THE ALARM VOCALIZATIONS OF

BRANTS' WHISTLING RAT, *PAROTOMYS BRANTSII*

by

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Declaration

I, the undersigned, hereby declare that the work contained in the thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature:

Date:

SUMMARY

The alarm calls of a colonial rodent, Brants' whistling rat (*Parotomys brantsii*), were investigated at Goegap Nature Reserve in the Northern Cape, South Africa. At this site *P. brantsii* occurs in sympatry with the congeneric *P. littledalei*, and the alarm calls in response to humans was compared between the two species. *Parotomys brantsii*'s typical call in reaction to a human is a simple whistle, characterized by an initial upward frequency sweep and high frequency plateau, whereas the alarm whistle of *P. littledalei* has three overlapping components. *Parotomys littledalei*'s calls are significantly shorter and lower in dominant frequency than those of *P. brantsii*, and have a significantly wider frequency bandwidth. These distinctions were attributed to species discrimination and habitat preferences. The acoustic adaptation hypothesis is supported in part, as *P. littledalei*, which inhabits a closed habitat in comparison with *P. brantsii*, has calls which are lower in frequency than *P. brantsii* calls, but contrary to the hypothesis, *P. brantsii* calls show less frequency modulation than those of *P. littledalei*. The high pitch of both species' vocalizations may be a convergent feature making the callers difficult for predators to locate.

The alarm call repertoire of *P. brantsii* was investigated by presenting members of the *P. brantsii* colony with models of some typical predators, a raptor and puff adder, as well as a human observer. Virtually no variation was detected in the structure of alarm whistles elicited by different predators, indicating that *P. brantsii* did not identify different predator types by means of vocalizations, even though behavioural responses showed that *P. brantsii* do distinguish between different predators and non-predators. Note duration varied in conjunction with the physical reaction of the caller. When the

caller bolted towards safety, the whistle was significantly shorter than when it remained aboveground. During an encounter with a snake or far-off human the caller would utter relatively long duration calls, signifying a low-risk situation, while high-risk situations such as a nearby human or raptor provoked short calls, emitted just before the whistling rat bolted underground. I regard *P. brantsii*'s alarm call repertoire as a graded "urgency-based" system, indicating threat level perceived rather than predator type. This system is widespread among ground squirrels and is usually associated with animals inhabiting a two-dimensional environment.

Playback experiments were conducted to determine the meaning of alarm calls to conspecifics, focusing specifically on the effect of variation in single call duration and function of alarm-calling bouts. All alarm calls induced heightened vigilance in receivers, but the behavioural response did not differ between short and long single calls. Multiple calls lead to significantly longer periods of high vigilance than single calls even after calling bouts have ended, showing that one of the functions of multiple calls is to maintain high vigilance in conspecifics for relatively long periods. The non-iconic nature of their alarm calls and the undiscriminating response of receivers to different calls emphasizes the importance of contextual clues in the communication system of animals living in an open habitat like that of *P. brantsii*.

OPSOMMING

Die alarm-roepgeluide van 'n koloniale knaagdier, Brants se fluitrot (*Parotomys brantsii*), is ondersoek by Goegap Natuurreservaat in the Noordkaap, Suid-Afrika, waar hulle simpatries voorkom met die naverwante *P. littledalei*. Die species se alarmroepe in reaksie op mense is met mekaar vergelyk. Die tipiese alarmroep van *P. brantsii* is 'n eenvoudige fluit, gekenmerk deur 'n aanvanklike skerp frekwensiestyging en hoë-frekwensie plato. *Parotomys littledalei* se fluitroep het drie komponente wat mekaar gedeeltelike oordek. *Parotomys littledalei* se roepgeluide is beduidend korter en laer in heersende toonhoogte as dié van *P. brantsii*, en hul frekwensie-wydte is ook beduidend wyer. Hierdie verskille word toegeskryf aan species-verskille en habitat-voorkeure. Die akoestiese aanpassingshipotese word gedeeltelik deur die studie ondersteun, aangesien *P. littledalei*, wat 'n geslote habitat verkies in vergelyking met *P. brantsii*, alarmroepe het met 'n laer dominante toonhoogte as *P. brantsii*. In teenstelling met die hipotese, toon *P. brantsii* se fluitgeluide minder frekwensie-modulasie as *P. littledalei* se geluide. Die hoë toonhoogte van beide species se alarmroepe kan 'n konvergente verskynsel wees wat dit vir roofdiere moeilik maak om fluitende individue te lokaliseer.

Die alarm-repertoire van *P. brantsii* is ondersoek deur individue bloot te stel aan 'n menslike waarnemer en modelle van tipiese predatore, naamlik 'n jakkalsvoël en pof-adder. Daar was omtrent geen variasie in die klank-struktuur van alarmroepe in reaksie op verskillende roofdiere nie. Dit wys daarop dat *P. brantsii* nie roofdiere deur middel van roepgeluide klassifiseer nie, hoewel gedragsresponse getoon het dat individue wel tussen roofdiere kan onderskei. Die duur van alarmroepe varieer na

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gelang van die gedrag van die fluitende individue – 'n fluitrot wat vlug, se roep is beduidend korter as die geluid van een wat bogronds bly. 'n Pofadder en 'n veraf mens ontlok lankdurende geluide, wat dui op 'n lae-risiko situasie, terwyl rotte op vlug slaan in reaksie op 'n hoë-risiko situasie, soos met 'n nabygeleë mens of jakkalsvoël, wanneer kort alarmroepe geuiter word. Ek beskou *P. brantsii* se alarm-repertoire as 'n gegradeerde "nood-gebaseerde" stelsel, wat die mate van bedreiging aandui, eerder as die identiteit van die spesifieke roofdier. Hierdie sisteem is tipies van grondeekhorings en word gewoonlik verbind met diere wat 'n twee-dimensionele omgewing bewoon.

Parotomys brantsii se reaksie op die terugspeel van die species se geluide is hierna ondersoek. Ek het gefokus op die effek van 'n verandering in die duur van alleenstaande fluitnote, asook hulle reaksie op fluitreekse. Alle alarmroepe het gelei tot hoër vlakke van waaksaamheid in luisterende individue, maar reaksies op kort en lang enkelnote het nie van mekaar verskil nie. Fluitreekse het beduidend langer periodes van hoë waaksaamheid veroorsaak as enkele geluide, en waaksaamheid het hoog gebly selfs nadat reekse geëindig het. Dit beteken dat fluitreekse onder andere die funksie vervul om waaksaamheid in kolonielede vir relatief lang tye te onderhou. *Parotomys brantsii* se eenvoudige alarm-repertoire en nie-onderskeidende reaksie op verskillene roepgeluide, beklemtoon die belangrikheid van aanvullende inligting uit die omgewing vir diere in 'n twee-dimensionele habitat wanneer die akoestiese kommunikasiestelse slegs 'n algemene waarskuwingsfunksie vervul.

ACKNOWLEDGEMENTS

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cases, the initial upward frequency sweep and high frequency plateau. Human (stay) calls are often part of a bout of whistles and differ from human (bolt) calls in terms of call duration. **48**

CHAPTER ONE

GENERAL INTRODUCTION

Vocal communication is a prominent feature of the behaviour of many group-living animals, and has been studied in a broad range of mammals, for example African elephants (McComb *et al.*, 2000), vervet monkeys (Cheney & Seyfarth, 1982), seals (Insley, 1992) and timber wolves (Schassbuger, 1993). The function of vocalizations is to mediate social interaction among group members, and animal calls are generally divided into categories such as mating calls, territory-defense signals, species recognition signals, and alarm calls (Lanyon & Tavolga, 1960; Bradbury & Vehrencamp, 1998). The focus of this study is alarm vocalizations of Brants' whistling rat, *Parotomys brantsii* (Nel & Rautenbach, 1974; Kerley, 1997).

The alarm vocalizations of colonial rodents have received considerable attention in the literature (e.g.: *Spermophilus beecheyi* : Owings *et al.*, 1977; *S. beldingi*: Leger *et al.*, 1984; *S. columbianus*: Betts, 1976; genus *Marmota*: Blumstein, 1999; *Cynomys ludovicianus*: Towers & Coss, 1991; *C. gunnisoni*: Slobodchikoff *et al.*, 1998; *Tupaia belangeri*: Binz & Zimmerman, 1989; *Helogale undulata*: Beynon & Rasa, 1989; genus *Callosciurus*: Tamura & Yong, 1993). A well-developed frame-work of empirical evidence therefore exists concerning the evolution of rodent alarm calls and their functional significance, environmental and phylogenetic factors affecting call structure, and reasons for interspecific convergence and divergence in alarm call structures. While mate-attraction signals, such as the prominent vocal displays of birds, have evolved primarily under the pressures of sexual selection (Kroodsma,

1977), alarm calling is apparently altruistic behaviour and different selective pressures are thought to have led to its evolution. In sciurids kin selection is most often invoked to explain alarm signaling (Smith, J. M., 1965; Sherman, 1977; Hoogland, 1983). The possibility that alarm calling evolved as selfish behaviour, used to manipulate conspecifics to the benefit of the caller (Charnov & Krebs, 1975), or as predator-deterrent signals (Blumstein *et al.*, 1997) is not excluded (see Klump & Shalter, 1984, for detailed review).

1.1 Environment: Physiological and physical factors

Like all acoustic signals, alarm calls are subject to constraints imposed by the environment of the calling animal, which affects the spectral structure of the vocalizations (Wiley & Richards, 1978). In a closed, forested habitat, call structure can be degraded by reflections off vegetation, scattering and ambient noise, whereas in an open savanna habitat sound is typically distorted by irregular gusts of wind (Ryan & Brenowitz, 1985; Forrest, 1994). Morton's (1975) acoustic adaptation hypothesis takes these environmental pressures into account and states that animals typically have calls that are adapted to propagate optimally in their native habitat. According to Morton, we should expect open-habitat species to have high-pitched, repetitive calls with considerable frequency modulation, whereas forest-dwellers should have tonal songs of a lower pitch. This theory has been supported at an intraspecific level by Hunter & Krebs (1979) but disputed by Wiley (1991), amongst others, in various studies on bird vocalizations. The structure of vocalizations is

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further affected by the physical characteristics of the vocalizing species, such as body size and shape of the larynx (Ryan & Brenowitz, 1985; Ploog, 1992), and the perceptual abilities of both prey and predator (Klump, 2000). Alarm vocalizations are usually species-specific, and in certain genera, for example *Eutamias*, the difference in alarm calls between species have been used to distinguish accurately between closely-related taxa (Gannon & Lawlor, 1989). Geographic variation in alarm call structure is also found in some species, for example, Gunnison's prairie dog, *C. gunnisoni* (Slobodchikoff *et al.*, 1998).

There is evidence of convergence in the spectral structure between mammalian and avian alarm calls in some call types, specifically vocalizations warning against aerial attack (e.g. Marler, 1955; Vencl, 1977). Such calls usually have a high frequency, begin and end imperceptibly, and show little frequency modulation. These characteristics make them hard for a raptor to locate (Marler, 1955; Klump, 2000), and purportedly cause confusion in the predator. Calls that are highly repetitive and of wide frequency bandwidths are easier to locate and are typical of intraspecific contact calls, e.g. the mobbing calls of birds (Marler, 1955; Klump & Shalter, 1984), when it is important for receivers to know the location of the caller in order to effectively attack the targeted predator.

1.2 The nature of alarm call repertoires

In spite of spectral differences between the alarm calls of different rodent species, there is an underlying similarity between alarm call repertoires with regard to their functional significance. Alarm call repertoires are generally described as one of two systems – either "urgency-based," or "externally referential" (Macedonia & Evans, 1993), alternatively labeled "motivational" and "referential" signals respectively (Marler *et al.*, 1992). The prevalent type of sciurid alarm repertoire is a system in which different call types are used to indicate the level of risk experienced by the caller, rather than the type of predator present (Macedonia & Evans, 1993). This urgency-based system is found in most colonial rodents, for example marmots (Blumstein, 1999), Belding's ground squirrels, *S. beldingi* (Leger *et al.*, 1984) and California ground squirrels, *S. beecheyi* (Leger *et al.*, 1980; see also Betts, 1976, for review). Because aerial attacks are usually fast, and terrestrial attacks slower, a spurious correlation between high-risk calls and aerial threat, and between low-risk calls and terrestrial threat exists in most rodent alarm call systems. It has been shown that far-off raptors elicit the same response as a nearby canid predator (e.g. Blumstein & Armitage, 1997), which suggests that risk is the determinant of call type rather than predator identity. The latter is a completely different way of classifying danger; the externally referential system of alarm calling is clearly differentiated from the urgency-based system, as calls remain specific to a predator type, regardless of the distance between predator and prey. This system of predator identification is found in, for example, red squirrels, *Tamiasciurus hudsonicus* (Greene & Meagher, 1998), *Eutamias sonomae* (Smith, 1978), and Malaysian trees squirrels, genus *Callosciurus*

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(Tamura & Yong, 1993). Macedonia and Evans (1993) proposed that one of the main reasons that the two different systems have developed is the effect of habitat complexity on the prey species. Animals that live in a three-dimensional habitat, such as vervet monkeys and tree squirrels, have a number of escape options open to them (e.g. flee up into a tree, down the tree, or freeze), and choosing the wrong option may increase the risk of death. It is important for conspecifics to know which predators are present in order to choose an appropriate escape response. On the other hand, animals that inhabit a two-dimensional environments, like ground squirrels and prairie dogs, typically have only one escape option – flee into a burrow. The most important information to them would be to know how fast to escape. Escaping too fast as a response to a low-level threat might unnecessarily reduce foraging time, whereas escaping too slowly to an imminent threat could mean death. In a relatively open environment contextual clues are expected to play a large role in mediating conspecifics' response to the alarm signals, as they are quite simple displays (Smith, 1969). The distinction between the two systems is not absolute, however, as motivational elements are found in "referential" signaling, and referential (contextual) information can play a very important role in the meaning of "motivational" signals (Marler *et al.*, 1992).

1.3 The functional significance of alarm calls

The exact meaning of a signal to conspecifics as it occurs in the natural context is difficult to determine if the effects of confounding contextual elements are not

excluded (Smith, W. J., 1965). A signal may have one or more referents, which can be "external" or "internal" factors (Smith, 1981). External referents include the specific predator present, whereas internal referents are mostly motivational factors, indicated by caller behaviour. In order to ascertain the exact meaning of an alarm call, one has to remove any confounding factor that could provide contextual information, in particular the referents of a call, which could be both predator and caller. The meaning of a vocal signal can then be gleaned from the behavioural response that conspecifics choose in reaction to the call (Smith, W. J., 1965). Playback experiments, in which all contextual information is removed – i.e. only the call itself is played – are a common method for determining the exact meaning of a signal (e.g. Seyfarth *et al.*, 1980; Owings *et al.*, 1986; Hare, 1998). Such experiments are also necessary to determine whether calls are functionally referential. For a signal to be functionally referential, it has to be produced under a fixed set of circumstances, and elicit particular, predictable responses – i.e. be production and perception specific (Macedonia & Evans, 1993). Both urgency-based and externally referential systems can be functionally referential, and this enables conspecifics to interpret and act upon messages without the need for gathering extra information from the environment.

