The perception of response urgency by juvenile and adult Richardson's ground squirrels (*Spermophilus richardsonii*); the relative importance of multiple alarm callers and temporal call bout properties

by

Jennifer Leanne Sloan

A thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Zoology
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THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

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ABSTRACT

Communication provides a window through which cognitive ethologists may explore the mental processes of animals. I conducted field research examining alarm communication by Richardson's ground squirrels (*Spermophilus richardsonii*), and through a series of field experiments, examined how individuals assess response urgency conveyed by alarm vocalizations. Call recipients incorporated information from the number of calling squirrels, the temporal properties of call bouts, or a combination of these mechanisms. I also addressed potential age differences in reliance on those mechanisms, thereby testing for developmental changes in perceptual abilities of the squirrels. In one study juvenile and adult Richardson's ground squirrels received playbacks containing two call bouts broadcast sequentially from either the same caller or two different individuals to address the importance of caller number discrimination in the perception of signal veracity. Juveniles responded similarly to both treatments, while adults responded with greater vigilance to multiple calling individuals. In another study I presented juveniles and adults with three playback experiments, each consisting of call bouts from one and four simultaneously calling squirrels. Behavioural responses suggested that juveniles preferentially attend to information encoded within call rate factors while adults focus on the number of calling squirrels. A final experiment examining adult responses to juvenile-emitted calls varying in rate and length confirmed that adults ignore information contained in those signal parameters, though it remains possible that adults decode and respond to temporal information contained in signals emitted by other adults. Information conveyed within juvenile vocalizations may be devalued by adults given the relative inexperience of juveniles with predators. Overall, my findings are consistent with those of other investigators who have suggested that alarm call recipients place a premium on the quality, and in essence "reliability", of information conveyed in alarm signals. Individuals of different ages, however, place differential emphasis on different signal components in ascertaining the underlying veracity of those signals, with juveniles attending largely to temporal properties of calls and adults attending to the number of calling individuals. This age difference suggests a developmental change in the squirrel's ability to extract information from alarm vocalizations, although both juveniles and adults clearly manifest adaptive cognitive abilities allowing them to decode and integrate information from multiple signal parameters.

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CHAPTER 1: GENERAL INTRODUCTION

Members of group-living species may profit via the communication of information concerning the presence and nature of predators (Sherman 1977). Many ground-dwelling sciurids (tribe Marmotini, including the genera *Marmota*, *Cynomys*, and *Spermophilus*) warn conspecifics of potential danger through the production of alarm calls (Davis 1984; Macedonia & Evans 1993). Receivers accrue fitness benefits through decoding information encoded within these signals and weighting their responses accordingly (Sherman 1977; Evans et al. 1993; Hare & Atkins 2001). These calls can convey information about the attributes of the predator (e.g. Cheney & Seyfarth 1988) or the extent of threat a predator may pose (e.g. Blumstein 1999). Through calling, individuals suffer energetic costs (Bradbury & Vehrencamp 1998) and place themselves at a greater risk of predation in warning other individuals (Sherman 1977).

Numerous studies have illustrated a positive correlation between vocalization in ground squirrels and the proximity of relatives (Dunford 1977; Owings & Leger 1980; Davis 1984). Alarm calling may have evolved in the context of kin selection (Sherman 1977), though reciprocity among calling individuals (Hare 1998) may also contribute to the evolution and maintenance of alarm signaling.

The degree of risk that a squirrel is faced with during a predator encounter depends on a multitude of factors, some of which include the physical attributes of the predator, the satiation level of the predator, the location of the predator relative to the squirrel, the number of conspecifics and their locations relative to the squirrel and predator, the anti-predator behaviour of conspecifics, as well as conspecific alarm calls

(Figure 1). Alarm call microstructure may serve a referential function, encoding semantic information regarding predator attributes as is observed in vervet monkeys (*Cercopithecus aethiops*, Cheney & Seyfarth 1988). The signaling systems of ground-dwelling squirrels, however, are generally considered to be based on the communication of response urgency (or the perceived necessity of anti-predator behavioural response by receivers) via the transfer of information encoded within alarm signals (Marler et al. 1992). The disparate call types ground squirrels produce in response to aerial and terrestrial predators are thought to communicate the degree of threat different predator classes pose to the signaler rather than communicating information concerning attributes of the predator (Warkentin et al. 2001). This does not preclude the possibility of referentiality as well, however, and further studies documenting the perception of call recipients using live or life-like predators are necessary to examine a referentiality-based component to ground squirrel alarm communication systems (Marler et al. 1992).

Alarm vocalizations may be produced in a non-repetitive fashion where discrete acoustic elements are temporally isolated from other elements, or in a repetitive fashion where multiple acoustic elements are emitted, separated by silences of varying durations. Both repetitive and non-repetitive alarm vocalizations communicate information concerning predator contexts (Sherman 1977); however, much speculation exists over the extent and nature of information conveyed within repetitive call bouts. The repetition of alarm calls may serve as a form of tonic communication (Owings & Hennessy 1984) whereby each additional element adds to the residual effects of previously received elements (Schleidt 1973). Vigilance would therefore be maintained through the repetition of alarm calls, with longer call bouts promoting longer lasting vigilance in signal recipients (Loughry & McDonough 1988). Limited support for the tonic communication hypothesis can be derived from studies with Columbian (*S. columbianus*, Harris et al. 1983) and California ground squirrels (*S. beecheyi*, Loughry & McDonough 1988); however, these studies, and recent research on Richardson's ground squirrels (*S. richardsonii*, Sloan & Hare 2004) reveal only short-term increases in vigilance in response to the repetition of syllables. Alternatively, the number of syllables produced within a repetitive bout may vary depending on the perceived response urgency a predator poses (Owings & Hennessy 1984; Hasson 1991). For example, the number of syllables produced by alpine (*M. marmota*, Blumstein & Arnold 1995) and golden marmots (*M. caudata*, Blumstein 1995) is inversely related to the response urgency perceived by the signaler.

Other proposed functions of repetitive alarm vocalizations are based on the temporal patterning of syllables within the call bout. Hartshorne's monotony-threshold hypothesis states that signals containing intervening silences of variable duration maintain 'receiver interest', while those signals with intervening silences of similar length result in receiver habituation and therefore reduced responsiveness (Hartshorne 1956). According to this hypothesis, alarm call bouts with varying intersyllable latencies (variable calls) will promote long-term vigilance more so than bouts with similar intersyllable latencies (monotonous calls). Richardson's ground squirrel call recipients, however, selectively attend to monotonous calls and show reduced responsiveness to variable calls as these communicate low signaler certainty as to extent of threat the predator poses (signal certainty hypothesis, Sloan & Hare 2004). The repeated alarm calls of Richardson's ground squirrels are produced at rates that are inversely correlated with the predator-signaler distance, and call recipients perceive call rate as an indication of the response urgency posed by a potential predator (rate-related response urgency hypothesis; Warkentin et al. 2001). Certainly, the rate of repeated alarm calls may communicate the response urgency of the threatening situation to receivers so that they may respond accordingly (see also Waring 1966; Nikol'skii et al. 1994).

In nature numerous factors exist that may inhibit the successful transfer of a signal, some of which include the level of ambient noise, attenuation of signal intensity with distance from the source, and pattern losses due to medium absorption, scattering, and boundary reflections (Bradbury & Vehrencamp 1998). Repetitive calling may prove beneficial in terms of enhancing transmission where the repetition of the signal increases the probability of reception by receivers (Bradbury & Vehrencamp 1998). Furthermore, perhaps signal transmission would be facilitated in a situation where not one but many signalers contribute to a chorus of alarm calling.

In a multiple-caller system, each caller would presumably increase its own risk of predation (Sherman 1977), while potentially confounding the assessment of call rate from any one signaler. However, all callers should enjoy proportionately less additional risk with each additional caller, and concurrently reduce the risk for others. In addition to increasing the signal-to-noise ratio, through a multiple-caller system, signal receivers may also integrate information decoded from each caller to determine predator location and movement through the colony (Warkentin et al. 2001), a process analogous to trilateration (Leick 1995). Columbian ground squirrels appear to track predator movements and communicate these movements through alterations in call rate (Harris et al. 1983). Wilson

& Hare (2003) have found, however, that while Richardson's ground squirrels alter call rate depending on predator-signaler distance (Warkentin et al. 2001), callers do not communicate predator movements via changes in call rate. This does not preclude the possibility that Richardson's ground squirrels use trilateration to communicate a predator's current location rather than its movements through the colony.

Tonic communication may partially explain the existence of multiple-caller signaling, whereby the recruitment of additional alarm callers functions to maintain vigilance in conspecifics in situations where the predator may still be present in the surrounding area (Owings et al. 1986). However, as limited support has been provided for tonic communication in alarm calling systems of ground-dwelling squirrels (Harris et al. 1983; Loughry & McDonough 1988; Sloan & Hare 2004), perhaps a multiple-caller system functions to communicate response urgency to call recipients, whereby more calling ground squirrels communicates to receivers a heightened assurance of impending threat posed by a predator (referred to as the multiple callers hypothesis). Robinson (1981) found in an observational study that multiple callers produced a larger number of highly vigilant Belding's ground squirrels (*S. beldingi*) compared with a single caller. Similarly, Blumstein et al. (2004) reported that yellow-bellied marmots (*M. flaviventris*) utilize their ability to discriminate among individual alarm callers (Blumstein & Daniel 2004) to perceive more calling squirrels as denoting a higher-risk predatory threat. Subjects were more vigilant in response to two sequentially calling marmots versus two sequential calls produced by a single calling individual. Richardson's ground squirrels have also been demonstrated to individually discriminate among alarm callers (Hare 1998) to distinguish reliable from unreliable signalers, adjusting their vigilance responses appropriately (Hare & Atkins 2001). Hare (1998) has suggested that identity discrimination by the Richardson's ground squirrel may also function to make caller number discriminations.

Multiple-caller signaling systems based on the utilization of caller number discriminations can be found throughout the literature (e.g. Belding's ground squirrels, Robinson 1981; African lions, *Panthera leo*, Grinnel & McComb 1996, Heinsohn et al. 1996; chimpanzees, *Pan troglodytes*, Wilson et al. 2001; yellow-bellied marmots, Blumstein et al. 2004). For example, a chimpanzee community may produce an alarm call chorus to signal to another community its relative vulnerability or power (Wilson et al. 2001). The listeners may then discriminate among the identities of the signalers as well as the number of signaling individuals to gauge the minimal group size (Wilson et al. 2001). Indeed, the ability to make at least rudimentary numerical discriminations may be selected to reduce injury or predation risks the signalers and/or receivers may experience (Hauser 1997).

Few studies have addressed the role of multiple callers in alarm communication systems (but see Robinson 1981; Blumstein et al. 2004). Using Richardson's ground squirrels as subjects, I examined the role of multiple-caller systems as tools for the communication of response urgency via signal veracity assessment associated with the number of calling squirrels. To address the relative contribution of the role of temporal patterning of syllables within repetitive call bouts, I tested for an influence of call rate effects on the perception of response urgency by receivers (addressing the rate-related response urgency hypothesis; Warkentin et al. 2001), variation in call rate on the signal assessment by call recipients (testing the signal certainty hypothesis, Sloan & Hare 2004), and syllable number on the tonicity of receiver vigilance (addressing the tonic communication hypothesis, Schleidt 1973).

Much of the perceptual work on Richardson's ground squirrels has involved the use of juvenile subjects only (see Hare 1998; Hare & Atkins 2001; Wilson & Hare 2003; Sloan & Hare 2004; Sloan et al. in press), precluding an examination of age-related differences in alarm call perception. Research across a broad range of taxa reveals significant differences in the behavioural responses of younger versus older individuals to conspecific alarm calls and/or predator encounters (e.g. fish, Giles 1984, Fuiman 1993; mammals, Seyfarth & Cheney 1986, Ramakrishnan & Coss 2000, McCowan et al. 2001; birds, Rajala et al. 2003). These age-dependent differences reflect the ontogeny of anti-predator behaviour, which occurs at each stage of a four-stage response process whereby the receiver 1) detects the signal; 2) differentiates the signal from other stimuli; 3) assesses the necessity to respond; and 4) selects and performs a response from a repertoire of available responses (Galef 1981; Mateo 1996a). Young may possess some anti-predator ability upon first exposure to an alarm-provoking stimulus, which will ultimately be improved through experience (Giles 1984; Herzog & Hopf 1984). Some naïve young, however, may exhibit poor initial response ability (Rydén 1982; Cheney & Seyfarth 1990). For example, juvenile vervet monkeys do not fully discriminate among acoustically distinct call types designating predator class until the age of 4 to 6 months due to the gradual development and fine-tuning of their vigilance responses (Seyfarth & Cheney 1986). Furthermore, correct alarm call production (i.e. elicited by the proper referent and possessing the appropriate acoustic structure), does not occur until individuals are 1.5 to 3 years old (Seyfarth & Cheney 1986).

Juveniles may exhibit heightened responsiveness to conspecific alarm calls regardless of the predictive value associated with the calls (Robinson 1981). Furthermore, young tend to exhibit anti-predator responses to non-threatening stimuli at a higher frequency compared with adult individuals (Robinson 1981; Cheney & Seyfarth 1990; Hanson & Coss 1997). Consequentially, adults may show reduced responsiveness to the alarm calls of juveniles relative to those of adults presumably due to the unreliability of such calls (Seyfarth & Cheney 1980). Both adult squirrel monkeys (*Saimiri sciureus*, McCowan et al. 2001) and bonnet macaques (*Macaca radiata*, Ramakrishnan & Coss 2000) respond with less vigilance to the alarm calls of juveniles than to those of adults.

Age-dependent differences in anti-predator responses have also been documented in ground-dwelling sciurids (California ground squirrels, Loughry & McDonough 1989, Hanson & Coss 2001; Belding's ground squirrels, Mateo 1996a, b, Mateo & Holmes 1997, Mateo & Holmes 1999a, b; steppe marmots, *M. bobac*, Nesterova 1996; thirteen-lined ground squirrels, *S. tridecemlineatus*, Arenz & Leger 2000). For instance, Belding's ground squirrels learn to discriminate alarm from non-alarm calls within the first few days following emergence, while anti-predator responses to these calls continue to develop over the first few weeks post-emergence (Mateo 1996a). The physical environment (Mateo 1996b), the behaviour of dams (Mateo & Holmes 1997), and early rearing history (Mateo & Holmes 1999a) facilitate this development. Juvenile California ground squirrels exhibit higher response urgency than do adults in response to chatter vocalizations (elicited by slower-moving predators, including terrestrial species); however, the reverse is true in response to whistle vocalizations (produced by faster-moving predators, including avian species; Hanson & Coss 2001). Furthermore, adult California (Hanson & Coss 2001), Belding's ground squirrels (Robinson 1981), and steppe marmots (Nesterova 1996) show reduced responsiveness to juvenile alarm calls compared with those vocalizations produced by adults, presumably due to the lower predictive value of juvenile calls.

Through demonstrating that adult golden-mantled ground squirrels (*S. lateralis*) can learn to associate a novel sound with the appearance of a model hawk using a classical conditioning protocol, Shriner (1999) provides evidence for associative learning as the mechanism through which anti-predator behaviours may be acquired and modified with age (see also Curio et al. 1978; Herzog & Hopf 1984; McLean et al. 1996). The ability of young to associate a sound (such as an alarm call produced by an experienced individual) that is repeatedly paired with a threatening stimulus (such as an approaching predator) is favoured for behavioural adaptation to temporally and spatially varying compositions of predator species within the local area (Robinson 1980; Towers & Coss 1990; Shriner 1999). In this thesis I contrast adult and juvenile responses to variation in the number of callers and temporal properties of call bouts to assess potential developmental changes concerning the relative importance of caller number discrimination, and temporal call bout factors in the perception of response urgency.

Richardson's ground squirrels are semi-fossorial, group-living rodents, found throughout the northern Great Plains and the Canadian prairies (Michener & Koeppl 1985). These squirrels emit anti-predator vocalizations, or alarm calls, to warn conspecifics of potential danger posed by predators (Davis 1984; Macedonia & Evans 1993; Hare 1998; Warkentin et al. 2001). Ground squirrels are ideal research subjects because they are known for their alarm vocalizations, are diurnal and large enough to be marked, and habituate well to humans (Robinson 1980). Addressing the role of multiple-signaler systems, temporal structuring of repetitive alarm calls, and age-related perceptual differences in Richardson's ground squirrel will further our understanding of the cognitive processes underlying alarm communication in ground squirrels. As such, it will contribute significantly to our understanding of mammalian communication systems and to the developing field of cognitive ethology.

SYNOPSIS OF STUDIES

A variety of playback studies were performed to address perception of multiple calling squirrels and individual call rate and length properties by Richardson's ground squirrels (Figure 1). Playback studies involve trials where behavioural responses of subjects to recorded alarm calls, previously elicited by a predator model, are recorded on video for subsequent data coding and analysis. Unlike receiver responses to alarm calls produced in situ, the playback method precludes the possibility of differential receiver response owing to contextual cues that normally accompany call production, such as non-vocal anti-predator behaviour of the signaler or the stimulus that originally elicited the alarm vocalizations (Macedonia & Evans 1993). Furthermore, the use of recorded alarm call exemplars allows the experimenter to manipulate aspects of alarm call bout morphology to control for or test influences of properties such as call rate and amplitude, as well as call bout length and duration.

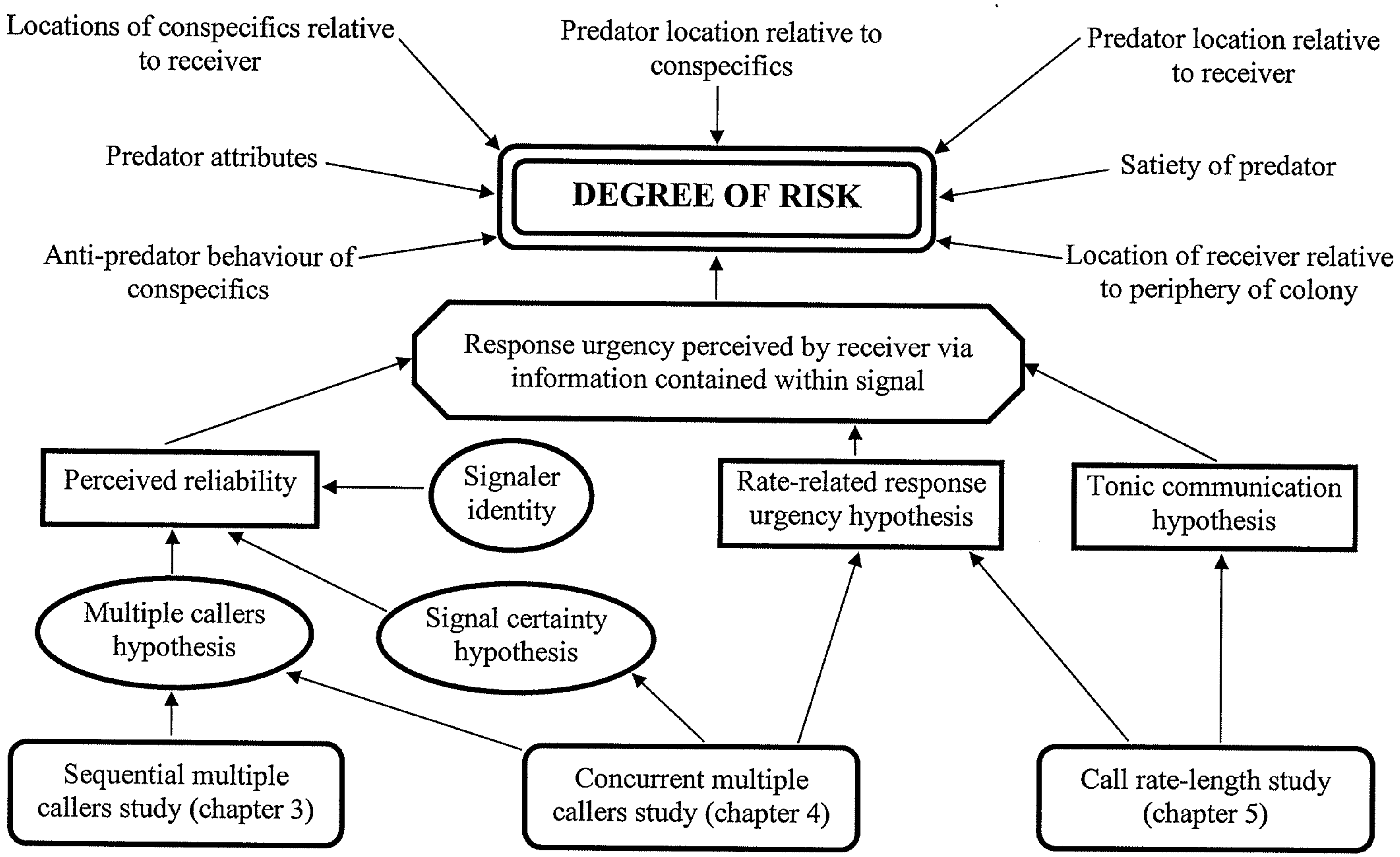

Figure 1. Conceptual diagram illustrating the relationship among each study, the hypotheses tested, and how these hypotheses relate to the perception of response urgency by Richardson's ground squirrels and the actual degree of risk the threat poses.

