



Neighbourhood watch: multiple alarm callers communicate directional predator movement in Richardson's ground squirrels, *Spermophilus richardsonii*

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ARTICLE INFO

Article history:

Received 4 August 2009
Initial acceptance 10 December 2009
Final acceptance 14 April 2010
Available online 7 June 2010
MS. number: A09-00516R2

Keywords:

alarm calling
communication network
indirect detection
Richardson's ground squirrel
Sciuridae
sociality
Spermophilus richardsonii

Richardson's ground squirrels are social animals that warn conspecifics of a predator's presence through the production of alarm vocalizations. Their ability to discriminate among individual alarm callers and to identify the location of those callers may allow receivers to track predator movement from acoustic information in multiple-caller bouts. Observations of encounters with live terrestrial and avian predators revealed that squirrels were significantly more likely to produce a multiple-caller bout that tracked predator movement when avian predators were airborne than when predators remained on the ground. To test whether receivers perceived such differences, squirrels were presented with playbacks of multiple-caller bouts composed of either chirps (commonly issued in response to airborne predators), or whistles (commonly issued in response to predators on the ground) from callers that were either unfamiliar or familiar to the receiver. In response to unfamiliar chirps, but not unfamiliar whistles, receivers were significantly more vigilant when call bouts progressively increased in proximity than when call bouts progressively decreased in proximity. Thus, Richardson's ground squirrels use multiple alarm callers to track airborne avian but not terrestrial predators, presumably owing to the more immediate threat that airborne predators pose, but also because of the relative paucity of directional information in bouts of whistle calls associated with potential threats on the ground. Squirrels were more responsive to calls from familiar neighbours, however, and despite our relatively small sample of familiar caller playbacks, receivers showed limited evidence of differential response to approaching versus receding bouts of whistle calls when they were familiar with callers.

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As is the case for many group-living species (Hass & Valenzuela 2002; Uetz et al. 2002), antipredator benefits have contributed substantially to the evolution and maintenance of ground squirrel sociality (Blumstein 2007; Hare & Murie 2007). Enhanced predator detection (i.e. the 'many eyes' hypothesis) is one means by which such benefits accrue (Lima 1990; Uetz et al. 2002). With more eyes scanning the environment, larger groups detect predators sooner (Kenward 1978) and each individual within the group is able to devote less time to vigilance, and more time to foraging (Kildaw 1995; Lima 1995), where alarm signals communicate the presence of a potential predatory threat to otherwise unwary individuals (Beauchamp & Ruxton 2007; Blumstein 2007).

Beyond enhanced detection, alarm signals convey a wealth of information regarding the precise nature of the threat at hand. Davis (1984) reported that Richardson's ground squirrel alarm calls

are referential, with short, typically singular, frequency-modulated chirps being issued in response to avian predators, and longer duration, repeated, stable-frequency whistles being issued in the presence of terrestrial predators. Warkentin et al. (2001), however, noted that chirps and whistles were not associated uniformly with terrestrial and avian predators, respectively, but rather with the context and response urgency implicit in the encounter with a presumptive predator. Thus, Richardson's ground squirrel alarm vocalizations appear to be context specific rather than functionally referential per se.

In addition to that general contextual information, Richardson's ground squirrels discriminate among individual alarm callers (Hare 1998a) and use this ability to adjust their response to the number of individuals calling (Sloan & Hare 2008), as well as the past reliability of individual alarm callers (Hare & Atkins 2001). Alarm calls also provide receivers with information on the location of the caller in space (Sloan et al. 2005), and with repeated whistles, the proximity of the predator to the caller (Warkentin et al. 2001).

While changes in the rate of repeated calling by an individual caller does not communicate predator movement (Wilson & Hare 2003), the ability of receivers to discriminate among individual callers (Hare 1998a), to locate those callers in space (Sloan et al.

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2005) and to enumerate callers (Sloan & Hare 2008) presents the possibility of receivers integrating information from multiple callers to track the direction of predator movement within the colony. The integration of information from multiple callers would prove highly adaptive in tailoring behavioural responses to the context at hand, and would represent a novel example of the proximate value of social networks (Fitzsimmons et al. 2008; Wey et al. 2008) in group-living species.

We examined alarm call production through field observations of encounters with avian and terrestrial predators to determine whether individual squirrels joined multicaller bouts in accordance with the direction of predator movement through the colony. We also conducted playbacks of multicaller bouts of chirp or whistle calls from both unfamiliar and familiar signallers that progressively approached or moved away from receivers to test whether receivers perceive directionality in multicaller bouts as indicative of predator movement.