Repetitive vocalizations are common in the communicative systems of invertebrates and vertebrates (e.g. see Lanyon & Tavolga, 1960). Repetition is a highly regular feature of sciurid alarm calls (Owings *et al.*, 1986; Burke da Silva *et al.*, 1994; Weary & Kramer, 1995; Blumstein & Armitage, 1997), and yet its functional significance remains uncertain. Whereas single alarm calls of various types usually function to warn conspecifics of impending danger, subsequent repetitive calls fall on the ears of already-warned animals, and should therefore serve a different function. In animals

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such as yellow-bellied marmots, *M. flaviventris* (Blumstein & Armitage, 1997), variation in the call interval within a bout communicates changes in predator behaviour to conspecifics. It has been proposed that a large number of callers calling in an alarm "chorus" of multiple calls can induce a predator to leave the area (Burke da Silva *et al.*, 1994), or that a high number of callers is indicative to receivers that the threat is substantial (Leger & Owings, 1978). A related theory proposed by Schleidt (1973) deserves some attention, as it remains largely uninvestigated. His theory of tonic communication (Schleidt, 1973) proposes that any signal emitted continuously functions to heighten and maintain the effect of the initial signal; accordingly, alarm calling bouts should induce longer periods of high vigilance than single calls do. This tonic communication theory has been cited by some authors to explain the occurrence of calling bouts (e.g. Owings *et al.*, 1986; Hare, 1998) but has not been subjected to rigorous testing. We found only two studies that specifically investigated the effect of calling bouts compared with single calls (Loughry & McDonough, 1988; Blumstein, 1999). Results from both studies suggest that tonic communication occurs in Olympic marmots, *M. olympus* (Blumstein, 1999), and California ground squirrels, *S. beecheyi* (Loughry & McDonough, 1988). In many animal species, however, it seems that receivers quickly habituate and stop reacting to multiple calls (Hartshorne, 1956), and in the black-tailed prairie dog, *C. ludovicianus*, it has been noted that continuous barking induced some initial vigilance, but not necessarily long periods of vigilance (Smith *et al.*, 1977). Thus it cannot be unequivocally stated that tonic communication is the purpose of calling bouts in most animals, and this phenomenon requires further investigation, particularly in the light of evidence of habituation to continual signals (Hartshorne, 1956).

1.4 The present study

In this study I investigate various aspects of the alarm calls of Brants' whistling rat, *P. brantsii*. Apart from anecdotal evidence mentioning the very conspicuous alarm vocalizations of this rodent (Nel & Rautenbach, 1974; Kerley, 1997), no research has been performed on the function, spectral structure, or meaning of *P. brantsii* whistles. *Parotomys brantsii* is a medium-sized, semi-fossorial otomyine rodent endemic to the southwest arid region of southern Africa (Skinner & Smithers, 1990). They are territorial animals, building and defending their burrow systems in sandy areas with little vegetation, forming colonies that vary dramatically in size depending on environmental conditions (Coetzee & Jackson, 1999; Jackson, 1999; Jackson, 2000*a*). They are generalist herbivores, acting as central place foragers, with each individual's home burrow as the refuge around which it forages (Coetzee & Jackson, 1999; Jackson, 2000*b*). At Goegap Nature Reserve in the Northern Cape, where my study site was located, the predators of *P. brantsii* include the jackal buzzard, *Buteo rufofuscus*, puff adder, *Bitis arietans*, and black-backed jackal, *Canis mesomelas*, and *P. brantsii* forms a substantial part of the diet of pale chanting goshawks, *Melierax canorus* (Malan & Crowe, 1996), which also occur near said study site.

Parotomys brantsii shares common predators with *P. littledalei*, a closely related species found in sympatry with *P. brantsii* at Goegap Nature Reserve. The calls of *P. littledalei* are reported to be more "melancholy" in nature than those of *P. brantsii* (De Graaff, 1981). In the second chapter of this thesis I investigate the differences in alarm calls between these two otomyine species, focusing on alarm calls made in response to a human observer. Differences are predicted based on the fact that the

calls should be species-specific and affected by the divergent habitats of the subjects. The two species are quite similar in population structure and social behaviour, but differ markedly in the habitat types they prefer (Coetzee & Jackson, 1999). *Parotomys brantsii* is found in open, sandy areas with limited vegetative cover, whereas *P. littledalei* inhabits a more closed environment, their burrows exclusively built underneath large bushes. I made the prediction that *P. littledalei* calls should be adapted to a closed environment, and *P. brantsii* calls to an open one, expecting the former's calls to be lower in frequency and less frequency-modulated that those of *P. brantsii*.

In the third chapter I investigate the alarm calling system of *P. brantsii* as it relates to various predators. I present colony members with models of different predators, a method that is well reported in the literature (e. g. Seyfarth *et al.*, 1980; Leger *et al.*, 1984; Greene & Meagher, 1998) and intend to establish whether *P. brantsii* can distinguish acoustically between predators or not. The third chapter deals with the production-specificity of *P. brantsii*'s alarm call repertoire (Macedonia & Evans, 1993). It is expected that they should have an urgency-based system of communication, as the rodents inhabit a two-dimensional habitat, and their alarm call repertoire may be relatively simple, reflecting the social structure of the species (Blumstein & Armitage, 1997; Jackson, 1999).

In chapter four I used playback experiments to determine whether the alarm calls of *P. brantsii* are perception-specific (Macedonia & Evans, 1993) and therefore externally referential. I also add to the limited body of evidence concerning the theory of tonic

communication by examining receiver reaction to calling bouts, which are typical of

P. brantsii's vocal repertoire.

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CHAPTER TWO

DIFFERENCES IN ALARM VOCALIZATIONS OF SYMPATRIC POPULATIONS OF THE WHISTLING RATS, *PAROTOMYS BRANTSII* AND *P. LITTLEDALEI* [†]

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Short title: Alarm vocalizations of whistling rats.

2.1 Summary

The alarm vocalizations of the whistling rats *Parotomys brantsii* and *P. littledalei* were investigated at the Goegap Nature Reserve in the Northern Cape, South Africa, where they occur sympatrically. *Parotomys brantsii*'s call is a single note vocalization, characterized by an upward frequency sweep and high frequency plateau with a dominant frequency of 10.0 ± 0.3 kHz and duration of 164 ± 11 ms. The alarm whistle of *P. littledalei* has three overlapping components and is both shorter (53 ± 5 ms) and lower in dominant frequency (7.7 ± 0.1 kHz) than that of *P. brantsii*. The frequency bandwidth of *P. littledalei* calls (10.2 ± 0.7 kHz) is significantly wider than that of *P. brantsii* (6.8 ± 0.4 kHz). These significant distinctions were attributed to habitat preferences of the two species. Data support the acoustic adaptation hypothesis in that *P. littledalei*, which inhabits a more closed habitat, has calls which are lower in frequency than *P. brantsii* calls, but contrary to the hypothesis, *P. brantsii* calls do not show greater frequency modulation than those of *P. littledalei*. Despite these differences, the alarm calls of the two species are both high-pitched, and may have converged in structure to be difficult for predators to locate.

Keywords: adaptation, alarm call, whistling rat.

2.2 Introduction

The alarm vocalizations of a variety of ground-dwelling, colonial rodents have been investigated extensively, for instance, in Columbian ground squirrels, *Spermophilus columbianus columbianus*, (Betts, 1976), Gunnison's prairie dogs, *Cynomys gunnisoni*, (Slobodchikoff *et al.*, 1991), and the yellow-bellied marmot, *Marmota flaviventris* (Waring, 1966). These alarm calls are uttered in the presence of predators such as raptors, snakes, canids and humans, and could convey information on either the level of risk perceived (Betts, 1976; Macedonia & Evans, 1993), or the identity of the predator (Slobodchikoff *et al.*, 1991; Macedonia & Evans, 1993). Alarm vocalizations, like the acoustic mate-attraction signals of many animals, are often species-specific and can therefore be used to distinguish between closely-related rodent species. For example, in Townsend chipmunks of the genus *Eutamias* (Gannon & Lawlor, 1989) species distinctions between related taxa were reaffirmed by the marked differences in their alarm calls.

Habitat dissimilarities could also play an important role in the evolution of interspecific call variation (Morton, 1975; Bradbury & Vehrencamp, 1998). The effectiveness of sound propagation is affected not only by intrinsic characters of the caller, such as body size, but by properties of the habitat in which it is emitted (Ryan & Brenowitz, 1985). Morton's (1975) acoustic adaptation hypothesis predicts that different habitats should shape the vocalizations of species which inhabit them uniquely, proposing that, in a more densely vegetated habitat, vocalizations would be lower in frequency, with fewer rapid frequency modulations than those affected by animals in a more open environment. The hypothesis, originally applied to the

vocalizations of birds, has been controversial (Wiley & Richards, 1978; Hunter & Krebs, 1979; Wiley, 1991).

Brants' whistling rat, *Parotomys brantsii*, and Littledale's whistling rat, *P. littledalei*, are closely related species of semi-fossorial otomyine rodents endemic to the southwest arid region of southern Africa (Skinner & Smithers, 1990). These colonial rodents have distributional ranges that overlap (Fig. 2.1) but are seldom found in sympatry due to differences in microhabitat preferences. *Parotomys littledalei* frequents a more densely vegetated habitat than *P. brantsii*, which often builds its burrow systems in areas with minimal vegetation (Coetzee & Jackson, 1999; Jackson, 2000). The two species are very similar in physical appearance and are best distinguished anatomically on the basis of grooves present on the upper incisors present in *P. brantsii,* but not in *P. littledalei* (De Graaff, 1981). Their social structures are comparable – both species are territorial, each animal defending a burrow system or part of a bush hummock against conspecifics (Coetzee & Jackson, 1999; Jackson, 1999). At low population densities animals are solitary, though colony and population numbers fluctuate dramatically with changing environmental patterns. Whistling rats are central place foragers (Coetzee & Jackson, 1999; Jackson in press) and share similar predators. At our study site these included the jackal buzzard *Buteo rufofuscus*, puff adder *Bitis arietans* and black-backed jackal *Canis mesomelas* (Jackson, personal observations.).
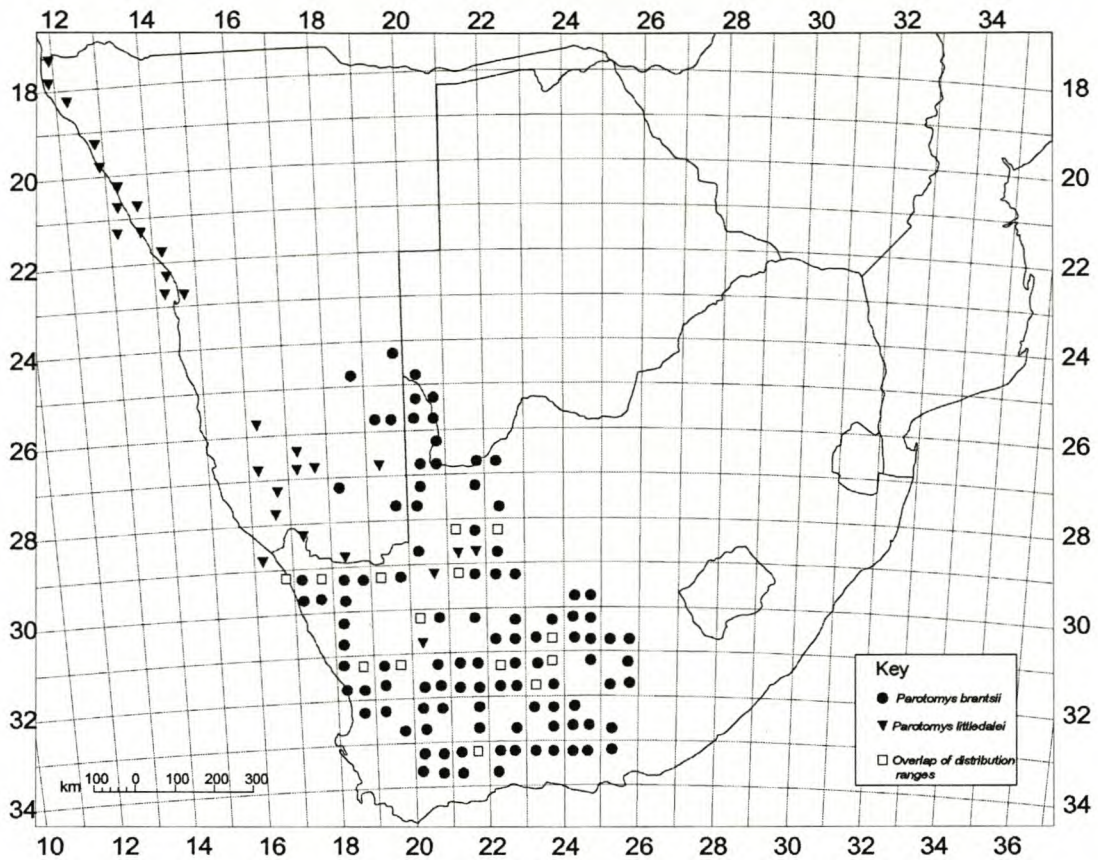
Fig. 2.1 Map showing the distribution ranges of *Parotomys brantsii* and *P. littledalei*, as well as the areas in which they occur in sympatry (adapted from Coetzee & Jackson, 1999). *Parotomys littledalei* prefers habitats with dense low shrubs and bushes, and its range extends up the Namibian coast, while *P. brantsii* occurs in more open habitats, especially in the Karoo and Kalahari.

Although the rodents' common name (whistling rat) alludes to their typical alarm whistle, no studies have been conducted on the spectral structure or function of this alarm vocalization. Authors have noted that both species emit short, high-pitched whistles when alarmed (Nel & Rautenbach, 1974; Kerley, 1997), and that the whistle of *P. littledalei* is somewhat "melancholy" in nature compared to that of *P. brantsii*

(De Graaff, 1981). This study is the first investigation into the nature of *Parotomys* alarm calls, and we focus on their reaction to humans. Our aim is to examine the possible nature of species distinction in relation to alarm call structure, and further to examine whether any variation can be related to habitat preferences. In terms of the acoustic adaptation hypothesis, we should expect the alarm call structure of the two species to be different: we predict a lower frequency for *P. littledalei* than *P. brantsii* calls, and *P. brantsii* whistles should show greater frequency modulation than *P. littledalei* calls, as *P. littledalei* inhabits a more closed habitat than *P. brantsii* (Morton, 1975).

2.3 Materials and Methods

2.3.1. Study Site and Animals

Parotomys brantsii and *P. littledalei* occur in sympatry at Goegap Nature Reserve (29°37'S, 17°59'E) in the Northern Cape Province, South Africa (Fig. 2.1). The study population of *P. brantsii* occurred in an open, sandy area dominated by winter ephemerals and Mesembryanthemaceae, whereas *P. littledalei* inhabited a sandy area almost completely covered by low shrubs, predominantly *Psilicaulon absimile* (Jackson, 2000). Both species dig burrows, though these are restricted to bush cover in the case of *P. littledalei*. The burrows of *P. brantsii* are often centred around *Lycium* bushes (Jackson, 1998) but radiate outwards extensively, with most entrances found outside the protection afforded by bush cover. Brants' whistling rat burrows usually have many entrances (more than 500 entrances have been recorded for one burrow system) and serve to protect the inhabitants against predators and environmental

extremes, whereas those of Littledale's whistling rat are less extensive (Jackson, 2000).

2.3.2. Sound Recording

Tape recordings were made of both species' alarm vocalizations in response to a human observer walking among colony members. In the case of *P. brantsii*, individuals had been marked with colour-coded neckbands made out of cable-ties on which electric heatshrink had been melted in unique colour combinations (Jackson, 1998). It was possible to obtain numerous calls from each whistling rat. The same methods could not be repeated for *P. littledalei*, as individuals are normally hidden by vegetation and seldom seen in the field. Within a colony of *P. littledalei*, occupied burrow systems could easily be recognized by the presence of recent droppings, spoor and nesting material at entrances, which are usually under bushes. As only one individual normally occupies any given burrow system (Coetzee & Jackson, 1999), only one recording was made per burrow system to ensure we sampled from different individuals, thus avoiding pseudoreplication.

Call data were obtained using a Marantz stereo cassette recorder (model CP430) fitted with a Sennheiser ME-66 microphone. Calls were subsequently digitised at a 32 kHz sampling rate and analysed using the Canary software program (Charif *et al.*, 1995) that displays sound waves as spectrograms (sonograms). The call parameters were set at 699.40 Hz bandwidth, -140dB clipping level, logarithmic amplitude, boxy display style, and the "Hamming" window function. Calls for 10 individual *P. littledalei* were analysed, as well as the average values of three or more calls per individual for 19 *P. brantsii*. Dominant frequency (peak frequency at peak amplitude), call duration, and

frequency bandwidth (maximum minus minimum frequency) were measured for each call.