Sequential Multiple Callers Study

In the sequential multiple callers study, juvenile and adult Richardson's ground squirrels received playbacks composed of two call exemplars, each with five syllables from either the same or two different individuals. These call exemplars were broadcast sequentially through two spatially separated loudspeakers to determine whether these animals use caller identity discrimination (Hare 1998) to distinguish a single caller that moves between two areas from a situation where two individuals issue alarm vocalizations. Using a different call exemplar from the same individual to produce the second set of syllables in the one-caller playback ensured that any differential receiver response was due to discrimination of a novel caller rather than a difference in acoustic morphology. Thus, the sequential multiple callers study addressed the multiple callers hypothesis that receivers discriminate the number of callers to gauge signal veracity. Further, comparisons of responses of juvenile and adult subjects allowed an exploration of age-related perceptual differences in potential numerical assessments.

Concurrent Multiple Callers Study

The concurrent multiple callers study addressed the relative roles of multiple callers and the decoding of temporal properties of repeated alarm calls based upon receiver behavioural responses. Trials were performed on adult and juvenile Richardson's ground squirrels addressing the multiple callers hypothesis and comprised three playback experiments, each involving playbacks of one versus four concurrently calling squirrels. The construction of four-caller playbacks varied across the three experiments to address the influence on receiver response of simultaneously presented call bouts, permitting the interpretation of the effects of temporal call bout properties in the context of additional hypotheses. Experiment one tested for effects of one versus four callers where the one-caller and four-caller playbacks possessed the same overall call rate but the individual call rates characterizing the four-caller condition were on average lower and were more variable. This experiment addressed three hypotheses: multiple callers, signal certainty (Sloan & Hare 2004) and rate-related response urgency (Warkentin et al. 2001). Increased receiver responsiveness to the one-caller condition would support the latter two hypotheses, and refute the multiple callers hypothesis, while greater vigilance in response to the four-caller playback would be inconsistent with signal certainty and rate-related response urgency in support of multiple callers. In experiment two, potential influences of signal-certainty effects were controlled for: the same one-caller playback was compared to a four-caller playback characterized by individual call rates that were lower on average but uniform like in the one-caller playback. Greater receiver responsiveness to the four-caller playback would support the multiple callers hypothesis, and refute the rate-related response urgency hypothesis, while the opposite finding would be inconsistent with the former and support the latter. The individual call rates of the four-caller condition of experiment three were uniform and equal to the individual call rate of the one-caller playback, controlling for effects of both signal certainty and rate-related response urgency. Therefore, support for the multiple callers hypothesis would be provided by greater receiver responsiveness to the four-caller condition. To be conservative in rejecting null hypotheses, I examined signal certainty and rate-related response urgency independent of multiple-caller influences through comparisons of the responses to the four-caller playbacks from each experiment. Furthermore, I addressed multiple-caller influences independent of signal certainty and rate-related response urgency in the sequential multiple callers study (see Chapter 3). Thus, through one-caller and four-caller treatment comparisons of behavioural responses to experiments one, two and three, and comparisons of responses to the four-caller treatments from these experiments, the concurrent multiple callers study addressed the mechanisms Richardson's ground squirrels utilize to perceive and assess the response urgency of predatory threat; i.e. whether they decode the number of callers through numerical assessment, the individual call rate, the extent of uniformity of individual call rate, or a combination of all of these mechanisms in assessing that conveyed in repeated calls. Finally, contrasts between the performance of juveniles and adults in this study permitted an assessment of developmental changes in alarm call responses and perceptual abilities.

Call Rate-length Study

Much of the perceptual research on Richardson's ground squirrels has failed to address potential differences between juvenile and adult responses to alarm calls (see Hare 1998; Hare & Atkins 2001; Warkentin et al. 2001; Wilson & Hare 2003; Sloan & Hare 2004; Sloan et al. in press). Warkentin et al. (2001) found that receivers respond with greater vigilance to higher versus lower call rates as higher rates are correlated with the degree of risk experienced by the signaler (supporting the rate-related response urgency hypothesis; Warkentin et al. 2001). Additionally, Sloan & Hare (2004) found that the number of syllables within a call bout produces no differential response by Richardson's ground squirrels (disproving the tonic communication hypothesis as it applies to the repetitive calling in juvenile Richardson's ground squirrels; Schleidt 1973; Owings & Hennessy

1984; Loughry & McDonough 1988). The method of scanning colonies of unmarked ground squirrels of unknown ages for receiver postures in Warkentin et al.'s (2001) study, and the restriction of subjects to juveniles in Sloan's & Hare's (2004) study, however, precluded examination of potential influences of age-class on response. Therefore, the call rate-length study examined the perception of call rate and length properties by adult Richardson's ground squirrels, testing the rate-related response urgency hypothesis that increased call rate communicates to the receiver increased response urgency posed by the predator (Warkentin et al. 2001), and the tonic communication hypothesis that additional syllables add to the residual effects experienced by subjects of previously received elements (Schleidt 1973). Each subject received three playbacks produced using a single caller, which differed in the temporal structure of the call bout. Playback one was composed of six syllables, each separated by a 6-s intersyllable latency, producing a call bout duration of approximately 30 s. Playback two also contained six syllables; however, the intersyllable latency was reduced to 3 s resulting in a higher-rate call bout comprising a total duration of approximately 15 s. Playback three maintained a 3-s intersyllable latency and contained 11 syllables, producing a total duration of approximately 30 s. Comparison of the vigilance response by recipients to playback one versus playback two tested the influence of increasing an individual's call rate, while controlling for the number of syllables (resulting in a difference in call bout duration). Comparison of the vigilance response by recipients to playback one versus playback three examined the influence of increasing an individual's call rate while controlling for the total duration of the call bout (resulting in a difference in total syllable number). If the rate-related response urgency is supported, Richardson's ground squirrels should exhibit greater vigilance in response to the playbacks with higher call rates, regardless of the number of syllables; Sloan & Hare (2004) have found that syllable number produces no differential vigilance response in juvenile Richardson's ground squirrels. Comparison of the vigilance response by recipients to playback two versus playback three allowed testing of the influence of call bout length on adult response while controlling for call rate (resulting in a difference in call bout duration). Support will be provided for the tonic communication hypothesis if call recipients exhibit greater vigilance in response to the playback with more syllables (Owings & Hennessy 1984), whereby additional signal elements add to the residual effects of previously received elements (Schleidt 1973). No differential response is expected to result from this treatment comparison.

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CHAPTER 2: GENERAL METHODS

This chapter contains a description of the research methods conducted during this thesis that are common across all studies. Any exceptions in methodology with respect to particular studies are indicated where appropriate.

SITE PREPARATION

Research was conducted from 12 April to 15 July 2003 on a 2.5-ha sub-section (50° 17′ N, 97° 70′ W) of grazed cattle pasture near Warren, Manitoba and from 11 April to 24 May 2004 at Winnipeg, Manitoba's Assiniboine Park Zoo (49° 52′ N, 97° 14′ W). Additional data used for this thesis were collected by James F. Hare & Brent A. Atkins from 1 May to 12 August 1997 on a 1.5-ha sub-section (49° 47′ N, 99° 59′ W) of grazed cattle pasture near Brandon, Manitoba. Adult (considered age 1 year and older) and juvenile (young of the year) Richardson's ground squirrels were live-trapped using National or Tomahawk live-traps baited with peanut butter and were permanently marked with metal ear tags (National Band and Tag Company, Monel #1). Hair dye (Clairol Hydrience^{TM}, Pearl Black, # 52S) was applied to the dorsal pelage of each animal in unique patterns to distinguish individuals in the context of field observations. In 1997 colored wire-pin flags formed a 10x10 m grid to obtain relative locations of and distances between animals, equipment, and human observers, while in 2003 and 2004 a Global Positioning System unit (Garmin GPS12XL) and measuring tape were used to obtain these measures.

PLAYBACK CONSTRUCTION

Fifty-four calling bouts of juvenile Richardson's ground squirrels recorded by Hare between 1994 and 1998 were transferred from Digital Audio Tape (DAT) onto the computer program Canary™ using a Sony TCD-D8 recorder. All bouts chosen were elicited initially by tossing a tan Biltmore hat (32.5 x 19.5 cm brim x 13.0 cm high) to within 1 to 8 m of a juvenile squirrel (see Hare 1998), thereby keeping contextual information conveyed within bouts as similar as possible. Though an unnatural stimulus, the hat as a predator model is a light-weight and portable object that reliably elicits alarm vocalizations, making it ideal for fieldwork. Playback exemplars were produced and edited using Canary™ and were constructed with syllables of callers from years and/or sites differing from the years and/or sites in which experiments took place to avoid potential effects of call recipient familiarity with callers. Syllables were chosen according to the clarity of recording and low level of background noise. Playbacks were then transferred from Canary™ onto mini disc using a Sony MZ-N707S MiniDisc Recorder. In 1997, however, Hare & Atkins employed SoundEdit™ for playback exemplar production and editing, and transferred those exemplars onto DAT using a Sony TCD-D8 recorder.

PLAYBACK TRIALS

Each prospective target individual was approached to within 25 to 10 m. An assistant erected a tripod holding a Sony DCR-TRV110 camcorder, while I placed a Genexxa Pro LX5 loudspeaker 9 m left of the tripod oriented toward the subject (concurrent multiple callers study and call rate-length study), or two loudspeakers 9 m to the left and right of the tripod, respectively, in the case of the sequential multiple callers study. The appropriate track was played using a Sony MZ-N707S MiniDisc Recorder, and broadcast to the subject through the loudspeaker(s) using a Sony XM-2025 amplifier. In 1997, however, Hare & Atkins used a Sony CCD-TR700 camcorder, Realistic Minimus-77 loudspeaker, and Sony TCD-D8 recorder during playback trials. Unless otherwise noted, playbacks were broadcast at 84 – 91 dB SPL (measured at 1 m from the loudspeaker using a Techcessories 33-2050 Sound Level Meter, weighting C, response fast). The same outerwear was worn every day to ensure any differential responses were attributable to the variables of interest.

Miscellaneous grouping factors, or measures other than the independent variables of interest that could potentially influence behavioural responses of subjects, were recorded and include: trial time (hours), trial date (truncated Julian day, equivalent to the Julian day minus 2440000.5, where the starting day is midnight May 24, 1968), subject to observer distance (m), subject to loudspeaker distance (m), and loudspeaker angle relative to subject (degrees; except in 1997 where loudspeaker angle was not recorded). Physical factors that could potentially influence behavioural responses were also measured during trials, including cloud cover [1 (clear) – 4 (overcast)], wind [1 (calm) – 5 (high)], and temperature (°C). A Kestrel 3000 Pocket Weather Meter was used to measure temperature (°C) and wind speed (kph; converted to ordinal values 1, 2, 3, 4, and 5, equivalent to 0 – 5 kph, 6 – 10 kph, 11 – 15 kph, 16 – 20 kph, and 21 – 25 kph, respectively). During 1997 trials, observers estimated wind speeds, employing a similar ordinal wind scale; however temperature measurements were not recorded. Furthermore, no physical measurements were obtained for the 2003 adult trials. During the course of experiments attempts were made to balance miscellaneous grouping factors across treatments for all studies. These variables, along with the physical factors, were also subject to statistical analysis following the completion of trials to check for balance across treatments, and to ensure any imbalanced factors did not significantly influence interpretation of results (see Appendix A).

Subjects were videotaped for the duration of the playback, and 30 s preceding and following the playback, though no pre-playback footage was obtained by Hare & Atkins in 1997. In all 2004 trials, subjects were required to maintain foraging behaviour in an all-fours posture for over 50% of the pre-playback, though in most (98%) trials, this proportion exceeded 80%, increasing the probability that vigilance responses were attributable to the treatment and not some external source. Trials were aborted if subjects were out of sight for 33% or more of the 30-s pre- and/or post-playback. Trials were removed where subjects were out of sight for 20% or more of the playback period or if the subject went down a burrow and remained underground during the playback of two or more syllables. Trials were also removed where non-target individuals called during the playback period and the first 20 s of the post-playback period, or if the subject engaged in an interaction with another individual during the playback or post-playback periods. To minimize the risk of habituation to particular playback types and individual callers, squirrels were sampled from widely dispersed (greater than 50 m) sub-areas of the field sites. Trials within the same field area located less than 50 m apart were separated by at least 1 hour.

DATA CODING AND ANALYSIS

Data were coded from videotape during August and September 2003 and July and August 2004 using a Sony Trinitron KV 20FV10 television, a Sony DCR-TRV110 camcorder, and a stopwatch. During an initial run-through, the time codes on the videotapes were determined for the pre-playback, playback, and post-playback periods. The proportion of time the animal was visible during these segments was also recorded and trials in which individuals did not meet the minimum visibility requirements (outlined above) were eliminated from further consideration.

Behavioural responses can be arranged in an ordinal series representing increasing vigilance/alarm. In order of increasing response, Hare (1998) defined: standing on all four feet with head lowered (S4hd; considered non-vigilant behaviour), standing on all four feet with head raised (S4hu; considered the lowest level of vigilant behaviour), resting on the hind legs with back arched forward (slouch), standing on the hind legs with back erect (alert; considered the highest level of vigilant behaviour), and running (considered escape-related behaviour) as potential responses (see Owings & Virginia 1978 for a similar categorization). Thus vigilant behaviour is defined in this thesis as any posture in which the head is above the horizontal plane (i.e. s4hu, slouch, and alert). The proportion of time recipients spent vigilant while they were visible was coded for pre-playback, playback, and post-playback periods. To eliminate experimenter bias, I muted the sound and used the time codes to distinguish each period so as to not be privy to the treatment condition while coding. As the concurrent multiple callers study trials were not subject to a pre-playback foraging criterion, the proportion of time spent vigilant during the pre-playback period was subtracted from those proportions coded from the playback and post-playback periods to create the following dependent variables for both the concurrent multiple callers study and the call rate-length study: change in the proportion of time spent vigilant from pre- to playback period and change in the proportion of time spent vigilant from the pre- to post-playback period. However, as pre-playback data were not obtained during the 1997 trials, for adult and juvenile comparison purposes, the proportion of time spent vigilant during the playback and the post-playback periods, rather than changes in proportions from the pre-playback period, were used in analyses of the sequential multiple callers study.

Appendix B provides behavioural assays corresponding to all treatment comparisons for all studies. These assays include the individual vigilance postures (S4hu, slouch, and alert), non-vigilant behaviour (S4hd), and escape-related behaviour (running). Means and standard errors of the change in proportion of time spent eliciting the different behaviours from pre- to playback and from pre- to post-playback periods are reported for the concurrent multiple callers study and the call rate-length study, while proportions of time spent performing the different behaviours during the playback and post-playback periods are reported for the sequential multiple callers study. A formal discussion of these behavioural assays is not provided; however, notable contributions of individual behaviours are referenced in the main text where appropriate.

Statistical tests were performed using SigmaStat™ 3.1 on a personal computer. As 62 out of 138 sets of data tested using Kolmogorov-Smirnov tests were not drawn from an underlying population of normally-distributed differences, non-parametric Wilcoxon's signed-ranks tests were performed to examine the influence of comparisons of the following treatments on the dependent variables: one-caller and four-caller treatments, and the four-caller treatments of the concurrent multiple callers study; one-caller and two-caller treatments of the sequential multiple callers study; and the three treatments of the call rate-length study, each differing in rate and length properties. Wilcoxon's signed-ranks tests, however, were not performed on the individual behaviours comprising the behavioural assays for the sequential multiple callers study and call rate-length study as squirrels during the 2004 field season exhibited little or no high vigilance behaviour (i.e. slouch and alert) or running (see Appendix B). A formal discussion of the test results documented in Appendix B is not provided; however, notable significant differences are referenced in the main text where appropriate. All differences were considered significant where $P \leq 0.05$, though given the extensive variability in behavioural responses implicit in conducting field playbacks, trends were also discussed where $P \leq 0.06$. For a description of the analyses performed on physical and miscellaneous grouping factors see Appendix A. Appendix C explores correlations among the physical factors cloud cover, wind, and temperature, and the miscellaneous grouping factors year, trial date, and trial time, with the use of a Spearman's correlation matrix.

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CHAPTER 3: THE SEQUENTIAL MULTIPLE CALLERS STUDY; A TEST OF CALLER NUMBER DISCRIMINATION BY JUVENILE AND ADULT RICHARDSON'S GROUND SQUIRRELS

INTRODUCTION

Experimental studies to date have examined alarm communication in ground squirrels via controlled experiments involving playbacks of single callers. Seldom is it the case, however, that only a single squirrel vocalizes in response to a predator. Rather, multiple individuals vocalize, each presumably increasing their own risk of predation (Sherman 1977), and potentially confounding the assessment of call rate from any one signaler. With each additional calling squirrel, however, all callers should enjoy proportionately less additional risk, and simultaneously reduce the risk for others. To evolve and persist, the benefits of a multiple-caller system must somehow outweigh the potential costs.

One hypothesis that may explain the recruitment of multiple callers into a chorus is an increase in the likelihood that the signal will be perceived in a noisy environment (Bradbury & Vehrencamp 1998). In nature there are numerous factors that may confound the transfer of a signal from the sender to the receiver, some of which include the level of ambient noise, spreading losses of sound with the distance from the source, pattern losses in frequency by medium absorption and scattering, and pattern losses due to boundary reflections (Bradbury & Vehrencamp 1998). Indeed, a multiple-caller system may facilitate transmission of the signal so that conspecifics may respond in a way that benefits not only themselves but also the signaler (Bradbury & Vehrencamp 1998).

Ground squirrels may enhance their safety by monitoring a predator's location (Lima & Dill 1990). Through a multiple-caller system signal recipients may also integrate information received from callers to resolve predator location and movement through the colony (Warkentin et al. 2001) in a process analogous to trilateration (Leick 1995). Each calling ground squirrel may communicate the distance the predator is away from itself thereby producing a unique point of intersection. The recipient individual may then reference the positions of the known individual callers (Hare 1998) and determine the predator's position. Predator monitoring may exist in Columbian ground squirrels, which alter call rate as a function of predator movement (Harris et al. 1983). Similarly, California ground squirrels have been shown to produce more syllables per bout with change of speed or direction of predator movement (Owings & Virginia 1978). Conversely, Wilson & Hare (2003) found that Richardson's ground squirrels do not communicate predator movements through changes in call rate. However, these findings do not preclude the possibility that a group of calling Richardson's ground squirrels could trilaterate a predator's current location, as call rate is inversely correlated with predator-signaler distance and call recipients adjust vigilance responses accordingly (Warkentin et al. 2001).

The tonic communication hypothesis states that repeated signal elements may add to the residual effects of previously received elements, and therefore produce a cumulative effect in the signal recipient (Schleidt 1973). Limited support for the tonic communication hypothesis has been obtained in Columbian (Harris et al. 1983) and California ground squirrels (Loughry & McDonough 1988) where repeated calls produced greater short-term vigilance in call recipients than did single vocalizations, though no differential extents of vigilance were observed in response to call bouts with more versus fewer syllables. Analogously, the addition of callers into a chorus of calling could serve as a form of tonic communication whereby the production of alarm vocalizations in response to another squirrel's calls serves to maintain vigilance in conspecifics in situations where the predator may still be present in the surrounding area (Owings et al. 1986). Tonic communication, however, does not appear to be a principle mechanism underlying the functioning of the alarm communication system of Richardson's ground squirrels; Sloan & Hare (2004) have found that more versus fewer repeated alarm syllables by a single caller does not promote tonic vigilance in juvenile Richardson's ground squirrel call recipients.

Alternatively, a multiple-caller system may be predicated simply upon the communication of response urgency, whereby an increase in the number of calling individuals lends credence to the assertion that there is a threat present (Blumstein et al. 2004). Call recipients may then respond according to degree of veracity related to the number of callers. Evidence of species with multiple-signaler systems can be found throughout the literature (e.g. Belding's ground squirrels, Robinson 1981; African lions, McComb et al. 1994, Heinsohn et al. 1996; chimpanzees, Wilson et al. 2001; yellow-bellied marmots, Blumstein et al. 2004). Lima (1994) describes a multiple-signaler system characterized by the departure of birds from a flock in the presence of danger. This fleeing behaviour serves as a signal to conspecifics of possible threat of injury or predation. Because of the contextual ambiguity of such a signal (departure may not be predator-driven), conspecific individuals are more likely to flee in response to simultaneous departures of two or more individuals rather than departure by a single individual (increased certainty of predator presence and thus increased perceived extent of threat; Lima 1994). A community of chimpanzees may produce a chorus of calls to communicate to another community its relative power or vulnerability (Wilson et al. 2001). The listeners within a nearby community may distinguish the number of individuals calling to determine the minimal size of the group, and possibly the identities of those callers (Wilson et al. 2001). Furthermore, defending adult female lions adjust their agonistic approach towards intruding lion groups according to the number of roaring individuals within their own group and the number of roaring intruders from opposing groups (McComb et al. 1994). Within ground-dwelling sciurids, yellow-bellied marmots are more vigilant in response to two sequentially calling marmots versus two sequential calls from a single caller, suggesting that multiple calling individuals is indicative of a more high-risk situation (Blumstein et al. 2004). Additionally, Robinson (1981) has found that multiple callers result in a greater number of highly vigilant Belding's ground squirrels compared with a single caller. Indeed, social species may benefit from numerical discriminations due to the reduced risk of injury or predation.

