# The song remains the same: Juvenile Richardson's ground squirrels do not respond differentially to mother's or colony member's alarm calls

James F. HARE[1*], Kurtis J. WARKENTIN[2]

[1] Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada R3T 2N2
[2] Department of Zoology, Brandon University, Brandon, MB R7A 6A9

**Abstract** Alarm calls are emitted by Richardson's ground squirrels *Urocitellus richardsonii* in response to avian and terrestrial predators. Conspecifics detecting these calls respond with increased vigilance, promoting predator detection and evasion, but in doing so, lose time from foraging. That loss can be minimized if alarm call recipients discriminate among signalers, and weight their response accordingly. For juvenile ground squirrels, we predicted that the trade-off between foraging and vigilance could be optimized via selective response to alarm calls emitted by their own dam, and/or neighboring colony members over calls broadcast by less familiar conspecifics. Alarm calls of adult female Richardson's ground squirrels were elicited in the field using a predator model and recorded on digital audio tape. Free-living focal juveniles were subjected to playbacks of a call of their mother, and on a separate occasion a call from either another adult female from their own colony, or an adult female from another colony. Neither immediate postural responses and escape behavior, nor the duration of vigilance manifested by juveniles differed with exposure to alarm calls of the three adult female signaler types. Thus, juveniles did not respond preferentially to alarm calls emitted by their mothers or colony members, likely reflecting the high cost of ignoring alarm signals where receivers have had limited opportunity to establish past signaler reliability [*Current Zoology* 58 (5): 773–780, 2012].

**Keywords** Alarm Signal, Communication, Maternal Call Recognition, Signal Reliability, Ground Squirrel, Social Discrimination

Alarm signals emitted by animals in the presence of predators reduce the probability of predation either by deterring attack (e.g. pursuit-deterrent signals; Hasson, 1991; Caro, 1995; Zuberbühler et al., 1999), or by providing signal recipients with information allowing them to take appropriate evasive action (Smith, 1969; Klump and Shalter, 1984; Blumstein, 2007). At the proximate level, both conspecifics (e.g. Weary and Kramer, 1995) and heterospecifics (e.g. Templeton and Greene, 2007; Kitchen et al., 2010) detecting alarm signals respond with increased vigilance, which allows receivers to obtain additional information (Swan and Hare, 2008a) promoting escape from predation (Seyfarth et al., 1980).

Despite the advantages inherent in detecting the presence of a predator, a trade-off exists between vigilance and foraging (Lima and Dill, 1990, Bachman, 1993). That trade-off should be particularly pronounced among ground-dwelling squirrels, where predation pressure is intense (e.g. Michener and Michener, 1977; Schmutz et al., 1980) and where rapid mass accrual over the relatively short-growing season leading up to winter

hibernation is essential (Michener, 1974). Because of the former, squirrels must be vigilant; though in deference to the latter, they must temper that vigilance with sufficient foraging effort to attain the mass necessary to survive the winter and emerge in reproductive condition the following spring (Michener, 1974; McNamara and Houston, 1990; Michener and Locklear, 1990). Given this trade-off, a selective advantage would accrue to animals that could discriminate among alarm signalers, and forego foraging only when danger was imminent.

Hare (1998a) demonstrated that juvenile female Richardson's ground squirrels recognize alarm callers as individuals using a field playback experiment employing a habituation-discrimination paradigm (Halpin, 1974; Johnston and Jernigan, 1994). Subsequent research has revealed that Richardson's ground squirrels use that ability to: 1) weight their response according to the past reliability of individual signalers (Hare and Atkins, 2001), 2) assess the veracity of predatory threat by enumerating the number of alarm signalers (Sloan and Hare, 2008), and, 3) discriminate situations in which a

multi-caller bout of alarm signaling is progressing toward or moving away from them, hence implying increasing or decreasing threat respectively (Thompson and Hare, 2010).

Immediate postural responses of Richardson's ground squirrels to signalers that reliably communicated the presence of threat did not wane with repeated alarm signaling, and call recipients ultimately remain vigilant significantly longer in response to alarm calls of reliable as opposed to unreliable alarm signalers (Hare and Atkins, 2001). Beyond selective response to reliable individuals (Cheney and Seyfarth, 1988; Hare and Atkins, 2001; Blumstein et al., 2004), selection may favor differential response to certain alarm signalers, which, based upon their social relationship and/or typical spatial proximity to a given receiver, produce alarms that are particularly salient to that receiver (Pollard, 2011). Indeed, Hare (1998a) reported that juvenile female Richardson's ground squirrels tended to manifest longer vigilance durations in response to the alarm calls of neighbors in comparison to the calls of non-neighboring colony members, perhaps owing to the immediacy of threat the calls of neighbors convey.