We used the program Statistica for Windows to perform all statistical tests (StatSoft Inc., 1996), which were predominantly Student's t-tests (Zar, 1984). The normality of data distribution for data sets was ascertained by Kolmogorov-Smirnov tests.

2.4 Results

The spectrogram of *P. brantsii*'s alarm call is characterized by a single note, with or without an upward frequency sweep, leading to a uniform frequency plateau at which the highest amplitude usually occurs (Fig. 2.2 a & b). The duration of *P. brantsii* calls is 164 ± 11 ms (mean $\pm$ SE), with a dominant frequency of 10.0 ± 0.3 kHz, and 6.8 ± 0.4 kHz frequency bandwidth. There is a structural difference between the species' calls, as *P. littledalei*'s alarm whistle consists of two or more overlapping frequency components (Fig. 2.2 c), lasting for 53 ± 5 ms, with a dominant frequency of 7.7 ± 0.1 kHz and frequency bandwidth of 10.2 ± 0.7 kHz.
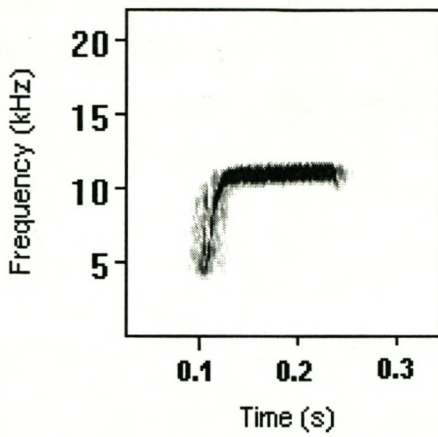
Fig. 2.2 (a) The typical alarm whistle of *Parotomys brantsii*, with a short upward frequency sweep.
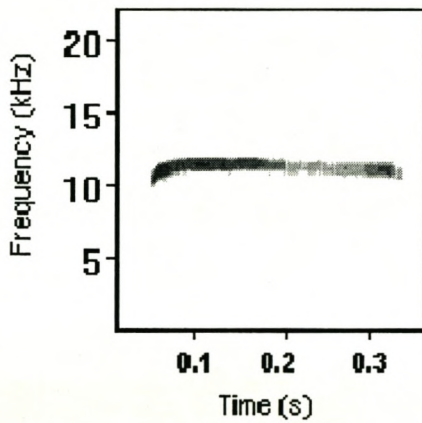
Fig. 2.2 (b) The *P. brantsii* alarm call can sometimes be seen without the initial frequency sweep. Note, in both (a) and (b), the high frequency plateau where the dominant frequency lies.
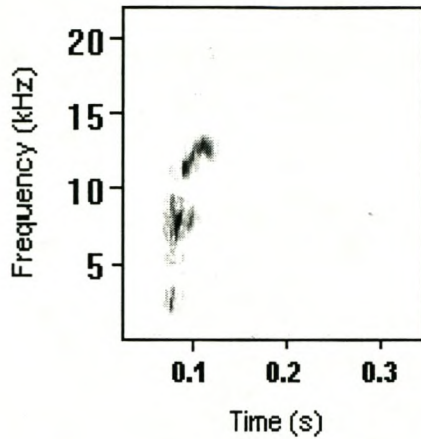
Fig. 2.2 (c) The typical alarm whistle of *Parotomys littledalei*. The call has more than one part, though to a human observer it sounds continuous and simple, like the call of *P. brantsii*. The dominant frequency of (c) lies between 5 and 10 kHz.

The call duration of *P. littledalei*'s calls was significantly shorter than that of *P. brantsii* (Fig. 2.3 a: t = -7.406; df = 27; p < 0.001) with a significantly lower dominant frequency (Fig. 2.3 b: t = -5.124; df = 27; p < 0.001). The frequency bandwidth of *P. littledalei* calls is significantly wider than *P. brantsii* calls (Fig. 2.3 c: t = 4.403; df = 27; p < 0.001).
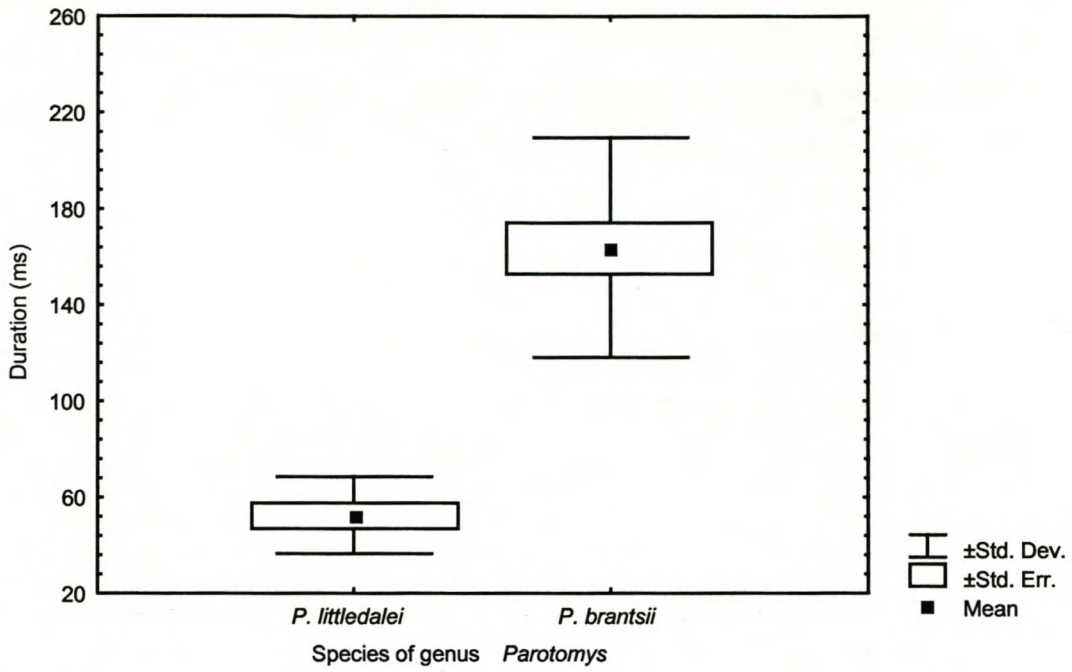
Fig. 2.3 (a) Boxplot demonstrating the comparative call durations between *Parotomys littledalei* and *P. brantsii*, which differs significantly between species (t-test: *p* < 0.001).
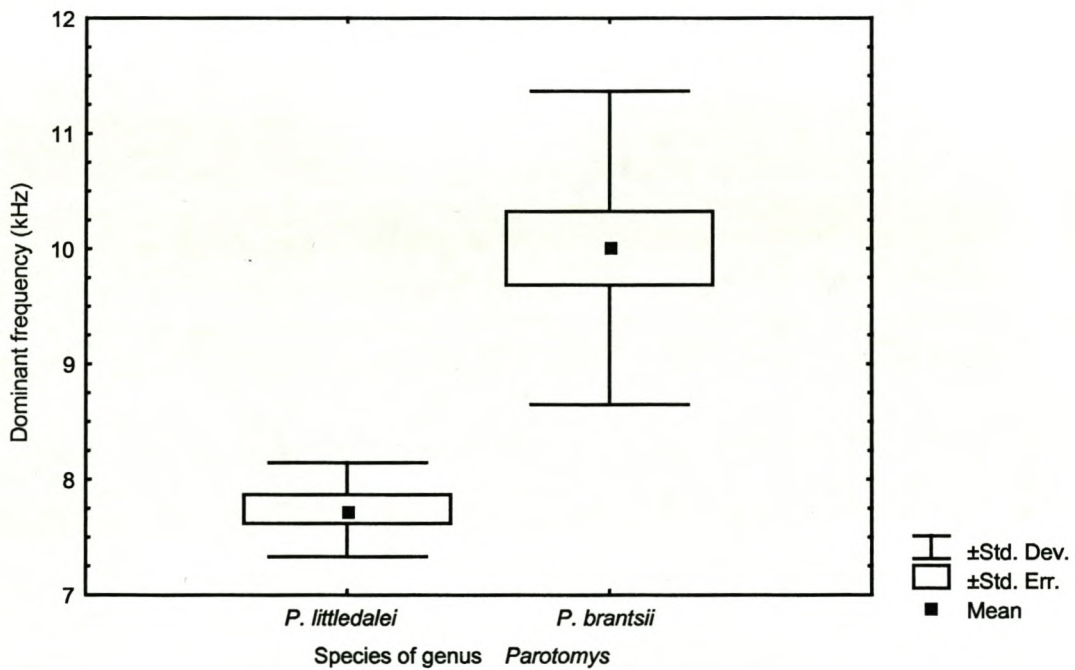
Fig. 2.3 (b) The dominant frequency compared between the two species, showing a significant difference (t-test: *p* < 0.001).
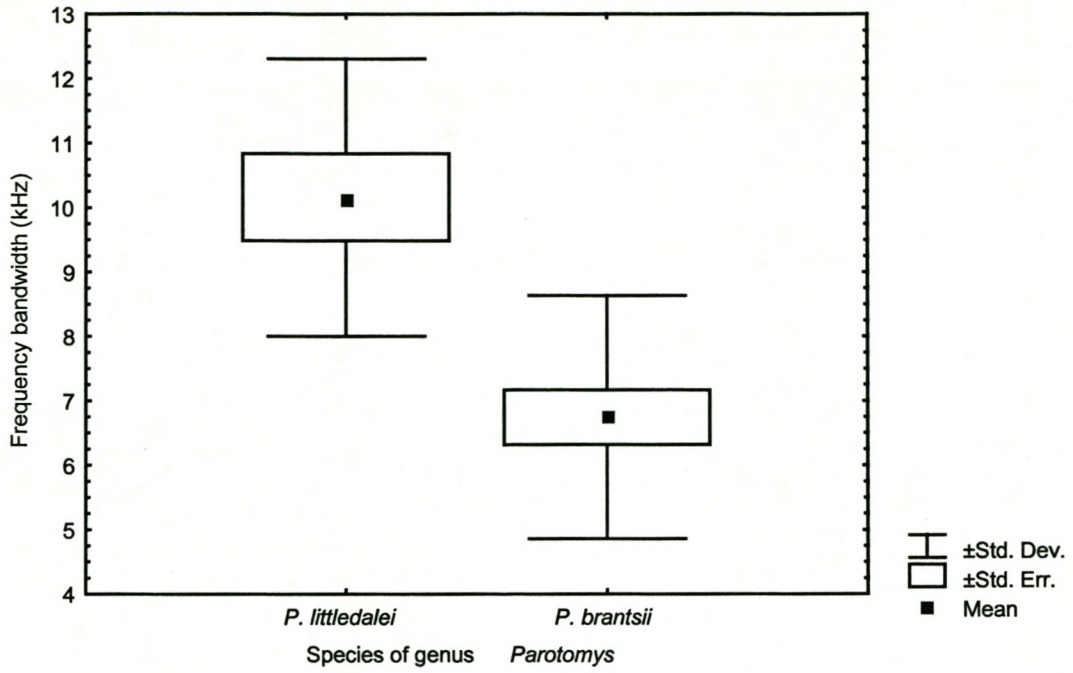
Fig. 2.3 (c) The frequency bandwidths were compared between the two species, and found to be significantly different (t-test: $p < 0.001$).

2.5 Discussion

The two species in the genus *Parotomys* both display relatively simple calls in response to humans, and the high pitch of their whistles is common in alarm calls of colonial rodents, such as ground squirrels of the genus *Spermophilus* (Koeppl *et al.*, 1978). Marler, in a seminal study (1955), suggested that the alarm calls of small birds were remarkably similar to each other, and that this represented convergent evolution resulting from selection for high-pitched 'seet' sounds that were difficult for predators to locate, thereby reducing the risk to the caller of attracting the predator to itself. In both rodents and birds, alarm types may have converged between species exposed to similar predators, allowing them to respond to heterospecific calls. This is certainly true for the mobbing calls of birds (Klump & Shalter, 1984), as several species may react to one species' mobbing call. For the Otomyine rodents of southern Africa the species relationships have not been well resolved. However, approaches using immuno-electrotransfer analysis (Contrafatto *et al.*, 1994) and allozymes (Taylor *et al.*, 1989) suggest that *P. brantsii* and *P. littledalei* may be more closely related to other Otomyine species, whose vocal repertoire does not include a distinct alarm whistle (Kerley, 1997), than to each other. Thus the distinction of two otomyine genera, Otomys and Parotomys, the latter distinguished by its inflated ear bullae, may be misleading. Indeed Pocock (1976) argues that the development of inflated ear bullae may have developed independently in the two species as an adaptation to arid environments. If so, it follows that the alarm whistles of *P. brantsii* and *P. littledalei* may have evolved independently but have converged to become similar. This convergence may be even more similar in areas in which the two species overlap, as it

could allow recognition of heterospecific as well as conspecific alarm calls, although this hypothesis remains untested.

The difference in alarm call structure between the two species could theoretically be attributed to alarm calls playing a role in species recognition, which is a common function of many vocal signals (Marler & Hamilton, 1968), particularly in closely-related species. Within the genus *Eutamias* (Townsend chipmunks), for example, uncertainties about species-distinctions have been ruled out by confirmation of differences not only in morphological characters, but also in vocalizations (Dunford & Davis, 1975). Related taxa diverge in vocalizations as much as they do in other characters, and reproductive character displacement in alarm calls has been reported, with vocal differences being enhanced at parapatric sites of some populations of *Eutamias* (Gannon & Lawlor, 1989). However, we regard this scenario as being unlikely in the case of whistling rats, as not only do they not appear to be sibling species (see above), but personal observations with habituated individuals (Jackson, personal observations) indicate that neither species calls outside an alarm context.

The alarm whistles of the two species do, however, show some consistent differences, and these may be related to differences in their microhabitat. Morton's (1975) hypothesis of acoustic adaptation suggests that animals inhabiting a more closed habitat should have vocalizations of lower frequency, and containing purer tones than those of related species in more open habitats. These predictions are based on environmental factors such as scattering by obstructions, echoes, background noise, and irregular amplitude fluctuations – factors which all differ between habitats (Morton, 1975; Ryan & Brenowitz, 1985). We have found that *P. littledalei*'s calls are

lower in dominant frequency than *P. brantsii*'s, which supports Morton's hypothesis, as did Wiley's (1991) study on oscine birds. On the other hand, the frequency bandwidth of *P. littledalei* calls is wider than *P. brantsii* calls. This implies that there is a higher amount of frequency modulation in *P. littledalei* vocalizations: the closed habitat species emits calls that are less pure in tone than those of the open habitat species, which is contrary to the predictions of the acoustic adaptation hypothesis (Morton, 1975).

Similarly, a study on marmots of the genus *Marmota* (Daniel & Blumstein, 1998) did not support Morton's hypothesis. One of its implications is that an animal's typical alarm signal should transmit further without becoming unrecognisably degraded in its native habitat, and degrade faster in a structurally foreign habitat. Daniel and Blumstein (1998) played the typical alarm calls of four species of marmots in the species' own habitats and in each other's habitat, to ascertain how much each call is degraded in each habitat type during transmission. None of the calls transmitted significantly better in the callers' native habitats compared to the others, even though there were significant differences in the acoustic properties of the four habitats. The acoustic adaptation hypothesis was therefore not supported by their study at all. The combined evidence appears to indicate that Morton's hypothesis is, at least, applicable only partially to rodent calls, but that it may nonetheless explain the observed differences in call structure between the two whistling rat species.

2.6 Acknowledgements

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CHAPTER THREE

DOES BRANTS' WHISTLING RAT (*PAROTOMYS BRANTSII*) USE AN URGENCY-BASED ALARM SYSTEM IN REACTION TO AERIAL AND TERRESTRIAL PREDATORS? [†]

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Short title: Whistling rat predator reaction.

