**, 23-38.

Ficken, M. S. 1989. Acoustic characteristics of alarm calls associated with predation risk in chickadees. *Animal Behaviour*, **39**, 400-401.

Gyger, M., Marler, P. & Pickert, R. 1987. Semantics of an avian alarm call system: the male domestic fowl, *Gallus domesticus*. *Behaviour*, **102**, 15-40.

Hare, J. F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. *Animal Behaviour*, **55**, 451-460.

Hare, J. F. & Atkins, B. A. 2001. The squirrel that cried wolf: reliability detection by Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and Sociobiology*, **51**, 108-112.

Holmes, W. G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. *Behavioral Ecology and Sociobiology*, **15**, 293-301.

Klump, G. M. & Shalter, M. D. 1984. Acoustic behaviour of birds and mammals in the predator context. *Zeitschrift für Tierpsychologie*, **66**, 189-225.

Koeppl, J. W., Hoffman, R. S. & Nadler, C. F. 1978. Pattern analysis of acoustical behavior in four species of ground squirrels. *Journal of Mammalogy*, **59**, 677-696.

Lima, S. L. & Dill, L. M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.

Macedonia, J. M. & Evans, C. S. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177-197.

Machlis, L., Dodd, P. W. D. & Fentress, J. C. 1978. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Zeitschrift für Tierpsychologie*, **68**, 201-214.

MacWhirter, R.B. 1992. Vocal and escape responses of Columbian ground squirrels to simulated terrestrial and aerial predator attacks. *Ethology*, **91**, 311-325.**Marler, P.** 1955. Characteristics of some animal calls. *Nature*, **176**, 6-8.

Michener, G. R. & Koeppl, J. W. 1985. *Spermophilus richardsonii*. *Mammalian Species*, **243**, 1-8.

Owings, D. H. & Hennessy, D. F. 1984. The importance of variation in sciurid visual and vocal communication. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. O. Murie & G.R. Michener), pp. 169-200, University of Nebraska Press, Nebraska,

Owings, D. H., Hennessy, D. F., Leger, D. W. & Gladney, A. B. 1986. Different functions of 'alarm' calling for different time scales: a preliminary report on ground squirrels. *Behaviour*, **99**, 101-116.

Pereira, M. E. & Macedonia, J. M. 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Animal Behaviour*, **41**, 543-544.

Rand, A. S. & Ryan, M. J. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Zeitschrift für Tierpsychologie*, **57**, 209-214.

Ryan, M. J. 1985. *The Túngara Frog - A Study in Sexual Selection and Communication*. The University of Chicago Press, Chicago IL. 230 pp.

Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a Neotropical frog. *American Naturalist*, **119**, 136-139.

Schleidt, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *Journal of Theoretical Biology*, **42**, 359-386.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, **28**, 1070-1094.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science*, **197**, 1246-1253.

Sloan, J. L. & Hare, J. F. 2004. Monotony and the information content of Richardson's ground squirrel (*Spermophilus richardsonii*) repeated calls: tonic communication or signal certainty? *Ethology*, **110**, 147-156.

Slobodchikoff, C. N., Kiriazis, J., Fischer, C. & Creef, E. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour*, **42**, 713-719.

Terhune, J. M. 1974. Directional hearing of a harbor seal in air and water. *Journal of the Acoustic Society of America*, **56**, 1862-1865.

Warkentin, K. J., Keeley, A. T. H. & Hare, J. F. 2001. Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. *Canadian Journal of Zoology*, **79**, 569-573.

Wilson, D. R. & Hare, J. F. 2003. Richardson's ground squirrels (*Spermophilus richardsonii*) do not communicate predator movements via changes in call rate. *Canadian Journal of Zoology*, **81**, 2026-2031.