In addition to neighbors, there is reason to believe that juvenile ground squirrels may respond selectively to alarm calls emitted by their own mother (dam). Female philopatry to the natal area results in matrilineal kin-clustering within Richardson's ground squirrel colonies (Michener, 1983), and thus dams are commonly found in close proximity to their offspring (van Staaden et al., 1994). Further, both the nepotistic patterns of alarm call production in closely-related Belding's (*Urocitellus beldingi*; Sherman 1980) and Columbian (*Urocitellus columbianus*; MacWhirter 1992) ground squirrels, along with the potent role mothers play in the development of alarm call responses of juvenile Belding's ground squirrels (Mateo and Holmes, 1997), suggest there may be enhanced responsiveness to alarm calls emitted by a juvenile's own mother, as is common for other social signals including contact calls, isolation calls, food calls, mobbing calls, and recruitment calls among other species (Fischer et al., 2000; Sèbe et al., 2008, Seyfarth and Cheney, 1997; Radford and Ridley, 2006). Heightened responsiveness in terms of waking from sleep to an alarm raised in a mother's voice relative to a tonal alarm has been documented for human children (Smith et al., 2006), though apart from the work of Mateo and Holmes (1997), we could find no other research focusing explicitly on the differential efficacy of alarm signals relative to social relationships among sig-

nalers and receivers, despite the possible existence of such relationships (Hollén and Radford, 2009). We compared responses of juvenile Richardson's ground squirrels to alarm calls of their own mothers, unrelated adult females from their own colony, or unrelated adult females residing in another colony to determine whether juveniles adjust their response according to their social relationship with the alarm signaler.

# 1 Materials and Methods

## 1.1 General methods

Squirrels used in this study occupied two sites, designated arbitrarily as 1 and 2, situated approximately 2.5 km north and 0.5 km southeast of Oak Lake Provincial Recreational Park (49°41'N, 100°43'W; elevation ca. 425 m) respectively in southwestern Manitoba, Canada. Site 1, a 10 × 50 m area, was an undisturbed remnant of a larger 2 ha cattle pasture where Richardson's ground squirrels were studied in 1994 and 1995 (Hare, 1998a; Hare, 1998b; Warkentin et al., 2001). Site 2 was a 50 × 50 m area artificially established in the spring of 1995 using methods described by Michener (1996) to transplant squirrels from the aforementioned 2 ha pasture prior to the majority of that site being disc-harrowed for agricultural purposes. For location reference, colored wire-pin surveyor's flags were used to form 10 × 10 m Cartesian grids on both sites. Throughout, our research conformed to the guidelines of the Canadian Council on Animal Care and the Animal Behavior Society for the use of animals in research.

Individuals were tagged for permanent identification with numbered metal ear tags (Monel #1, National Band and Tag Co., Newport, KY) and marked with human hair dye (Clairol "Nice 'n Easy" Blue-Black #124, Clairol Corp., Stamford, CT) on their dorsal pelage to allow identification at a distance. Juveniles were reliably associated with their dams by live-trapping them for marking (using Tomahawk live traps baited with peanut butter) as they emerged from their mother's nest burrow for the first time (Hare et al. 2004). Where that was not possible, we regarded juveniles to be from a given dam if they shared that female's nest burrow overnight within three days of the expected emergence date of her litter. Further information on Richardson's ground squirrel life-history can be found in Michener and Koeppl (1985).

## 1.2 Recording alarm calls

Alarm calls were elicited by presenting adult females with a tan-colored Biltmore™ hat that served as a predator model. As detailed in Hare (1998a), the hat was

tossed from experimenter hip level with a flip of the wrist toward each possible caller so that it landed on the ground within 1-8 m of the prospective caller. Calls were recorded on Digital Audio Tape (DAT) using a SONY TCD-D7 recorder (SONY Corp., Oradell, NJ) and a Dan Gibson EPM P-650 microphone (set to 'M' for low frequency roll-off; RD Systems of Canada, Toronto, ON). To further reduce wind noise, a foam windscreen was placed over the microphone head. All alarm calls used were recorded on 24 June 1996, between 13 and 20 days after juveniles first emerged from their natal burrows.