Through the playback of syllables from two versus one caller broadcast sequentially through two spatially separated loudspeakers, the sequential multiple callers study tested the multiple callers hypothesis to determine whether Richardson's ground squirrels use their ability to discriminate among individual callers (Hare 1998) to distinguish a single caller that moves between two areas from a situation where two individuals issue alarm vocalizations. Furthermore, comparisons of juvenile and adult responses permitted an exploration of age-related differences in perceptual abilities.

METHODS

In 1997, on a 1.5-ha sub-section (49° 47′ N, 99° 59′ W) of grazed cattle pasture near Brandon, Manitoba, Hare & Atkins collected data that addressed whether juvenile Richardson's ground squirrels use their ability to identify individual callers to distinguish a single caller that moves between two areas from the situation where two separate individuals sequentially issue alarm vocalizations. I adopted these methods and conducted a similar experiment on adult Richardson's ground squirrels at the Winnipeg, Manitoba Assiniboine Park Zoo (49° 52′ N, 97° 14′ W) in 2004. All procedures performed in conducting this study followed those outlined under General Methods (Chapter 2). Thirteen and 19 callers were used in the construction of playbacks for the 1997 and 2004 sequential multiple callers experiments, respectively. Restriction to female juvenile callers avoided any potential confounds between caller sex and age, playback type, and vigilance response. This study involved 10 playback sets in 1997 and 12 playback sets in 2004, each consisting of a one-caller and a two-caller playback. Each playback set was constructed using an arbitrary assignment of callers in 1997, and in 2004, a systematic arrangement of callers according to spectrographical similarity of syllables, balancing amplitude and frequency characteristics across treatments. In both years, some callers were assigned to more than one playback set. Using a paired-sample design, subjects received two playback trials. The one-caller treatment consisted of five syllables of the same exemplar of a single caller broadcast through one loudspeaker, followed by the playback of a different five-syllable call exemplar belonging to the same animal broadcast through a second loudspeaker located approximately 20 m away (thus mimicking an individual squirrel moving and calling from a second location). The two-caller treatment consisted of five syllables belonging to the caller featured in the one-caller treatment, but followed by five syllables broadcast from a second loudspeaker belonging to a different caller. The order of presentation of the two treatment types was randomized for each call recipient in 1997 and systematically balanced in 2004. Within both treatments, the intersyllable latency was 3 s and the playback of the first bout of five syllables was separated from the second bout by 15 s. As no pre-playback data were obtained in 1997, for data collected during both 1997 and 2004 the proportion of time squirrels spent vigilant was coded for bout one and bout two within the playback, as well as for the post-playback period, rather than changes in proportion of time spent vigilant from the pre-playback period. The initial vigilance duration, or the amount of time (s) that subjects maintained vigilance following the first syllable of the first and second bouts, was also coded in the sequential multiple callers study. The initial vigilance duration is a measure of the subject's first reaction to the onset of a bout of alarm calling, and is therefore an ideal variable to examine the influence of the introduction of a novel caller. Although differences in one-caller and two-caller treatment designs were only apparent during the second bout of the playback, the dependent variables were also measured during the first bout to serve as a baseline against which comparisons could be made. Wilcoxon's signed-ranks tests should reveal no differences in the initial vigilance duration or proportion of time spent vigilant when comparing the first bout of the one-caller versus two-caller playback as the first bout is from the same individual across both treatments. However, if the multiple callers hypothesis is supported and Richardson's ground squirrels perceive more individuals as an indication of greater response urgency due to greater signal veracity, Wilcoxon's signed-ranks tests should reveal a greater initial vigilance duration during the second bout of the playback and a greater proportion of time spent vigilant during the second bout of the playback and the post-playback period when this bout is produced by a novel caller.

To compare the initial vigilance duration in response to the first and second bouts, there had to be a coding cut-off point of 27 s (i.e. 12 s from bout one plus 15 s from the inter-bout period) as once the second bout begins, the initial vigilance duration for the first bout is no longer restricted to stimuli presented during that period. Data lacking the 27-s coding cut-off criterion, however, were also considered where the initial vigilance duration was coded for the second bout but not compared with the first bout.

Each of the 12 playback sets of 2004 was presented to one male and one female Richardson's ground squirrel resulting in a total sample size of 24 adults, while the 10 playback sets of the 1997 experiment were divided amongst five male and five female subjects for a total sample size of 10 juveniles. A total of 48 trials performed on adults in 2004 and 18 trials conducted on juveniles in 1997 (one subject's trials removed due to inability to hear the entire playback on videotape) were included for analysis. In 1997, playbacks were broadcast to juveniles at 84 – 91 dB SPL (measured at 1 m from the loudspeaker using a Techcessories 33-2050 Sound Level Meter, weighting C, response fast). Due to greater ambient noise and a greater number of boundary reflections characterizing the 2004 zoo site, however, playbacks were broadcast to adult subjects at a range of 95 – 100 dB SPL (measured at 1 m from the loudspeaker) to ensure receivers were able to hear the entirety of the calls. Differences in playback amplitude across years should not confound comparisons of adult and juvenile response data as Nicklaus (2000) has found that differences in amplitude have no apparent effect on the vigilance response of Richardson's ground squirrels.

RESULTS

Juvenile Richardson's Ground Squirrels

Vigilance Proportion

Juveniles did not exhibit greater vigilance in response to the second bout of a different rather than same individual (bout two: W = -5, n = 9, *P* = 0.688; post-playback: W = 0, n = 8, *P* = 1.000; Table 1). Juveniles also responded no differently during the first bout of the two-caller versus one-caller treatment (bout one: W = -16, n = 9, *P* = 0.219; Table 1) where the caller was always the same individual.

Initial Vigilance Duration

Juvenile Richardson's ground squirrels responded no differently to the same or to two different callers broadcast sequentially through two spatially separated loudspeakers. The initial vigilance duration of juveniles in response to a unique caller during the second bout of the playback was not significantly different from the initial vigilance duration in response to the same caller during the second bout. This was the case regardless of whether one examined data where a 27-s cut-off criterion was applied (bout one: W = -2, n = 9, *P* = 0.945; bout two: W = -31, n = 9, *P* = 0.074; Table 1) or data where no 27-s cut-off criterion was applied (bout two: one-caller playback – 34.280 ± 19.050, two-caller playback – 8.301 ± 2.505; W = -31, n = 9, *P* = 0.074).

Table 1. Wilcoxon's signed-ranks tests illustrate the influence of the one- versus two-caller playbacks from the sequential multiple callers study on the initial vigilance duration (IVD; mean ± SE sec) and the proportion of time spent vigilant [mean ± SE sec] during bouts one and two of the playback period and during the post-playback period by adult and juvenile Richardson's ground squirrels. (Statistically significant differences are in bold font).

Measured Period	Dependent Variable	Adults One Caller	Two Callers	W	*P*	n	Juveniles One Caller	Two Callers	W	*P*	n
Bout One	IVD	9.123 ± 2.026	8.082 ± 1.845	8	0.920	24	13.576 ± 3.440	12.062 ± 2.610	-2	0.945	9
	Playback Vigilance	0.718 ± 0.048	0.701 ± 0.050	4	0.966	24	0.924 ± 0.047	0.881 ± 0.049	-16	0.219	9
Bout Two	IVD	**5.152 ± 1.785**	**10.606 ± 2.287**	**138**	**0.050**	**24**	15.672 ± 3.905	8.301 ± 2.505	-31	0.074	9
	Playback Vigilance	**0.577 ± 0.053**	**0.731 ± 0.051**	**170**	**0.016**	**24**	0.865 ± 0.089	0.841 ± 0.063	-5	0.688	9
Post-playback	Post-playback Vigilance	0.578 ± 0.044	0.639 ± 0.060	32	0.637	24	0.792 ± 0.063	0.748 ± 0.071	0	1.000	8

Adult Richardson's Ground Squirrels

Vigilance Proportion

Adult Richardson's ground squirrels spent a greater proportion of time vigilant in response to two different callers versus the same caller broadcast sequentially through two spatially separated loudspeakers. Adults did not respond differently during the first bout of the two-caller versus one-caller playback (bout one: W = 4, n = 24, *P* = 0.966; Table 1). However, adults did exhibit greater vigilance during the second bout of calling by a different rather than same caller (bout two: W = 170, n = 24, *P* = 0.016; post-playback: W = 32, n = 24, *P* = 0.637; Table 1). This difference was attributable to a greater proportion of time spent in S4hu and slouch in response to two different callers (Table B.1.; Appendix B).

Initial Vigilance Duration

Adult Richardson's ground squirrels spent a greater amount of time initially vigilant to two different callers versus the same caller broadcast sequentially through two spatially separated loudspeakers. When examining data where a 27-s cut-off criterion was applied, the initial vigilance duration was greater in response to the unique versus same caller during the second bout of the playback (bout one: W = 8, n = 24, *P* = 0.920; bout two: W = 138, n = 24, *P* = 0.050; Table 1). However, this significant difference was not apparent when examining data with no 27-s cut-off criterion (bout two: one-caller playback – 9.580 ± 3.874, two-caller playback – 14.862 ± 4.479; W = 92, n = 24, *P* = 0.194).

DISCUSSION

Juvenile Richardson's Ground Squirrels

The sequential multiple callers study addressed whether or not Richardson's ground squirrels make caller number discriminations to perceive the degree of signal veracity (Blumstein et al. 2004), and therefore the response urgency, associated with the threat. No differential response was observed by juveniles to two different squirrels versus the same squirrel broadcast sequentially through two spatially separated loudspeakers, refuting the multiple callers hypothesis as it pertains to juvenile Richardson's ground squirrels.

As the sample size of the sequential multiple callers study was relatively small, only nine individuals, the finding of no differential vigilance response to more than one caller should be interpreted cautiously. Furthermore, upon review of the videotapes produced during this study, four trials were found to be conducted in very high winds (exceeding 30 kph), potentially biasing the results obtained for three subjects. Clearly, additional research is required to establish caller number discrimination by juvenile Richardson's ground squirrels (but also see Chapter 4).

Adult Richardson's Ground Squirrels

Adults responded with greater vigilance to two different callers versus the same caller broadcast sequentially through two spatially separated loudspeakers. Additionally, the initial vigilance duration was greater in response to the two-caller versus one-caller treatment. In the case of adult Richardson's ground squirrels, therefore, findings from the sequential multiple callers study provide support for the multiple callers hypothesis. Adult Richardson's ground squirrels utilize their ability to discriminate among individual callers to perceive increases in the degree of response urgency, where more callers is indicative of greater veracity associated with each signaler's call bout (Blumstein et al. 2004). Similarly, Blumstein et al. (2004) found that yellow-bellied marmots were more vigilant in response to two sequential callers versus a single caller (Blumstein et al. 2004), while Robinson (1981) documented more Belding's ground squirrel callers resulting in a greater number of highly vigilant receivers. Indeed, the ability to make caller number discriminations would prove beneficial in systems where survival is largely a function of the adaptive trade-off between anti-predator behaviour and foraging (Lima & Dill 1990).

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CHAPTER 4: THE CONCURRENT MULTIPLE CALLERS STUDY; AN EXAMINATION OF THE RELATIVE IMPORTANCE OF THE NUMBER OF CONCURRENT ALARM CALLERS AND THEIR CALL RATES IN THE PERCEPTION OF RESPONSE URGENCY BY JUVENILE AND ADULT RICHARDSON'S GROUND SQUIRRELS

INTRODUCTION

Multiple-signaler systems are a commonly observed phenomenon in nature (e.g. Belding's ground squirrels, Robinson 1981; African lions, McComb et al. 1994, Heinsohn et al. 1996; chimpanzees, Wilson et al. 2001; yellow-bellied marmots, Blumstein et al. 2004). Indeed, an increase in the number of signalers may increase the probability of successful signal transmission in a noisy environment (Bradbury & Vehrencamp 1998). By calling, each individual presumably increases its risk of predation (Sherman 1977), while potentially confounding the assessment of individual temporal call bout information by receivers. With each additional calling squirrel, however, the added risk experienced by each caller should be reduced, with a reduction in risk for receivers as well. The evolution and perseverance of such a system must result from higher benefits compared with the potential costs.

I propose that a multiple-caller system functions in the communication of response urgency to receivers, whereby an increase in the number of calling individuals communicates a greater perceived extent of threat. Ground-dwelling squirrels are generally considered to possess response-urgency based alarm communication systems (Marler et al. 1992). For example, Blumstein (1999) demonstrated that Olympic (*M.*

olympus), hoary (*M. caligata*), and Vancouver Island marmots (*M. vancouverensis*) produce call bouts that vary in frequency, duration, and bandwidth according to the distance between the caller and the alarming stimulus. Additionally, yellow-bellied marmots have been shown to increase their rate of calling according to the response urgency the signaler experiences (Waring 1966), while Columbian ground squirrels increase call rate with increased predator movement (Harris et al. 1983). Richardson's ground squirrels also vary call rate with perceived extent of threat; repeated alarm calls are produced at rates that are inversely related to the signaler-predator distance, and call recipients perceive call rate as an indication of the response urgency posed by a potential predator (rate-related response urgency hypothesis; Warkentin et al. 2001).

The multiple callers hypothesis suggests that the increased level of perceived response urgency to multiple calling individuals results from the increased level of signal veracity associated with more versus fewer callers (Blumstein et al. 2004). For instance, yellow-bellied marmots perceive higher predatory threat following the playback of call bouts from two sequentially calling marmots versus two sequential call bouts from a single caller (Blumstein et al. 2004). Similarly, a greater number of Belding's ground squirrels assume highly vigilant postures in response to multiple calling individuals versus a single caller (Robinson 1981). Reliability assessment of individual callers by call recipients, based on previous ability to communicate accurate risk information, has been observed in vervet monkeys (Cheney & Seyfarth 1988, 1990) and Richardson's ground squirrels (Hare & Atkins 2001). Richardson's ground squirrels also respond less vigilantly to call bouts that vary in their intersyllable latency (variable bouts) than to those that do not (monotonous bouts; Sloan & Hare 2004). As Richardson's ground squirrels communicate the distance to a predator via call rate (Warkentin et al. 2001), recipients essentially come to ignore callers producing variable bouts because they are in effect communicating uncertainty of predator location and/or extent of threat (signal certainty hypothesis; Sloan & Hare 2004).

Seldom is it the case that callers segregate their calls temporally as in the sequential multiple callers study (Chapter 3). Rather, calls from multiple individuals are typically produced concurrently in response to a predator's presence. Therefore, to better assess how Richardson's ground squirrels in the field extract information from multiple callers, I performed three controlled playback experiments of one versus four concurrently calling squirrels on juvenile and adult Richardson's ground squirrels. The concurrent multiple callers study, then, addressed the multiple callers hypothesis that more calling squirrels communicates greater response urgency to recipients via the perception of signal veracity associated with numerical discriminations, while taking into consideration that Richardson's ground squirrels communicate response urgency through call rate (rate-related response urgency hypothesis; Warkentin et al. 2001), and perceive variation in call rate as uncertainty on the part of the signaler (signal certainty hypothesis; Sloan & Hare 2004). Indeed, the temporal structure of the four-caller playbacks were constructed such that in addition to testing the multiple callers hypothesis, experiment one also addressed both rate-related response-urgency and signal-certainty effects, experiment two considered the relative role of rate-related response urgency, while experiment three addressed the multiple callers hypothesis alone. Four-caller comparisons permitted testing of the rate-related response urgency and the signal certainty hypotheses independent of the influence of caller number. Thus, through one-caller and four-caller treatment comparisons of experiments one, two and three, and comparisons of four-caller treatments from these experiments, the concurrent multiple callers study examined the mechanisms by which squirrels decode information regarding the extent of predatory threat; i.e. whether they assess the total number of callers though numerical discriminations, individual call rate, the extent of uniformity of individual call rate, or a combination of all of these mechanisms in assessing that conveyed in the response urgency communicated by repeated calls. Furthermore, juvenile and adult responses were compared to assess potential age-related differences in perceptual ability.

METHODS

In 2003, on a 2.5-ha sub-section (50° 17′ N, 97° 70′ W) of grazed cattle pasture near Warren, Manitoba, I performed three playback experiments to address the influence of the number of callers and individual call rate properties on vigilance responses of adult and juvenile Richardson's ground squirrels. All procedures performed in conducting this study followed those outlined under General Methods (Chapter 2). Each experiment was composed of both a playback of one calling squirrel and a playback of four concurrently calling squirrels to examine whether or not a multiple-caller system is predicated upon the communication of response urgency, whereby an increase in the number of calling individuals would likely be correlated with the actual presence of a predatory threat, in essence increasing the veracity associated with the signal's predictivity of predator presence. A maximum of four callers was used as it is within the natural range of the number of calling squirrels in a chorus (pers. obs.). Temporal structuring of syllables of the one-caller playback remained constant across all three experiments, while those of the four-caller playback varied among the three experiments to account for potential effects of call rate and variability of call rate of each individual. This allowed for an examination of the relative importance of two additional hypotheses: the rate-related response urgency hypothesis, where call recipients perceive bouts of higher call rate as communicating greater danger (Warkentin et al. 2001), and the signal certainty hypothesis, where recipients essentially come to ignore callers producing variable bouts because they are in effect communicating uncertainty of predator location and/or extent of threat (Sloan & Hare 2004). To maintain similar call bout durations across all treatments, which would otherwise change with caller number and call rate modifications and potentially influence receiver response, the total number of syllables differed between one- and four-caller conditions. These differences in syllable number should be of no consequence on the behaviour of call recipients, however, as Sloan & Hare (2004) found that longer versus shorter call bouts do not produce differential vigilance responses in juvenile Richardson's ground squirrels.

This study involved 12 playback sets, each consisting of the one-caller playback and the four-caller playbacks from experiments one, two, and three. Each playback set was constructed using a randomly assigned and unique combination of four callers to produce the different playback types, though some callers were assigned to more than one playback set. To address and balance potential effects of caller sex on vigilance response, four playback sets contained two male and two female callers, another four playback sets contained four male callers, and the remaining four sets contained four female callers. Recipient individual squirrels were assigned a particular playback set, while maintaining a balance of the sex of call recipients with the sex of callers. Where possible, I followed a standard presentation order where the sexes of both callers and recipient would alternate to avoid bias associated with order of presentation and caller/recipient sex.

Experiment one addressed the issue of caller number while varying the individual call rate properties of the four-caller condition. It consisted of two playback types: one containing 12 syllables from the same individual caller (one-caller playback), and one composed of three syllables from each of four concurrently calling individuals (four-caller playback). The intersyllable latency characteristic of the one-caller condition was 4 s, comparable to the average intersyllable latency in natural calling bouts of Richardson's ground squirrels (Sloan & Hare 2004). Within the four-caller condition, the placement of an individual's syllables was randomized. Consequently, the mean individual intersyllable latency of the four-caller condition was greater than 4 s, reducing the apparent call rate for each individual caller. Furthermore, the call rate of each individual varied throughout the duration of the four-caller playback. Thus, both the one-caller and the four-caller playbacks consisted of 12 syllables, with a total duration of 44 s, and an overall (among callers) intersyllable latency of 4 s. The individual intersyllable latency differed between the two, however, with the four-caller condition bearing individual call rates that were on average lower and variable compared with the one-caller playback. Greater vigilance in response to four squirrels calling than to one would be inconsistent with rate-related response urgency and signal certainty, but support the hypothesis that multiple callers communicate greater response urgency than does a single caller. However, the opposite result of the one-caller condition producing greater vigilance in call recipients would support the rate-related response urgency and the signal certainty hypotheses, but be inconsistent with the predictions of the multiple callers hypothesis. Because the average individual call rate of the four-caller playback is lower than the one caller's rate, this may be perceived by recipients as the communication of lower response urgency (Warkentin et al. 2001). Additionally, the tendency for the four callers to produce variable call rates may communicate uncertainty of predator location and/or extent of threat to the call recipient (Sloan & Hare 2004). No differential response to either one- or four-caller treatment may refute all hypotheses, but would more likely represent a combined influence of call rate properties and multiple callers on the perception of response urgency by call recipients.

Experiment two was constructed to address the issue of multiple callers, while at the same time address the relative importance of individual call rate in the perception of response urgency by call recipients. The influence of individual call rate variability (or signal-certainty effects) was controlled for across treatments through making the call rates of each individual uniform within the four-caller playback. Both one-caller and four-caller playbacks possessed an overall intersyllable latency of 4 s, 12 syllables in total, and a total duration of 44 s. Each individual within the four-caller playback, however, was given a uniform individual intersyllable latency of 16 s with a randomization of the ordinal position of callers rather than the position of individual syllables. Therefore, while the four-caller playback contained more callers, the individual call rates were much lower than that of the one-caller playback. If squirrels are more vigilant in response to the four-caller condition of experiment two, support is provided for multiple callers, but is inconsistent with the rate-related response urgency hypothesis. However, if the one-caller condition elicits more vigilance, support is provided for rate-related response urgency, but is inconsistent with the multiple callers hypothesis.

