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

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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.

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 km^2 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 and1030 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 productional 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