Specific recording procedures followed those described in Hare (1998a), though to ensure contextual consistency in the present study, all calls were obtained from 4 females with surviving juveniles at the time of recording (1 on Site 1 and 3 on Site 2). All adult females for which successful recordings were obtained emitted repeated whistle calls, typical of those given to terrestrial predators (Davis, 1984) once the predator model was resting on the ground. These original call recordings were dubbed to a new Digital Audio Tape via SoundEdit 16 software (Macromedia Inc., San Francisco, CA) on a Macintosh computer (Apple Computer, Cupertino, CA). Using that software, each original repeated call was reduced to a series of five syllables for playback, chosen specifically to avoid multiple callers, excessive background noise, and to be of a similar call rate (ca. 0.3 chirp / sec), approximating the average syllable repetition rate for repeated whistle calls reported by Warkentin et al. (2001). Five syllable call exemplars have proven effective in allowing individual discrimination of alarm signalers (Hare, 1998a), the discrimination of reliable from unreliable signalers (Hare and Atkins, 2001), and receiver assessment of call rate variation (Warkentin et al., 2001) and thus, were deemed appropriate for the present study.

### 1.3    Playback trials

To determine whether juveniles respond preferentially to calls of their own dam over calls of other adult females, each of 12 juvenile Richardson's ground squirrels was presented with two alarm call playbacks on separate days. The design was balanced so that each of the 12 focal juveniles (7 females and 5 males ranging in age from 21 to 36 days post-emergence) was played a call of its own dam once; half of the focal juveniles were also played a call from another adult female from the same site, while the other half were played a call from an adult female from a different site. Thus, our data allow an assessment of response to calls of the ju-

veniles' mothers versus other adult females, and within those other females, calls of familiar female colony members versus unfamiliar female non-colony members that originated from the same source colony (thus limiting any effect of colony membership to differential familiarity). Although it would have been ideal to assess the response of all 12 juvenile subjects to each of the three possible adult-female call types, high-quality 5-syllable alarm call exemplars were available for only 1 adult female with surviving juveniles on Site 1, and 3 adult females with surviving juveniles on Site 2. That constraint limited the number of possible unique adult female caller/juvenile call recipient combinations to only 6 juveniles in each of the non-maternal call treatments, so that overall, 12 juvenile subjects from among 4 litters (3 from the single litter on Site 1 and 9 from the 3 litters on Site 2) contributed data to the "own dam" treatment, 6 of the juveniles from the 3 litters on Site 2 also contributed data to the "other dam own site" treatment, and the 6 remaining juveniles (3 from the single litter on Site 1 and 1 from each of 3 litters on Site 2) also contributed data to the "other dam other site" treatment. The order of presentation of call types was alternated among subjects to avoid any call order effect. Further, the playback of the second call to each subject was delayed from one to five days after the initial call playback (2.29 ± 0.48; mean ± *SE*) and a maximum of 4 playbacks employing unique adult female callers (1.39 ± 0.26; mean ± *SE*) were attempted on either site each day, with a minimum of 1 hour between consecutive playbacks to minimize potential habituation of subjects to call playbacks or other carry-over effects on subject response. Trials were divided equally with respect to the sex of the focal juvenile and treatment group to allow an assessment of whether call recognition is expressed differentially by males and females.

Playback trials involved the broadcast of alarm calls to subjects in the field using a SONY TCD-D7 DAT deck, a SONY XM-2025 amplifier, and a Realistic Minimus-77 loudspeaker (Tandy Corp., Fort Worth TX) at sound pressure levels of 84 to 91 dB SPL (1 m from source). Sound pressure levels in that range correspond to those measured from Richardson's ground squirrels in the field (Hare, 1998a). Once an eligible playback recipient was located (a juvenile belonging to a litter for which a successful recording had been made and that had not already been tested in both conditions), we approached that individual to a distance of between 25 and 15 m. While KJW erected a tripod-supported SONY CCD TR-700 8mm camcorder and prepared to video-

record, JFH placed the loudspeaker 9 m away from the tripod and sound system (but no nearer the focal animal than ourselves) so that it was facing the focal individual. Videotaping commenced as soon as the focal was clearly visible in the camera's view-finder. After the behavior of the focal was videotaped for one minute, the call was presented. Videotaping continued for three minutes or until the focal went out of sight of the observers. Because physical factors can influence vigilance behavior (Carter and Goldizen, 2003), we coded cloud cover as an ordinal ranging from 1–3 and wind intensity as an ordinal from 1–5, estimated the temperature in degrees Celsius, and recorded the time of day at the outset of each trial.