Furthermore, no differential vigilance response to either one- or four-caller treatments may refute the rate-related response urgency and multiple callers hypotheses; however, it may also represent a combined influence of both individual call rate and multiple callers.

Experiment three addressed the influence of multiple callers and controlled for both individual call rate and individual call rate variability. Within the four-caller playback, the ordinal position of callers was the same as in experiment two's four-caller playback, but the intersyllable latency for each individual caller was decreased from 16 to 4 s to produce equivalent individual call rates for both the one-caller and four-caller playbacks. For the total duration of the four-caller condition to approximate that of the one-caller playback (44 s), the total number of syllables contributed by each individual had to be increased from three to 11 syllables, resulting in a total overall syllable number of 44 (compared with the one-caller playback's 12) and a total duration of approximately 43 s. As Sloan & Hare (2004) reported that the number of syllables produced during a calling bout does not significantly influence vigilance response of juvenile Richardson's ground squirrels, the difference in overall syllable number across playbacks should not influence the vigilance responses of recipients. Thus, experiment three controlled for signal-certainty and individual call rate-related response-urgency effects, while permitting an examination of the potential influence of multiple callers on call recipient vigilance. If multiple callers are important in the communication of response urgency, squirrels should respond more vigilantly to the four-caller playback than to the one-caller playback. As an increase in each individual caller's rate in the four-caller playback inevitably resulted in the overall, emergent (among callers) call rate to be greater than that of the one-caller condition (i.e. an overall intersyllable latency of 1 s compared with an intersyllable latency of 4 s), higher vigilance in response to the four-caller playback could be interpreted as being the result of increased overall call rate. Indeed, perhaps the mechanism through which squirrels perceive increased threat, modulated via the recruitment of multiple callers into a chorus, is through increases in overall rate and not via increases in the number of individuals calling. Therefore, experiment three tests for a multiple-caller system predicated upon the communication of response urgency, with the perception of increased threat being the result of either an increase in overall call rate that naturally accompanies an increase in caller number or via an increase in the actual number of callers. Through comparison of these results with those from the sequential multiple callers study (Chapter 3) where additional callers were presented sequentially as opposed to simultaneously, I was able to identify the mechanism by which Richardson's ground squirrels perceive an increase in the response urgency a predator poses; through an increase in the perceived overall call rate or through an increase the actual number of callers.

All 2003 experiments were conducted on both adult and juvenile Richardson's ground squirrels. As trials contributing data to all three experiments were staged contemporaneously starting approximately 1 wk following the juvenile emergence of the last dam employed in this study, and as the same one-caller playback of each playback set was used as a control for all three possible four-caller treatments, the performance of the one-caller playback was only required once for each subject and prevented habituation to the one-caller playback. For adult call recipients, however, I conducted experiment one prior to juvenile emergence, and experiments two and three following juvenile emergence. Therefore, to eliminate influences associated with seasonal, physiological, or behavioural differences between pre- and post-emergence time frames, adult subjects received the one-caller playback twice during the field season: once during experiment one, and once during experiments two and three.

Each of the 12 playback sets of 2003 (composed of a one-caller playback, and the four-caller playbacks of experiments one, two, and three) was to be presented to two adult and two juvenile recipients to obtain a sample size of 24 adults and 24 juveniles. As a result of the occasional disappearance or dispersal of squirrels in the midst of experiments, however, subjects did not always receive all trials. Though not always possible, individuals were replaced by other squirrels to receive all four playbacks. With the elimination of trials that did not meet the data inclusion criteria outlined under Playback Trials (Chapter 2, General Methods), trials performed on 19 adults and 25 juveniles were included for final analyses. Forty-six trials performed on adults and 78 trials performed on juveniles were included in the final dataset.

To produce the illusion that callers within the four-caller playbacks were located at different locations rather than at a single point source, a range of amplitudes (from 75 to 95 dB SPL (measured at 1 m from the loudspeaker using a Techcessories 33-2050 Sound Level Meter, weighting C, response fast) were used. The application of amplitude values to callers was systematically balanced across all playback sets according to ordinal position of individuals within the four-caller conditions for experiments two and three. The individuals within the one-caller playbacks were assigned amplitudes equal to the loudest amplitude characterizing the four-caller condition to ensure differential responses were due to the variables of interest and not higher amplitudes in either treatment type.

Nicklaus (2000) found, however, that amplitude has no apparent effect on the vigilance response of Richardson's ground squirrels.

To be conservative in rejecting hypotheses, resulting from differential receiver responses owing to combined effects or to differences in relative saliency of any one particular hypothesis, I addressed signal certainty and rate-related response urgency independent of the influence of multiple callers through response comparisons (described below) to the four-caller playbacks from each experiment. Furthermore, I tested the influence of multiple callers independent of signal certainty and rate-related response urgency in the sequential multiple callers study (see Chapter 3). Therefore, the concurrent multiple callers study comprised the following two-group comparisons of the changes in the proportion of time spent vigilant from pre-playback to playback and from pre-playback to post-playback periods, analyzed using Wilcoxon's signed-ranks tests:

Experiment one – one-caller playback versus four-caller playback with variable and on average lower individual call rates;

Experiment two – one-caller playback versus four-caller playback with uniform but on average lower individual call rates;

Experiment three – one-caller playback versus four-caller playback with uniform individual call rates equal to that of the one-caller playback;

Experiment one's four-caller playback versus experiment two's four-caller playback to examine the influence that uniformity of individual call rate has on vigilance;

Experiment one's four-caller playback versus experiment three's four-caller playback to examine the influence that both individual call rate and individual call rate uniformity have on vigilance; and

Experiment two's four-caller playback versus experiment three's four-caller playback, examining the influence of individual call rate on vigilance response of recipients.

The four-caller conditions of experiment one versus experiment two and experiment one versus experiment three for adult subjects were not compared statistically as the passage of time between experiment one conducted prior to juvenile emergence and experiments two and three conducted following juvenile emergence may have coincided with physiological or behavioural changes in call recipients.

RESULTS

Juvenile Richardson's Ground Squirrels

Juvenile Richardson's ground squirrels displayed no more total vigilance to the playback of four callers with individual call rates that were on average lower and variable compared with one caller's uniform and higher rate (experiment one: playback – W = -58, n = 19, *P* = 0.258; post-playback – W = -24, n = 15, *P* = 0.524; Table 2). However, though not statistically significant, juveniles tended to exhibit greater slouch following the playback of four callers with lower on average and variable individual call rates than to one caller with a higher and uniform individual call rate (experiment one: post-playback – W = 79, n = 15, *P* = 0.055; Table B.2., Appendix B). Furthermore, it was determined that juveniles spent a significantly greater proportion of time in slouch plus

Table 2. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE s] adult and juvenile Richardson's ground squirrels spent vigilant from the pre- to the playback and post-playback periods in response to the one-caller treatment versus the four-caller treatments of varying temporal structure from the concurrent multiple callers study. (Statistically significant differences are in bold font).

		Adults					Juveniles				
		Number of Callers					Number of Callers				
Individual Call Rate Type	Measured Period	One	Four	W	*P*	n	One	Four	W	*P*	n
Experiment 1:											
High/Uniform	Playback	0.171 ± 0.066	0.080 ± 0.068	-32	0.389	16	0.189 ± 0.043	0.080 ± 0.064	-58	0.258	19
Vs.	Post Playback	0.076 ± 0.055	0.031 ± 0.081	-17	0.588	14	-0.030 ± 0.058	-0.040 ± 0.085	-24	0.524	15
Low/Variable											
Experiment 2:											
High/Uniform	Playback	0.249 ± 0.088	0.230 ± 0.074	-7	0.839	13	0.208 ± 0.044	0.269 ± 0.081	11	0.761	14
Vs.	Post Playback	0.004 ± 0.107	0.133 ± 0.090	14	0.577	11	-0.034 ± 0.074	0.208 ± 0.106	44	0.092	12
Low/Uniform											
Experiment 3:											
High/Uniform	Playback	0.204 ± 0.091	0.275 ± 0.083	19	0.583	14	**0.216 ± 0.047**	**0.379 ± 0.067**	**114**	**0.020**	**19**
Vs.	Post Playback	0.008 ± 0.101	0.150 ± 0.078	47	0.153	14	-0.038 ± 0.091	0.200 ± 0.079	60	0.095	15
High/Uniform											

alert (or in high vigilance) following the four-caller playback than the one-caller playback (experiment one, post-playback: one caller – -0.101 ± 0.058, four callers – 0.039 ± 0.083; W = 79.0, n = 15, *P* = 0.011). Juveniles were no more responsive to the playback of four callers with individual call rates that were constant but on average lower than the rate of one individual with a higher, uniform rate (experiment two: playback – W = 11, n = 14, *P* = 0.761; post-playback – W = 44, n = 12, *P* = 0.092; Table 2). However, juveniles were more vigilant in response to a greater number of callers when individual call rate factors were controlled. Subjects exhibited greater vigilance in response to the playback of four callers when individual call rates were uniform and equal to the rate of one caller's uniform rate (experiment three: playback – W = 114, n = 19, *P* = 0.020; post-playback – W = 60, n = 15, *P* = 0.095; Table 2). This difference was largely attributable to the contributions of the individual postures slouch and alert, which were both greater for the four-caller than the one-caller condition (Table B.2.; Appendix B).

The two-group comparisons of the four-caller treatments revealed that juveniles responded more vigilantly to higher and more uniform call rates when the number of callers was controlled. Juveniles were more vigilant after the playback of four squirrels calling simultaneously with uniform though on average lower individual call rates than to four simultaneously calling squirrels with variable individual call rates (experiment one, four callers versus experiment two, four callers: playback – W = 89, n = 18, *P* = 0.054; post-playback – W = 88, n = 15, *P* = 0.010; Table 3). This difference was largely attributable to a greater proportion of time spent in the individual vigilance postures S4hu, slouch, and alert, and a larger decrease in the proportion of time spent in non-vigilant S4hd (Table B.3.; Appendix B).

Table 3. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE sec] adult and juvenile Richardson's ground squirrels spent vigilant from the pre- to the playback and post-playback periods in a response comparison to the different four-caller treatments from the concurrent multiple callers study. (Statistically significant differences are in bold font).

Individual Call Rate Type	Measured Period	Adults Experiment Number of Four-caller Treatment		W	*P*	n	Juveniles Experiment Number of Four-caller Treatment		W	*P*	n
Low/ Variable vs. Low/ Uniform		One	Two				One	Two			
	Playback	---	---	---	---	---	0.040 ± 0.072	0.249 ± 0.066	89	0.054	18
	Post-playback	---	---	---	---	---	**-0.118 ± 0.097**	**0.204 ± 0.095**	**88**	**0.010**	**15**
Low/ Variable vs. High/ Uniform		One	Three				One	Three			
	Playback	---	---	---	---	---	**0.071 ± 0.058**	**0.332 ± 0.064**	**178**	**0.007**	**23**
	Post-playback	---	---	---	---	---	**-0.072 ± 0.084**	**0.148 ± 0.075**	**87**	**0.040**	**17**
Low/ Uniform vs. High/ Uniform		Two	Three				Two	Three			
	Playback	0.224 ± 0.068	0.312 ± 0.085	22	0.424	12	0.249 ± 0.066	0.349 ± 0.073	53	0.265	18
	Post-playback	0.202 ± 0.069	0.153 ± 0.075	-6	0.831	11	0.209 ± 0.098	0.199 ± 0.089	0	1.000	15

Juveniles were more vigilant in response to four callers with higher, uniform individual call rates than to four callers with variable individual call rates that were presented at a lower rate on average (experiment one, four callers versus experiment three, four callers: playback – W = 178, n = 23, *P* = 0.007; post-playback – W = 87, n = 17, *P* = 0.040; Table 3). These differences result from a greater proportion of time spent alerting particularly during the playback, and a greater proportion of time spent in S4hu, slouch, and alert during the post-playback (Table B.3.; Appendix B). Indeed, the proportion of time juveniles spent in non-vigilant S4hd decreased a larger amount from the pre- to the playback period in response to four callers with higher, uniform individual call rates than to four callers with variable and on average lower individual call rates (experiment one, four callers versus experiment three, four callers: playback – W = -170, n = 23, *P* = 0.050; Table B.3.; Appendix B) as a result of the increased time spent in high-vigilance alert. However, juveniles exhibited no differential response to four callers with higher, uniform individual call rates compared to four callers with lower, uniform individual call rates (experiment two, four callers versus experiment three, four callers: playback – W = 53, n = 18, *P* = 0.265; post-playback – W = 0, n = 15, *P* = 1.000; Table 3).

Adult Richardson's Ground Squirrels

Adult Richardson's ground squirrels exhibited equivalent proportions of vigilance regardless of whether one or four squirrels were calling. Adults were no more responsive to the playback of four callers with lower on average and variable individual call rates than to one caller with a higher and uniform call rate (experiment one: playback – W = -32, n = 16, *P* = 0.389; post-playback – W = -17, n = 14, *P* = 0.588;

Table 2). Adult Richardson's ground squirrels, however, spent a greater proportion of time in S4hu in response to one caller with a higher and uniform rate than to four squirrels calling at lower and variable individual call rates (experiment one: post-playback – W = -103, n = 14, *P* = 0.005; Table B.4.; Appendix B). Upon further examination, this difference appears to be the result of a greater proportion of time spent in the higher vigilance postures slouch and alert in response to four callers with variable and on average lower individual call rates. Indeed, performing a Wilcoxon's signed-ranks test on the change in the proportion of time spent in slouch and alert pooled from the pre- to the post-playback yields a significant difference in favor of the four-caller condition (experiment one, post-playback: one caller – -0.020 ± 0.045, four callers – 0.304 ± 0.138; W = 61, n = 14, *P* = 0.033), though slouch (experiment one: post-playback – W = 53, n = 14, *P* = 0.272; Table B.4, Appendix B) and alert (experiment one: post-playback – W = 9, n = 14, *P* = 0.939; Table B.4., Appendix B) are not individually significantly greater for the four-caller playback. Adults did not manifest differential vigilance in response to the playback of four callers with individual call rates that were constant but on average still lower than the rate of one individual with a higher, uniform rate (experiment two: playback – W = -7, n = 13, *P* = 0.839; post-playback – W = 14, n = 11, *P* = 0.577; Table 2). Finally, adults responded no differently to the playback of four callers with uniform individual call rates than to the equivalent and uniform rate of one caller (experiment three: playback – W = 19, n = 14, *P* = 0.583; post-playback – W = 47, n = 14, *P* = 0.153, Table 2).

The two-group comparison of the four-caller treatments of experiments two and three illustrated no differential response to four simultaneously calling squirrels with higher, uniform call rates than to four callers with lower, uniform call rates (experiment two, four callers versus experiment three, four callers: playback – W = 22, n = 12, *P* = 0.424; post-playback – W = -6, n = 11, *P* = 0.831; Table 3).

DISCUSSION

Juvenile Richardson's Ground Squirrels

Juvenile Richardson's ground squirrels responded with greater levels of vigilance in situations where multiple versus single squirrels called. Though not significant, call recipients tended to spend a greater proportion of time in slouch following the playback of four simultaneously calling squirrels with lower on average and variable call rates compared with one calling squirrel with a higher and uniform call rate. Furthermore, the proportion of time juveniles spent highly vigilant (pooling slouch plus alert) was significantly greater for the four-caller condition. Results of experiment one are inconsistent with the rate-related response urgency and signal certainty hypotheses, but support the multiple callers hypothesis that juveniles may discriminate the number of callers in an alarm chorus as a salient indicator of response urgency (but see Chapter 3).

Experiment two addressed the perception of increased caller number by juveniles, while controlling for variability of individual call rate across one- and four-caller treatments. Greater vigilance in response to the four-caller treatment would suggest caller number discrimination by juveniles, while greater vigilance in response to the one-caller condition would indicate higher perceived response urgency provoked by a higher individual call rate. No differential response, however, was observed by juveniles to the playback of one squirrel calling at a uniform rate compared with four callers with uniform and on average lower individual call rates. Unlike the results of experiment one, the lack of differential response to the treatments of experiment two suggests that caller number discrimination and the decoding of call rate information may be relatively unimportant in the perception of response urgency by juveniles (refuting both the multiple callers and the rate-related response urgency hypotheses). An alternative and more probable explanation, however, is that this finding is due to combined effects of call rate and caller number. Making the call rates of each individual within the four-caller treatment uniform resulted in an increase in the average individual intersyllable by 4.55 s from experiment one's four-caller playback to experiment two's four-caller playback. Accordingly, the average call rate per individual was considerably lower than the one-caller condition (16 s intersyllable latency compared with 4 s intersyllable latency). Therefore, in response to the four-caller condition of experiment two, squirrels may have perceived syllables from multiple individuals at considerably lower rates than that of the single caller, "canceling out" effects of higher call rate in the one-caller playback and caller number in the four-caller playback on the perception of response urgency. Indeed, call rate has shown to be an important mechanism by which Richardson's ground squirrels gauge extent of threat. The repeated alarm calls of Richardson's ground squirrels are produced at rates that are inversely correlated with the predator-signaler distance, and call recipients perceive call rate as an indication of the extent of threat posed by a potential predator (Warkentin et al. 2001). Furthermore, Wilson & Hare (2003) found that a higher overall call rate was the most likely explanation for greater vigilance by Richardson's ground squirrels to call bouts with increasing versus decreasing rates.

Through consistency of individual call rate factors across one-caller and four-caller treatments, experiment three controlled for individual call rate and variability of individual call rate, while permitting an examination of the potential influence of multiple callers on receiver vigilance. Juveniles spent a greater proportion of time vigilant in response to four simultaneously calling squirrels with uniform call rates compared with a single caller possessing an equal and uniform rate. This finding suggests that when individual call rate factors are equal, juvenile Richardson's ground squirrels perceive greater response urgency when multiple squirrels call than compared with situations where a single squirrel calls. As stated previously, however, an increase in overall call rate is coincident with increases in the call rates of each individual contributing to the chorus. Therefore, the results of experiment three provide support for a multiple-caller system based on the communication of response urgency where the mechanism used by juveniles to gauge response urgency is either through an increase in the actual number of individuals, or through an increase in perceived overall call rate. This perceived increase in overall call rate may be the natural mechanism by which recipients recognize an increase in predatory threat with the recruitment of additional callers into a chorus of alarm calling. Findings from the sequential multiple callers study (Chapter 3), where juveniles showed no differential response to two different squirrels versus the same squirrel broadcast sequentially through two spatially separated loudspeakers, suggest that this result may be explained by an increase in perceived overall call rate rather than an increase in the actual number of calling individuals. As mentioned previously, however, the findings from the sequential multiple callers study for juveniles must be interpreted cautiously as the sample size was only nine individuals, and three of these individuals received trials conducted in very high winds (exceeding 30 kph), potentially biasing results.

Hare (1998) has suggested that the ability of juvenile Richardson's ground squirrels to discriminate among individual alarm callers may be selected for the identification of situations where more versus fewer squirrels call. Indeed, both Belding's ground squirrels (Robinson 1981) and yellow-bellied marmots (Blumstein et al. 2004) exhibit greater vigilance in response to multiple callers versus a single signaler through the ability to distinguish caller identity. Juvenile Richardson's ground squirrels spent a significantly greater proportion of time highly vigilant (in slouch plus alert) following the playback of four simultaneously calling squirrels with lower on average and variable rates compared with one calling squirrel with a higher and uniform call rate (experiment one). Therefore, it remains possible that juveniles possess at least rudimentary numerical capacity to gauge the extent of threat based on the number of distinguished callers rather than from an inevitable increase in overall call rate observed in experiment three's four-caller playback (but see Chapter 3). Further research is required to ascertain whether or not juvenile Richardson's ground squirrels discriminate the number of calling squirrels or perceive an apparent increase in overall call rate, coincident with the recruitment of additional callers, in the perception of response urgency.

Comparisons of the four-caller treatments of experiments one, two, and three, where the number of callers was held constant, addressed the rate-related response urgency hypothesis based on differences in individual call rate, as well as the signal certainty hypothesis based on differences in the variability of individual call rate. Juveniles were more vigilant in response to four callers with uniform individual call rates that were on average lower (experiment two's four-caller condition) than to four callers with variable individual call rates that were higher on average (experiment one's four-caller condition), providing additional support for the signal certainty hypothesis. Juveniles were also more vigilant in response to four callers with uniform individual call rates (experiment three) than to four callers with variable individual call rates that were lower on average (experiment one). This result provides support for both the rate-related response urgency and signal certainty hypotheses. Indeed, Richardson's ground squirrels perceive higher call rates as indicative of greater predatory threat (Warkentin et al. 2001), and variable call rates as uncertainty on the part of the signalers of predator location and/or extent of threat (Sloan & Hare 2004).