METHODS

General Methods

Richardson's ground squirrels are ideal subjects for the study of alarm communication as they are readily observed during the day, are large enough to be distinguished individually, habituate well to human presence, and, most importantly, readily utter alarm vocalizations in response to potential threats in the environment (Hare 1998a). Both juvenile and adult Richardson's ground squirrels were used as subjects in the present study because juveniles and adults perceive certain aspects of alarm calls differently (Sloan & Hare 2006, 2008; but see Swan & Hare 2008).

Field research was conducted on a free-living colony of Richardson's ground squirrels at the Assiniboine Park Zoo (49°52'N, 97°14'W) in Winnipeg, Manitoba from 31 March through to 23 July 2008. At the site, squirrels inhabit mowed berms and fields surrounded by trees, around the musk ox and bison exhibits, covering approximately 2 km² of the zoo property. Squirrel density and dispersion is virtually indistinguishable from that seen in colonies occupying natural, grazed pasture, and noise levels are, on average, similar to other urban and rural sites inhabited by these squirrels. Given the zoo environment, these Richardson's ground squirrels are exposed to humans on a daily basis, although people other than experimenters were not present during playback trials.

Squirrels were live-trapped using National or Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI, U.S.A.) baited with No Name™ smooth peanut butter (Sunfresh Ltd, Toronto, ON, Canada). They were tagged with a metal eartag in one ear (National Band and Tag Company, Monel no. 1, Newport, KY, U.S.A.) and given a unique pattern of hair dye on the dorsal pelage (Clairol Hydrience™ 52S, Pearl Black, Stamford, CT, U.S.A.) for individual identification. Adult squirrels were trapped and marked upon their emergence from hibernation in late March through April, whereas juveniles were marked later upon their emergence from natal burrows in late May to early June. Sex, mass, breeding status and age class were recorded upon the capture of each individual squirrel. All research involving animals was conducted in accordance with the guidelines of the Canadian Council on Animal Care (CCAC) for the care and use of experimental animals and wildlife, as approved under Protocol F08-012 of the University of Manitoba's Fort Garry Campus Protocol Management and Review Committee, and in accordance with the guidelines of ASAB/ABS (2009).

Call production

Data on the production of multiple alarm calls were obtained during natural predator encounters. Observations of calling

behaviour in response to presumptive predators were collected during a 1 h time period (starting between 0730 and 1030 hours Central Standard Time, CST) each morning that squirrels were above ground from 8 June through 18 July. We also documented spontaneous bouts of antipredator calling by multiple signallers while trapping. For each encounter, we recorded the predator species, the context in which it was moving (airborne or on the ground), and whether or not alarm-calling Richardson's ground squirrels joined bouts of calling in a pattern coincident with the direction of predator movement, along with the estimated distance over which callers joined in the calling bout. Observations primarily involved avian predator species (Cooper's hawk, *Accipiter cooperii*; red-tailed hawk, *Buteo jamaicensis*; Swainson's hawk, *B. swainsoni*; common raven, *Corvus corax*), although we also documented alarm vocalizations issued to nonpredatory avian species (common peafowl, *Pavo cristatus*; wild turkey, *Meleagris gallopavo*). A few mammalian species (American mink, *Mustela vison*; fisher, *Martes pennant*; humans) also evoked alarm calls in Richardson's ground squirrels, although we did not attempt to quantify call bout characteristics in response to humans given their often erratic patterns of movement.

Call perception

Alarm call playbacks were conducted on 17 juvenile and 19 adult Richardson's ground squirrels ($N = 36$) from 17 June to 23 July to determine whether receivers extract information on predator movement from multiple calls. Alarm calls used in the majority of playback trials (83%) were recorded by J. F. Hare from 1994 to 1998 (details in Hare 1998a). These calls were recorded at sites other than the current study site to eliminate familiarity between callers and receivers, and were elicited by tossing a tan Biltmore hat through the air (32.5 × 19.5 cm brim, 13.0 cm high). The hat was considered an appropriate model as it is portable and reliably elicits alarm calls from Richardson's ground squirrels (Sloan & Hare 2006). Alarm calls were also recorded by J. F. Hare in 2008 at the Assiniboine Park Zoo in the context of the morning predator observations described above and were used in the remaining playback trials. Some subjects ($N = 6$ of 36) thus received playbacks from known neighbours. We may expect a more pronounced response to familiar callers, where past reliability and spatial relationships are known (Hare & Atkins 2001), although it may also prove imprudent to ignore calls issued by unfamiliar signallers. Thus, we used calls uttered by familiar and unfamiliar signallers to test whether the extraction of information regarding predator movements from multiple-caller bouts is contingent upon familiarity with neighbouring callers. Both chirps and whistles were used in playbacks as production specificity (chirps for airborne predators and whistles for predators on the ground has been reported for the alarm-calling system of Richardson's ground squirrels (Davis 1984; Warkentin et al. 2001; Sloan et al. 2005).