## 1.4  Data coding and analyses

JFH, who was blind with respect to the treatment conditions of each trial, coded the data from videotapes in 2012. The initial response of each subject as call playback commenced was coded as one of five possible behaviors used routinely in studies of Richardson's alarm communication to assess initial responsiveness to alarm signals (Hare, 1998a; Hare and Atkins, 2001; Warkentin et al., 2001; Wilson and Hare, 2003, 2004, 2006; Sloan and Hare, 2004, 2006, 2008; Sloan et al., 2005; Swan and Hare, 2008a, 2008b; Thompson and Hare, 2010). Four general postures typical of Richardson's ground squirrels were considered to represent varying degrees of vigilance ranging from non-vigilant to highly vigilant. Standing with all four feet on the ground with the head oriented on a plane less than parallel to the ground surface (S4-d) was considered non-vigilant. Standing with all four feet on the ground with the head oriented on a plane equal to or greater than that parallel to the ground surface (S4-u) was considered as the lowest degree of vigilance. Resting on the hind legs with back arched forward (slouch) was considered the second highest vigilance posture. Finally, standing on the hind legs with the back erect (alert) was considered the highest level of vigilance. Running was considered the most intense response, but is regarded as "escape-related" rather than vigilance. By coding the subject's posture immediately prior to playback and that manifested upon call playback, we were able to score each subject's immediate response as an ordinal change, ranging from zero (no change - the minimal response to playback in this study) through a maximum of 4 (S4-d to run) as employed previously to assess responsiveness to reliable versus unreliable alarm callers by Hare and Atkins (2001).

As in previous studies of Richardson's ground squir-

rel alarm communication (see references above), we also coded the duration of vigilance in response to each call presentation. We measured the length of time (in seconds) that each focal held any vigilant posture (see above) upon playback of the first call syllable and stopped timing when the focal shifted to any non-vigilant posture (initial vigilance duration). Because that measure may tend to underestimate overall vigilance, however, we also measured the total amount of time (in seconds) the focal engaged in any vigilant posture in the one minute subsequent to the onset of playback (total vigilance duration). Although some squirrels remained vigilant longer than one minute, it becomes increasingly uncertain that responses are associated with the playback alone as time from the presentation elapses (Hare and Atkins, 2001).

We tested whether the levels of the abiotic factors we coded (cloud, wind, temperature, and time of day) were balanced across treatment type (dam versus other female from own colony and other female from another colony) using Kruskal-Wallis tests. Those factors were balanced across the three alarm signaler types (cloud, $H_C = 2.38$, $P = 0.30$; wind, $H_C = 0.90$, $P = 0.64$; temperature, $H_C = 1.63$, $P = 0.44$; time of day, $H_C = 1.83$, $P = 0.40$), and thus do not confound our contrasts of responses to the three call types. Therefore, physical factors were not considered further in our analyses.

We also conducted exploratory analyses using unpaired Student's $t$-tests to contrast immediate responses, initial vigilance durations and total vigilance durations of male versus female juveniles in response to their own mother's call or another adult female's call, and found no effect of juvenile sex on response (all $t_{10} \leqslant 1.32$, all $P \geqslant 0.22$). Further, we could detect no significant interaction between adult female caller type and juvenile receiver sex in exploratory two-factor ANOVAs examining immediate response ($F_{2,17} = 0.11$, $P = 0.89$), initial vigilance duration ($F_{2,17} = 0.13$, $P = 0.88$), and total vigilance duration ($F_{2,17} = 0.33$, $P = 0.73$). Thus, as with previous studies of Richardson's ground squirrel alarm call responsiveness (Sloan and Hare, 2004; Swan and Hare, 2008a, 2008b; Thompson and Hare, 2010), we did not consider the sex of juvenile receivers further in our analyses, pooling results from both male and female juveniles to test for effects of signaler identity.