Interestingly, juveniles responded no differently to four callers each with higher individual call rates and thus a higher overall rate of calling (experiment three's four-caller condition) than they did to four callers each calling at a lower rate (experiment two's four-caller condition), contradictory to the rate-related response urgency hypothesis (Warkentin et al. 2001). Indeed, one would expect greater response urgency to result from the greater individual call rate or overall call rate characterizing experiment three's four-caller playback. One factor other than individual and overall call rate that differed across the four-caller treatments was individual syllable number. Experiment three's four-caller condition contained 11 syllables per caller, and therefore 44 syllables overall, to produce a playback with a duration approximating 43 s. Experiment two's four-caller playback, however, was composed of three syllables from each caller, producing a playback with a total of 12 syllables within 44 s. Though previous research has found that Richardson's ground squirrels do not respond differentially to differences in syllable number (Sloan & Hare 2004), perhaps there is a threshold corresponding to the number of syllables heard per unit time above which call recipients will habituate rather quickly, particularly when coupled with a lack of predator presence. One would expect additional contextual information, such as that provided by a predator's presence, to be important for the interpretation and appropriate behavioural response to alarm call bouts (Owings & Hennessy 1984). Therefore, the combined effect on perceived response urgency of high individual call rate, and more rapid habituation to a high number of syllables within a short time period characterizing experiment three's four-caller playback, may explain a lack of differential vigilance response observed between the two treatments.

Adult Richardson's Ground Squirrels

Limited evidence from the concurrent multiple callers study suggests that adult Richardson's ground squirrels may discriminate caller number. In experiment one, adult Richardson's ground squirrels were observed to spend a greater proportion of time highly vigilant (pooling slouch and alert), in response to four callers versus one caller, despite that individual call rates characteristic of the four-caller playback were variable and on average lower than the single caller's uniform and higher call rate. This finding suggests that adult Richardson's ground squirrels may possess at least rudimentary numerical skill used to perceive increases in the actual number of calling individuals (also see Chapter 3) because more callers would be indicative of greater signal veracity. It also suggests that while individual call rate factors may be important in the communication of response urgency (Warkentin et al. 2001; Sloan & Hare 2004), the importance of caller number discriminations in perceiving extent of threat may be relatively greater. Indeed, Robinson

(1981) found that adult Belding's ground squirrels perceive the number of juvenile or adult callers as predictive of response urgency.

Contrary to the above finding, however, results of experiment two revealed no differential vigilance response by adult Richardson's ground squirrels to four callers versus one caller, even with individual call rate variability controlled for across treatments. As with juveniles, the lack of differential vigilance observed in the treatment comparison of experiment two may be explained by the reduction of each individual's call rate through an increase in individual intersyllable latency by an average of 4.55 s from experiment one's four-caller playback to experiment two's four-caller playback. This rate reduction resulting in a relatively low average individual call rate (16 s intersyllable latency per individual) accompanied the control of uniformity of individual call rate across treatments while maintaining the ordinal position of callers. Therefore, while the individual call rates were uniform in both treatments, a low average call rate characterizing experiment two's four-caller playback may have overridden response by adults to a greater number of callers, and led to the discrepancy in findings across experiments one and two.

There was also no differential vigilance response in experiment three, despite the fact that individual call rate factors were controlled for across both one-caller and four-caller playbacks. Conversely, juvenile ground squirrels exhibited greater vigilance in response to the four-caller condition than to the one-caller condition of experiment three, presumably due to a greater number of callers or perhaps due to the increase in overall call rate. If adult Richardson's ground squirrels perceive caller number to gauge response urgency as experiment one suggests, why would the perception of multiple callers not be revealed through the controlling of individual call rate factors, and why would a differential response exist between juveniles and adults? This discrepancy in findings may be due to the rather unnatural sound of the four-caller playback of experiment three, and the degree of experience with which older individuals assess the predictive value of calls (Seyfarth & Cheney 1980, 1986; Robinson 1981; Ramakrishnan & Coss 2000; McCowan et al. 2001). Within the four-caller playback of experiment three, the intersyllable latency for each individual caller was 4 s, while the overall intersyllable latency resulting from this temporal structuring was 1 s. Based on my personal experience, this playback sounded rather artificial, almost too "temporally perfect" in its consistency of overall call rate with time to simulate a natural chorus of calling. Perhaps adult Richardson's ground squirrels possess the past experience required to discern unnatural from natural choruses of calls and therefore showed reduced responsiveness to the unnatural-sounding playback as it contained lower predictive value. Juveniles, however, presumably have less personal experience than do adults assessing predictive versus non-predictive signals, and must learn appropriate responses to both alarm calls and interspecific encounters (Rydén 1978; Robinson 1981; Seyfarth & Cheney 1986; Mateo 1996; Ramakrishnan & Coss 2000). Indeed, studies conducted on the Belding's ground squirrel illustrate that juvenile ground squirrels do not emerge with a full repertoire of anti-predator responses, but rather develop their discriminatory responses to alarm and non-alarm calls from the time of emergence to at least the time of natal dispersal (Mateo 1996). Selection favours this plasticity of behavioural responses (Johnston 1982) to alarm calls given the temporal and spatial changes in predator contexts that occur within a given environment (Robinson 1980; Towers & Coss 1990).

The lack of differential response by adults to the four-caller versus one-caller playback of experiment three may also be due to the discrepancy between juvenile and adult responses to the playback of juvenile calls (Robinson 1981). Juveniles tend to respond to more stimuli, a fair proportion of which are not threatening (Robinson 1981; Cheney & Seyfarth 1990; Hanson & Coss 1997; McCowan et al. 2001; Rajala et al. 2003). This behaviour may be explained by the inexperience of immature Richardson's ground squirrels, or the fact that juveniles may be more vulnerable to predation than adults (Seyfarth and Cheney 1986). It is not surprising, therefore, that numerous species, including vervet monkeys (Seyfarth & Cheney, 1980, 1986), bonnet macaques (Ramakrishnan & Coss 2000), steppe marmots (Nesterova 1996), California ground squirrels (Hanson & Coss 2001), and Belding's ground squirrels (Robinson 1981) show reduced responsiveness to juvenile alarm calls. Furthermore, as discussed earlier, experiment three's four-caller playback is characterized by a large number of syllables (44 overall) per unit time, which may contribute to more rapid habituation of receivers than a single caller's 12 syllables (one-caller playback) within the same time frame, particularly when coupled with a lack of predator presence. Therefore, as Richardson's ground squirrels are able to discriminate reliable from unreliable signalers (Hare & Atkins 2001), perhaps adult Richardson's ground squirrels showed reduced responsiveness to the four-caller playback because it represents an unnatural-sounding chorus containing a large number of syllables per unit time, produced by less reliable juvenile signalers. Juveniles, however, may not have detected this four-caller playback as unnatural-sounding, and therefore responded to the increase in caller number or the increase in perceived overall call rate.

Comparisons of the four-caller treatments of experiments two and three, where the number of callers was held constant, addressed the rate-related response urgency hypothesis based on differences in individual call rate. Adults responded no differently to four callers each with higher individual call rates and thus a higher overall rate of calling (experiment three's four-caller condition) than to four callers each calling at a lower rate (experiment two's four-caller condition). This finding, contradictory to the predictions of the rate-related response urgency hypothesis, where call recipients should be more responsive to higher call rates as these bouts communicate greater response urgency that a predator poses (Warkentin et al. 2001), may be explained by a multitude of factors. As suggested in the case of juvenile Richardson's ground squirrel responses, perhaps adult receivers habituated to experiment three's versus experiment two's four-caller playback more rapidly, as a result of a large overall number of syllables (44) within a small time frame coupled with a lack of predator context. Predator context is no doubt important for the interpretation and appropriate behavioural response to potentially ambiguous alarm call bouts (Owings & Hennessy 1984; Hebets & Papaj 2005). Furthermore, the lack of greater vigilance response to experiment three's four-caller playback may be due the unnatural-sounding temporal structure of a chorus of calls produced using unreliable juvenile syllables. Adults tend to ignore juvenile alarm calls as they are poorer predictors of the extent of threat a predator poses (Seyfarth & Cheney, 1980, 1986; Robinson 1981; Nesterova 1996; Ramakrishnan & Coss 2000; Hanson & Coss 2001). Therefore, the combined effects of urgency-provoking high individual call rates, coupled with the unnatural-sounding call chorus produced using syllables of less-predictive juvenile squirrels, may explain the lack of differential vigilance response in the case where individual call rate varies but the number of callers does not.

The Multiple-caller System of Richardson's Ground Squirrels

The concurrent and sequential multiple callers studies collectively suggest that adult, and perhaps juvenile, Richardson's ground squirrels discriminate caller number. While further evidence is required to resolve the mechanism by which juveniles perceive changes in the number of calling squirrels (i.e. through actual caller number or an increase in overall call rate), we may state with certainty that adult Richardson's ground squirrels possess the capacity to make numerical assessments of the number of callers based on vocal discrimination of individual callers (Hare 1998).

Adult Richardson's ground squirrels are not alone in their ability to make caller number discriminations. For example, juvenile Belding's ground squirrels maintain vigilance for a longer period of time in response to alarm vocalizations produced by one or more call recipients following alarm call playbacks (Mateo 1996) than in instances where no recipient squirrels produced novel alarm vocalizations. Additionally, in an observational study, Robinson (1981) found that multiple callers resulted in a greater number of highly vigilant Belding's ground squirrels within the ground squirrel colony compared with a single caller. Yellow-bellied marmots are also documented to exhibit greater vigilance in response to two sequentially calling squirrels versus one calling squirrel (Blumstein et al. 2004). Indeed, caller number discriminations prove beneficial in systems where surviving is largely a function of decisions dependent on the adaptive trade-off between anti-predation and other fitness-enhancing activities, such as foraging

(Lima & Dill 1990). Where more conspecifics produce alarm signals, greater predictive value or veracity may be attached to each signaler's call bout, thereby increasing the perceived response urgency that the threat may pose to the recipient, and consequently enhancing the receiver's likelihood of avoiding predation.

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CHAPTER 5: THE CALL RATE-LENGTH STUDY; AN EXAMINATION OF THE RELATIVE IMPORTANCE OF CALL RATE AND LENGTH FACTORS IN THE PERCEPTION OF RESPONSE URGENCY BY ADULT RICHARDSON'S GROUND SQUIRRELS

INTRODUCTION

Alarm vocalizations may be produced in a discrete fashion as single acoustic elements temporally isolated from other sounds, or in a repetitive fashion where multiple elements are each separated by varying durations of silence. Many hypotheses have been proposed for the function of repetitive alarm calls, as these signals presumably increase the probability of detection by predators and are energetically costly to produce (Marler 1955; Sherman 1977). Repetitive alarm calls may function to potentially offset the costs of unsuccessful signal transfer resulting from factors such as high ambient noise, sound attenuation with increased distance from receivers, and pattern losses due to medium absorption, scattering, and boundary reflections (Bradbury & Vehrencamp 1998). These receivers may then respond in a manner that benefits themselves and the signaler (Bradbury & Vehrencamp 1998).

The number of syllables in a repetitive bout may communicate information regarding the extent of threat a predator poses (Owings & Hennessy 1984; Hasson 1991). For example, dwarf mongooses (*Helogale undulata*) produce fewer pulses in their panic and excitement twitters as predators approach callers (Beynon & Rasa 1989). Furthermore, both alpine (Blumstein & Arnold 1995) and golden marmots

(Blumstein 1995a) vary syllable number inversely with the response urgency experienced by the caller.

The repetition of alarm vocalizations may function as a type of tonic communication (Owings & Hennessy 1984), with each additional signal element adding to the residual effects of previously received elements (Schleidt 1973). Accordingly, repetitive versus single alarm calls should maintain vigilance in call recipients (Owings & Hennessy 1984), while longer versus shorter call bouts should promote longer lasting vigilance in receivers (Loughry & McDonough 1988). Limited support for the tonic communication hypothesis comes from studies with Columbian (Harris et al. 1983) and California ground squirrels (Loughry & McDonough 1988), where receivers exhibited longer lasting vigilance in response to repetitive versus single alarm vocalizations, but did not maintain that vigilant behaviour beyond the completion of the repetitive call bouts. Furthermore, Richardson's ground squirrels displayed no differential vigilance response to longer versus shorter call bouts (Sloan & Hare 2004).

The temporal patterning of syllables within a bout of calling may also communicate contextual information regarding a predator encounter. For instance, the rate of repeated alarm calls may communicate to receivers the extent of threat the signaler is experiencing. Call recipients may then respond according to the perceived level of response urgency. For example, olympic, hoary, and Vancouver Island marmots vary the frequency, duration, and bandwidth of their call bouts relative to the distance between the signaler and predator (Blumstein 1999). Furthermore, yellow-bellied marmots increase call rate with the extent of threat the signaler experiences (Waring 1966), while Columbian ground squirrels vary call rate as a function of predator movement (Harris et al. 1983). Richardson's ground squirrels also communicate response urgency through the rate of repeated alarm calls (Warkentin et al. 2001). Call rate is inversely correlated with the distance the signaler is from the alarming stimulus, and call recipients perceive call rate as an indication of the extent of threat the eliciting stimulus presents (rate-related response urgency hypothesis; Warkentin et al. 2001).

Hartshorne's monotony-threshold hypothesis suggests that 'receiver interest' may be maintained if the elements within a signal are separated by varying durations of silence, while receivers will habituate and respond less to signals with elements separated by similar lengths of silence (Hartshorne 1956). Accordingly, alarm call bouts with varying intersyllable latencies (variable calls) should yield greater long-term vigilance than bouts with similar intersyllable latencies (monotonous calls). In Richardson's ground squirrels, however, call recipients selectively attend to monotonous calls and show reduced responsiveness to variable calls, presumably because these calls communicate low certainty on the part of the signaler as to the location of the predator or the degree of threat the predator poses (signal certainty hypothesis; Sloan & Hare 2004). Richardson's ground squirrels also use their ability to discriminate among individuals (Hare 1998) to modify their responses based on the past performance (reliability) of the signaler (Hare & Atkins 2001). Through the identification of the caller, and its proximity to the recipient, receivers may be able to perceive the extent of danger (Hare 1998).

Differences in anti-predator response behaviour by juvenile and adult individuals have been observed throughout the literature (e.g. fish, Giles 1984, Fuiman 1993; mammals, Seyfarth & Cheney 1986, Ramakrishnan & Coss 2000, McCowan et al. 2001; birds, Rajala et al. 2003). Similarly, ground squirrels do not emerge with a fully-developed response repertoire to alarm calls or threatening stimuli (e.g. California ground squirrels, Hanson & Coss 2001; Belding's ground squirrels, Mateo 1996a); rather juveniles develop their anti-predator response ability over time (Mateo 1996a). Much of the perceptual research on Richardson's ground squirrels has failed to address potential differences between juvenile and adult responses to alarm calls (see Hare 1998; Hare & Atkins 2001; Warkentin et al. 2001; Wilson & Hare 2003; Sloan & Hare 2004; Sloan et al. in press). Warkentin et al. (2001) found that Richardson's ground squirrels communicate response urgency through the rate of repeated alarm calls, where higher call rate is indicative of a closer predator and therefore perceived by recipients to be a greater threat (supporting the rate-related response urgency hypothesis, Warkentin et al. 2001). Additionally, Sloan and Hare (2004) found that Richardson's ground squirrels respond no differently to call bouts with more versus fewer syllables (disproving the tonic communication hypothesis as it applies to Richardson's ground squirrel alarm calling; Schleidt 1973; Owings & Hennessy 1984; Loughry & McDonough 1988). The limitation of subjects to juveniles in Sloan's and Hare's (2004) study, and the method of scanning ground squirrel colonies for the recording of receiver postural responses used in Warkentin et al.'s (2001) study, precluded assessment of potential age-class effects on response data. Therefore, I examined the perception of call rate and length properties by adult Richardson's ground squirrels through response comparisons of three playbacks varying in temporal structure. This was achieved through testing the rate-related response urgency hypothesis that greater response urgency is communicated through higher call rate (Warkentin et al. 2001), and the tonic communication hypothesis that call bouts with more versus fewer syllables produce longer lasting vigilance in call recipients (Schleidt 1973; Owings & Hennessy 1984; Loughry & McDonough 1988).

METHODS

The call rate-length study conducted at the Winnipeg, Manitoba Assiniboine Park Zoo (49° 52′ N, 97° 14′ W), addressed the perception of call rate information by adult Richardson's ground squirrels, and followed the procedures outlined under General Methods (Chapter 2). Twenty playback sets were constructed using 10 male and 10 female callers. Playback one was composed of six syllables, each separated by a 6-s intersyllable latency, producing a call bout duration of approximately 30 s. Playback two also contained six syllables; however, the intersyllable latency was reduced to 3 s resulting in a higher-rate call bout comprising a total duration of approximately 15 s. Playback three maintained a 3-s intersyllable latency; however those calls contained 11 syllables in order to produce a call bout with a total duration approximating 30 s, equal to playback one. Wilcoxon's signed ranks tests were performed on the following two-group comparisons:

Playback one versus playback two – addressing the influence of increasing an individual's call rate while controlling for the number of syllables;

Playback one versus playback three – addressing the influence of increasing an individual's call rate while controlling for the total duration of the call bout; and,

Playback two versus playback three – addressing the influence of call length while holding call rate constant.

With respect to the first two treatment comparisons, if adult Richardson's ground squirrels perceive increases in response urgency through higher call rate, adults should be more responsive to the treatments with higher call rates, regardless of the influence of the number of syllables as differential bout length has been demonstrated to produce no differences in vigilance response of juvenile Richardson's ground squirrels (Sloan & Hare 2004). No differential vigilance response is expected in the final treatment comparison as juvenile Richardson's ground squirrels do not differentially respond to call bouts of different lengths (Sloan & Hare 2004).

Each of 20 female subjects was arbitrarily assigned its own playback set consisting of three playback types, produced using a single, unique caller, and resulting in a total sample size of 20, and a total of 60 trials included for analysis. Restriction to female recipients avoided any potential confounds between recipient sex and vigilance response. Where possible, I followed a standard presentation order where the sex of the caller would alternate to avoid bias associated with order of presentation and caller sex. Treatment presentation order (i.e. playback one, two, and three) was systematically balanced so that there was no association between trial date and playback number. Due to high ambient noise levels and numerous potential boundary reflection surfaces at the zoo site, playbacks were broadcast at 95 – 100 dB SPL (measured at 1 m from the loudspeaker using a Techcessories 33-2050 Sound Level Meter, weighting C, response fast) to ensure subjects were able to hear the playbacks.

RESULTS

Adult Richardson's ground squirrels did not alter their vigilance response based on an individual's call rate properties. Adults responded similarly to playback one, composed of six syllables from the same caller, with an intersyllable latency of 6 s, and a total duration of 30 s, versus playback two, where the intersyllable latency was reduced to 3 s, resulting in a higher call rate and a total bout duration of 15 s (playback: W = 66, n = 19, *P* = 0.196; post-playback: W = 31, n = 17, *P* = 0.487; Table 4). Adults also responded similarly to playback one versus playback three, where not only the call rate but the total number of syllables was increased to 11, resulting in a bout duration of 30 s, equivalent to playback one's duration (playback: W = 54, n = 19, *P* = 0.293; W = 21, n = 17, *P* = 0.644; Table 4). There was no difference in the vigilance response of adults to playback two versus playback three where there was an increase in the number of syllables to 11 and a total duration of 30 s (playback: W = -58, n = 20, *P* = 0.294; post-playback: W = -19, n = 18, *P* = 0.702; Table 4).

DISCUSSION

The call rate-length study addressed the perception of individual call rate and length factors by adult Richardson's ground squirrels, specifically testing the rate-related response urgency (Warkentin et al. 2001) and tonic communication hypotheses (Schleidt 1973; Owings & Hennessy 1984; Loughry & McDonough 1988) through comparisons of behavioural responses to three single-caller playbacks with different temporal structures. Adults responded similarly to playback one versus playback two, where call rate was greater in playback two, resulting in a shorter bout duration. Adults also responded

Table 4. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE s] adult Richardson's ground squirrels spent vigilant from the pre- to the playback (PB) and the post-playback (Post-PB) periods in response to different combinations of call rate and bout length properties represented in three treatment comparisons from the call rate-length study.