All calls were transferred, using a SONY TCD-D8 recorder (SONY Corporation, Oradell, NJ, U.S.A.), from digital audiotape (DAT) to a Macintosh computer. Calls were then manipulated into the appropriate playback treatments using the program Canary (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). Terrestrial whistles were six syllables in length with a 4 s intersyllable latency. Intersyllable latencies in natural call bouts of Richardson's ground squirrels range from 2.79 ± 0.35 s to 6.93 ± 0.47 s (Sloan & Hare 2004); therefore, we chose an intermediate rather than a maximal latency to elicit a response from receivers. Whistle playbacks were thus approximately 76 s long (6 syllables × 4 s latency = 24 s × 3 callers + 2 × 2 s intercaller latency), given that calls were issued sequentially (2 s between callers) without overlap. Chirp playbacks, in contrast, consisted of single syllables from three callers (2 s between callers) and, thus, playbacks lasted approximately 8 s. While playbacks of bouts containing whistles

versus chirps differed in duration, repetitive whistles and non-repetitive chirps were used to keep playbacks as realistic as possible. In the field, encounters with airborne predators are typically fleeting, seldom persisting longer than 10 s, and involve the production of nonrepetitive chirps (Davis 1984). Predators on the ground tend to evoke longer bouts of alarm calling composed of repeated whistles (Davis 1984), which often extend over several minutes, as the predator moves within the caller's field of view (J. F. Hare, personal observation).

For each playback trial, individual subjects were approached to within 25–10 m. We erected a SONY DCR-TRV110 camcorder (SONY Corp., Oradell, NJ, U.S.A.) on a tripod and placed a Sony XM-2025 audio amplifier connected to a SONY MZ-N707S MiniDisc player and loudspeakers directly beside it. Three Centrios 4018173 indoor/outdoor loudspeakers (ORBYX Electronics, Walnut, CA, U.S.A.) were set up in a row behind the tripod at 12 m intervals, resulting in an intercaller dispersion that would fall towards the lower end of the range of distances between the centres of activity of neighbouring Richardson's ground squirrel females (Michener 1979). Loudspeakers were oriented towards the subject, and manipulated calls were broadcast at 83 dB SPL 1 m from each speaker, which falls within the natural range of alarm call amplitudes of Richardson's ground squirrels (Hare 1998a). For a given trial, calls were broadcast from each of the three loudspeakers, representing three unique callers, with a 2 s latency between calls from different speakers. Given that Richardson's ground squirrel receivers recognize callers as individuals (Hare 1998a) and use that ability to enumerate the number of individuals signalling in multiple-speaker playbacks (Sloan & Hare 2008), it was safe to assume that receivers recognized the calls from multiple speakers as emanating from different individuals. Calls were broadcast from the three speakers in sequence so that they would be perceived as moving either progressively towards or progressively away from the subject during playback. Each subject received four playback treatments: a series of whistles towards, the same series of whistles away, a series of chirps towards, and the same series of chirps away. Trials on each individual were conducted at least 1 h apart, and the order of treatments was determined randomly by rolling a four-sided die.

Video recording of trials commenced when subjects assumed a nonvigilant posture (i.e. standing on four feet with the head down). Subjects were recorded for 1 min before playback (pre-playback), during playback of three sequential alarm calls (playback) and for 2 min postplayback (postplayback), although a minimum of 30 s postplayback was required for data from a trial to be used in the study. Trials were discontinued if the subject remained out of view for more than 25% of the preplayback, playback or postplayback period, or if the subject remained in a burrow for more than one syllable of a call playback.

Other factors (wind speed, temperature and relative humidity) were recorded as continuous variables using a Kestrel 3000 pocket weather meter in the field. The extent of cloud cover was categorized subjectively as an ordinal ranging from 1 (clear) to 4 (completely overcast) (Sloan & Hare 2008).

Data analysis

All statistical analyses were performed on a Macintosh computer using JMP 8.0.1 (SAS Institute, Cary, NC, U.S.A.). Two-tailed significance tests were applied throughout, and results were considered significant at $P \leq 0.05$.

With the call production data, we used binomial tests to determine whether callers joined in multiple-caller bouts in a pattern coincident with the direction of predator movement more or less often than expected by chance. Presumptive predators were divided according to whether they were terrestrial or avian predators, and according to whether they were airborne (avian only) or

on the ground (terrestrial or avian) during the encounter. The latter category accounted for effects of context rather than predator taxonomic affiliation on calling bouts.