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

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)	Z_c	*P*
Proportion of syllables with a chuck	0.85 ± 0.09	0.90 ± 0.02	0.49	0.62
Chuck duration (msec)	22.5 ± 4.4	19.9 ± 3.5	0.65	0.52
Latency to chuck (msec)	20.9 ± 3.4	24.8 ± 3.6	0.73	0.46
Minimum frequency (KHz)	3.18 ± 0.15	3.76 ± 0.29	1.22	0.22
Maximum frequency (KHz)	5.86 ± 0.41	6.31 ± 0.28	0.89	0.37
Frequency change (KHz)	2.68 ± 0.35	2.56 ± 0.42	0.57	0.57
Frequency rate change (KHz / msec)	0.13 ± 0.01	0.13 ± 0.01	0.41	0.68
Frequency drop from primary offset to chuck onset (KHz)	3.40 ± 0.64	2.45 ± 0.32	1.06	0.29

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

		Preceding Syllable Amplitude Type		Majority Amplitude Type	
		Descending	Other	Descending	Other
Chucks	Yes	8	4	12	0
Present?	No	0	6	0	6

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
Chucks	Yes	0	12	0	12
Present?	No	6	0	6	0

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

Variable	Logistic Likelihood Logit(*P*) =	Chi-Square	*P*	Correct Predictions	Effect Size (R^2)
Date	15.07 - 0.08x	2.18	0.14	70%	0.08
Time	4.45 - 0.39x	0.75	0.38	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	69%	0.12
Caller/Hat Distance	5.90 - 2.50x	11.40	0.00	85%	0.44

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

	Call Type				Significance Tests		
	Whistle-like		Chirp-like		1° Syllable	Chuck	Interaction
Dependent Variable	With Chuck	No Chuck	With Chuck	No Chuck	$F_{1,53}$, *P*	$F_{1,53}$, *P*	$F_{1,53}$, *P*
Initial Vigilance Duration (sec)	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 (Post-playback)	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

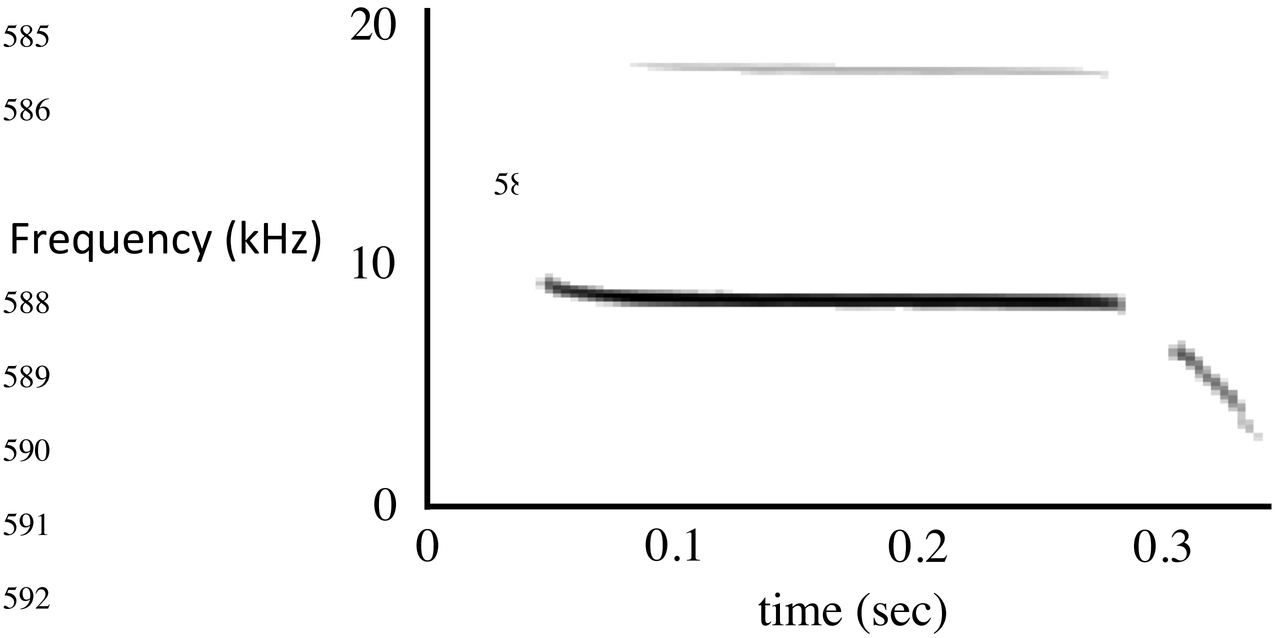

Figure 1. Spectrographic representation of the frequency versus time domain of a Richardson's ground squirrel "whistle" (*sensu* Davis 1984) with a "chuck" trailing the primary syllable.