3.1 Summary

It is predicted that differences in mammalian alarm call systems may be explained relative to the complexity of their habitat, with species inhabiting three-dimensional habitats classifying predator types (externally referential), and those living in two-dimensional environments indicating the level of risk (urgency-based). We tested this prediction in a two-dimensional environment for a small African rodent, Brants' whistling rat, *Parotomys brantsii*. Colony members were presented with predator models of a raptor and puff adder, as well as a human observer, to investigate their alarm call repertoire. Alarm calls consisted of simple, single-note vocalizations, often repeated in non-rhythmic bouts. Virtually no variation was detected in the structure of alarm whistles between the calls elicited by the two model predators and humans, indicating that *P. brantsii* did not identify different predator types by means of vocalizations. However, note duration was dependent on the reaction of the caller: when the caller bolted towards safety, the whistle was significantly shorter than when it remained stationary. A snake and far-off human elicited relatively long-duration calls and the caller would remain above ground, signifying a low-risk situation. High-risk encounters with a nearby raptor or human provoked short calls before the whistling rat bolted underground. We conclude that *P. brantsii*'s alarm call repertoire represents a graded "urgency-based" system, indicating perceived threat level rather than predator type. Our study supports the prediction that mammalian alarm call systems in two-dimensional environments primarily provide information indicating the level of risk and not predator type.

Key words: Externally referential, urgency-based.

3.2 Introduction

The alarm call repertoire of a variety of colonial rodents has been classified as a graded system conveying the degree of risk, for example in marmots (genus *Marmota*) (Blumstein, 1999), Belding's ground squirrels, *Spermophilus beldingi*, (Leger *et al.*, 1984) and a large number of other sciurids (review by Betts, 1976). By means of gradually changing vocalizations, these animals communicate fluctuating levels of risk to conspecifics. It is widely accepted that the degree of risk posed to an animal is associated with the response time imposed by the predator's hunting method (e.g. Sherman, 1977; Robinson, 1980). The variance in risk experienced by animals thus often coincides with the presence of different predator types. Raptors, for example, are fast hunters, and therefore present higher levels of risk to their prey than do canids, which attack less speedily. As vocalizations communicate this changing risk, usually raptors and terrestrial predators evoke different types of calls, but a raptor that is far away would elicit the same call type as a nearby terrestrial predator (e. g. Blumstein & Armitage, 1997a) because they present a similarly low level of risk. Alarm vocalizations that are distinct for each different predator type, regardless of the imminence of attack, constitute a different system of alarm calling. Rodents such as Gunnison's prairie dog, *Cynomys gunnisoni* (Slobodchikoff *et al.*, 1991), red squirrels, *Tamiasciurus hudsonicus* (Greene & Meagher, 1998), and Malaysian tree squirrels (genus *Callosciurus*) (Tamura & Yong, 1993) are among the species that classify predator types acoustically, with prairie dogs even discriminating between individual members of a certain predator species (Slobodchikoff *et al.*, 1991). These two types of alarm calling systems are referred to as "urgency-based" where different

calls signal different degrees of perceived risk, and "externally referential" where the predator type is indicated by vocalizations (Macedonia & Evans, 1993).

The present study investigates the alarm whistles of Brants' whistling rat, *Parotomys brantsii*, a colonial burrowing rodent occurring in the semi-arid regions of southern Africa (Kerley, 1997). These rodents have a number of aerial and terrestrial predators, including the pale chanting goshawk (*Melierax canorus*), jackal buzzard (*Buteo rufofuscus*), lanner falcon (*Falco biarmicus*), black-backed jackal (*Canis mesomelas*), yellow mongoose (*Cynicitis penicillata*), Cape cobra (*Naja nivea*) and puff adder (*Bitis arietans*) (Jackson, 1998a), and the alarm whistles evoked by intruders, including humans, are clearly audible (Nel & Rautenbach, 1974; Kerley, 1997).

Macedonia & Evans (1993) proposed that differences in the alarm call systems of mammals can be partly explained in terms of habitat complexity. Species that inhabit three-dimensional habitats, such as vervet monkeys and tree squirrels, typically have an alarm call system that classifies predator types (Seyfarth *et al.*, 1980; Tamura & Yong, 1993), whereas animals living in two-dimensional environments, such as ground squirrels, more simply indicate the perceived level of risk (Betts, 1976). This divergence is ascribed to the fact that tree-dwelling animals have a variety of escape options available to them, depending on the predator's hunting methods, which allows them to choose the most appropriate flight tactic. Ground squirrels, by contrast, simply flee into their burrows, and therefore the most crucial information that calls provide is an indication of the immediacy of the threat.

Parotomys brantsii are typically found in an open, treeless, sandy habitat (De Graaff & Nel, 1965; Jackson, 1999). As the only escape path is to flee into their burrows, their predator-avoidance options may be classified as two-dimensional, and we expect this species to have an urgency-based alarm call repertoire. However, behavioural observations reported in the literature indicate that *P. brantsii* can differentiate between types of predators. In reaction to birds of prey, the rats immediately flee into a burrow, whereas in response to a snake they remain above ground, vocalizing continuously (Kerley, 1997). This may be adaptive considering that a snake encountered within the tunnels of a burrow may be more dangerous than other predators. The aim of this study is thus to test whether *P. brantsii* has an urgency-based alarm call system or whether it differentiates between types of predators acoustically. For this purpose, we examine the structure of whistling rat alarm calls elicited by humans and compare them with the structure of those calls made in response to two other predators, the puff adder and jackal buzzard.

3.3 Materials and methods

3.3.1. Study area

The study was undertaken on a population of *P. brantsii* at Goegap Nature Reserve (29°37'S, 17°59'E) 10 km north-east of Springbok in the Northern Cape Province, South Africa. The vegetation characterizing this area is upland succulent Karoo (Low & Rebelo, 1996) with a mean annual rainfall of 160 mm. The study site was a sandy area 6 ha in extent, situated among hills dominated by Mesembryanthemaceae and winter ephemerals.

3.3.2. Study animals

Parotomys brantsii typically live singly within an extensive burrow system, except at high population densities when they may be forced to share burrow systems (Du Plessis & Kerley, 1990; Jackson, 1999), or prior to the dispersal of young from their natal burrow system (Jackson, 2000a). In the present study area, on average, burrows covered an area of 72.9 m^2, with 92 entrances (Jackson, 2000b). Burrow systems were situated 1 – 25 m apart and interconnected by a series of pathways along which rats travel freely (Jackson, 2000b). Together, this collection of burrow systems makes up a *P. brantsii* colony, which varied in size between 8 – 50 rats per ha during this investigation. *Parotomys brantsii* are strictly herbivorous (Du Plessis *et al.*, 1991; Jackson, 1998b) and forage almost exclusively within the boundaries of burrow systems (Jackson, in press). Consequently, for 79% of their foraging time, individuals remain within one metre of an entrance hole (Jackson, unpubl. data), making flight distances extremely small.

Individuals within the study population were live-trapped in mesh-wire cages baited with the succulent *Augea capensis*, sexed, weighed, and permanently marked by means of toe-clipping. Where the animals were not yet fully grown (under 85 g) they were marked for later identification in the field by dying their hair with *Clairol Nice 'n Easy* hair dye, and in the case of fully-grown adults, colour-coded neckbands consisting of cable-ties on which electric heatshrink had been melted (Jackson, 1998). Calls were recorded only from animals foraging independently and behaving as adult rats.

3.3.3. Experiment 1: Reaction to a human observer

Calls were recorded during fieldwork conducted intermittently between August 1999 and February 2000. During a preliminary study conducted in 1999, distances between calling rats and the observer (ALR) were recorded in addition to notes on the behaviour of the caller, to determine the effect of human distance on rats' acoustic and physical behaviour. In the main part of the study, the observer would walk around in the *P. brantsii* colony and identify callers while recording their vocalizations, noting only the caller's behavioural reaction. A constant slow walking rate was maintained, while distance between the rats and observer varied. Calls were classified as "human (bolt)" when a rat bolted towards safety, while calls emitted by a rat that remained above ground were classified as "human (stay)" calls. Hereafter these vocalizations are referred to as "human calls," with subsets of human (bolt) or (stay) calls. Calls uttered as part of a bout were considered separately in our initial analyses and will be referred to as "human (series)" calls. During calling bouts, callers would normally stand alert on their hind feet, watching the observer and tail-thumping irregularly.

3.3.4. Experiment 2: Reaction to a snake predator

Experiment 2 was conducted during January-February 2000. To test the reaction of *P. brantsii* to a puff adder, a stuffed adder skin (87 cm in length) was used, mounted on a narrow cardboard sledge attached to a 40 m long, thin nylon rope. A rat would be approached by the observer (ALR) while it was visible above ground at its burrow system, and as soon as it bolted into hiding, the recording equipment was placed close to the burrow system, hidden from view behind a bush 2 – 3 m from where the rat was expected to emerge. The snake model was then placed a short distance from the hole into which the rat had disappeared. The observer would walk away and stay at a

distance of approximately 20 m, where the rats would no longer react to her. The trial would begin as soon as the focal animal re-appeared and resumed foraging. The model was drawn past the rat by means of the rope, and only if the rat's reactions corresponded to the species' typical reaction to a live snake, were the recorded data utilized. If the rat did not display such behaviour it was assumed that it had not seen the model, or did not regard it as real. The typical reaction of the rat was to remain above ground, tail-thumping and producing a continuous bout of whistles, keeping its eyes fixed on the model while maintaining a stiff, quadrupedal body posture, and keeping a distance of approximately one metre between itself and the model as it approached. Twenty-nine of the 39 experiments were aborted because the rat failed to notice the snake, usually because the rat re-emerged from its burrow system too far from the path of the model snake. Control trials were run in February 2001 to verify that animals did not react merely to the presence of a nearby moving object, but recognized the model as a snake. Using the same protocol as above, the cardboard sledge (from which the model had been removed) was drawn past focal individuals and their vocal reactions were recorded on tape. These control trials were presented to 12 different individuals.

3.3.5. Experiment 3: Reaction to an avian predator

Experiment 3 was conducted over the same period as experiment 2. A stuffed buzzard (length from beak to tip of tail-feathers: 42 cm; wingspan: 93 cm) was "flown" across the burrow systems of marked individuals to simulate natural aerial attacks on *P. brantsii*. The experimental set-up comprised a model linked by a pulley system to a 50 m long stainless steel wire strung between two poles of different lengths. This was arranged so that the model would be between 1 and 1.5 m above the burrow system as

it "flew" past. Before the experiment, the sound equipment would be set up as per

experiment 2. The model raptor was mounted on the wire system, which had been set

up the previous day, and the observer would wait from a distance of approximately

20m for the focal animal to reappear. The model was released from this distance when

the rat had resumed normal foraging activities, and in each case resulted in the flight

of the focal individual. Although there was some noise when as the model ran along

the steel wire, it did not appear to affect the whistling rats. In all trials the rats would

look at the approaching model, and bolt only when it was right above them (a vertical

distance of between 1 and 1.5 m). In all cases the horizontal distance between the

model and the rat was less than 1.5 m. Vocalizations were rarely audible to the

observer but registered on the cassette tape. Ten successful trials were run, each from

a different individual.

All recordings were made on windless days during early morning (0645 – 1030) and

late afternoon (1630-1945) periods. A Marantz CP430 cassette recorder fitted with a

Sennheiser ME-66 microphone and windscreen was used throughout, and recordings

were made on tapes with a normal bias without filtering. The vocalizations were

digitised at a 32 kHz sampling rate on a personal computer and analysed by means of

the *Canary* software programme, which is largely dedicated to the analysis of

spectrograms (Charif *et al.*, 1995). For the analysis of our data we used a 699.40 Hz

bandwidth, -140 dB clipping level, logarithmic amplitude, and the Hamming window

function to create the graphics. A number of manual measurements had to be made

and a boxy display style was therefore chosen to facilitate the determination of call

duration, peak frequency at the overall peak amplitude of the call (hereafter referred

to as "dominant frequency"), and frequency bandwidth (the range between maximum

and minimum frequencies). No harmonics were observed. Additionally, call interval was measured as the time between subsequent calls in a bout, for both human and snake bouts.

3.3.6. Statistical analysis

Data were analysed using Statistica for Windows (StatSoft, Inc., 1996). For the statistical comparison of single human calls, the average of a minimum of three calls per individual was used. In the experiments with the raptor model, only one trial was run per individual and we could therefore analyse only a single bird call per individual. In the case of human (series) and snake calls, as well as the calls in response to the control sledge, the average values of all calls within a bout were used in making comparisons. Data were tested for normality and parametric or nonparametric tests were conducted as appropriate. Mann-Whitney U tests were used to compare human (bolt) with human (stay) calls, and these two call types were contrasted with human (series) calls using a nonparametric Kruskal-Wallis ANOVA. Whenever the Kruskal-Wallis ANOVA revealed a significant difference between groups, appropriate post-hoc tests were performed on the groups in question (following Siegel & Castellan, 1988). For human calls, stay and series calls were pooled because they were statistically indistinguishable. This combined data set was used in further comparisons with bird and snake calls. Snake and bird trials were conducted with the same 10 individuals, and therefore snake calls were compared with bird calls by means of paired t-tests. Snake calls were then compared with human (bolt) and (stay) calls, using one-way ANOVAs, and, where necessary, post-hoc comparisons of means were conducted using Newman-Keuls tests (Zar, 1984). Bird calls were compared similarly with the two human call types. Data from the control

trials were also contrasted with human, snake and bird trials using Kruskal-Wallis ANOVAs.

All calls were compared in terms of dominant frequency, total call duration, slope and plateau duration (to see which part of the call contributed most to variation in call duration), and frequency bandwidth.

3.4 Results

3.4.1. Experiment 1: Response to human observer

Noting behavioural responses in relation to distance between rat and observer, it was found the distance between an observer and rat was significantly smaller when it bolted than when it remained above ground (Students' t-test: $t = 8.571$, df $= 76$, $p < 0.001$). In the 17 cases in which the rat remained above ground, the animal was an average of 14.0 ± 1.0 m (mean $\pm$ SE) away from the observer, whereas bolting ($N = 61$ cases) resulted when the observer was an average of 5.5 ± 0.5 m away. These data were derived from a preliminary experiment on different rats to those used in subsequent experiments, excluding the possibility of habituation to humans affecting their outcome.