For the call perception component, videotaped trials (17 h in total) were coded using a SONY Trinitron KV 20FV10 television and a stopwatch to determine vigilance times as well as ordinal postural responses. General coding methods were modelled after those used in previous studies (Hare 1998a; Wilson & Hare 2003; Sloan et al. 2005; Swan & Hare 2008). For each trial, we first qualified individual responses based on time spent engaged in low vigilance (standing on four feet with the head up, S4u; sensu Hare 1998a), high vigilance (standing on the hindlegs with the back either arched or erect; slouch; alert) and running during each period. We also noted the ordinal postural response (standing on four feet with the head down: S4d = 1; S4u = 2; slouch = 3; alert = 4; run = 5) at certain points throughout the playback period. For whistle playbacks, the ordinal postural response was noted immediately before playback and following the first syllable of the first call during playback. We did not formally quantify initial postural responses to each subsequent caller for whistle playbacks, given that we noted in situ that receivers consistently raised their head when the call of each new signaller was played in bouts moving towards or away from the receiver. As such, immediate postural responses to each individual caller in those whistle bouts were deemed uninformative, and we focused instead on initial responsiveness, to assess how proximity of the receiver to the signaller affected vigilance, and, as is appropriate where whistle calls are repeated over a longer time frame and either progress towards or away from the receiver, the proportion of time devoted to vigilance and escape behaviour in the playback and postplayback periods. For chirp playbacks, the ordinal postural response was again noted immediately before playback and following each of the three calls during playback, as postural responses showed a tendency to change with each call during these trials, as would be expected where calls occur in close temporal succession. The overall highest postural response reached throughout the entire playback period was also determined for all trials and call types.

Two-tailed Wilcoxon's signed-ranks tests were used (the parametric assumptions of normality and homoscedasticity were violated for several dependent variables: not all $P > 0.05$) to examine the effects of the pattern in which callers contributed to calling bouts (towards versus away) on the proportion of time spent vigilant and the ordinal postural response of subjects for both chirp and whistle bouts. Separate tests were performed for unfamiliar and familiar trials to determine whether effects were contingent upon caller familiarity. Because of the relatively small sample size obtained for trials involving signallers that were familiar to receivers ($N = 6$), we computed the exact probability associated with the outcome of all tests, rather than using the asymptotic approach, to establish significance (Mundry & Fischer 1998). To assist in interpreting our findings, we calculated effect sizes (Cohen's d) for all contrasts.

Two-factor ANOVA tests, which are considered robust enough to operate with little bias even when assumptions of normality and homoscedasticity are violated (Zar 1974), showed that while there was a differential response between age classes during both the playback and postplayback periods, there were no significant differences between age classes for call direction (all $P > 0.05$) and no significant interaction between age class and call direction (all $P > 0.05$). Therefore, the interpretation of directional effects was not affected by the differential responses of adults and juveniles, and the data for all sex and age classes were pooled for further analysis. Abiotic factors, including time of trial (0630–1200 hours CST), date (17 June–23 July 2008), average wind speed (0–13.4 km/h), maximum wind speed (0–21.9 km/h), temperature (11.2–28.5 °C), relative humidity (50.7–92.3%) and cloud cover (1–4), were

balanced across all treatments (all $P > 0.05$) and did not confound interpretation of the directional effects of callers in multicaller bouts.

RESULTS

Call Production

Richardson's ground squirrels produced multiple calls that coincided with the direction of potential predator movement (mapped travel) more often than expected by chance when a bird (predator or otherwise) was in the air (17 of 20 encounters; binomial test: $P = 0.003$), but failed to do so when presumptive avian or terrestrial predators remained on the ground (2 of 9 encounters; binomial test: $P = 0.180$). When encounters were categorized according to the taxonomic affiliation of the potential predator as opposed to the context of their movement, neither of the two encounters with terrestrial predators resulted in multicaller bouts tracking predator movement (binomial test: $P = 0.50$), while 19 of 27 encounters with avian species resulted in callers joining multicaller bouts in a pattern coincident with the movement of the potential predator (binomial test: $P = 0.052$).

Call Perception

Unfamiliar chirp trials

While no differences were detected during the playback period (Table 1), individuals showed significant differences in the total proportion of time spent vigilant (low and high vigilance combined) between trials where calls were progressively issued towards versus away from subjects during the postplayback period (Table 1). Receivers spent more time vigilant following multiple-caller bouts in which callers joined bouts in increasing proximity to the subject ($\bar{X} \pm SE = 0.445 \pm 0.046$) as compared to bouts in which callers joined in decreasing proximity ($\bar{X} \pm SE = 0.348 \pm 0.038$). This pattern was also evident in the proportion of time spent in high vigilance during the postplayback period, although it fell short of statistical significance (Table 1).