Treatment Comparison	Period	Playback Number		W	*P*	n
		PB One	PB Two			
PB One (Short Bout/Slow Rate/Thirty-second Duration) Versus PB Two (Short Bout/Fast Rate/Fifteen-second Duration)	PB	0.119 ± 0.047	0.255 ± 0.065	66	0.196	19
	Post-PB	0.041 ± 0.036	0.084 ± 0.043	31	0.487	17
		PB One	PB Three			
PB One (Short Bout/Slow Rate/Thirty-second Duration) Versus PB Three (Long Bout/Fast Rate/Thirty-second Duration)	PB	0.119 ± 0.047	0.169 ± 0.038	54	0.293	19
	Post-PB	0.015 ± 0.044	0.060 ± 0.035	21	0.644	17
		PB Two	PB Three			
PB Two (Short Bout/Fast Rate/Fifteen-second Duration) Versus PB Three (Long Bout/Fast Rate/ Thirty-second Duration)	PB	0.254 ± 0.062	0.168 ± 0.036	-58	0.294	20
	Post-PB	0.111 ± 0.043	0.074 ± 0.033	-19	0.702	18

similarly to playback one versus playback three, where not only the call rate in playback three was increased, but also the total number of syllables, to equal playback one's total duration. These data suggest that adults do not perceive differences in individual call rate as communicating differences in response urgency. This result was unexpected as Richardson's ground squirrels have been shown to increase vigilance response with an increase in call rate (Warkentin et al. 2001). The method of scanning ground squirrel colonies for postural responses of receivers in Warkentin et al.'s (2001) study, however, precluded examination of potential influences of age-class on response data, and given the time of year during which the Warkentin et al. playbacks were conducted, many of the unmarked respondents were likely to be juveniles. Much of the perceptual research on Richardson's ground squirrels has involved the manipulation of alarm calls produced by juvenile squirrels only and the examination of juvenile (and not adult) responses to these playbacks (see Hare 1998; Hare & Atkins 2001; Wilson & Hare 2003; Sloan & Hare 2004; Sloan et al. in press). Therefore, differences apparently exist given the results between juvenile and adult Richardson's ground squirrels in their responses to alarm vocalizations. Adult Richardson's ground squirrels may base their perception of response urgency upon the number of callers rather than temporal properties encoded by calling individuals. Whereas the ability to encode contextual information through temporal properties of call bouts may vary among individual callers and the accuracy of decoding these temporal properties may be reduced by ambient noise and calling by multiple individuals, adult squirrels may focus attention on caller number discrimination as it may prove to be a more reliable indication of extent of threat. Alternatively, the lack of response by adults to changes in call rate may be the result of the broadcast of playbacks produced using juvenile syllables and that adult Richardson's ground squirrels have a tendency to show reduced responsiveness to juvenile vocalizations. The unreliability of juvenile alarm calls would presumably result from lack of experience in associating the correct alarm calls with appropriate contexts and the greater vulnerability of juveniles to predation compared with adults (Seyfarth & Cheney 1980; Mateo 1996a, b). Indeed, juvenile animals alarm call in response to non-threatening stimuli at a higher frequency than do adult animals (Robinson 1981; Cheney & Seyfarth 1990; Hanson & Coss 1997; McCowan et al. 2001; Rajala et al. 2003). Studies of the Belding's ground squirrel (Robinson 1981; Mateo 1996a) and the California ground squirrel (Hanson & Coss 1997) illustrate that juvenile ground squirrels may not emerge with a full repertoire of responses to alarming stimuli; rather, juveniles may develop their discriminatory responses to alarm and non-alarm calls over time by associating the vocalizations of experienced individuals with the appropriate eliciting stimuli (Mateo 1996a; Shriner 1999). Certainly, adult vervet monkeys (Seyfarth & Cheney, 1980, 1986), bonnet macaques (Ramakrishnan & Coss 2000, steppe marmots (Nesterova 1996), California ground squirrels (Hanson & Coss 2001), and Belding's ground squirrels (Robinson 1981) respond to the alarm calls of other adults but not to juvenile alarm calls, as these vocalizations are less reliable indicators of threat. Therefore, through the ability to discriminate reliable from unreliable individuals (Hare & Atkins 2001), perhaps adult Richardson's ground squirrels come to be less responsive to variations in the temporal signaling of juvenile calling bouts as these variations are less likely to be as predictive as those produced by adult Richardson's ground squirrels. Juvenile Richardson's ground squirrels, however, are predicted to respond to alarm calls regardless of caller age as juveniles have less personal experience than do adults assessing predictive versus non-predictive signals, and must learn appropriate responses to both alarm calls and interspecific encounters (Rydén 1978). Indeed, Robinson (1981) found that juvenile Belding's ground squirrels respond to alarm calls regardless of the age of the caller.

Adult Richardson's ground squirrels exhibited no differential vigilance response to playback two versus playback three where there was an increase in the total number of syllables and an increase in the total duration. Therefore, as observed with juvenile Richardson's ground squirrels (Sloan & Hare 2004), additional signal elements do not appear to promote tonic vigilance in adult recipients. Alternatively, the lack of differential response may be explained by the broadcast of playbacks produced using juvenile syllables and the tendency for adult Richardson's ground squirrels to show reduced responsiveness to juvenile vocalizations. Clearly, additional research is warranted to further examine the age-dependent differential perceptual processes exhibited by Richardson's ground squirrels.

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CHAPTER 6: A GENERAL DISCUSSION OF RESPONSE URGENCY IN RICHARDSON'S GROUND SQUIRRELS; INTERGRATING THE INFLUENCES OF MULTIPLE ALARM CALLERS, TEMPORAL CALL BOUT PROPERTIES, AND CALLER ATTRIBUTES.

Richardson's ground squirrels possess a response-urgency based alarm communication system (Warkentin et al. 2001; Wilson & Hare 2003; Sloan & Hare 2004; Sloan et al. in press), where the extent of threat a predator poses is communicated through the use of alarm calls. My results suggest that juvenile Richardson's ground squirrels perceive the response urgency imposed by a predator through the extent of call rate variability, with greater variability indicative of lower response urgency due to greater ambiguity with respect to predator distance (supporting the signal certainty hypothesis; Sloan & Hare 2004). Furthermore, limited evidence suggests that juvenile Richardson's ground squirrels also perceive the response urgency a predator poses through the actual call rate, with higher rates indicative of greater perceived threat, supporting the rate-related response urgency hypothesis and the findings of Warkentin et al. (2001). Finally, while further research is required to establish caller number discrimination in juvenile Richardson's ground squirrels, limited evidence supports the multiple callers hypothesis that more than one individual calling lends credence to the assertion that a predatory threat is present. Adult Richardson's ground squirrels performed caller number discriminations, exhibiting greater vigilance to multiple callers versus a single caller, supporting the multiple callers hypothesis in adults. Examination of the influence of temporal call bout properties revealed that adults do not differentially respond to call bouts with higher versus lower call rates (refuting rate-related response urgency), monotonous versus variable call bouts (refuting signal certainty), and longer versus shorter call bouts (inconsistent with the tonic communication hypothesis as it applies to repetitive calling in Richardson's ground squirrels; Schleidt 1973; Owings & Hennessy 1984; Loughry & McDonough 1988). The lack of differential vigilance response to bouts with greater versus fewer syllables is consistent with findings for juvenile playback recipients (Sloan & Hare 2004). It is speculated that the reduced responsiveness of adult subjects to call bouts differing in call rate properties may have been the result of adult receivers devaluing less predictive juvenile alarm calls (Seyfarth & Cheney 1980), or perhaps due to the lower efficacy of call rate factors as compared to the number of calling individuals in eliciting receiver response given the greater perceived veracity of the message when multiple signalers call.

The complexity of the alarm communication system of Richardson's ground squirrels is evident through the multitude of signal variants produced by signalers and the multiplicity of mechanisms with which receivers decode these signals. For instance, Richardson's ground squirrels produce disparate call types (Davis 1984) that communicate to receivers the extent of threat the signaler experiences (Sloan et al. in press), while the repetition of alarm calls allows signalers to communicate information regarding the extent of threat a predator poses based on how close the predator is to a signaler, allowing recipients to gauge their vigilance responses accordingly (Warkentin et al. 2001). Furthermore, Richardson's ground squirrels produce ultrasonic vocalizations, potentially directing alarm calls to close kin, while limiting predator attention to the caller (Wilson & Hare 2004).

Rather than employ one mechanism to perceive the response urgency communicated by a caller, receivers utilize numerous mechanisms, thereby maximizing the likelihood of making appropriate trade-offs between foraging and vigilance. In addition to those mechanisms, my research suggests that adult, and perhaps juvenile, Richardson's ground squirrels perceive the response urgency a predator presents through discrimination of the number of calling ground squirrels, where more signalers increase the perceived veracity of predatory threat (Blumstein et al. 2004). Similar discrimination of number of callers has been observed in Belding's ground squirrels (Robinson 1981) and yellow-bellied marmots (Blumstein et al. 2004), suggesting that such numerical abilities may be characteristic of ground-dwelling squirrels in general.

Such numerical discrimination is consistent with observations suggesting that Richardson's ground squirrels place a premium on the reliability of alarm signals. For example, more uniform-rate call bouts of Richardson's ground squirrels communicate predator location and/or extent of threat with greater certainty than variable call bouts (signal certainty; Sloan & Hare 2004, this thesis). Furthermore, Richardson's ground squirrels adjust vigilance response according to the perceived reliability of the individual calling based on past performance during predator encounters (Hare & Atkins 2001) and, if receivers are adults, perhaps the age of the calling individual (as speculated in this thesis). Caller assessments based on age discrimination have been documented in other ground-dwelling sciurids including California ground squirrels (Hanson & Coss 2001), Belding's ground squirrels (Robinson 1981), steppe marmots (Nesterova 1996), and yellow-bellied marmots (Blumstein et al. 2004), and among primates including humans (Bliss et al. 1995), vervet monkeys (Cheney & Seyfarth 1988, 1990), and bonnet macaques (Ramakrishnan & Coss 2000). Discrimination of reliable from unreliable signalers may prove selectively advantageous where call recipients face life or death, either immediately due to a predator's presence (Sherman 1985) or over the long term due to trade-offs between foraging and vigilance (Bachman 1993).

Overall then, Richardson's ground squirrels possess a complex alarm communication system, where callers produce alarm vocalizations to communicate information concerning the presence and nature of predatory threat (Sherman 1977), and call recipients perceive response urgency through caller number discriminations (at least in the case of adults; this thesis), the decoding of temporal signal properties (at least in the case of juveniles; Warkentin et al. 2001; Wilson & Hare 2003; Sloan & Hare 2004; this thesis), and identifications of caller attributes (Hare 1998; Hare & Atkins 2001; Chapters 4 and 5, this thesis).

The relative importance of each particular mechanism (i.e. caller number discrimination, caller attribution, and the decoding of temporal properties) in the communication of response urgency may be situationally dependent. For example, the number of calling ground squirrels may take precedence in response urgency perception, over call rate properties and signaler reliability. Experiment one of the concurrent multiple callers study revealed that both juvenile and adult Richardson's ground squirrels assume greater high vigilance in response to four versus one caller, despite the presumed discrimination by juveniles of lower and more variable individual call rates in the four-caller condition, and despite the speculated perception by adults of unreliable juvenile-produced alarm vocalizations.

In this thesis I have proposed that the greater vigilance exhibited by Richardson's ground squirrels to an increase in caller number is the result of the perception of greater response urgency due to heightened signal veracity. This does not preclude, however, that additional adaptive mechanisms may also contribute to the maintenance of a multiple-caller system in Richardson's ground squirrels. For instance, in addition to increasing signal veracity, numerous callers may facilitate transmission of the signal in an environment where the signal-to-noise ratio may be rather low due to ambient noise, sound losses with distance from the source, and pattern losses due to medium absorption, scattering, and boundary reflections (Bradbury & Vehrencamp 1998). Furthermore, though Richardson's ground squirrels do not display tonic vigilance in response to bouts with greater versus fewer syllables (Sloan & Hare 2004), experiment one of the concurrent multiple callers study does provide limited support for the hypothesis that more callers may promote tonic vigilance (adapted from the predictions of the tonic communication hypothesis; Schleidt 1973; Owings & Hennessy 1984), where both juvenile and adult squirrels exhibited high vigilance only following the completion of the playback of four simultaneously calling squirrels with lower on average and variable rates compared with one calling squirrel with a higher and uniform call rate. Therefore, in addition to increasing signal veracity and response urgency a receiver may experience, tonic vigilance may be maintained in call recipients to guard against the possibility of a predator still being present in the surrounding area (Owings et al. 1986). However, as long-term vigilance was not maintained in all cases where greater vigilance was observed in response to more callers, tonic communication is unlikely to serve as a selective force in the maintenance of a multiple-caller system in Richardson's ground squirrels.

Examination of the communicative processes of animals allows researchers to make inferences about the cognitive mechanisms underlying animal behaviour (Griffin 1991). The complexity and versatility with which Richardson's ground squirrels communicate with one another is suggestive of the occurrence of mental processes. Indeed, the ability of Richardson's ground squirrels to adapt their alarm signals according to the extent of threat a predator poses, and their responses to those calls according to the information encoded within the temporal and other spectral attributes of the signal, the number of signalers calling, and reliability of the signaler, implies some form of information processing (Pepperberg 1991). It remains to be determined, however, whether such higher order processing ultimately manifests itself as a form of conscious awareness (Griffin 1992).

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APPENDIX A: EXAMINATION OF THE INFLUENCE OF INDEPENDENT VARIABLES, INCLUDING PHYSICAL AND MISCELLANEOUS GROUPING FACTORS, ON THE VIGILANCE RESPONSE OF RICHARDSON'S GROUND SQUIRRELS IN ALL STUDIES

METHODS

Miscellaneous grouping factors are measures other than the independent variables of interest that could potentially influence behavioural responses of subjects. The miscellaneous grouping factors trial time (hours), trial date (truncated Julian day, equivalent to the Julian day minus 2440000.5, where the starting day is midnight May 24, 1968), subject to observer distance (m), subject to loudspeaker distance (m), and loudspeaker angle relative to subject (degrees) were recorded following the completion of each trial. Physical factors that could potentially influence the behaviour of subjects were also recorded, and include cloud cover [1 (clear) – 4 (overcast)], wind [1 (calm) – 5 (high)], and temperature (^{o}C). A Kestrel 3000 Pocket Weather Meter was used to measure wind speed (kph; converted to ordinal values 1, 2, 3, 4, and 5, equivalent to 0 – 5 kph, 6 – 10 kph, 11 – 15 kph, 16 – 20 kph, and 21 – 25 kph, respectively) and temperature (^{o}C). In 1997, Hare & Atkins estimated wind speeds, using a similar ordinal wind scale, and did not record temperature and loudspeaker measurements. Additionally, no physical measurements were obtained for the 2003 adult trials.

STATISTICAL ANALYSIS

Statistical tests to examine the influence of physical and miscellaneous grouping factors were performed using SigmaStat^{TM} 3.1, unless otherwise indicated. As 67 out of 117 sets of treatment data failed Bartlett's tests for homogeneity of variance and/or Kolmogorov-Smirnov tests to determine whether or not data were drawn from an underlying population of normally-distributed differences, non-parametric Mann-Whitney rank sum tests were performed to determine if physical and miscellaneous grouping factors were balanced across the treatment comparisons for all three studies. These treatment comparisons included: the one-caller versus two-caller treatment comparisons of the sequential multiple callers study, the one-caller versus four-caller treatment comparisons and the four-caller treatment comparisons of the concurrent multiple callers study, and comparisons of the three treatments of the call rate-length study each differing in rate and length properties. For those treatment combinations where imbalance of a factor existed, the influence of the factor was determined by performing Spearman's rank order correlation tests in two ways. Correlations of factors and relevant dependent variables were examined within each treatment. As a confirmatory test, however, Spearman's rank order correlation tests were also performed on the relevant dependent variable(s), pooling across the main independent variables of interest. All differences were considered significant where $p \leq 0.05$. Any factors shown to be correlated with the dependent variables were then evaluated for potential influences on the interpretation of results.

RESULTS

Sequential Multiple Callers Study

Trials Performed on Juvenile Richardson's Ground Squirrels

Trial time, trial date, subject to observer distance, subject to left loudspeaker distance, and subject to right loudspeaker distance were balanced across one-caller and two-caller treatments (all $P \geq 0.05$; Table A.1.). These factors ranged from 9.3 to 19.7 hours, day 10668 to 10672, 6.3 to 21.2 m, 7.2 to 16.3 m, and 9.2 to 18.6 m, respectively. The physical factors, cloud cover and wind, were also balanced across one-caller and two-caller treatments (all $P \geq 0.05$; Table A.2.), and ranged from 0 to 3, and 1 to 5. Spearman's rank order correlation tests were therefore not required.

Trials Performed on Adult Richardson's Ground Squirrels

Trial time, trial date, subject to observer distance, subject to left loudspeaker distance, subject to right loudspeaker distance, left loudspeaker angle relative to subject, and right loudspeaker angle relative to subject were balanced across the one-caller and two-caller treatments (all $P \geq 0.05$; Table A.1.), and ranged from 8.1 to 13.8 hours, day 13110 to 13129, 9.6 to 22.2 m, 10.1 to 30.3 m, 9.3 to 40.5 m, 0 to 30 degrees, and 0 to 30 degrees, respectively. Temperature, cloud cover, and wind were also balanced across one-caller and two-caller treatments (all $P \geq 0.05$; Table A.2.), and ranged from –1.9 to 15.8 °C, 1 to 3, and 1 to 5, respectively. Spearman's rank order correlation tests were therefore not required.

Table A.1. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including trial date (truncated Julian day), trial time (hours), distance to observer (D to O; m), distance to left loudspeaker (D to Sp_L; m), distance to right loudspeaker (D to Sp_R; m), left loudspeaker angle (Sp_L Ang; degrees), and right loudspeaker angle (Sp_R Ang; degrees) across one- and two-caller treatments from the sequential multiple callers study for trials performed on both adult and juvenile Richardson's ground squirrels.

	Adults						Juveniles					
	Number of Callers						Number of Callers					
Independent Variable	One	Two	T	*P*	n_1	n_2	One	Two	T	*P*	n_1	n_2
Date	13120.2 ± 1.2	13121.0 ± 1.2	570.5	0.726	24	24	10669.3 ± 0.5	10669.3 ± 0.5	85.5	0.965	9	9
Time	9.9 ± 0.3	10.0 ± 0.2	551.0	0.452	24	24	13.2 ± 1.1	13.8 ± 1.2	81.0	0.724	9	9
D to O	14.3 ± 0.7	14.2 ± 0.5	563.0	0.613	24	24	11.5 ± 1.5	10.5 ± 0.8	86.0	1.000	9	9
D to Sp_L	16.6 ± 0.8	16.4 ± 0.8	620.0	0.516	24	24	12.2 ± 0.8	13.3 ± 0.8	75.0	0.377	9	9
D to Sp_R	15.0 ± 0.7	16.0 ± 1.2	573.0	0.765	24	24	12.7 ± 1.1	11.8 ± 0.6	87.0	0.930	9	9
Sp_L Ang	6.7 ± 1.7	5.3 ± 1.2	598.0	0.845	24	24	---	---	---	---	---	---
Sp_R Ang	5.7 ± 1.9	7.2 ± 1.8	530.0	0.236	24	24	---	---	---	---	---	---

Table A.2. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including temperature (°C), cloud cover (ordinal), and wind (ordinal) across one- and two-caller treatments of the sequential multiple callers study for trials performed on both adult and juvenile Richardson's ground squirrels.

	Adults						Juveniles					
Independent Variable	Number of Callers One	Number of Callers Two	T	*P*	n_1	n_2	Number of Callers One	Number of Callers Two	T	*P*	n_1	n_2
Temperature	4.7 ± 0.7	7.2 ± 1.0	501.5	0.076	24	24	---	---	---	---	---	---
Cloud Cover	1.7 ± 0.2	1.6 ± 0.1	596.5	0.869	24	24	0.3 ± 0.2	0.7 ± 0.3	79.5	0.625	9	9
Wind	1.8 ± 0.2	1.7 ± 0.2	613.0	0.613	24	24	2.9 ± 0.5	3.3 ± 0.3	77.0	0.479	9	9

Concurrent Multiple Callers Study

Trials Performed on Juvenile Richardson's Ground Squirrels

Trial time, trial date, and subject to observer distance were balanced across one-caller and four-caller treatments, and the four-caller treatment comparisons of experiments one, two and three (all $P \geq 0.05$; Table A.3.; A.4.). Subject to the loudspeaker distance, however, was greater for trials with playbacks of four squirrels calling at lower and variable rates compared with trials containing playbacks of four squirrels calling at higher and uniform rates (experiment one, four callers versus experiment three, four callers: $T = 636.5$, $n_1 = n_2 = 23$, $P = 0.036$; Table A.4.). The loudspeaker angle relative to the subject was greater during trials with playbacks of four squirrels calling at higher uniform rates compared with trials containing playbacks of four squirrels calling at lower and variable rates (experiment one, four callers versus experiment three, four callers: $T = 388.0$, $n_1 = 23$, $n_2 = 21$, $P = 0.048$; Table A.4.). The distance of the subject to the loudspeaker and the angle of the loudspeaker relative to the subject were balanced across the other four-caller treatment comparisons and the one-caller versus four-caller treatments (all $P \geq 0.05$; Table A.3.; A.4.). Trial time, trial date, subject to observer distance, subject to loudspeaker distance, and loudspeaker angle ranged from 7.8 to 18.8 hours, day 12803 to 12835, 6.9 to 21.8 m, 7 to 22.5 m, and 0 to 45 degrees, respectively.

Temperature, cloud cover, and wind were balanced across one-caller and four-caller treatments, as well as four-caller treatment comparisons from experiments one, two and three (all $P \geq 0.05$; Table A.5.; A.6.). These factors ranged from 13.2 to 28.6 °C, 1 to 4, and 1 to 5, respectively.

Table A.3. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including trial date (truncated Julian day), trial time (hours), distance to observer (D to O; m), distance to loudspeaker (D to Sp; m), and loudspeaker angle (Sp Ang; degrees) across one- and four-caller treatments from the concurrent multiple callers study for trials performed on both adult and juvenile Richardson's ground squirrels. (Statistically significant differences are in bold font).