Further calls in response to a human observer were obtained for 13 female and 7 male *P. brantsii*. The typical call had a short upward frequency slope, falling between 6.2 and 12.0 kHz (for variation in this basic structure, see chapter 2). The call then leveled into a relatively uniform frequency plateau, which comprised the main part of the

vocalization. The dominant frequency was 10.0 ± 0.3 kHz, and the average duration of a whistle was 167 ± 1 ms. Of these twenty individuals, we had at least three calls of one type which could be classified as bolt ($N = 8$) and as stay ($N = 7$) calls respectively (in each case from different individuals). Comparing these two categories, we found no difference in dominant frequency (Mann-Whitney U tests: $U = 20$; $p = 0.355$)) or frequency bandwidth between the calls ($U = 28$; $p = 1.000$), but call duration was longer in stay calls ($U = 0$; $p = 0.001$) (Table 3.1, Fig. 3.1). Human (series) calls ($N = 13$) were then compared with human (bolt) and (stay) single notes. The dominant frequency (Kruskal-Wallis ANOVA: $H = 0.947$; df $= 2$; $p = 0.623$) and frequency bandwidth ($H = 0.953$; df $= 2$; $p = 0.621$) did not differ significantly between the three groups, but again, they differed in call duration ($H = 10.282$; df $= 2$; $p = 0.003$). Post hoc tests showed that human (bolt) calls were significantly shorter than human (series) and (stay) calls ($p < 0.05$), whereas human (stay) and (series) calls were equal in duration.
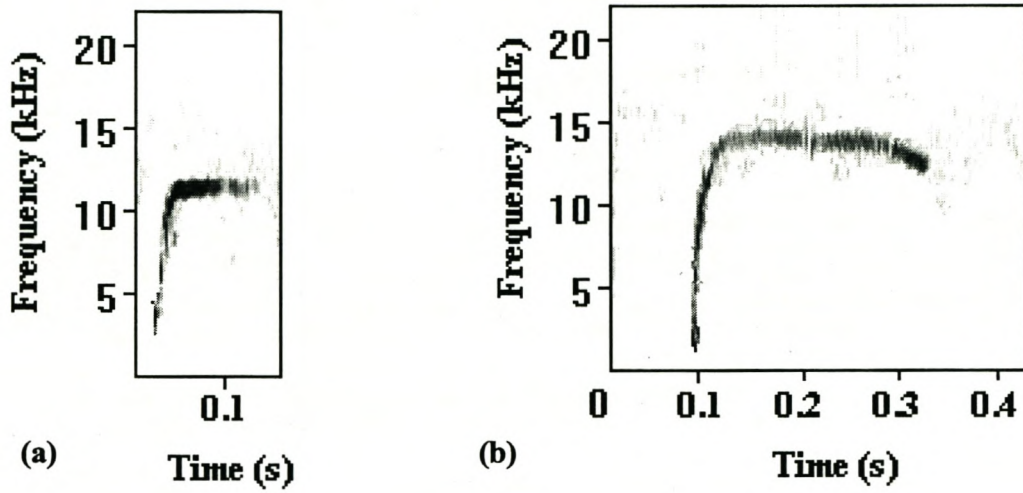
Fig. 3.1 The typical alarm calls of *P. brantsii* in reaction to humans. Spectrogram (a) represents a human (bolt) call, and (b), a human (stay) call. Note, in both cases, the initial upward frequency sweep and high frequency plateau. Human (stay) calls are often part of a bout of whistles and differ from human (bolt) calls in terms of call duration

TABLE 3.1 *The average values (±SE) for the dominant frequencies and duration of all call types of* **P. brantsii**. *There were no significant differences in dominant frequency, frequency bandwidth or slope duration between any call types. Different superscripts indicate significant differences between groups. Data for human stay and series calls did not differ in any respect, and were thus pooled before comparison with snake and bird calls*

Call type	Human (bolt)	Human (stay)	Human (series)	Bird	Snake	Sledge control
Dominant frequency (kHz)	9.7 ± 0.6	10.7 ± 0.5	9.9 ± 0.5	10.6 ± 0.4	10.9 ± 0.4	10.5 ± 0.6
Frequency bandwidth (kHz)	5.9 ± 0.8 [a, b]	6.4 ± 0.5 [a, b]	5.5 ± 0.7 [a, b]	7.4 ± 0.9 [a]	6.5 ± 0.6 [a]	3.3 ± 0.5 [b]
Total call duration (ms)	108 ± 20 [a]	243 ± 20 [b]	215 ± 25 [b, c]	98 ± 20 [a]	184 ± 13 [b]	351 ± 15 [c]
Slope duration (ms)	18 ± 3	22 ± 4	31 ± 2	27 ± 4	28 ± 2	31 ± 4
Plateau duration (ms)	96 ± 10 [a]	221 ± 21 [b]	183 ± 24 [b]	71 ± 17 [a]	158 ± 12 [b]	320 ± 14
N	8	7	13	10	10	5

On this basis, calls uttered in series were classified as human (stay) calls that were performed repetitively and human (stay) calls were pooled with (series) calls in comparisons with bird and snake calls. Even though the difference between these pooled stay and bolt calls was highly significant, there was some overlap in duration between the shorter (pooled stay) and longer (bolt) calls (Fig. 3.2), indicating that there is a gradual, not abrupt, transition between human (bolt) and (pooled stay) calls. The average call interval within a bout of whistles was found to be 7.0 s (range 0.5 – 23.0s). In all observed bouts, there was substantial variability in call intervals.
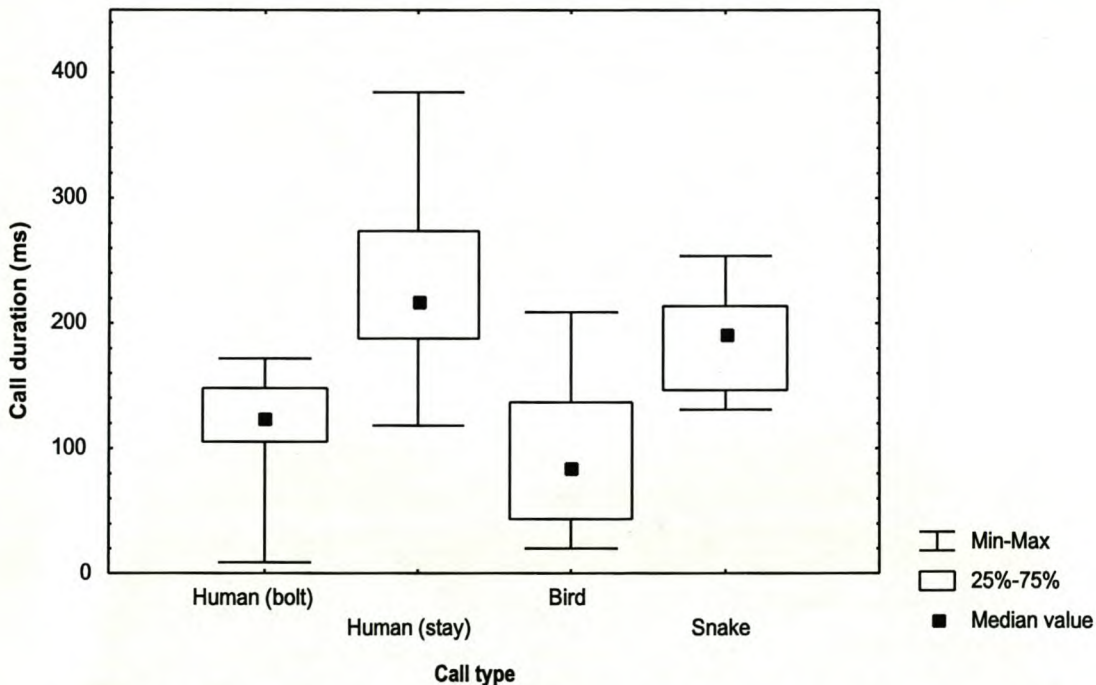
Fig. 3.2 The duration of the alarm calls made by *P. brantsii* in response to different predators. The human (stay) calls indicated on this figure are the pooled data from single human (stay) and (series) data, which were identical to one another (see text). These pooled human (stay) calls are different from human (bolt) and bird calls in terms of call duration. Snake calls are significantly longer than bird and human (bolt) calls, but there is considerable overlap in duration between all different call groups

3.4.2. Experiment 2 and 3: Response to a snake or aerial predator

The alarm call profiles in response to snake and aerial predators were not different from those of alarm calls to humans, and both consisted of an upward frequency slope leading to a high, relatively constant plateau that was short in bird calls, and long in snake calls (Fig. 3.3 a, b; Table 3.1).
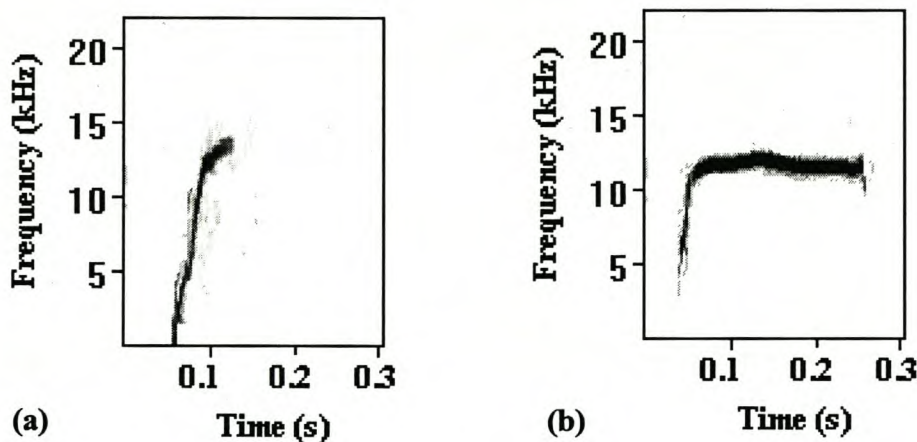
Fig. 3.3 The alarm calls made by *P. brantsii* in response to (a) the avian model, and (b) the snake model, which differ from one another in terms of call duration.

Therefore, we suspected that *P. brantsii* did not classify predators acoustically. Dominant frequency differed between snake and bird calls (Paired t-test: $t = -2.537$; df $= 9$; $p = 0.032$), with that of snake calls being only marginally higher. In comparisons between human, snake and bird calls, trials repeated with the same individuals were omitted from the data set, resulting in $N = 10$ for human (bolt) calls, $N = 14$ for pooled human (stay) calls, and $N = 10$ each for the bird and snake calls (total N for each ANOVA = 34). There were no differences between snake and human calls ($F = 1.107$;

df = 2; *p* = 0.343) or bird and human calls (*F* = 0.184; df = 2; *p* = 0.833) in terms of peak frequency. Frequency bandwidth did not differ between snake and bird calls (*t* = 0.828; df = 9; *p* = 0.429) nor between snake, human (bolt) and (stay) calls (*F* = 0.678; df = 2; *p* = 0.515). There was also no difference in frequency bandwidth between bird, human (stay) and (bolt) calls (*F* = 1.669; df = 2; *p* = 0.205).

Total call duration was considerably higher in snake than bird calls (*t* = -4.202; df = 9; *p* = 0.002). Total duration between snake and human calls also differed significantly (*F* = 7.845; df = 2; *p* < 0.002), as did bird and human calls (*F* = 10.688; df = 2; *p* < 0.001). Post hoc Newman-Keuls tests showed that the differences (*p* < 0.05 in all cases) lay between human (stay) and (bolt) calls, snake and human (bolt) calls, and human (stay) and bird calls. Human (stay) calls were similar to snake calls and human (bolt) calls were similar to bird calls.

The duration of the slope and plateau (table 3.1) were compared between the different call types. The slope duration was similar between snake and bird calls (*t* = -0.313; df = 9; *p* = 0.762), snake and human calls (*F* = 3.179; df = 2; *p* = 0.056), as well as bird and human calls (*F* = 2.060; df = 2; *p* = 0.145). Plateau duration differed between snake and bird calls (*t* = -4.982; df = 9; *p* < 0.001), snake and human calls (*F* = 4.819; df = 2; *p* = 0.015), and bird and human calls (*F* = 10.233; df = 2; *p* < 0.001). According to post hoc Newman-Keuls tests, the differences (*p* < 0.05) lay between human (bolt) and (stay) calls, and human (stay) and bird calls. Human (stay) calls were similar to snake calls, and bird calls were similar to human (bolt) calls. On average, for all call types, the plateau comprised 79 $\pm$ 3 % of the total call duration. Calls made in response to snakes are always uttered in bouts, with the average call

interval of 14s (range between 3 s and 44 s), which is longer than the call interval between human (series) calls (t-test: $t = 3.009$; df = 8; $p = 0.017$).

The behavioural reactions of animals in response to the control sledge on no occasion resembled the reaction exhibited in response to the snake model. Focal rats ($N = 12$) would notice the sledge and visually track it as it approached, in some cases vocalizing (5 out of the 12 times). In three instances rats bolted underground as the sledge jerked unexpectedly, but the animals always reappeared. The fact that they bolted into the burrows implies that the sledge was not regarded as a snake, because snakes are more dangerous if encountered within a burrow than above ground. On the other nine occasions the rats were simply more vigilant for a short period, and then resumed foraging. The vocalizations made in response to the control sledge did not have a unique spectral structure (Fig. 3.4, Table 3.1).
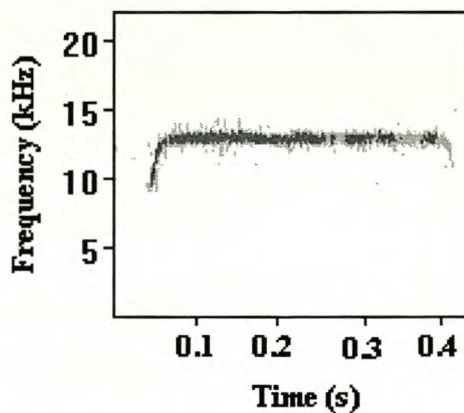
Fig. 3.4 An example of the alarm calls made by *P. brantsii* in response to a control sledge moved past the warrens. The calls were similar to human (stay) calls, and the behavioural responses of *P. brantsii* showed that the sledge was not mistaken for a snake.

These calls were compared with human, bird and snake calls in two sets of Kruskal-Wallis ANOVAs (this was necessary in order to avoid repeated measures for the snake and bird trials, which were performed on the same individuals), and the results are summarized in table 3.2. Total duration and frequency bandwidth differed significantly between the groups for both comparisons, and post hoc tests were performed to determine which groups were distinct. These tests indicate that control sledge calls had a narrower frequency range than either snake or bird calls and longer duration than either of these two calls and human (bolt) calls ($p < 0.05$ in all cases). The control sledge calls are, in other words, extremely long duration vocalizations of a rather narrow bandwidth (Table 3.1), similar to human (stay) calls in all respects (post-hoc test; $p > 0.05$).

TABLE 3.2 – *Results of the comparisons between* **P. brantsii** *calls from control sledge trials and the four other call types: snake, bird, human (stay) and human (bolt) calls. Kruskal-Wallis ANOVAs were performed in each comparison. Control* **N = 5;** *bird* **N = 10;** *snake* **N= 10;** *bolt* **N = 10;** *and stay* **N = 14. Two sets of comparisons were performed in order to avoid repeated measures for snake and bird calls.**

Parameter used	For control: snake: bolt: stay		For control: bird: bolt: stay	
Test statistics	*H*	*p*	*H*	*p*
Call duration	19.980	< 0.001	21.675	< 0.001
Dominant frequency	2.307	0.511	0.298	0.960
Frequency bandwidth	8.138	0.043	8.518	0.036

In summary, the alarm calls of *P. brantsii* do not vary in spectral structure with predator type. Only call duration varies between call "types:" long duration being associated with remaining stationary above ground; and short duration being associated with bolting towards the safety of a burrow. *Parotomys brantsii* alarm calls may therefore be divided into two call "types" namely "stay" and "bolt" calls. "Bird" and human (bolt) calls fall in the latter category, whereas "snake", "control sledge" and human (stay) calls are all in the former group.

3.5 Discussion

Parotomys brantsii's typical alarm call is a high-pitched whistle of short duration that can be uttered singly or in bouts of calls. The calls are simple, with an initial upward frequency sweep leading to a relatively uniform frequency plateau. This basic call structure does not vary significantly between individual callers, or in relation to call-evoking stimuli.

Once it has been seen, a snake presents a relatively low predation threat, as rats will usually be able to escape, remaining above ground, before a snake can attack. However, a raptor flying overhead presents a higher risk due to the speed with which it can mount an attack (Curio, 1976; Robinson, 1980). The danger associated with a human presence is variable and reflected by the distance between the observer and rat. While the distance between an observer and the rat determines whether the rat bolts or not, the distance between the rat and a bolt-hole should not normally affect this

decision greatly, as rats spend most of their time within 1 m of a burrow entrance (Jackson, in press). The duration of vocalizations varies consistently between calls elicited during high-risk and low-risk situations: long calls being associated with low risk (snake and distant human threats) and short calls with high risk (raptor and close human threats). It could be deduced from their differential behavioural responses to humans, the two predator models, and the control sledge, that *P. brantsii* can distinguish between different predators and choose the appropriate response in any situation, but this discriminative ability is not necessarily reflected in their alarm call repertoire. Similarly, Belding's ground squirrels, *S. beldingi*, discriminate between predators and non-predators, but their alarm vocalizations are indications of the risk presented by the predator, not its identity (Robinson, 1980).