Richardson's ground squirrels showed a significant difference in the ordinal posture expressed in response to the first and third calls in a bout between trials where calls were progressively issued towards versus away from subjects (Table 1). In response to the first call, the ordinal posture was greater during bouts in which callers

joined bouts in decreasing proximity to the subject ($\bar{X} \pm SE = 3.033 \pm 0.265$) than in bouts in which callers joined in increasing proximity to the subject ($\bar{X} \pm SE = 2.267 \pm 0.214$). Conversely, in response to the third call, the ordinal posture was greater during bouts in which callers joined in increasing proximity to the subject ($\bar{X} \pm SE = 2.833 \pm 0.215$) than in bouts in which callers joined bouts in decreasing proximity to the subject ($\bar{X} \pm SE = 2.233 \pm 0.164$). There was no significant difference in the ordinal posture expressed to the second call in a bout between trials where calls were progressively issued towards versus away from subjects (Table 1).

Unfamiliar whistle trials

During the playback period, Richardson's ground squirrels showed a significant difference in the proportion of time spent in high vigilance between trials where calls were progressively issued towards versus away from subjects (Table 1). Receivers spent more time highly vigilant during multiple-caller bouts in which callers joined in decreasing proximity to the subject ($\bar{X} \pm SE = 0.139 \pm 0.040$) than in bouts in which callers joined in increasing proximity to the subject ($\bar{X} \pm SE = 0.060 \pm 0.020$). No significant differences in the proportion of time spent vigilant were observed in the postplayback period (Table 1). There were also no significant differences in ordinal postural responses during the playback period between trials where calls were progressively issued towards versus away from subjects (Table 1).

Familiar chirp trials

There were no significant differences in vigilance times or ordinal vigilance postures between trials where calls were progressively issued towards versus away from subjects in either the playback or postplayback period (Table 1). There was a nonsignificant tendency towards a difference, however, in the ordinal posture expressed in response to the second call in a bout (Table 1). Receivers tended to manifest a more pronounced response to the second call during multiple-caller bouts in which callers joined bouts in increasing proximity to the subject ($\bar{X} \pm SE = 4.167 \pm 0.543$) as compared to bouts in which callers joined in decreasing proximity to the subject ($\bar{X} \pm SE = 2.333 \pm 0.333$).

Familiar whistle trials

There were no significant differences in vigilance times or ordinal vigilance postures between trials where calls were

Table 1
Responses of Richardson's ground squirrels during and after playback of multiple-caller bouts progressing towards (T) versus away (A) from receivers ($N = 30$ unfamiliar call playbacks, $N = 6$ familiar call playbacks), significance (two-tailed Wilcoxon signed-ranks tests) and effect sizes (Cohen's d)

Variable	Unfamiliar chirps			Unfamiliar whistles			Familiar chirps			Familiar whistles		
	Trend	P	d	Trend	P	d	Trend	P	d	Trend	P	d
Playback												
Low vigilance	T<A	0.361	0.181	T>A	0.816	0.077	T=A	0.938	0.000	T<A	0.063	0.936
High vigilance	T>A	0.195	0.278	T<A	0.042	0.456	T>A	0.750	0.271	T>A	0.250	0.674
Total vigilance	T>A	0.592	0.112	T<A	0.391	0.250	T>A	1.000	0.270	T>A	1.000	0.074
Run	T>A	0.774	0.110	T<A	0.295	0.294	T>A	0.250	1.068	T<A	1.000	0.566
Postplayback												
Low vigilance	T>A	0.771	0.096	T<A	0.235	0.261	T<A	0.563	0.236	T<A	0.156	1.000
High vigilance	T>A	0.081	0.369	T>A	0.978	0.048	T>A	0.625	0.466	T>A	0.250	0.954
Total vigilance	T>A	0.041	0.424	T<A	0.380	0.245	T>A	1.000	0.030	T>A	0.844	0.416
Run	T<A	0.681	0.000	T>A	0.787	0.107	T>A	0.500	0.793	T<A	0.500	0.849
Posture												
1st syllable	T<A	0.036	0.581	T<A	0.713	0.089	T<A	1.000	0.165	T<A	1.000	0.496
Highest	T=A	1.000	0.000	T<A	0.108	0.391	T>A	0.125	1.633	T<A	1.000	0.496
2nd syllable	T>A	0.250	0.288	N/A	N/A	N/A	T>A	0.063	1.663	N/A	N/A	N/A
3rd syllable	T>A	0.028	0.573	N/A	N/A	N/A	T>A	0.250	0.735	N/A	N/A	N/A

Bold values indicate significance at $P \leq 0.05$.

progressively issued towards versus away from subjects in either the playback or postplayback period (Table 1). Squirrels tended to devote more time to low vigilance during multiple-caller bouts in which callers decreased in proximity to the subject ($\bar{X} \pm SE = 0.409 \pm 0.077$) than in bouts in which callers increased in proximity to the subject ($\bar{X} \pm SE = 0.189 \pm 0.112$), although the difference was not statistically significant (Table 1).