Because each subject juvenile was exposed to both an alarm call from its own mother and from another adult female ground squirrel, we employed paired-sample tests to evaluate whether juveniles responded

differentially to those adult female signaler classes. The distributions of differences between responses to mother's calls versus calls of other females for the three dependent variables were likely to have been derived from normally-distributed populations of differences (all D'Agostino's $D \leqslant 0.29$, $P > 0.16$), and thus, we employed paired-sample $t$-tests to test for differential response to one's own versus another mother's alarm call for our 12 subject juveniles. Because half of our subject juveniles were exposed to another female's alarm call from their own colony, while the other half received alarm calls of females from a different colony, we also contrasted immediate response, initial vigilance duration and total vigilance duration of the unique juvenile subjects between those groups (own versus other colony) using unpaired Student's $t$-tests (both the assumption of normality and homogeneity of variance were met for all variables; all D'Agostino's $D \leqslant 0.22$, $P \geqslant 0.14$, and all

$Fmax \leqslant 2.31$, $P > 0.05$). Differences in our two-tailed tests were considered significant at $\alpha = 0.05$.

## 2   Results

No differences in the subject's responses to the broadcast of alarm calls of their own mother versus another adult female were detected for the intensity of immediate response ($t_{11} = 0.38$, $P = 0.71$), initial vigilance duration ($t_{11} = -1.34$, $P = 0.21$), or total vigilance subjects engaged in over the one minute subsequent to call playback ($t_{11} = -0.76$, $P = 0.46$) (Table 1). Further, no differences were detected in immediate responsiveness ($t_{10} = -0.92$, $P = 0.38$), initial vigilance duration ($t_{10} = -1.85$, $P = 0.09$) or total vigilance ($t_{10} = -0.68$, $P = 0.51$) shown by juveniles that received an alarm call from a familiar adult female residing in their own colony versus an unfamiliar adult female residing in a remote colony (Table 1).

**Table 1   Magnitude of immediate response (mean ± *SE* ordinal change), initial vigilance duration (mean ± *SE* sec) and total vigilance duration (mean ± *SE* sec) of juvenile Richardson's ground squirrels to calls of their own mother ($n = 12$), other reproductive adult females in general ($n = 12$), and within those, females from their own site ($n = 6$), or from a different site ($n = 6$)**

|  | Own Dam | Other Dam: Overall | Other Dam: Own Site | Other Dam: Other Site |
|---|---|---|---|---|
| Immediate Response | 2.08 ± 0.42 | 1.92 ± 0.45 | 1.50 ± 0.50 | 2.33 ± 0.76 |
| Initial Vigilance | 21.33 ± 5.33 | 32.08 ± 6.23 | 21.67 ± 6.77 | 42.50 ± 9.02 |
| Total Vigilance | 41.25 ± 5.06 | 45.92 ± 3.96 | 43.17 ± 4.66 | 48.67 ± 6.66 |

## 3   Discussion

Juvenile Richardson's ground squirrels did not respond differentially to repeated whistle alarm calls of their own mother, an adult female colony member or an adult female from another colony. Mateo and Holmes (1997) reported a similar finding for Belding's ground squirrels in that captive juveniles did not show greater responsiveness to alarm calls of their own dam versus calls of another adult, despite the pronounced influence of their dam's presence on the rate at which newly emerged juveniles develop the ability to discriminate alarm calls from non-alarm calls.

Our failure to detect any differential response for Richardson's ground squirrel juveniles is not likely to be an artifact of limited statistical power in that contrasts of juvenile responses to their own versus another mother's call were based upon a dependent-groups design employing 12 individual subjects. A sample size this large compares favorably to that employed in studies of Richardson's ground squirrel alarm communication that have revealed individual discrimination of alarm signal-

ers ($n = 14$ in Hare 1998a), differential response relative to past signaler reliability ($9 \leqslant n \leqslant 18$ in Hare and Atkins 2001), the role of brief, frequency-modulated "chucks" in enhancing receiver vigilance and promoting localization of the signaler ($10 \leqslant n \leqslant 15$ in Sloan et al. 2005), and receiver discrimination of multi-signaler alarm call bouts wherein signalers recruit sequentially toward versus away from the receiver ($6 \leqslant n \leqslant 20$ in Thompson and Hare 2010). Thus, we can conclude that Richardson's ground squirrel juveniles do not accord alarm signals emanating from their own dam any greater credence than those propagated by other adult females.

Because the mortality rate of juvenile ground squirrels due to predation is high, alarm calls emitted by any adult colony member may indicate a risk too great to be ignored. All adult ground squirrels are, by virtue of their very survival, successful at predator detection and avoidance and thus should represent a reliable source of warning to juveniles. While juvenile females reduce the duration of their vigilance responses to alarm callers that are rendered unreliable by playing back their calls

repeatedly when no predator is present, the extent to which alarm signaler reliability varies in nature remains undocumented, and requires additional research.