We conclude that the alarm call repertoire of *P. brantsii* is an urgency-based system, as contrasted with an externally referential system in which predator types are identified (Macedonia & Evans, 1993). In externally referential systems calls for different predator types are completely distinct (e.g. Pereira & Macedonia, 1991). Repertoires conveying risk, by contrast, are often graded (e.g. Blumstein, 1999), as appears to be the case in *P. brantsii* calls, for which call duration changes gradually, not abruptly (see Fig. 3.2). An urgency-based alarm structure is the predominant type of call system amongst ground-dwelling colonial sciurids (Betts, 1976), which are faced with limited escape options compared to animals living in a three-dimensional habitat. In *P. brantsii*, decreasing the duration of single calls seems to communicate increased risk, and in calling bouts levels of danger could also be indicated by varying the call interval, as reported by Weary and Kramer, (1995) for eastern chipmunks, *Tamias striatus,* and Blumstein and Armitage, (1997a) for yellow-bellied marmots,

Marmota flaviventris. Alternatively, bouts could maintain a high level of vigilance in conspecifics (Schleidt, 1973; Owings *et al.*, 1986).

Furthermore, as *P. brantsii* inhabits a quite sparsely vegetated environment, external contextual clues such as the sighting of a predator can play a substantial role in mediating the behaviour of conspecifics (Marler *et al.*, 1992) and complex alarm signals should not be necessary to specify the exact nature of the referent that elicited the calls (Smith, 1969). Another factor associated with such an open habitat is that callers might be conspicuous to predators. In birds it has been observed that alarm calls with a narrow frequency bandwidth are hard for predators to locate (Marler, 1955; Klump & Shalter, 1984), and this may be the reason why human (series) calls have such a narrow frequency bandwidth, making the calls ventriloquial in nature.

Compared to the vocalizations of colonial rodents in the genus *Marmota* (Blumstein, 1999), or *Spermophilus* (Leger *et al.*, 1984), the dominant frequency of *P. brantsii* calls is relatively high, which could be attributed to the comparatively smaller body size of *P. brantsii* (Nowak & Paradiso, 1983; Coetzee & Jackson, 1999). As the size of the animal producing the sound constrains its frequency (smaller animals usually emitting higher calls), and due to acoustic impedance mismatch, it is often energetically advantageous for small animals to generate high frequency vocalizations (Ryan & Brenowitz, 1985). Strong winds frequent the area where the investigation was centred (Jackson, 1998b) and wind-generated noise occurs predominantly at low frequencies (Ryan & Brenowitz, 1985). Thus, even though high-pitched sounds attenuate rapidly in any given habitat, they may be advantageous in overcoming this ambient noise (Konishi, 1970). The simplicity of *P. brantsii*'s alarm call repertoire

may be linked with their simple social structure, as defined by Blumstein & Armitage (1997b), but this needs to be tested by comparing their repertoire with that of closely related species. Unfortunately, the data available on the vocalizations of the family Muridae, reports mainly on social calls elicited in laboratories, and not predator-induced alarm calls (e.g. Houseknecht, 1968; Watts, 1975; Hafner & Hafner, 1979)

Parotomys brantsii has a relatively simple alarm call repertoire consisting of simple whistles that indicate the level of threat perceived by means of graded variation in call duration, low risk being associated with long calls and high risk with short calls. However, playback experiments are needed to confirm that receivers respond differentially to differences in call duration. Vocalizations made in bouts probably function to maintain a heightened state of vigilance in conspecifics, and an increase in risk may be reflected by an increased rate of calling.

3.6 Acknowledgements

3.7 References

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CHAPTER FOUR

THE EFFECT OF CHANGING CALL DURATION AND CALLING BOUTS ON VIGILANCE IN BRANTS' WHISTLING RAT, *PAROTOMYS BRANTSII* [†]

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Short title: Whistling rat reaction to alarm calls

4.1 Summary

The function of variation in single call duration and alarm calling bouts was investigated in Brants' whistling rat, *Parotomys brantsii,* by means of playback experiments and video analyses of the resultant vigilance. Short calls are produced in high-risk situations, and long calls in low-risk encounters, but apparently do not communicate this variance in risk to conspecifics. Both short and long single calls induced heightened vigilance in receivers, but rats did not respond differentially to the two call types, and it was concluded that *P. brantsii* alarm calls are not functionally referential. Multiple calls maintain a state of increased alertness in receivers for a longer period than single calls, even after the bouts had ended, but long bouts did not lead to longer periods of vigilance than shorter bouts. Natural variation in alarm call intervals may prevent rats' habituation to the continuous alarm signal.

Key words: playback experiments, tonic communication.

4.2 Introduction

The alarm call repertoires of many colonial rodents have been investigated by means of experiments using both live and model predators (e.g. see review by Betts, 1976; Robinson, 1980; Schwagmeyer, 1980; Greene & Meagher, 1998). A few studies have also focused on reactions to conspecific alarm calls using playback experiments (e.g. Owings *et al.,* 1986; Blumstein & Armitage, 1997; Hare, 1998), as an understanding of any alarm call repertoire is incomplete without knowing how animals react to conspecific vocalizations (Macedonia & Evans, 1993). Investigating animals'

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reactions to vocalizations is important to ascertain the biological significance of "scientific" classifications of calls, as differences between vocalizations perceived by humans may not be perceived by animals themselves as differences (Smith, 1965).

Alarm vocalizations can generally be described as either single or repetitive signals. Alarm calling repertoires consisting of single calls and calling bouts have been recorded in a variety of colonial rodents such as the eastern chipmunk, *Tamias striatus* (Burke da Silva *et al.*, 1994), and numerous members of the genera *Spermophilus* (Leger *et al.*, 1984; Owings *et al.* 1986; Hare, 1998) and *Marmota* (Blumstein, 1999). Single alarm calls usually serve to warn unalert group members, but subsequent vocalizations reach the ears of conspecifics that have already been warned. Such multiple calls must therefore have another function. Schleidt (1973) proposed the theory of tonic communication, defined as "a form of communication in which discrete signs are repeated by the transmitting animal… [having]… a continual effect on the receiving animal, reflected in a gradually changing or steadily maintained behavioural output." In the case of alarm calling behaviour, a tonic effect would therefore lead to a maintained level of heightened vigilance in receivers.

This tonic communication theory has been cited by some authors to explain the occurrence of calling bouts (e.g. Owings *et al.*, 1986; Hare, 1998) but the theory has not yet been widely tested. We found only two studies that had set out to test the long term effect of multiple calls on conspecifics, one in California ground squirrels, *Spermophilus beecheyi* (Loughry & McDonough, 1988), and another on marmots of the genus *Marmota* (Blumstein, 1999). In both studies evidence was found that alarm

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calling bouts cause the maintenance of longer periods of high vigilance than do single calls.

Brants' whistling rat, *Parotomys brantsii,* has a relatively simple alarm calling system consisting of single calls (whistles) that vary in length to indicate gradually changing levels of risk, and these simple calls are often uttered in bouts (chapter 3). The classification of *P. brantsii*'s alarm call repertoire as a graded, urgency-based system has been made on the grounds of a correlation between the callers' behavioural context, and call duration. Long (stay) calls are associated with low-risk situations such as the presence of far-off humans, whereas short (bolt) calls are uttered in high-risk encounters, usually with raptors or nearby humans. *Parotomys brantsii* calls satisfy the criteria for production specificity, as production specific signals must be consistently produced in reaction to specific, unchanging referents (Macedonia & Evans, 1993). Referents of a display can either be "external" factors such as the presence of a predator, or may be "internal" factors, such as motivation (Smith, 1981). In the case of *P. brantsii* these referents are not specific predators, but distinct behavioural responses of callers – i.e. bolting rats utter short calls, and stationary rats, long calls, which are statistically distinguishable from one another and reflect the degree of risk experienced by the caller (chapter 3). The response of *P. brantsii* to conspecific alarm calls remains unknown, and is examined in this study. The first aspect of the investigation is the study of the effect that single calls of varying duration have on rats. Secondly, the function of calling bouts is examined. Loughry and McDonough's paper (1988) detailed some clearly defined predictions of the tonic communication theory, whereas Blumstein (1999) tested only the general effect calling bouts have on vigilance. In the former paper, the researchers studied receiver

vigilance during naturally occurring calling bouts, whereas in the latter, controlled playback experiments were conducted. In this experiment, we use call playbacks instead of naturally occurring bouts, and examine vigilance according to two predictions based on those detailed in Loughry and McDonough's paper (1988). Our playback experiment is designed to control for confounding factors such as the identity of the callers (Hare, 1998), fluctuating call interval (Blumstein & Armitage, 1997), as well as the distance between the receiver and the unseen risk (Leger & Nelson, 1982). All these factors may influence the vigilance behaviour of receivers (see Elgar, 1989, for review), and by controlling for them, we should be able to demonstrate the effect of calling bouts on *P. brantsii*, and investigate whether tonic communication occurs in these rodents.

4.3 Materials and methods

The study was conducted in January-February 2001 at Goegap Nature Reserve, in the Northern Cape Province of South Africa. A previously recorded alarm call of *P. brantsii* was manipulated using the software programme Cool Edit Pro to produce a long single call, short single call, short and long bout of calls (Table 4.1). The durations for the short and long calls are the average durations of short (bolt) and long (stay) calls in *P. brantsii,* and vocalizations in *P. brantsii* alarm calling bouts are typically long (stay) calls, with an average call interval of seven seconds (chapter 3). These calls were presented to a colony of *P. brantsii,* in which individuals had been marked by means of neckbands made out of cable ties on which colour-coded electric heatshrink had been melted. The calls were presented at a constant volume that was

similar to the average volume of naturally produced calls (pers. obs.). The exact playback volume was determined by means of a Brüel Kjaer integrating sound level meter (model NL-05) set at C frequency weighting and slow time weighting. The average volume was 61.1 dB, measured from a horizontal distance of 1m at ground level (with an error of $\pm$ 1.0 dB). Average wind speed at the site was 9.1 $\pm$ 0.5 km/ h (mean $\pm$ SE), with an average temperature of 24.3 $\pm$ 0.8 °C.

TABLE 4.1 – *The calls used in playback trials. Members of a* **P.** **brantsii** *colony were presented with each of these trials, and their responses were recorded. A control period, during which no calls occurred, was also recorded for each individual.*

Trial	Call duration (ms)	Number of calls	Total duration (s)
Short single	117	1	0.1
Long single	238	1	0.2
Short bout	238	5	29
Long bout	238	10	64

Each one of the trials (Table 4.1) was presented to 22 different rats in a random order, and control trials were also run, by observing the behaviour of individuals when no alarm calls were sounded. Trials were conducted by placing the right speaker of the AIWA Active Speaker System, model SC-A47, obscured behind some vegetation, on the warren closest to the home warren of each individual (an average distance of 8.5 m away, ranging between 7 m and 11.5 m). The position of the speaker was varied slightly between trails for each individual. During each trial calls were played through the speaker, and the behaviour of rats was recorded on a Sony Handicam camcorder,

model CCD-TR 315E PAL from a distance of 17 – 20 m. The camcorder was mounted on a tripod to reduce the effects of observer movement on the focal rats. Trials were commenced only when no natural alarm calls had been made for 3 minutes, and if the focal individual was unalert. Each video recording was 3 minutes long, measured from the moment the first alarm call was played (or simply three minutes without calls when control trials were conducted). No more than one trial was conducted per rat per day, and we did not repeat a trial more than once per animal if the trials failed, in order to reduce the possibility of habituation.

Recordings were carefully viewed to measure the time every rat spent vigilant and unalert. Each trial period of three minutes was divided into a first and second half (1.5 minutes each), hereafter referred to as the first and second time divisions. A rat that was eating, digging, or foraging, was classified as unalert, whereas a vigilant rat would cease all foraging activities and look at the observer, either in a quadrupedal or bipedal position (Fig. 4.1). The levels of vigilance were determined as the proportion of time spent either quadrupedally or bipedally alert during the first and second time divisions, and during the entire three minute period of each trial. These ratios were arcsine transformed to ensure homogeneity of variance and data were tested for normality by means of the Kolmogorov-Smirnov test. All statistical tests were non-parametric because the data were not normally distributed for all trials (Siegel & Castellan, 1988).
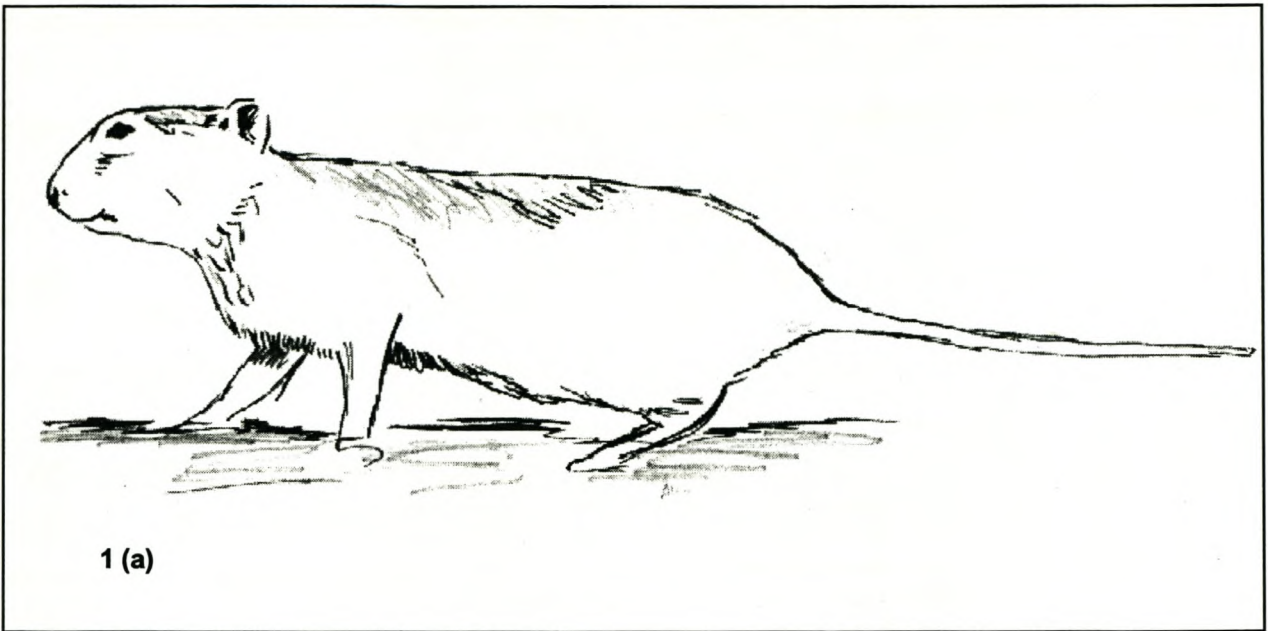
Fig. 4.1 (a-b). These figures illustrate the postures that vigilant *P. brantsii* individuals exhibit. Fig. 4.1 (a) shows a quadrupedally alert rat, and fig. 4.1 (b) depicts a bipedally alert rat. Individuals ceased all foraging and feeding behaviour while in either of these vigilant states. (Drawings by ALR)

4.3.1. Variation in single call duration

The first hypothesis we set out to test was that short single calls indicate a higher level of risk than long single calls based on predictions made in an earlier paper (chapter 3). This implied that (a) rats would be more likely to bolt in reaction to short calls than long calls, and (b) vigilance in response to short calls would be higher than in response to long calls. Both types of single call were predicted to induce higher levels of vigilance than control trials. The frequency with which rats bolted was calculated for each call type and compared between short and long calls by means of a chi-square test. Variation in vigilance was tested as follows: For each single call, vigilance in the first and second time division was compared with control data using a Friedman ANOVA. The two call types were contrasted with one another by means of Wilcoxon matched pairs tests, contrasting the first and second time division with the corresponding time division in the comparative call type.

4.3.2. Tonic communication theory

The second hypothesis tested was that calling bouts fulfil the function of tonic communication. The predictions stemming from this hypothesis, were that (a) calling bouts would induce longer periods of high vigilance than single calls, and (b) longer bouts would lead to longer periods of high vigilance than short bouts. Bouts were compared with long single calls, as natural calling bouts typically consist of long calls (chapter 3). Each time division of the long single call trials was compared with the corresponding time divisions of the short and long bout, using a Friedman ANOVA. Wilcoxon matched pairs tests were done to compare the two types of bout with one another, comparing each time division between bout types.