DISCUSSION

Vigilance increases an animal's likelihood of detecting a predator (Dimond & Lazarus 1974) and, thus, as predicted, Richardson's ground squirrels are more vigilant when a predator is approaching than when it is retreating (Wilson & Hare 2003). Our findings reveal that differential vigilance to approaching versus retreating predators can also come about through a receiver's reliance on indirect detection, extracted from the emergent pattern of alarm signalling among neighbouring signallers. For unfamiliar chirp trials, squirrels spent significantly more time vigilant following playbacks in which multiple calls were progressively issued towards them than they did following playbacks in which multiple calls were progressively issued away from them. Given that calls broadcast towards the subject would imply that a predator is approaching and calls broadcast away from the subject would imply that a predator is retreating, these vigilance responses indicate that receivers extracted information on airborne predator movement from the multiple-call playbacks. Consistent with these results, data on call production during predator encounters provided evidence that squirrels produced multiple calls that tracked the predator's movement during encounters with airborne predators.

Multiple callers thus more than simply verify the presence of a predator as suggested by Weary & Kramer (1995) and Sloan & Hare (2008). The emergent pattern of calls issued by multiple callers communicates information on the direction of predator movement, which would allow receivers to optimize the trade-off between foraging and vigilance, and their escape response. The use of indirect information gathered from calls of surrounding individuals allows receivers to respond rapidly without assuming the increased risk implicit in gathering direct information regarding the location of the predator, providing a selective advantage to individuals that integrate information from multiple callers (Fitzsimmons et al. 2008) where such signals reliably indicate a predator's presence (Beauchamp & Ruxton 2007). The ability to discriminate among individual callers (Hare 1998a) is likely to be maintained, at least in part, by the selective pressures derived from these benefits.

Squirrels also showed a significantly greater postural response to chirps that were broadcast nearby (i.e. the first call in trials issued away from subjects and the third call in trials issued towards subjects) than to chirps that were broadcast further away. This suggests that there is a proximity effect associated with receiver responsiveness to calls, with a tight association between the location of the caller and the location of the predator. A chirp that is produced in close proximity to the receiver appears to indicate that the predator is also nearby and, therefore, warrants a more urgent response, as has been suggested by Hare (1998a). If the proximity of a caller reliably indicates the proximity of a predator, calls must only be produced once the predator has crossed a certain distance threshold. This logic offers insight into how calls from multiple signallers can provide receivers with information on predator movement. Valuable information is, in effect, extracted after an individual has ceased calling, consistent with Owings et al.'s (1986) proposition that alarm calls can serve as a form of tonic communication, priming receivers to remain attentive beyond the period encompassed by a single individual's call. Future studies

documenting how variation in the temporal and spatial elements of multicaller bouts influence the behaviour of receivers would prove useful in defining the limits over which receivers use such information.

The notion of such integration of information within a communication network has only recently been considered (Fitzsimmons et al. 2008). Thus far, communication networks have been interpreted to result largely from competition among signallers for the receiver's attention (McGregor & Peake 2000). This study provides new evidence for de facto cooperation rather than competition between signallers, communicating information to receivers beyond what could be communicated by a single individual. There seem to be few advantages to signallers, however, of communicating in a social network (McGregor & Peake 2000). Rather, it is the receivers that reap the benefits of multiple calls and, therefore, receivers are a more probable source of selection on the nature of information provided through communication networks (McGregor & Peake 2000).

Contrary to our results for chirps, there was limited evidence of predator tracking through multiple whistles produced by unfamiliar signallers. Squirrels spent significantly more time engaged in high vigilance during the playback period when callers joined in bouts that progressed away from them than when callers progressively joined bouts moving towards them. This result is contrary to what would be expected if multiple calls that progressively decrease in proximity imply that a predator is retreating, and thus may reflect an influence of signaller proximity on receiver response. In trials where calls were broadcast in sequence moving away from the subject, the first call was closest to the subject. Furthermore, increased high vigilance did not continue into the postplayback period, suggesting again that it was the proximity of the first call in trials broadcast away from subjects, and not the overall pattern of all calls, that influenced squirrels' vigilance responses.