Further, despite Hare's 1998a report of a strong, but non-significant trend toward greater initial vigilance duration in response to alarm calls of neighboring versus non-neighboring juvenile Richardson's ground squirrel colony members, we found no evidence of enhanced responsiveness to alarm calls of adult female colony members relative to non-colony members in the present study. While our sample sizes for this contrast were relatively small ($n = 6$ subjects in each group), any non-significant differences in the magnitude of immediate response, total vigilance duration and initial vigilance duration in particular, tended toward greater responsiveness of juveniles to unfamiliar adult females from the other colony rather than adult females from their own colony (Table 1). These apparently opposite trends, with greater initial vigilance duration in response to more familiar neighboring as opposed to non-neighboring juvenile alarm signalers (Hare 1998a), and lesser initial vigilance in response to more familiar adult colony-members as opposed to unfamiliar adult non-colony members, are unlikely to be attributable to signaler age class. Swan and Hare (2008b) found that productional attributes of Richardson's ground squirrel alarm calls do not differ according to signaler age class, and neither adult nor juvenile receivers show differential response to juvenile- versus adult-produced alarm calls. While the active space of Richardson's ground squirrel alarm calls has yet to be formally documented, juveniles residing in the population studied by Hare (1998a) on a 2 ha cattle pasture would have had the opportunity to become familiar to a greater or lesser extent with all colony members. As such, squirrels would have been able to discriminate alarm calls as originating from juvenile neighbors (those reared in nest burrows ⩽ 25 m apart) versus more remote juvenile non-neighbors (reared in nest burrows ⩾ 70 m apart), with calls of the former likely implying a greater extent of threat based on the signaler's spatial proximity to the receiver. In the present study juvenile squirrels occupying the relatively small 10 × 50 m and 50 × 50 m sites would have been familiar with the alarm calls of all colony members but completely unfamiliar with those of adult females from the other colony. Thus, the most likely explanation for the trend toward heightened responsiveness to calls of adult females from another colony is that those calls were entirely novel to receivers. Such novel signalers would

represent unknown commodities in terms of their reliability, and thus could not be safely ignored (Hare and Atkins, 2001; Blumstein and Daniel, 2004; Blumstein, 2006; Pollard, 2011). Indeed, heightened initial vigilance to those novel individuals could represent an adaptive mechanism via which individuals would gather personal information regarding predator presence so as to obtain associative data with which to assess the reliability of a previously unknown signaler (Pollard, 2011).

Our present findings indicate that for alarm signals, unlike a variety of other social signals, receivers do not respond preferentially to signals emanating from their mother's or colony members. This is not particularly surprising in that receivers would benefit from displaying antipredator behavior to any signal that is reliably associated with the presence of a predatory threat (Hauser, 1988; Lind and Cresswell, 1995; Shriner, 1999; Schibler and Manser, 2007), though as Leonard et al. (2005) have argued, receivers cannot increase their responsiveness to signals without simultaneously increasing their risk of responding to inappropriate signals. Future studies of social discrimination in the context of ground squirrel alarm signaling should thus focus on documenting the active space of alarm signals and how that relates to the development of differential responsiveness to reliable versus unreliable individual signalers, along with the costs and benefits of such discrimination.

# References

Bachman GC, 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Anim. Behav. 46: 233–244.

Blumstein DT, 2006. The multi- predator hypothesis and the evolutionary persistence of antipredator behavior. Ethology 112: 209–217.

Blumstein DT, 2007. The evolution, function, and meaning of marmot alarm communication. Adv. Stud. Behav. 37: 371–400.

Blumstein DT, Daniel JC, 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. Anim. Behav. 68: 1257–1265.

Blumstein DT, Verneyre L, Daniel JC, 2004. Reliability and the adaptive utility of discrimination among alarm callers. Proc. Roy. Soc. Lond. B. 271: 1851–1857.

Caro TM, 1995. Pursuit-deterrence revisited. Trends Ecol. Evol. 10: 500–503.

Carter K, Goldizen AW, 2003. Habitat choice and vigilance behaviour of brush-tailed rock-wallabies *Petrogale penicillata* within their nocturnal foraging ranges. Wildl. Res. 30: 355–364.