In all statistical tests, each comparison was made firstly for the separate levels of vigilance, and secondly for total vigilance (sum of quadrupedal and bipedal vigilance) calculated per time division. Lastly, the total vigilance across the entire three-minute period was compared between trials. All statistical tests were performed using the software program Statistica (StatSoft Inc., 1996).

4.4 Results

Twenty-two different animals (12 males and 10 females) were used in the experiment. Two individuals were killed by predators before the end of the study. Animals typically reacted to playbacks by looking at the observer (ALR), and not at the speaker, indicating that the playbacks were perceived as naturally produced calls in response to the presence of possible danger (i.e. natural calls elicited by the observer). Total vigilance measured over the total three minute period during control trials, was 0.065 ± 0.020 (mean $\pm$ SE) ($N = 22$), during short single call trials, 0.438 ± 0.103 ($N = 21$), and during long single call trials, 0.250 ± 0.078 ($N = 21$). Short bouts evoked a total vigilance of 0.643 ± 0.106 ($N = 21$) over three minutes, and long bouts, 0.589 ± 0.082 ($N = 21$).

### *4.4.1. Variation in duration of single calls*

Vigilance induced by both long and short single calls was significantly higher than control data (Fig. 4.2 a-c). For the short single calls, there were significant differences between control trials, first and second time divisions in terms of quadrupedal (Friedman ANOVA: χ^2 ($N = 21$, df = 2) = 6.537; $p < 0.038$), bipedal (χ^2 ($N = 21$; df = 2) = 8.037; $p < 0.018$) and the total vigilance within each time division (χ^2 ($N = 21$; df = 2) = 14.354; $p < 0.001$). Post hoc tests indicated that in all three cases, the vigilance in the first time division of short single call trials was significantly higher than the vigilance during control trials ($p < 0.05$). For quadrupedal and total vigilance, the vigilance in the second time division of short single call trials was also higher than during control trials ($p < 0.05$).

In similar comparisons between long single calls and control trials, significant differences between groups were detected for quadrupedal (χ^2 ($N = 20$; df =2) = 6.533; $p < 0.038$) and total vigilance (χ^2 ($N = 20$; df = 2) = 11.49, $p < 0.003$), but not for bipedal vigilance (χ^2 ($N = 20$; df = 2) = 4.308; $p < 0.116$). The source of the significant variation in both quadrupedal and total vigilance was the difference between control data and the first time division of long single calls, and the difference between first and second time division vigilance of long single calls (all post hoc tests: $p < 0.05$).

The two single call trials were compared with each other, but showed no significant differences. In the first time division neither quadrupedal (Wilcoxon matched pairs test: $N = 20$; $T = 72.0$; $z = 0.926$; $p = 0.355$), bipedal ($N = 20$; $T = 26.0$; $z = 1.931$; $p = 0.054$), nor total vigilance ($N = 20$; $T = 79.0$; $z = 0.971$; $p = 0.332$) differed between

the two trials. This was also true for quadrupedal ($N = 19$; $T = 40.0$; $z = 0.785$; $p =$ 0.433), bipedal ($N = 19$; $T = 24.0$; $z = 1.177$; $p = 0.239$) and total vigilance ($N = 19$; $T = 45.0$; $z = 1.764$; $p = 0.078$) in the second time division. The rats seldom bolted in reaction to playbacks, and the proportion of times that rats bolted did not differ between the two types of single call (chi-squared test: $\chi^2 = 0.23$; df $= 1$; $p = 0.634$).
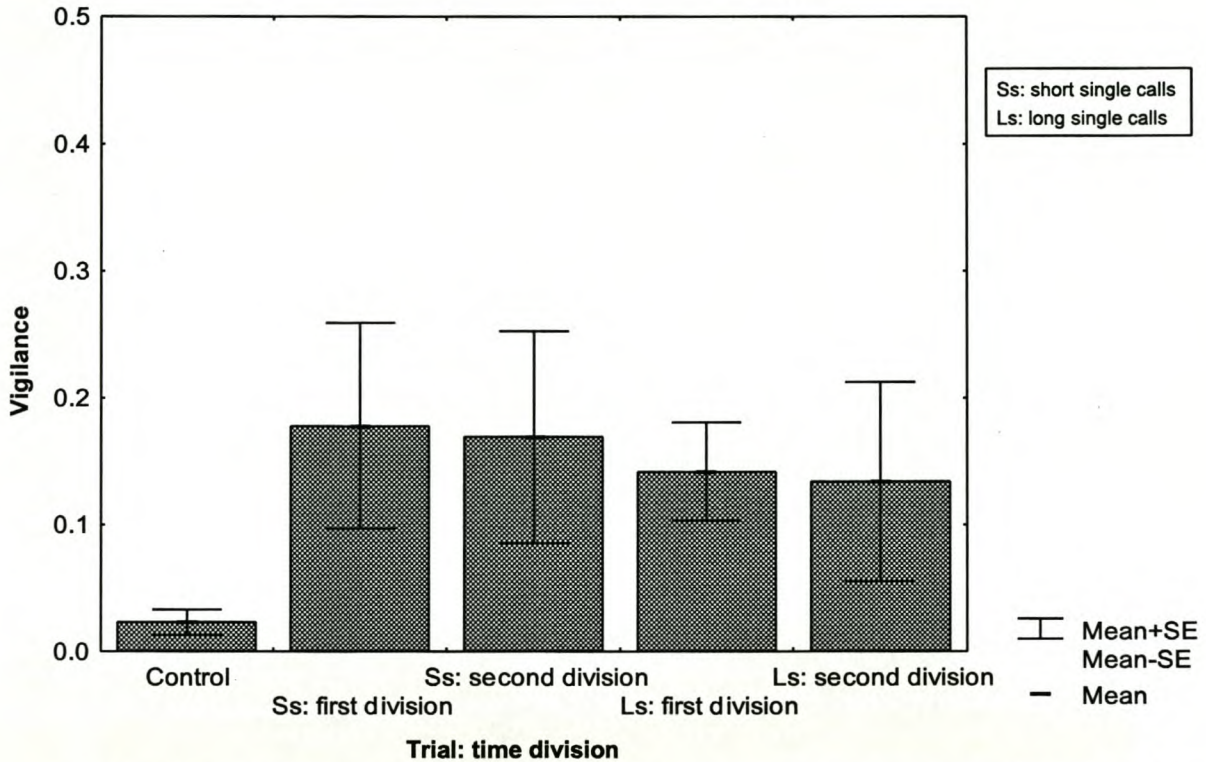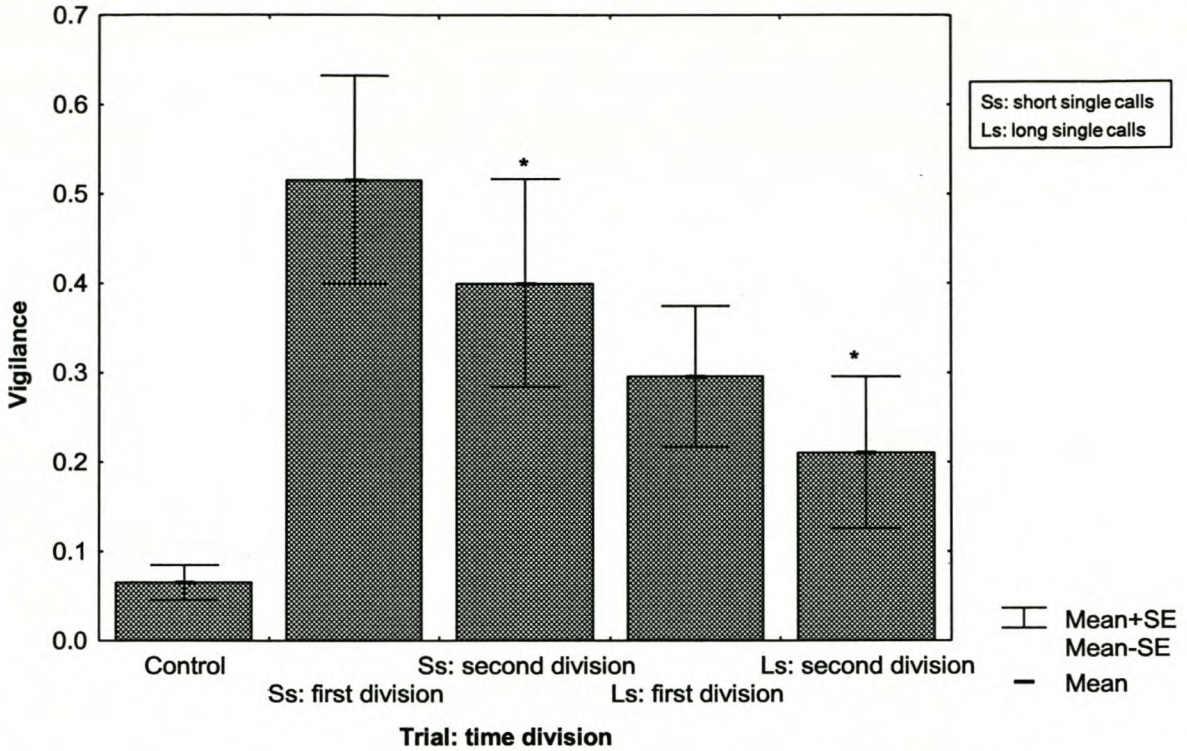

Fig. 4.2 (a) Quadrupedal vigilance compared between long and short single calls of *P. brantsii*. In all trials quadrupedal vigilance was significantly higher than control levels (Friedman ANOVA: $p < 0.05$ in each case; $N = 20$), but the two call types did not differ from one another.
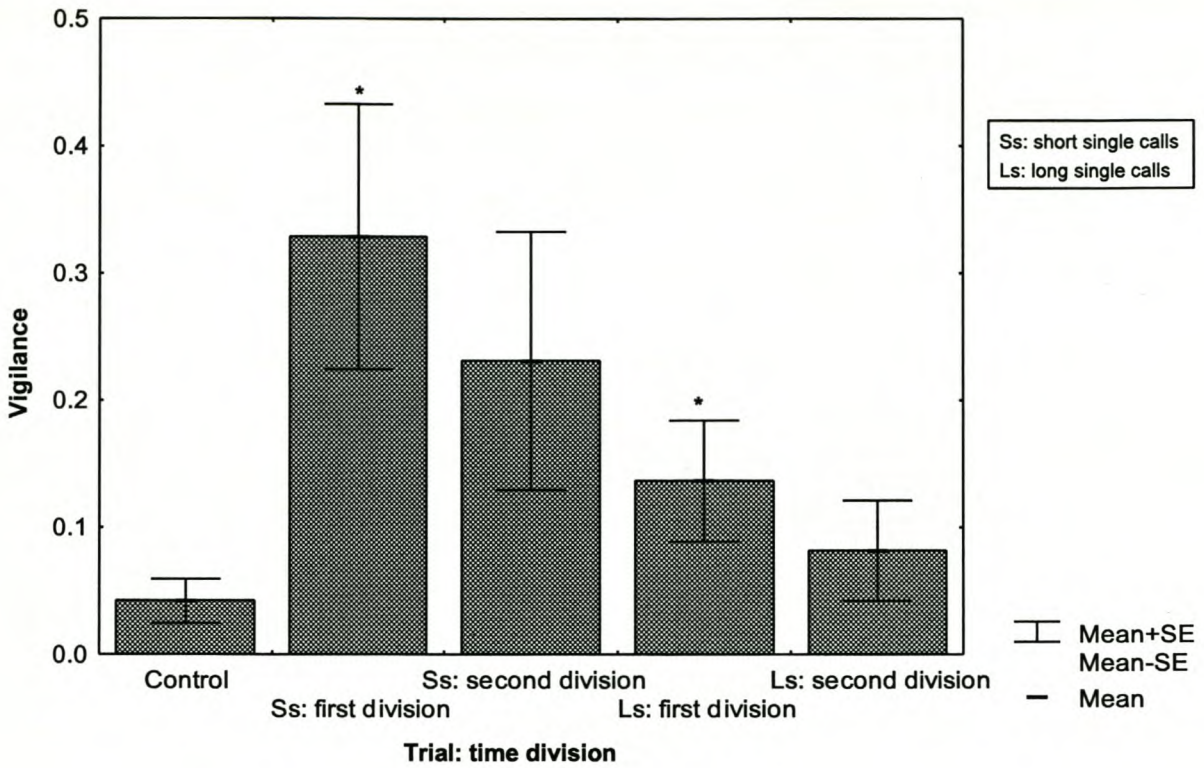
Fig. 4.2 (b) Bipedal vigilance compared between short and long single calls in *P. brantsii*. Bipedal vigilance was significantly higher than control levels for each time division (Friedman ANOVAs: $p < 0.05$; $N = 20$) except between the long single calls' second time division and control (post-hoc test: $p > 0.05$). Vigilance during the first time division of the short single calls was marginally higher than that of the long single calls (Wilcoxon matched pairs test: $p = 0.054$; $N = 20$; indicated by *); other comparisons are not significantly different.

Fig. 4.2 (c) Comparison of total vigilance between single calls of *P. brantsii*. Again, for all time divisions, vigilance was significantly higher than control levels (Friedman ANOVAs: *p* < 0.05; *N* = 20). A marginally significant difference was found between the second time divisions of short and long calls (Wilcoxon matched pairs test: *p* = 0.078; *N* = 20; indicated by *); other comparisons are not significantly different.

4.4.3.Tonic communication

The comparisons between long single calls, short and long bouts supported the first prediction of the tonic communication hypothesis. The separate levels of vigilance did not differ significantly between any of the groups, but the total vigilance calculated for each time division, showed substantial variation (Fig. 4.3 a-c). For the first time division, quadrupedal (Friedman ANOVA: χ^2 ($N = 19$; df $= 2$) $= 1.971$; $p < 0.373$) and bipedal vigilance (χ^2 ($N = 19$; df $= 2$) $= 1.508$; $p < 0.471$) did not vary between the three groups. This was also true for the second time division's quadrupedal (χ^2 ($N = 18$; df $= 2$) $= 1.926$; $p < 0.382$) and bipedal vigilance (χ^2 ($N = 18$; df $= 2$) $= 4.203$; $p < 0.122$). The total vigilance for the first time division did not differ between the three trials (χ^2 ($N = 19$; df $= 2$) $= 5.528$; $p < 0.063$), but the second time division did vary significantly (χ^2 ($N = 19$; df $= 2$) $= 11.425$; $p < 0.003$). Post hoc tests showed that the single call elicited significantly lower levels of vigilance than both the short bout and long bout ($p < 0.05$). Total vigilance across the three minute periods of each trial differed significantly between the three trials (χ^2 ($N = 19$; df $= 2$) $= 11.760$; $p < 0.003$). The long single call again proved to be lower in vigilance than both the short bout and long bout (post hoc test, $p < 0.05$).