Individual Call Rate Type	Independent Variable	Trials on Adults						Trials on Juveniles					
		Number of Callers						Number of Callers					
		One	Four	T	*P*	n_1	n_2	One	Four	T	*P*	n_1	n_2
Experiment 1: High/ Uniform vs. Low/ Variable	Date	12784.5 ± 6.5	12786.3 ± 6.9	259.5	0.880	16	16	12821.5 ± 1.9	12823.1 ± 2.0	348.5	0.530	19	19
	Time	12.7 ± 0.8	14.5 ± 0.7	228.0	0.181	16	16	12.1 ± 0.8	11.7 ± 0.8	387.5	0.630	19	19
	D to O	17.7 ± 1.1	17.3 ± 0.8	197.5	0.930	16	13	14.4 ± 0.7	14.8 ± 0.6	345.0	0.465	19	19
	D to Sp	18.9 ± 1.0	16.2 ± 0.8	279.0	0.128	16	15	13.4 ± 0.7	14.4 ± 0.7	317.5	0.125	19	19
	Sp Ang	12.7 ± 3.6	7.9 ± 3.5	175.0	0.132	15	14	11.3 ± 2.6	7.4 ± 2.6	272.0	0.183	19	17
Experiment 2: High/ Uniform vs. Low/ Uniform	Date	12812.2 ± 2.0	12812.6 ± 1.5	168.0	0.720	13	13	12822.6 ± 2.2	12823.9 ± 2.1	193.5	0.679	14	14
	Time	13.0 ± 0.9	12.4 ± 0.9	185.5	0.626	13	13	13.1 ± 1.0	12.5 ± 1.2	213.0	0.662	14	14
	D to O	15.1 ± 0.5	15.7 ± 0.8	166.5	0.663	13	13	14.7 ± 0.9	15.2 ± 0.8	187.0	0.476	14	14
	D to Sp	14.6 ± 0.6	14.6 ± 0.8	170.5	0.817	13	13	13.5 ± 0.7	14.2 ± 0.7	186.5	0.462	14	14
	Sp Ang	10.0 ± 2.9	8.1 ± 3.2	192.5	0.397	13	13	7.9 ± 1.8	8.6 ± 3.1	210.5	0.747	14	14
Experiment 3: High/ Uniform vs. High/ Uniform	Date	12815.5 ± 2.9	12815.6 ± 2.3	195.0	0.730	14	14	12821.3 ± 2.0	12821.7 ± 2.1	364.0	0.861	19	19
	Time	**13.9 ± 0.8**	**11.7 ± 0.9**	**250.0**	**0.033**	**14**	**14**	**12.2** ± 0.8	11.9 ± 0.8	379.0	0.815	19	19
	D to O	15.1 ± 0.5	15.1 ± 0.5	196.5	0.783	14	14	14.3 ± 0.7	15.2 ± 0.7	329.5	0.237	19	19
	D to Sp	14.8 ± 0.7	15.3 ± 0.7	194.5	0.713	14	14	13.4 ± 0.7	14.0 ± 0.6	333.0	0.280	19	19
	Sp Ang	10.7 ± 2.9	7.1 ± 2.0	223.5	0.358	14	14	11.3 ± 2.6	12.6 ± 2.0	349.0	0.540	19	19

Table A.4. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including trial date (truncated Julian day), trial time (hours), distance to observer (D to O; m), distance to loudspeaker (D to Sp; m), and loudspeaker angle (Sp Ang; degrees) across four-caller treatments from the concurrent multiple callers study for trials performed on both adult and juvenile Richardson's ground squirrels. (Statistically significant differences are in bold font).

		Trials on Adults						Trials on Juveniles					
Individual Call Rate Type	Independent Variable	Experiment Number of Four-caller Treatment		T	*P*	n_1	n_2	Experiment Number of Four-caller Treatment		T	*P*	n_1	n_2
		One	Two					One	Two				
Low/ Variable vs. Low/ Uniform	Date	---	---	---	---	---	---	12823.9 ± 2.3	12823.6 ± 1.8	338.5	0.874	18	18
	Time	---	---	---	---	---	---	11.4 ± 0.8	11.8 ± 1.0	337.0	0.912	18	18
	D to O	---	---	---	---	---	---	16.0 ± 0.6	15.5 ± 0.6	350.0	0.602	18	18
	D to Sp	---	---	---	---	---	---	15.2 ± 0.6	14.7 ± 0.7	364.5	0.327	18	18
	Sp Ang	---	---	---	---	---	---	5.6 ± 2.1	8.3 ± 2.7	302.0	0.334	18	18
		One	Three					One	Three				
Low/ Variable vs. High/ Uniform	Date	---	---	---	---	---	---	12822.6 ± 2.0	12820 ± 2.1	566.5	0.575	23	23
	Time	---	---	---	---	---	---	12.2 ± 0.8	12.6 ± 0.8	522.0	0.693	23	23
	D to O	---	---	---	---	---	---	15.5 ± 0.6	14.6 ± 0.8	568.0	0.553	23	23
	D to Sp	---	---	---	---	---	---	**14.9 ± 0.6**	**13.3 ± 0.6**	**636.5**	**0.036**	**23**	**23**
	Sp Ang	---	---	---	---	---	---	**8.3 ± 2.4**	**12.2 ± 1.8**	**388.0**	**0.048**	**23**	**21**
		Two	Three					Two	Three				
Low/ Uniform vs. High/ Uniform	Date	12812.8 ± 1.5	12814.5 ± 2.6	144.5	0.773	12	12	12823.6 ± 1.8	12822.1 ± 2.2	347.5	0.658	18	18
	Time	12.3 ± 0.7	12.2 ± 1.0	153.0	0.885	12	12	11.8 ± 1.0	12.1 ± 0.8	309.5	0.467	18	18
	D to O	15.7 ± 0.8	14.5 ± 0.5	164.5	0.419	12	12	15.5 ± 0.6	15.2 ± 0.8	338.5	0.874	18	18
	D to Sp	15.0 ± 0.9	14.7 ± 0.7	159.0	0.624	12	12	14.7 ± 0.7	13.9 ± 0.7	345.0	0.716	18	18
	Sp Ang	11.7 ± 3.7	12.1 ± 3.0	148.0	0.931	12	12	8.3 ± 2.7	11.9 ± 2.1	278.5	0.087	18	18

Table A.5. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including temperature (^{o}C), cloud cover (ordinal), and wind (ordinal) across one- and four-caller treatments from the concurrent multiple callers study for trials performed on both adult and juvenile Richardson's ground squirrels. (Statistically significant differences are in bold font).

Individual Call Rate Type	Independent Variable	Trials on Adults Number of Callers One	 Four	 T	 *P*	 n_1	 n_2	Trials on Juveniles Number of Callers One	 Four	 T	 *P*	 n_1	 n_2
Experiment 1: High/ Uniform vs. Low/ Variable	Temperature	---	---	---	---	---	---	21.3 ± 1.0	20.0 ± 0.8	339.0	0.414	19	19
	Cloud Cover	---	---	---	---	---	---	2.7 ± 0.2	2.5 ± 0.2	291.5	0.644	18	17
	Wind	---	---	---	---	---	---	2.3 ± 0.2	2.2 ± 0.1	380.0	0.792	19	19
Experiment 2: High/ Uniform vs. Low/ Uniform	Temperature	24.4 ± 0.9	21.9 ± 1.1	210.0	0.081	13	13	21.3 ± 1.3	22.2 ± 0.9	188.5	0.520	14	14
	Cloud Cover	2.5 ± 0.3	2.7 ± 0.3	74.5	0.679	11	8	2.8 ± 0.3	2.2 ± 0.3	156.0	0.215	14	13
	Wind	2.6 ± 0.3	2.4 ± 0.2	163.0	0.723	13	12	2.4 ± 0.2	2.4 ± 0.1	205.5	0.926	14	14
Experiment 3: High/ Uniform vs. High/ Uniform	Temperature	**24.7 ± 0.9**	**19.7 ± 1.3**	**262.0**	**0.007**	**14**	**14**	21.3 ± 4.2	21.3 ± 0.9	369.5	0.988	19	19
	Cloud Cover	2.6 ± 0.3	3.0 ± 0.4	68.0	0.341	11	8	2.7 ± 0.2	2.9 ± 0.2	330.5	0.428	18	17
	Wind	2.5 ± 0.2	2.4 ± 0.2	184.0	0.942	14	13	2.3 ± 0.2	2.2 ± 0.1	388.5	0.608	19	19

Table A.6. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including temperature (°C), cloud cover (ordinal), and wind (ordinal) across four-caller treatments from the concurrent multiple callers study for trials performed on both adult and juvenile Richardson's ground squirrels.

		Trials on Adults						Trials on Juveniles					
Individual Call Rate Type	Independent Variable	Experiment Number of Four-caller Treatment		T	*P*	n_1	n_2	Experiment Number of Four-caller Treatment		T	*P*	n_1	n_2
Low/ Variable vs. Low/ Uniform		One	Two					One	Two				
	Temperature	---	---	---	---	---	---	19.7 ± 0.8	21.6 ± 0.9	281.5	0.107	18	18
	Cloud Cover	---	---	---	---	---	---	2.5 ± 0.2	2.5 ± 0.2	276.0	0.900	17	16
	Wind	---	---	---	---	---	---	2.1 ± 0.2	2.3 ± 0.1	306.0	0.400	18	18
Low/ Variable vs. High/ Uniform		One	Three					One	Three				
	Temperature	---	---	---	---	---	---	20.4 ± 0.8	21.5 ± 0.8	497.0	0.345	23	23
	Cloud Cover	---	---	---	---	---	---	2.6 ± 0.2	2.9 ± 0.2	376.0	0.364	20	20
	Wind	---	---	---	---	---	---	2.2 ± 0.1	2.2 ± 0.2	551.5	0.817	23	23
Low/ Uniform vs. High/ Uniform		Two	Three					Two	Three				
	Temperature	22.4 ± 1.0	20.6 ± 1.6	160.5	0.564	12	12	21.6 ± 0.9	20.8 ± 0.7	353.5	0.527	18	18
	Cloud Cover	2.8 ± 0.3	3.3 ± 0.4	88.0	0.306	10	8	2.5 ± 0.2	2.9 ± 0.2	262.5	0.234	17	17
	Wind	2.4 ± 0.2	2.3 ± 0.2	151.0	0.977	12	12	2.3 ± 0.1	2.2 ± 0.2	363.0	0.349	18	18

Spearman's rank order correlation tests were performed, pairing subject to loudspeaker distance with the change in the proportion of time spent vigilant from pre- to playback period and the change in the proportion of time spent vigilant from pre- to post-playback period. Correlations were first examined within the four-caller treatments of experiment one and three, followed by an examination of the correlations of pooled four-caller treatment data. The same procedure was followed with loudspeaker angle relative to subject. No significant relationships existed between subject to loudspeaker distance and the dependent variables within the four-caller treatments of experiments one and three or when the data from these treatments were pooled (all $P \geq 0.05$; Table A.7.). A correlation did exist, however, between loudspeaker angle relative to subject and the change in proportion of time spent vigilant from the pre- to the playback period within experiment one's four-caller treatment ($r_s = 0.444$, $n = 21$, $P = 0.043$; Table A.7.). Nicklaus (2000) has found, however, that changes in amplitude (that would accompany greater speaker angle relative to the receiver) do not result in differential vigilance responses by Richardson's ground squirrels. Furthermore, a greater deviation of the loudspeaker angle relative to the receiver would presumably represent a decreased likelihood from the receiver's perspective that the predator is close by. Therefore, the change in the proportion of time spent vigilant from the pre- to the four-caller playback period is unlikely influenced by greater deviation in the loudspeaker angle relative to the receiver, and perhaps the correlation observed occurred by chance. No significant relationships were observed between loudspeaker angle relative to subject and the other dependent variables within or among treatments (all other $P \geq 0.05$; Table A.7.).

Table A.7. Spearman's rank order correlation tests to determine if any relationships exist between loudspeaker angle as well as subject to loudspeaker distance and the changes in proportion of time spent vigilant from the pre- to the playback period and from the pre- to the post-playback period, both within and pooling across four-caller treatments of experiment one and three from the concurrent multiple callers study trials on juvenile Richardson's ground squirrels. (Statistically significant differences are in bold font).

		Playback			Post-playback		
Independent Variable	Treatment Comparison	r_s	*P*	n	r_s	*P*	n
Loudspeaker Angle (exp 1, four callers vs. exp 3, four callers)	Exp 1, Four Callers: Low/Variable Individual Call Rates	**0.444**	**0.043**	**21**	0.192	0.441	18
	Exp 3, Four Callers: High/Uniform Individual Call Rates	-0.148	0.495	23	-0.121	0.608	20
	Pooled: Exp 1 and Exp Three	0.256	0.093	44	0.145	0.382	38
Subject to Loudspeaker Distance (exp. 1, four callers vs. exp 3, four callers)	Exp 1, Four Callers: Low/Variable Individual Call Rates	0.138	0.524	23	-0.044	0.846	20
	Exp 3, Four Callers: High/Uniform Individual Call Rates	0.212	0.328	23	0.284	0.220	20
	Pooled: Exp 1 and Exp Three	0.030	0.844	46	-0.019	0.905	40

Trials Performed on Adult Richardson's Ground Squirrels

Trial date, subject to observer distance, subject to loudspeaker distance, and loudspeaker angle relative to subject were balanced across one-caller and four-caller treatments and the four-caller treatment comparisons of experiments two and three (all $P \geq 0.05$; Table A.3.; A.4.). Trial time, however, was later during playbacks with one squirrel calling at a uniform rate versus playbacks where each of four squirrels called at uniform rates equal to the rate of the one caller (experiment three: $T = 250.0$, $n_1 = n_2 = 14$, $P = 0.033$; Table A.3.). Trial time was balanced across all other treatment comparisons (all $P \geq 0.05$; Table A.3.; A.4.). Trial time, trial date, subject to observer distance, subject to loudspeaker distance, and loudspeaker angle ranged from 8.12 to 19.13 hours, day 12764 to 12835, 11.5 to 24.7 m, 8.8 to 26.8 m, and 0 to 45 degrees, respectively.

Temperature, cloud cover, and wind were balanced across one-caller and four-caller treatment comparisons ($P \geq 0.05$; Table A.5.), except for experiment three where the temperature was greater during playbacks with one squirrel calling at a uniform rate versus playbacks where each of four squirrels called at uniform rates equal to the rate of the one caller (experiment three: $T = 262.0$, $n_1 = n_2 = 14$, $P = 0.007$; Table A.5.). Temperature, cloud cover, and wind were balanced across the four-caller treatment comparisons of experiments two and three (all $P \geq 0.05$; Table A.6.). Temperature, cloud cover, and wind ranged from 11.7 to 30.2 °C, 1 to 4, and 1 to 4, respectively.

Spearman's rank order correlation tests were performed, pairing time as well as temperature with the change in the proportion of time spent vigilant from pre- to playback and the change in the proportion of time spent vigilant from pre- to post-playback. Correlations were first examined within the one-caller treatment and the four-caller treatment of experiment three, followed by an examination of the correlations of pooled one-caller and four-caller treatment data. No significant relationships were found to exist (all $P \geq 0.05$; Table A.8.).

Call Rate-length Study

Trial time, trial date, subject to observer distance, subject to loudspeaker distance, and loudspeaker angle were balanced across the three treatment combinations of playbacks one, two, and three (all $P \geq 0.05$; Table A.9.), and ranged from 7.3 to 12.6 hours, day 13131 to 13149, 10.8 to 26.7 m, 12.2 to 26.2 m, and 0 to 30 degrees, respectively. Temperature, cloud cover, and wind were balanced across the three treatment combinations (all $P \geq 0.05$; Table A.10.). These factors ranged from 1.8 to 22.8 °C, 1 to 3, and 1 to 3, respectively. Spearman's rank order correlation tests were therefore not required.

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Table A.8. Spearman's rank order correlation tests to determine if any relationships exist between trial time as well as temperature and the changes in proportion of time spent vigilant from the pre- to the playback period and from the pre- to the post-playback period, both within and pooling across one-caller and four-caller treatments of experiment three from the concurrent multiple callers study trials on adult Richardson's ground squirrels.

		Playback			Post-playback		
Independent Variable	Treatment Comparison	r_s	*P*	n	r_s	*P*	n
Temperature	One Caller: High/Uniform Individual Call Rate	-0.015	0.952	14	-0.015	0.952	14
	Four Callers: High/Uniform Individual Call Rates	0.042	0.880	14	-0.007	0.976	14
	Pooled: One-caller Treatment and Four-caller Treatment	0.050	0.799	28	-0.082	0.677	28
Trial Time	One Caller: High/Uniform Individual Call Rate	0.000	1.000	14	-0.020	0.940	14
	Four Callers: High/Uniform Individual Call Rates	-0.002	0.988	14	-0.033	0.904	14
	Pooled: One-caller Treatment and Four-caller Treatment	-0.101	0.607	28	-0.188	0.334	28

Table A.9. Mann-Whitney rank sum tests illustrate the degree of balance of miscellaneous grouping factors [mean ± SE s] including trial date (truncated Julian day), trial time (hours), distance to observer (D to O; m), distance to loudspeaker (D to Sp; m), and loudspeaker angle (Sp Ang; degrees) across the different combinations of call rate and bout length properties of the call rate-length study for trials performed on adult Richardson's ground squirrels.

Treatment Comparison	Independent Variable	Playback Number		T	*P*	n_1	n_2
		PB One	PB Two				
PB One (Short Bout/Slow Rate/Thirty-second Duration) Versus PB Two (Short Bout/Fast Rate/Fifteen-second Duration)	Date	13141.9 ± 1.5	13141.3 ± 1.5	380.0	0.793	19	19
	Time	8.9 ± 0.3	9.0 ± 0.3	364.5	0.872	19	19
	D to O	16.8 ± 0.8	17.7 ± 1.0	345.5	0.474	19	19
	D to Sp	17.6 ± 0.7	18.5 ± 0.8	339.0	0.365	19	19
	Sp Ang	6.8 ± 1.5	6.0 ± 1.7	400.5	0.389	19	19
		PB One	PB Three				
PB One (Short Bout/Slow Rate/Thirty-second Duration) Versus PB Three (Long Bout/Fast Rate/Thirty-second Duration)	Date	13141.9 ± 1.5	13141.7 ± 1.3	378.5	0.827	19	19
	Time	8.9 ± 0.3	9.0 ± 0.3	357.0	0.704	19	19
	D to O	16.8 ± 0.8	17.8 ± 0.8	339.5	0.373	19	19
	D to Sp	17.6 ± 0.7	18.6 ± 0.8	337.5	0.343	19	19
	Sp Ang	6.8 ± 1.5	6.8 ± 1.4	365.5	0.895	19	19
		PB Two	PB Three				
PB Two (Short Bout/Fast Rate/Fifteen-second Duration) Versus PB Three (Long Bout/Fast Rate/ Thirty-second Duration)	Date	13140.8 ± 1.5	13141.2 ± 1.3	409.5	1.000	20	20
	Time	9.0 ± 0.3	9.0 ± 0.3	409.0	0.989	20	20
	D to O	17.6 ± 0.9	17.6 ± 0.8	401.0	0.818	20	20
	D to Sp	18.5 ± 0.8	18.4 ± 0.8	410.0	0.989	20	20
	Sp Ang	5.7 ± 1.7	6.8 ± 1.4	427.5	0.187	20	19

Table A.10. Mann-Whitney rank sum tests illustrate the degree of balance of physical factors [mean ± SE s] including temperature (°C), cloud cover (ordinal), and wind (ordinal) across the different combinations of call rate and bout length properties of the call rate-length study for trials performed on adult Richardson's ground squirrels.