Cheney DL, Seyfarth BM, 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. Anim. Behav. 36: 477–486.

Davis LS, 1984. Alarm calling in Richardson's ground squirrels *Spermophilus richardsonii*. Z. Tierpsychol. 66: 152–164.

Fischer J, Cheney DL, Seyfarth RM, 2000. Development of infant baboons' responses to graded bark variants. Proc. R. Soc. Lond. B. 267: 2317–2321.

Halpin ZT, 1974. Individual differences in the biological odors of the Mongolian gerbil *Meriones unguiculatus*. Behav. Biol. 11: 253–259.

Hare JF, 1998a. Juvenile Richardson's ground squirrels *Spermophilus richardsonii* discriminate among individual alarm callers. Anim. Behav. 55: 452–460.

Hare JF, 1998b. Juvenile Richardson's ground squirrels *Spermophilus richardsonii* manifest both littermate and neighbour/stranger discrimination. Ethology 104: 991–1002.

Hare JF, Atkins BA, 2001. The squirrel that cried wolf: Reliability detection by Richardson's ground squirrels *Spermophilus richardsonii*. Behav. Ecol. Sociobiol. 51: 108–112.

Hare JF, Todd G, Untereiner WA, 2004. Multiple mating results in multiple paternity in Richardson's ground squirrels *Spermophilus richardsonii*. Can. Field-Nat. 118: 90–94.

Hasson O, 1991. Pursuit deterrent signals: The communication between prey and predator. Trends Ecol. Evol. 6: 325–329.

Hauser MD, 1988. How infant vervet monkeys learn to recognize starling alarm calls: The role of experience. Behaviour 105: 187–201.

Hollén, LI, Radford AN, 2009. The development of alarm call behaviour in mammals and birds. Anim. Behav. 78: 791–800.

Johnston RE, Jernigan P, 1994. Golden hamsters recognize individuals, not just individual scents. Anim. Behav. 48: 129–136.

Kitchen DM, Bergman TJ, Cheney DL, Nicholson JR, Seyfarth RM, 2010. Comparing responses of four ungulate species to playbacks of baboon alarm calls. Anim. Cogn. 13: 861–870.

Klump GM, Shalter MD, 1984. Acoustic behaviour of birds and mammals in the predator context. Z. Tierpsychol. 66: 189–226.

Leonard ML, Horn AG, Mukhida A, 2005. False alarms and begging in nestling birds. Anim. Behav. 69: 701–708.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Can. J. Zool. 68: 619–640.

Lind J, Cresswell W, 2005. Determining the fitness consequences of antipredator behavior. Behav. Ecol. 16: 945–956.

MacWhirter RB, 1992. Vocal and escape responses of Columbian ground squirrels to simulated terrestrial and aerial predator attacks. Ethology 91: 311–325.

Mateo JM, Holmes WG, 1997. Development of alarm-call responses in Belding's ground squirrels: The role of dams. Anim. Behav. 54: 509–524.

McNamara JM, Houston AI, 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheor. 38: 37–61.

Michener DR 1974. Annual cycle of activity and weight changes in Richardson's ground squirrel *Spermophilus richardsonii*. Can. Field Nat. 88: 409–413.

Michener GR, 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Eisenberg JF, Kleiman DG ed. Advances in the Study of Mammalian Behaviour: The American Society of Mammalogists Special Publication No. 7. Lawarence Kansas: Allen Press, 528–572.

Michener GR, 1996. Establishment of a colony of Richardson's ground squirrels in southern Alberta. In: Willms WD, Dormaar JF ed. Proceedings of the Fourth Prairie Conservation and Endangered Species Workshop. Provincial Museum of Alberta Natural History Occasional Paper 23, 303–308.

Michener GR, Koeppl JW, 1985. *Spermophilus richardsonii*. Mamm. Spec. 243: 1–8.

Michener GR, Locklear L, 1990. Overwinter weight loss by Richardson's ground squirrels in relation to sexual differences in mating effort. J. Mamm. 71: 489–499.

Michener GR, Michener DR, 1977. Population structure and dispersal in Richardson's ground squirrels. Ecology 58: 359–368.

Pollard KA, 2011. Making the most of alarm signals: The adaptive value of individual discrimination in an alarm context. Behav. Ecol. 22: 93–100.

Radford AN, Ridley AR, 2006. Recruitment calling: A novel form of extended parental care in an altricial species. Curr. Biol. 16: 1700–1704.