The short bout and long bout were compared with one another, and showed no significant variation in terms of separate levels of vigilance or total vigilance (Table 4.2).
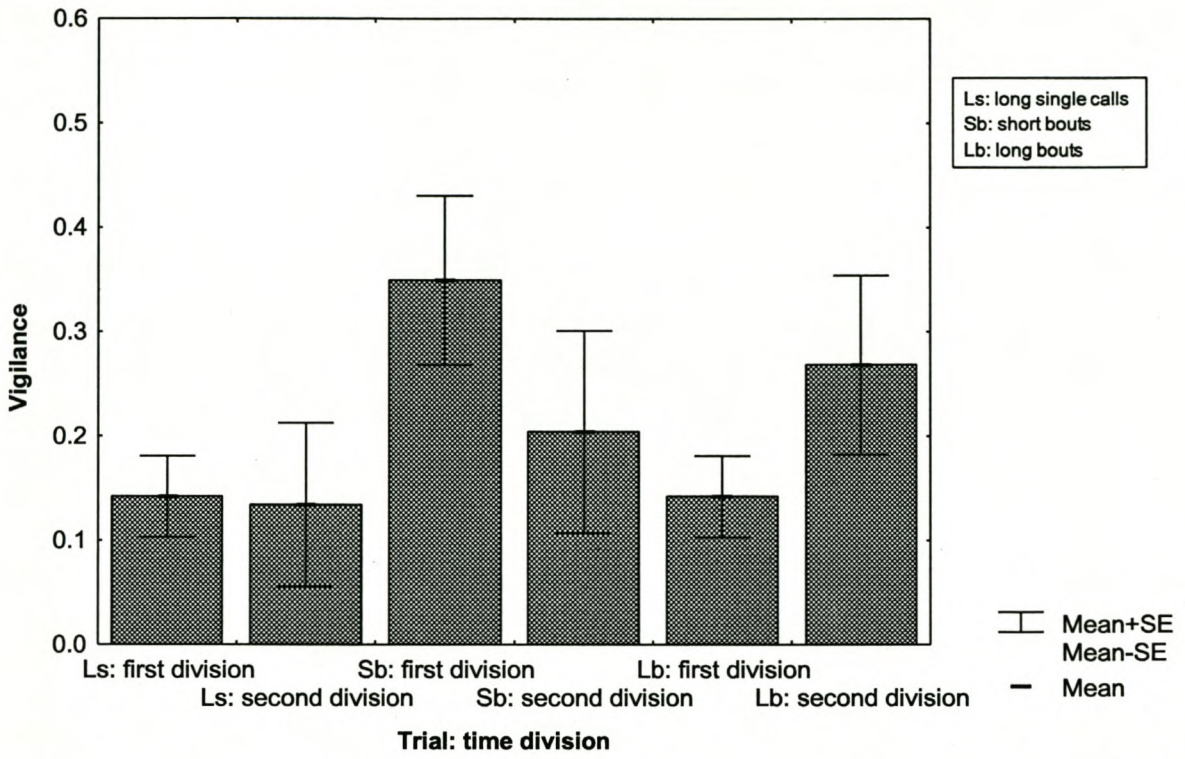
Fig. 4.3 (a) A comparison of quadrupedal vigilance between long single calls and call bouts of *P. brantsii* (*N* = 19). There were no significant differences between the trials.
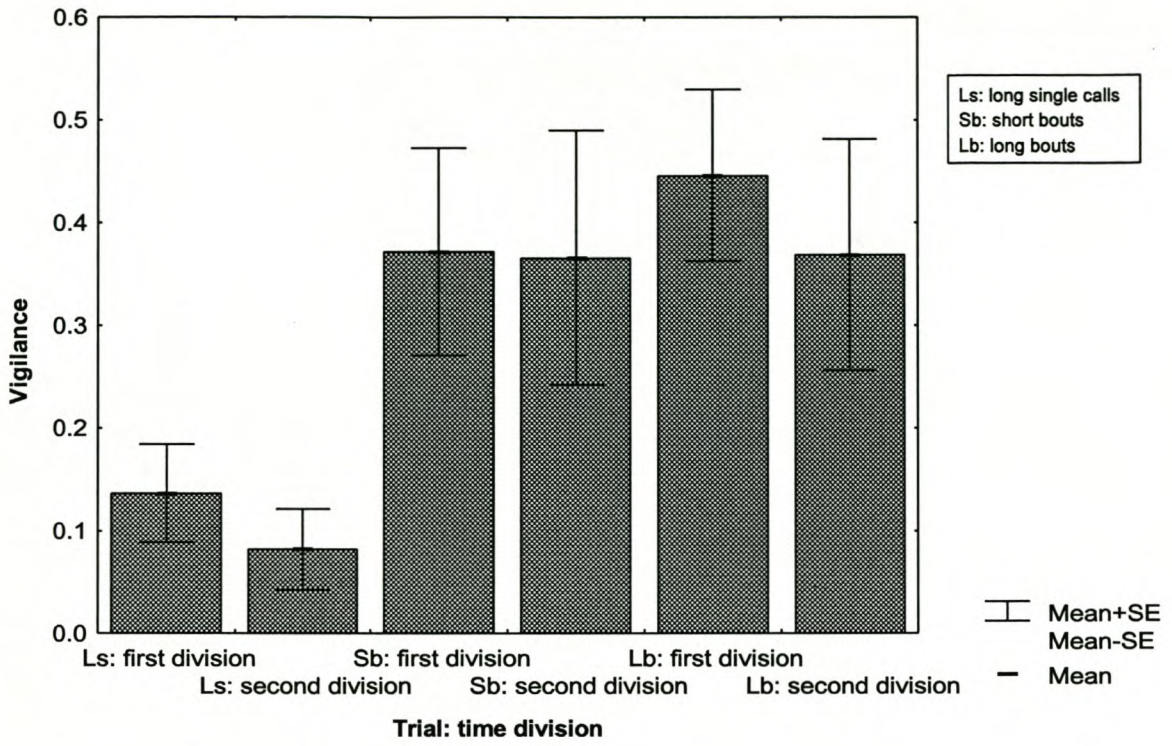
Fig. 4.3 (b) A comparison of bipedal vigilance between single calls and bouts of *P. brantsii* (*N* = 19). There were no significant differences between the trials.
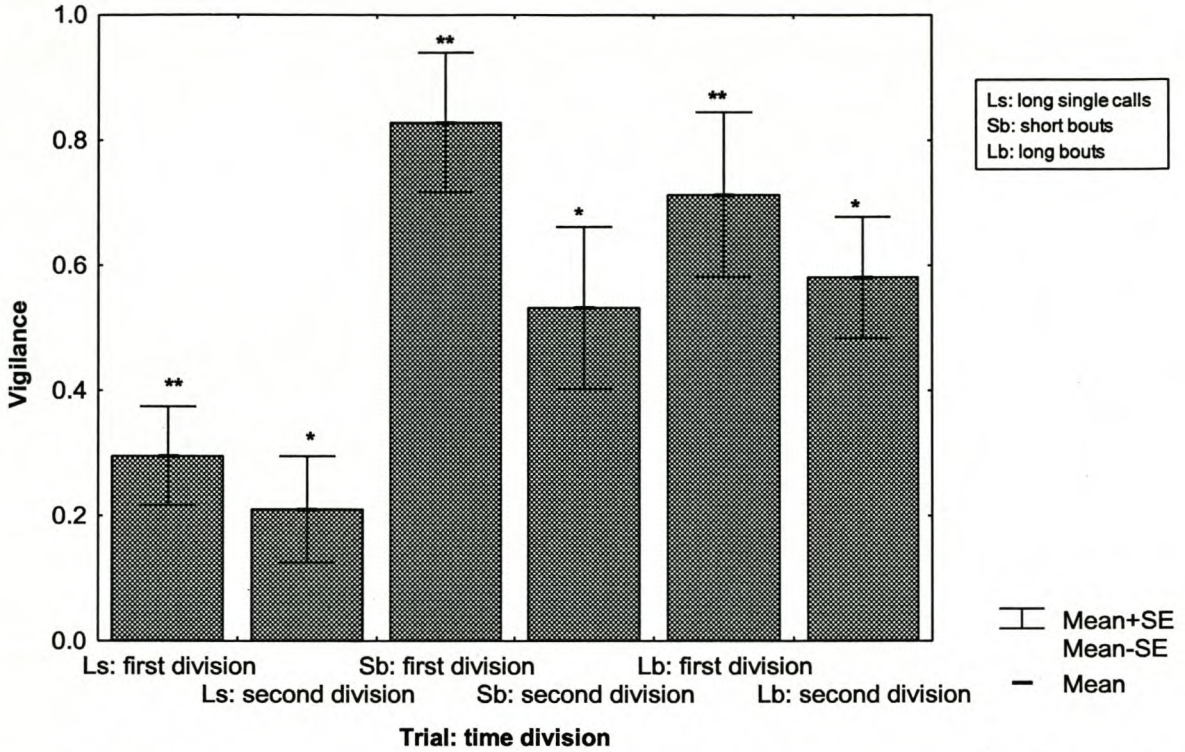
Fig. 4.3 (c) Total vigilance compared between single calls and bouts of *P. brantsii*. A significant difference was detected between the second time divisions of the single calls and two types of bout (Friedman ANOVA: $p < 0.003$; $N = 19$; indicated by *). There was a marginal difference in total vigilance between the first time divisions of these groups (Friedman ANOVA: $p < 0.063$; $N = 19$; indicated by **).

TABLE 4.2 – *The results of comparisons between the short bout and long bout, using Wilcoxon matched pairs tests.* **Parotomys brantsii***'s reaction did not differ between the two types of bouts; the total vigilance over 3 minutes was virtually identical.*

Type of vigilance	Time division	*N*	*T*	*Z*	*P*
Quadrupedal vigilance	First	21	87.5	0.302	0.763
	Second	20	54.0	1.372	0.170
Bipedal vigilance	First	21	65.0	1.208	0.227
	Second	20	44.5	0.880	0.379
Total vigilance	First	21	81.5	0.543	0.587
	Second	20	55.0	1.018	0.309
Total vigilance over 3 minutes	--	20	93.0	0.0805	0.936

4.5 Discussion

The playback of alarm vocalizations to *P. brantsii* induced high levels of vigilance in receivers, whether the calls were single or made in bouts. Receivers did not appear to distinguish between short and long single calls. We found that, although short ("high risk") single calls induced marginally higher, longer duration vigilance than long ("low risk") calls, these differences were not significant. Rats did not bolt more frequently in reaction to short calls than long calls, indicating that *P. brantsii* alarm whistles are not perception specific, as distinct call types do not lead to unique reactions in nearby conspecifics. This means that *P. brantsii*'s alarm calls are not functionally referential as they do not meet the criterion of both being produced under specific circumstances, and leading to specific responses (Macedonia & Evans, 1993). The calls alone, therefore, do not provide sufficient, exact information to which conspecifics can react.

The tonic communication theory was supported in this study. The predictions stemming from the theory were that (a) calling bouts should induce longer periods of heightened vigilance than single calls, and (b) longer bouts should lead to longer periods of high vigilance than short bouts. In Loughry and McDonough's (1988) study on California ground squirrels, *S. beecheyi,* the first, primary prediction was supported by the experimental evidence, which is similar to our findings for *P. brantsii*. High levels of vigilance were maintained for a long period of time in *P. brantsii* individuals, even after calling bouts have ended, inducing much longer periods of high vigilance than single calls did. For *P. brantsii*, as with *S. beecheyi,* the second prediction of the hypothesis is not met, as longer bouts did not cause longer

periods of vigilance than shorter bouts. This is probably because receivers become habituated to the signal, and therefore react less strongly to such a long, continuous stimulus (Hartshorne, 1956). In natural calling bouts of *P. brantsii*, calls are never uniformly spaced (chapter 3), and this fluctuation may prevent habituation in receivers to maintain vigilance more effectively, according to the dishabituation hypothesis of Hartshorne (1956). Hartshorne argued that in vocalizations with a social function such as alarm calls, signal types must be varied frequently or pauses between identical signals should be long enough to prevent "intolerable monotony" within the receivers. Both Hartshorne's dishabituation theory (1956) and Schleidt's theory of tonic communication (1973) regard it necessary for receivers to remain interested in, or affected by the continual signal. Based on the findings of this paper and those of Loughry & McDonough (1988) and Blumstein (1999), we propose that tonic communication is a feature of the vocalizations of at least some colonial rodents, but that habituation appears to hamper this effect in very long calling bouts.

Here we have explored the possible meanings of *P. brantsii*'s vocal alarm signals. Meaning can be interpreted as the sum of the effects of a message plus the context in which it is sent, as reflected in the behavioural response chosen by the recipient (Smith, 1965). Therefore, if an animal bolts in response to a certain alarm signal made under controlled circumstance (i.e. the context will not affect the receiver), the meaning of the message is that the receiver should bolt. The meaning of all *P. brantsii* alarm whistles appears to be that receivers must be vigilant, but the level of risk is not communicated by the call length alone. We suspect that animals can distinguish between short and long calls (as there was slightly higher vigilance in response to short calls compared to long calls), but that the situational context plays an important

role in determining the receiver's subsequent behavioural response to a *P. brantsii* alarm whistle. In a sparsely vegetated environment such as that which *P. brantsii* inhabits, the sighting of a predator's approach, or the behaviour of the calling animal may be important in mediating the behavioural response of receivers to non-iconic alarm signals (Marler *et al.,* 1992). As is found in other sciurids like *S. columbianus* (Betts, 1976), *S. beecheyi* (Owings *et al.,* 1977) and *Cynomys ludovicianus* (Smith *et al.,* 1977), *P. brantsii* typically reacts to alarm calls by running towards the safety of a burrow, and then scanning the environment for signs of danger. Non-specific, simple signals like the alarm whistles of *P. brantsii* may compel receivers to receive sufficient contextual information to make a behavioural decision (Smith, 1969). It has been found in chipmunks that alarm calling by conspecifics make individuals more responsive to external stimuli (Weary & Kramer, 1995) and it is generally assumed that animals are able to assess risk and adapt their behaviour accordingly (Lima & Dill, 1990). Whistling rats are central place foragers that are mostly close to the safety of burrow entrances while feeding (Jackson, in press). It may therefore be advantageous for an animal to first scan the environment to determine the immediacy of a threat to itself, rather than simply bolting underground without knowing the nature and extent of the danger. Especially in reaction to bouts, bipedal vigilance plays a larger role in vigilant behaviour than quadrupedal vigilance (compare figures 4.2a and b). As animals scanning in a more elevated posture should become aware of danger sooner than those in horizontal ones, this behaviour stresses the importance of visual perception of danger in *P. brantsii*'s communication system.

The phenomenon of contagious calling has been noted in *C. gunnisoni* (Smith *et al.,* 1977) and *Eutamias sonomae* (Smith, 1978). This occurs when animals respond to

conspecific alarm calls by beginning to call themselves, even if the predator remains unseen by the new callers. Alarm calling in *P. brantsii* does not appear to be contagious, implying that individuals call only if they have observed the source of threat themselves. The number of callers are thus a good indication to receivers as to the extent of the danger (Leger & Owings, 1978) and conspecifics should be able to glean contextual information about the position and possible behaviour of the predator by listening to multiple callers. This is consistent with the assumption that alarm calls provide information that conspecifics use to choose an appropriate response (Smith, 1969; Leger & Owings, 1978). However, it is possible that alarm calls are used by the caller to manipulate conspecifics (Charnov & Krebs, 1975). In *P. brantsii*, as in ground squirrels, the alarm callers probably use the alerted colony members as added "look-outs" to maintain visual contact with predators after they had moved out of the original caller's sight (Owings *et al.*, 1986). An added function of calling bouts may be to deter predator attacks (Woodland *et al.*, 1980). For example, in klipspringers (*Oreotragus oreotragus*) animals have alarm-calling duets that are loud and continual signals directed at the predator (Tilson & Norton, 1981). The vocalizing animals are safe while calling, making no attempt to hide from the predator, and may start calling even before the predator has noticed them. The calls direct the predator's attention to the fact that it has been seen, and often lead to abandoning the hunt (Tilson & Norton, 1981). Similarly, in the presence of a human "predator," *P. brantsii* alarm calls are often sounded before the callers are seen and they are made from positions of relative safety (ALR pers. obs.). We propose that alarm calling bouts in *P. brantsii* are not aimed solely at conspecifics, but also at the predator, encouraging it to abandon the hunt because it is being constantly monitored.

We conclude that alarm calling bouts in *P. brantsii* tonically maintain high levels of vigilance in receivers, even after bouts have ended. Single calls induce vigilance in conspecifics, but in the absence of contextual clues, variation in call length alone does not prescribe exact behavioural responses, for example bolting as opposed to remaining aboveground. In addition, alarm calls may function as pursuit-deterrent signals aimed at the predator.

4.6 Acknowledgements

4.7 References

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