The possibility that the emergent pattern of whistle calling influenced receiver response cannot, however, be dismissed altogether. An alternative explanation for enhanced vigilance during call bouts where unfamiliar callers issued whistles in decreasing proximity to receivers is that retreating whistle bouts represent a low-urgency situation, which renders the accrual of direct information through individual vigilance more adaptive than responding to indirect information garnered from multiple calls. The lower response urgency implied by a progression of repeated whistles moving away from the receiver effectively allows receivers more time to collect reliable, direct information on the presumptive predatory threat. During an approaching terrestrial call bout, increased response urgency may select against increasing vigilance, favouring instead individuals that remain on all fours, prepared to run. Furthermore, individuals surrounded by conspecifics that have proven to be reliable alarm signallers in the past, and hence that could rely on indirect information to adjust their escape response (see Beauchamp & Ruxton 2007), would be at an advantage in using such information in the context of the higher risk imposed by an approaching terrestrial predator. If this were the case, we would have expected a more pronounced effect with the broadcast of whistles derived from familiar as opposed to unfamiliar signallers, although a statistically significant difference in vigilance responses to approaching versus receding call bouts was detected only for whistle playbacks involving unfamiliar callers. This latter result must be interpreted cautiously, however, given the small sample of playback trials using signallers familiar to receivers. Further research manipulating the temporal properties of multicaller repeated whistle bouts is necessary to explore how variation in response urgency can modulate receiver responses. In particular, playbacks involving overlapping repeated whistles from multiple

callers, thus reducing the overall length of the multicaller whistle bouts to the same length as multicaller chirp bouts would also address the extent to which the different call types are functionally referential. Overlap in call production is not unusual for Richardson's ground squirrels in the wild, but individuals also routinely join calling bouts in a discrete and sequential fashion, which we opted to explore in our study. Our productional data, indicating that squirrels rarely produced multiple calls that followed the direction of predator movement on the ground, further suggest that Richardson's ground squirrels do not use multiple calls from unfamiliar callers to communicate information on the movement of terrestrial predators. In effect, playbacks of repeated whistles served as controls in our study, documenting the response of receivers to calls that do not routinely coincide with predator movement.

Callers joined into multiple-caller bouts in a pattern coinciding with the direction of predator movement significantly more often than would be expected by chance alone when avian predators were airborne, but failed to do so when either avian or terrestrial predators were on the ground. Furthermore, multicaller bouts that tracked predator movements did not appear more often than expected by chance for the two encounters observed with nonhuman mammalian predators, or for the 27 encounters with potential avian predators where we included observations of avian predators in the air and on the ground in our analysis. That productional differences in the tendency for callers to join in multicaller bouts is more contingent on the context of the encounter than the presumptive predator's taxonomic affiliation is consistent with the fact that differential calls in the antipredator signalling system of Richardson's ground squirrels appear to be based on the perceived threat posed by predators (response urgency; Macedonia & Evans 1993), and not on the specific predator type (referential; Davis 1984). This has been suggested previously for Richardson's ground squirrels (Warkentin et al. 2001), and is consistent with findings for other rodent species (golden marmot, *Marmota caudata aurea*: Blumstein 1995; alpine marmot, *Marmota marmota*: Blumstein & Arnold 1995; Brants' whistling rat, *Parotomys brantsii*: Le Roux et al. 2001). As such, our categorization of call bout production by encounter context rather than by taxonomic affiliation of presumptive predators seems most appropriate. Avian predators remaining on the ground would be perceived by Richardson's ground squirrels as posing a lesser threat and, given earlier findings, would not be tracked by multiple callers.

The extraction of information from multiple calls in the face of avian but not of terrestrial predators also probably results from the different levels of threat imposed by each predator type. Belding's ground squirrels, *Spermophilus beldingi*, recognize that aerial and terrestrial predators pose different levels of threat (Robinson 1980). Avian predators typically appear suddenly and attack, presenting an immediate threat, whereas terrestrial predators approach more slowly, allowing their presumptive prey more time to respond to the threat (Warkentin et al. 2001; Sloan et al. 2005). Avian predators can also attack from essentially anywhere, including the centre of the colony, while terrestrial predators must approach from the edge of the colony, further increasing the level of threat posed by avian predators (Brunton 1997). Richardson's ground squirrels appear to recognize the differential threat posed by the different predator types because they produce different call types and respond differentially to those call types. Squirrels typically respond to a chirp by running into a burrow, and they respond to a whistle by standing upright (Michener & Koepl 1985). Thus, the tracking of predators through multiple callers may have evolved with chirps to allow for a rapid, precise response in the presence of immediate danger. In this situation, movement in the wrong direction could prove fatal and, thus, indirect information on the

direction of predator movement could greatly increase the probability of survival. Selection should, as a result, strongly favour individuals that integrate information from multiple chirps. This degree of information may not be necessary, however, in response to slower moving predators on the ground that must approach from the edge of the colony, as squirrels have more time to locate the predator themselves. By becoming vigilant, the receiver's visual and auditory receptors are elevated above the vegetation, allowing them to gather more exact information through their own senses (i.e. direct detection) regarding the nature and extent of the threat before determining an appropriate escape response.