Schibler F, Manser MB 2007. The irrelevance of individual discrimination in meerkat alarm calls. Anim. Behav. 74: 1259–1268.

Sèbe F, Aubin T, Boué A, Poindron P, 2008. Mother-young vocal communication and acoustic recognition promote preferential nursing in sheep. J. Exp. Biol. 211: 3554–3562.

Seyfarth RM, Cheney DL, 1997. Some general features of vocal development in non-human primates. In: Snowdon CT, Hausberger M ed. Social Influences on Vocal Development. Cambridge: Cambridge University Press, 249–273.

Seyfarth RM, Cheney DL, Marler P, 1980. Vervet monkey alarm calls: Semantic communication in a free-ranging primate. Anim. Behav. 28: 1070–1094.

Sherman PW, 1977. Nepotism and the evolution of alarm calls. Science 197: 1246–1253.

Sherman PW, 1980. The limits of ground squirrel nepotism. In: Barlow GW, Silverberg J ed. Sociobiology: Beyond Nature/Nurture? Boulder: Westview Press, 505–544.

Shriner WM, 1999. Antipredator responses to a previously neutral sound by free-living adult golden-mantled ground squirrel *Spermophilus lateralis* (Sciuridae). Ethology 105: 747–757.

Sloan JL, Hare JF, 2004. Monotony and the information content of Richardson's ground squirrel *Spermophilus richardsonii* repeated calls: tonic communication or signal certainty? Ethology 110: 147–156.

Sloan JL, Hare JF, 2006. Adult Richardson's ground squirrels *Spermophilus richardsonii* ignore rate changes in juvenile alarm calls: Age-differential response urgency perception? Ethology 112: 896–902.

Sloan JL, Hare JF 2008. The more the scarier: Adult Richardson's ground squirrels *Spermophilus richardsonii* assess response urgency via the number of alarm signalers. Ethology 114: 436–443.

Sloan JL, Wilson DR, Hare JF, 2005. Functional morphology of Richardson's ground squirrel *Spermophilus richardsonii* alarm calls: The meaning of chirps, whistles and chucks. Anim. Behav. 70: 937–944.

Smith WJ, 1969. Messages of vertebrate communication. Science 165: 145–150.

Smith GA, Splaingard M, Hayes JR, Xiang H, 2006. Comparison of a personalized parent voice smoke alarm with a conventional residential tone smoke alarm for awakening children. Pediatrics 118: 1623–1632.

Swan DC, Hare JF, 2008a. The first cut is the deepest: Primary syllables of Richardson's ground squirrel *Spermophilus richardsonii* repeated calls alert receivers. Anim. Behav. 76: 47–54.

Swan DC, Hare JF, 2008b. Signaler and receiver ages do not affect responses to Richardson's ground squirrel alarm calls. J. Mamm. 89: 889–894.

Templeton CN, Greene E, 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. Proc. Nat. Acad. Sci. U.S.A. 104: 5479–5482.

Thompson AB, Hare JF, 2010. Neighbourhood watch: Multiple alarm callers communicate directional predator movement in Richardson's ground squirrels *Spermophilus richardsonii*. Anim. Behav. 80: 269–275.

van Staaden MJ, Chesser RK, Michener GR, 1994. Genetic correlations and matrilineal structure in a population of *Spermophilus richardsonii*. J. Mamm. 75: 573–582.

Warkentin KJ, Keeley ATH, Hare JF, 2001. Repetitive calls of Richardson's ground squirrels *Spermophilus richardsonii* communicate response urgency. Can. J. Zool. 79: 569–573.

Weary DM, Kramer DL, 1995. Response of eastern chipmunks to conspecific alarm calls. Anim. Behav. 49: 81–93.

Wilson DR, Hare JF, 2003. Richardson's ground squirrels *Spermophilus richardsonii* do not communicate predator movements via changes in call rate. Can. J. Zool. 81: 2026–2031.

Wilson DR, Hare JF, 2004. Ground squirrel uses ultrasonic alarms. Nature 430: 523.

Wilson DR, Hare JF, 2006. The adaptive utility of Richardson's ground squirrel *Spermophilus richardsonii* short- range ultrasonic alarm signals. Can. J. Zool. 84: 1322– 1331.

Zuberbühler K, Jenny D, Bshary R, 1999. The predator deterrence function of primate alarm calls. Ethology 105: 477–490.