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
University of Manitoba
Winnipeg, Manitoba

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.

ACKNOWLEDGEMENTS

I first and foremost thank Dr. James F. Hare for the invaluable advice and support he has given me throughout the years I have known him. Jim, the feedback you have provided me with concerning field methods, statistical analysis, and drafts of my work has been extremely helpful in producing a thesis to which I am proud to attach my name. Thank you for the many times you have set my mind at ease about thesis concerns and life tribulations. I thank you for your patience and for your fun-loving and good-hearted nature, but most of all I thank you for believing in me. It has been a pleasure being your student.

I am grateful to my other committee members, Dr. Darren Gillis and Dr. Sue Cosens, for their very helpful questions and suggestions regarding statistical analysis and data interpretation and presentation. I thank Dr. Nathan Lovejoy for suggesting early on in my project a more efficient means to an end with respect to methodology. I thank my lab mate, David Wilson, for his advice and for his friendship throughout the duration of my degree program. I thank the Sorenson family of Warren, Manitoba, and Dr. Bob Wrigley of the Assiniboine Park Zoo for providing access to ground squirrel colonies. I also thank Glenda Todd, Geoff Heath, Dr. James F. Hare, and David Wilson for excellent field assistance. You are all pleasant and highly competent people to work with! I also thank Dr. Gail Davoren for being such a pleasant person to work with and for thesis advice. Many thanks go to the staff of the Department of Zoology, particularly Madeleine Harris and Urmilla Deonauth for their assistance and kindness in guiding me through departmental bureaucracy.

I cannot forget my mother, Merle, and father, Gary, to whom I owe a great deal of appreciation. You have always been there for me through thick and thin and I could not ask for better parents and friends. I thank my sister, Angela, for a cherished friendship and for being a positive source of energy in my life, particularly during the final stages of my thesis writing. I also thank my fellow graduate students for the fun we have shared over the years. I thank my good friends (you know who you are) for the many great times, the encouragement, the support, and the inspiration. Last but not least I thank the little "gophers" that have made this milestone in my life possible. My research was funded by a University of Manitoba Student Union Scholarship, a Natural Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Scholarship, and an operating grant to Dr. James F. Hare.

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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),