Treatment Comparison	Independent Variable	Playback Number		T	*P*	n_1	n_2
		PB One	PB Two				
PB One (Short Bout/Slow Rate/Thirty-second Duration) Versus PB Two (Short Bout/Fast Rate/Fifteen-second Duration)	Temperature	9.7 ± 1.4	9.5 ± 1.3	336.0	0.937	18	18
	Cloud Cover	2.2 ± 0.2	2.3 ± 0.2	356.5	0.693	19	19
	Wind	1.6 ± 0.2	1.6 ± 0.1	329.0	0.912	18	18
		PB One	PB Three				
PB One (Short Bout/Slow Rate/Thirty-second Duration) Versus PB Three (Long Bout/Fast Rate/Thirty-second Duration)	Temperature	9.7 ± 1.4	9.3 ± 1.1	334.0	0.987	18	18
	Cloud Cover	2.2 ± 0.2	2.1 ± 0.2	374.5	0.918	19	19
	Wind	1.6 ± 0.2	1.5 ± 0.2	345.0	0.715	18	18
		PB Two	PB Three				
PB Two (Short Bout/Fast Rate/Fifteen-second Duration) Versus PB Three (Long Bout/Fast Rate/ Thirty-second Duration)	Temperature	9.5 ± 1.2	9.0 ± 1.1	372.0	0.977	19	19
	Cloud Cover	2.3 ± 0.2	2.1 ± 0.2	434.0	0.524	20	20
	Wind	1.6 ± 0.2	1.5 ± 0.2	391.0	0.558	19	19

APPENDIX B: BEHAVIOURAL ASSAYS OF RICHARDSON'S GROUND SQUIRRELS FOR TREATMENT COMPARISONS IN ALL STUDIES

METHODS

Behavioural assays of Richardson's ground squirrels for all treatment comparisons are provided to supplement the reader's understanding of the contribution of individual behaviours to the behavioural response results of the sequential multiple callers study, the concurrent multiple callers study, and the call rate-length study described in chapters 3, 4, and 5, respectively. Receiver responses may be categorized in an ordinal series representing increasing vigilance/alarm. As potential responses, these include: standing on all four feet with head lowered (S4hd; considered non-vigilant behaviour), standing on all four feet with head raised (S4hu; considered the lowest level of vigilant behaviour), resting on the hind legs with back arched forward (slouch), standing on the hind legs with back erect (alert; considered the highest level of vigilant behaviour), and running (considered escape-related behaviour; Hare 1998; see Owings & Virginia 1978 for a similar categorization). The proportion of time recipients exhibited these different behaviours while they were visible was coded for pre-playback, playback, and post-playback periods. As the concurrent multiple callers study trials were not subject to a pre-playback foraging criterion, the proportion of time subjects displayed these responses during the pre-playback period was subtracted from those proportions coded from the playback and post-playback periods to produce the following dependent variables: change in the proportion of time spent in S4hd, S4hu, slouch, alert, and running from pre- to playback period and from the pre- to post-playback period. To compare adult and juvenile responses, however, the proportion of time spent displaying these behaviours during the playback and the post-playback periods (instead of changes in proportions from the pre-playback period) were used in analyses within the sequential multiple callers study as pre-playback data were not obtained during the 1997 sequential multiple callers study trials.

Wilcoxon's signed ranks tests were performed on these dependent variables for the concurrent multiple callers study using SigmaStat™ 3.1 on a personal computer; however, as proportions of time spent in the individual behaviours are dependent upon one another, p-values presented have been subjected to sequential Bonferroni (Rice 1989). Only means and standard errors are reported for the sequential multiple callers study and call rate-length study as squirrels during the 2004 field season exhibited little or no high vigilance behaviour (i.e. slouch and alert) or running. A formal discussion of the behavioural assays is not provided; however, notable contributions of individual behaviours to proportions of time spent vigilant are referenced in the main text where appropriate.

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Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223 –225.

Table B.1. Proportions of time [mean ± SE s] adult and juvenile Richardson's ground squirrels spent on all fours with heads down (S4hd), on all fours with heads up (S4hu), on hind legs with backs arched forward (Slouch), on hind legs with backs straight (Alert), and running during bout one and two of the playback period and during the post-playback period in response to one-caller versus two-caller treatments from the sequential multiple callers study.

Measured Period	Dependent Variable	Adults			Juveniles		
		One Caller	Two Callers	n	One Caller	Two Callers	n
	S4hd	0.268 ± 0.049	0.289 ± 0.052	24	0.072 ± 0.048	0.072 ± 0.038	9
	S4hu	0.619 ± 0.058	0.577 ± 0.062	24	0.190 ± 0.118	0.267 ± 0.110	9
Bout One	Slouch	0.078 ± 0.050	0.095 ± 0.049	24	0.132 ± 0.068	0.395 ± 0.135	9
	Alert	0.022 ± 0.022	0.029 ± 0.029	24	0.601 ± 0.151	0.218 ± 0.108	9
	Run	0.014 ± 0.007	0.009 ± 0.006	24	0.005 ± 0.005	0.048 ± 0.016	9
	S4hd	0.396 ± 0.057	0.265 ± 0.051	24	0.128 ± 0.083	0.151 ± 0.058	9
	S4hu	0.512 ± 0.057	0.619 ± 0.065	24	0.166 ± 0.078	0.269 ± 0.118	9
Bout Two	Slouch	0.023 ± 0.020	0.113 ± 0.063	24	0.332 ± 0.143	0.432 ± 0.129	9
	Alert	0.042 ± 0.042	0.000 ± 0.000	24	0.368 ± 0.148	0.140 ± 0.111	9
	Run	0.003 ± 0.002	0.004 ± 0.003	24	0.006 ± 0.006	0.008 ± 0.006	9
	S4hd	0.413 ± 0.046	0.349 ± 0.061	24	0.200 ± 0.063	0.234 ± 0.073	8
	S4hu	0.533 ± 0.045	0.538 ± 0.066	24	0.240 ± 0.095	0.461 ± 0.119	8
Post-playback	Slouch	0.017 ± 0.010	0.095 ± 0.058	24	0.250 ± 0.136	0.106 ± 0.059	8
	Alert	0.028 ± 0.028	0.006 ± 0.006	24	0.302 ± 0.131	0.181 ± 0.116	8
	Run	0.005 ± 0.002	0.008 ± 0.004	24	0.008 ± 0.006	0.017 ± 0.017	8

Table B.2. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE s] from the pre- to the playback and post-playback periods juvenile Richardson's ground squirrels spent on all fours with heads down (S4hd), on all fours with heads up (S4hu), on hind legs with backs arched forward (Slouch), on hind legs with backs straight (Alert), and running in response to one-caller versus four-caller treatments of varying temporal structure from the concurrent multiple callers study.

Individual Call Rate Type	Dependent Variable	Playback Period Number of Callers One	Four	W	*P*	n	Post-playback Period Number of Callers One	Four	W	*P*	n
Experiment 1: High/ Uniform vs. Low/ Variable	S4hd	-0.163 ± 0.047	-0.084 ± 0.063	44	1.000	19	0.017 ± 0.056	0.044 ± 0.085	24	1.000	15
	S4hu	-0.030 ± 0.064	-0.077 ± 0.073	-2	1.000	19	0.071 ± 0.062	-0.079 ± 0.107	-52	0.604	15
	Slouch	0.042 ± 0.068	0.076 ± 0.042	39	1.000	19	-0.082 ± 0.034	0.048 ± 0.035	79	0.055	15
	Alert	0.177 ± 0.059	0.082 ± 0.067	-30	1.000	19	-0.019 ± 0.065	-0.008 ± 0.073	3	1.000	15
	Run	0.009 ± 0.017	-0.003 ± 0.007	-22	1.000	19	0.017 ± 0.016	-0.004 ± 0.004	-30	0.798	15
Experiment 2: High/ Uniform vs. Low/ Uniform	S4hd	-0.209 ± 0.042	-0.191 ± 0.066	7	1.000	14	-0.001 ± 0.062	-0.115 ± 0.103	-26	1.000	12
	S4hu	-0.140 ± 0.058	0.142 ± 0.072	69	0.150	14	0.017 ± 0.072	0.066 ± 0.080	16	1.000	12
	Slouch	0.131 ± 0.077	0.016 ± 0.029	-47	0.612	14	-0.030 ± 0.033	0.033 ± 0.074	12	1.000	12
	Alert	0.218 ± 0.077	0.111 ± 0.094	-22	1.000	14	-0.021 ± 0.083	0.109 ± 0.103	12	1.000	12
	Run	-0.004 ± 0.012	0.012 ± 0.009	21	1.000	14	0.016 ± 0.012	-0.008 ± 0.008	-28	1.000	12
Experiment 3: High/ Uniform vs. High/ Uniform	S4hd	-0.180 ± 0.053	-0.386 ± 0.070	-116	0.090	19	0.026 ± 0.095	-0.205 ± 0.076	-58	0.475	15
	S4hu	-0.017 ± 0.067	-0.010 ± 0.046	4	1.000	19	0.068 ± 0.064	0.079 ± 0.082	4	1.000	15
	Slouch	0.062 ± 0.068	0.085 ± 0.084	14	1.000	19	-0.104 ± 0.055	0.078 ± 0.090	60	0.475	15
	Alert	0.172 ± 0.060	0.304 ± 0.084	50	0.844	19	-0.002 ± 0.070	0.043 ± 0.071	1	1.000	15
	Run	-0.002 ± 0.010	0.006 ± 0.011	38	1.000	19	0.021 ± 0.013	-0.002 ± 0.017	-50	0.507	15

Table B.3. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE s] from the pre- to the playback and post-playback periods juvenile Richardson's ground squirrels spent on all fours with their heads down (S4hd), on all fours with their heads up (S4hu), on hind legs with backs arched forward (Slouch), on hind legs with backs straight (Alert), and running in a response comparison to the different four-caller treatments from the concurrent multiple callers study. (Statistically significant differences are in bold font).

		Playback Period					Post-playback Period				
Individual Call Rate Type	Dependent Variable	Experiment Number of Four-caller Treatment		W	*P*	n	Experiment Number of Four-caller Treatment		W	*P*	n
		One	Two				One	Two			
Low/ Variable vs. Low/ Uniform	S4hd	-0.038 ± 0.073	-0.194 ± 0.055	-77	0.495	18	0.123 ± 0.100	-0.136 ± 0.094	-60	0.475	15
	S4hu	-0.089 ± 0.072	0.092 ± 0.064	73	0.495	18	-0.148 ± 0.102	0.056 ± 0.081	44	0.916	15
	Slouch	0.061 ± 0.043	0.071 ± 0.047	-4	1.000	18	0.017 ± 0.033	0.039 ± 0.078	-10	1.000	15
	Alert	0.068 ± 0.080	0.086 ± 0.073	6	1.000	18	0.013 ± 0.058	0.110 ± 0.077	5	1.000	15
	Run	-0.009 ± 0.009	0.015 ± 0.009	59	0.522	18	-0.008 ± 0.011	-0.000 ± 0.010	-7	1.000	15
		One	Three				One	Three			
Low/ Variable vs. High/ Uniform	S4hd	**-0.069 ± 0.060**	**-0.341 ± 0.067**	**-170**	**0.050**	**23**	0.079 ± 0.087	-0.158 ± 0.072	-97	0.100	17
	S4hu	-0.034 ± 0.065	-0.005 ± 0.040	44	1.000	23	-0.050 ± 0.097	0.018 ± 0.058	15	1.000	17
	Slouch	0.047 ± 0.038	0.044 ± 0.068	23	1.000	23	0.014 ± 0.036	0.067 ± 0.083	11	1.000	17
	Alert	0.057 ± 0.062	0.294 ± 0.078	103	0.096	23	-0.036 ± 0.070	0.064 ± 0.065	21	1.000	17
	Run	-0.008 ± 0.008	0.008 ± 0.010	75	0.690	23	-0.010 ± 0.010	-0.000 ± 0.015	-8	1.000	17
		Two	Three				Two	Three			
Low/ Uniform vs. High/ Uniform	S4hd	-0.194 ± 0.055	-0.359 ± 0.076	-91	0.210	18	-0.129 ± 0.095	-0.219 ± 0.084	-28	1.000	15
	S4hu	0.092 ± 0.064	0.026 ± 0.044	-37	1.000	18	0.027 ± 0.079	0.083 ± 0.078	16	1.000	15
	Slouch	0.071 ± 0.047	-0.023 ± 0.072	-35	1.000	18	0.095 ± 0.086	0.011 ± 0.076	-25	1.000	15
	Alert	0.086 ± 0.073	0.346 ± 0.089	52	0.210	18	0.087 ± 0.083	0.105 ± 0.066	4	0.813	15
	Run	0.015 ± 0.009	0.009 ± 0.012	3	1.000	18	-0.000 ± 0.010	0.008 ± 0.017	3	1.000	15

Table B.4. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE s] from the pre- to the playback and post-playback periods adult Richardson's ground squirrels spent on all fours with their heads down (S4hd), on all fours with their heads up (S4hu), on hind legs with backs arched forward (Slouch), on hind legs with backs straight (Alert), and running in response to the one-caller versus the four-caller treatments of varying temporal structure from the concurrent multiple callers study. (Statistically significant differences are in bold font).

Individual Call Rate Type	Dependent Variable	Playback Period					Post-playback Period				
		Number of Callers					Number of Callers				
		One	Four	W	*P*	n	One	Four	W	*P*	n
Experiment 1:	S4hd	-0.134 ± 0.057	-0.084 ± 0.059	12	1.000	16	-0.055 ± 0.063	-0.039 ± 0.074	-9	1.000	14
High/	S4hu	-0.117 ± 0.083	-0.130 ± 0.071	-4	1.000	16	**0.095 ± 0.062**	**-0.273 ± 0.097**	**-103**	**0.005**	**14**
Uniform vs.	Slouch	0.159 ± 0.093	-0.002 ± 0.080	-46	1.000	16	-0.043 ± 0.037	0.102 ± 0.112	53	0.272	14
Low/	Alert	0.129 ± 0.059	0.212 ± 0.083	21	1.000	16	0.024 ± 0.016	0.202 ± 0.108	9	0.939	14
Variable	Run	-0.004 ± 0.011	0.001 ± 0.008	2	1.000	16	0.017 ± 0.032	0.001 ± 0.012	-1	1.000	14
Experiment 2:	S4hd	-0.219 ± 0.083	-0.279 ± 0.075	-11	1.000	13	-0.004 ± 0.108	-0.177 ± 0.068	-24	1.000	11
High/	S4hu	-0.530 ± 0.075	-0.106 ± 0.084	-5	1.000	13	0.026 ± 0.115	-0.056 ± 0.118	-12	1.000	11
Uniform vs.	Slouch	0.075 ± 0.086	0.074 ± 0.112	-10	1.000	13	0.029 ± 0.103	-0.063 ± 0.102	-2	1.000	11
Low/	Alert	0.227 ± 0.093	0.262 ± 0.107	9	1.000	13	-0.052 ± 0.064	0.251 ± 0.131	17	0.470	11
Uniform	Run	-0.002 ± 0.012	0.010 ± 0.013	14	1.000	13	0.033 ± 0.042	0.002 ± 0.013	-9	1.000	11
Experiment 3:	S4hd	-0.175 ± 0.085	-0.226 ± 0.068	-31	0.716	14	-0.039 ± 0.115	-0.091 ± 0.057	-25	1.000	14
High/	S4hu	-0.099 ± 0.079	-0.032 ± 0.105	19	0.716	14	-0.043 ± 0.129	0.058 ± 0.070	23	1.000	14
Uniform vs.	Slouch	0.079 ± 0.091	0.253 ± 0.085	43	0.582	14	0.006 ± 0.082	0.064 ± 0.067	12	1.000	14
High/	Alert	0.224 ± 0.088	0.053 ± 0.049	-34	0.080	14	0.045 ± 0.051	0.027 ± 0.081	-6	1.000	14
Uniform	Run	-0.003 ± 0.011	0.016 ± 0.012	53	0.272	14	0.050 ± 0.039	0.006 ± 0.013	-5	1.000	14

Table B.5. Wilcoxon's signed-ranks tests illustrate the change in the proportion of time [mean ± SE s] from the pre- to the playback and post-playback periods adult Richardson's ground squirrels spent on all fours with their heads down (S4hd), on all fours with their heads up (S4hu), on hind legs with backs arched forward (Slouch), on hind legs with backs straight (Alert), and running in a response comparison of experiment two's four-caller treatment and experiment three's four-caller treatment from the concurrent multiple callers study.

Individual Call Rate Type	Dependent Variable	Playback Period Experiment Number of Four-caller Treatment		W	*P*	n	Post-Playback Period Experiment Number of Four-caller Treatment		W	*P*	n
		Two	Three				Two	Three			
Low/ Uniform vs. High/ Uniform	S4hd	-0.250 ± 0.069	-0.240 ± 0.068	4	1.000	12	-0.206 ± 0.072	-0.146 ± 0.069	4	1.000	11
	S4hu	-0.097 ± 0.090	0.089 ± 0.101	26	1.000	12	0.014 ± 0.122	0.095 ± 0.088	-4	1.000	11
	Slouch	0.060 ± 0.112	0.154 ± 0.071	16	1.000	12	-0.050 ± 0.100	-0.033 ± 0.040	-2	1.000	11
	Alert	0.261 ± 0.119	0.070 ± 0.047	-14	1.000	12	0.237 ± 0.134	0.091 ± 0.091	-5	1.000	11
	Run	0.009 ± 0.014	0.008 ± 0.014	-10	1.000	12	0.004 ± 0.013	0.005 ± 0.017	1	1.000	11

Table B.6. Change in the proportion of time [mean ± SE s] from the pre- to the playback and post-playback periods adult Richardson's ground squirrels spent on all fours with heads down (S4hd), on all fours with heads up (S4hu), on hind legs with backs arched forward (Slouch), on hind legs with backs straight (Alert), and running in response comparisons of three different playback treatments with varying temporal structure from the call rate-length study.

Treatment Comparison	Dependent Variable	Playback Period Playback Number		n	Post-playback Period Playback Number		n
		PB One	PB Two		PB One	PB Two	
PB One (Short Bout/Slow Rate/ Thirty-second Duration) Versus PB Two (Short Bout/Fast Rate/Fifteen-second Duration)	S4hd	-0.126 ± 0.049	-0.262 ± 0.067	19	-0.044 ± 0.037	-0.094 ± 0.045	17
	S4hu	0.096 ± 0.044	0.074 ± 0.061	19	-0.040 ± 0.035	-0.009 ± 0.041	17
	Slouch	0.021 ± 0.018	0.083 ± 0.046	19	0.081 ± 0.051	0.031 ± 0.011	17
	Alert	0.002 ± 0.002	0.098 ± 0.068	19	0.000 ± 0.000	0.062 ± 0.055	17
	Run	0.007 ± 0.004	0.007 ± 0.004	19	0.003 ± 0.002	-0.002 ± 0.002	17
		PB One	PB Three		PB One	PB Three	
PB One (Short Bout/Slow Rate/ Thirty-second Duration) Versus PB Three (Long Bout/Fast Rate/Thirty-second Duration)	S4hd	-0.126 ± 0.049	-0.175 ± 0.039	19	-0.018 ± 0.044	-0.097 ± 0.044	17
	S4hu	0.096 ± 0.044	0.029 ± 0.061	19	-0.066 ± 0.039	0.017 ± 0.056	17
	Slouch	0.021 ± 0.018	0.068 ± 0.056	19	0.081 ± 0.051	0.029 ± 0.044	17
	Alert	0.002 ± 0.002	0.072 ± 0.051	19	0.000 ± 0.000	0.014 ± 0.010	17
	Run	0.007 ± 0.004	0.006 ± 0.004	19	0.003 ± 0.002	0.011 ± 0.004	17
		PB Two	PB Three		PB Two	PB Three	
PB Two (Short Bout/Fast Rate/ Fifteen-second Duration) Versus PB Three (Long Bout/Fast Rate/ Thirty-second Duration)	S4hd	-0.260 ± 0.064	-0.173 ± 0.037	20	-0.120 ± 0.044	-0.109 ± 0.041	18
	S4hu	0.083 ± 0.058	0.035 ± 0.058	20	0.023 ± 0.045	0.034 ± 0.054	18
	Slouch	0.079 ± 0.044	0.065 ± 0.054	20	0.030 ± 0.011	0.027 ± 0.042	18
	Alert	0.093 ± 0.064	0.068 ± 0.048	20	0.058 ± 0.052	0.013 ± 0.010	18
	Run	0.006 ± 0.004	0.006 ± 0.004	20	-0.002 ± 0.002	0.011 ± 0.004	18

APPENDIX C: CORRELATIONS OF PHYSICAL AND MISCELLANEOUS GROUPING FACTORS

A Spearman's correlation matrix of the miscellaneous grouping factors year, trial date, and trial time, and the physical factors cloud cover, wind, and temperature was constructed with Statview 5.1.1. pooling across all studies, using 407 observations (Table C.1.). Correlations are described where $| r_s | \geq 0.300$ (designated arbitrarily). Trial date and year were both inversely proportional to trial time, indicating that more recent trials were conducted earlier in the day (-0.364 and -0.359, respectively). Trial date and year were also both inversely correlated with cloud cover, wind, and temperature because these factors are typically lower during early hours of the day and trials were performed earlier in the morning as years progressed (trial date: cloud cover – -0.332, wind – -0.411, temperature – -0.798; year: cloud cover – -0.339, wind – -0.401, temperature – -0.805). Temperature readings were higher for trials conducted later during the day (0.546), while wind and temperature were positively correlated (0.318) because wind levels and temperature typically increase from morning to afternoon hours. All factors are balanced across the different treatment comparisons and/or do not significantly confound interpretation of results from any studies conducted for this thesis.

Table C.1. Spearman's correlation matrix of the factors year, trial date, trial time, cloud cover, wind, and temperature pooling across all trials for all studies (n = 407). (Correlations where | r_s | ≥ 0.300 are in bold font).

	Year	Trial Date	Trial Time	Cloud Cover	Wind	Temperature
Year	**1.000**					
Trial Date	**0.998**	**1.000**				
Trial Time	**-0.359**	**-0.364**	**1.000**			
Cloud Cover	**-0.339**	**-0.332**	0.206	**1.000**		
Wind	**-0.401**	**-0.411**	0.190	0.028	**1.000**	
Temperature	**-0.805**	**-0.798**	**0.546**	0.259	**0.318**	**1.000**