Familiarity between callers and receivers may affect the extent to which receivers rely on indirect detection in that colonies of Richardson's ground squirrels are composed of cooperating related and unrelated individuals (Michener 1983; Hare 1998b; Hare & Murie 2007). While no statistically significant differences were detected among responses to multicaller bouts of chirps or whistles from familiar callers that progressed towards versus away from receivers, sample sizes were small and thus the power of these tests was limited. In spite of that, effect sizes were reasonable (Cohen's $d \geq 0.4$ for 15 of 22 contrasts, and $d \geq 0.7$ for 9 of those; Table 1), and differences that approached significance ($P < 0.10$) were evident in responses to playbacks using familiar callers. In response to familiar chirps, Richardson's ground squirrels expressed a greater postural response to the second call in a bout when calls were issued towards them as compared to away from them. Unlike the increased postural response to the third (i.e. closest) call in a bout of calling by unfamiliar callers, this cannot be attributed to a proximity effect as the second call in a bout was always the same distance from the subject regardless of the direction of calls. This indicates that the spatial pattern in which callers join in a multiple-caller bout was resolved by receivers of familiar calls after only two calls. Such rapid resolution of the spatial pattern of calling from bouts including familiar callers could reflect the receiver's greater reliance on familiar, reliable signallers, although the small sample size ($N = 6$) of playbacks involving familiar callers precludes drawing any definitive conclusion. Even given this small sample size, general trends in the familiar chirp trials were similar to those observed in the unfamiliar trials, although the differences were not statistically significant (Table 1). Therefore, it appears that the tracking of avian predators through multiple callers occurs whether or not receivers are familiar with callers, which is a logical outcome given the selective advantage of relying upon indirect detection in the face of the high-risk airborne predators pose.

In response to whistles from familiar callers, squirrels tended to spend more time in low vigilance during the playback period when calls were progressively issued away from them as opposed to towards them. This observation may result from the trade-off between low and high vigilance, however, given that squirrels tended to spend more time in high vigilance during the playback period when calls were issued towards them as opposed to away from them. Taken together, along with the fact that these two trends continued into the postplayback period, it is possible that familiarity is necessary for tracking terrestrial predators through multiple whistles. The overall pattern of multiple calls clearly affected the proportion of time receivers spent vigilant when whistles were from familiar callers, unlike the results obtained in trials using unfamiliar callers. Familiarity is important in the social interactions of numerous species (macaques, *Macaca nemestrina*: Fredrickson & Sackett 1984; collared lizards, *Crotaphytus collaris*: Husak 2004; guinea pigs, *Cavia aperea* f. *porcellus*: Kober et al. 2007), including Richardson's ground squirrels (Hare 1998b). In Richardson's ground squirrels, individuals remain vigilant longer in response to alarm calls of known neighbours (Hare 1998a) and in response to individuals that are deemed reliable (Hare & Atkins

2001). Hare (1998a) proposed that a neighbour's call would typically correspond with greater proximity of the predator to the receiver and, consequently, more immediate danger, leading to increased vigilance in the receiver. Thus, multiple callers possibly communicate terrestrial predator movement to known neighbours and selection consequently acts on receivers to integrate that information because of the increased level of threat, as well as the greater known veracity of those familiar, and hence, presumably, more reliable, signalers. Because of the aforementioned small sample size, however, this hypothesis requires additional testing in future studies.

Our research takes the study of sociality, in the context of antipredator communication, beyond the study of individuals. It examines how information is propagated and integrated among multiple colony members, enhancing our understanding of Richardson's ground squirrel communication as well as the cognitive abilities underlying sociality in these squirrels, and potentially many other group-living species.

Acknowledgments

We thank Bob Wrigley for allowing access to Richardson's ground squirrels at the Assiniboine Park Zoo and all zoo staff for their kindness and patience during our field work. We also thank Christine Legal for her assistance in the field, and Gail Davoren, Brenda Hann and Spencer Sealy for valuable feedback on the thesis from which this manuscript was derived. D.T. Blumstein and two anonymous referees provided extraordinarily valuable input on previous drafts of the manuscript, which greatly improved the quality of our offering. Funding for this study was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) via an Undergraduate Student Research Award to A.B.T. and a Discovery Grant to J.F.H.

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