WARNING VOCALISATIONS AND PREDATOR INFORMATION TRANSFER IN SOCIAL BIRDS

by

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ABSTRACT

Alarm or warning vocalizations are produced by many animals when they detect a potential predator. However little is known about the information contained in these vocalizations. This study investigated the warning vocalisations of three passerine species, viz. the Buff-streaked Chat *Oenanthe bifasciata*, the Stonechat *Saxicola torquata* and the Bronze Mannikin *Spermestes cucullatus*. The study investigated whether the alarm calls for terrestrial predators differ in their acoustic structure from alarm calls emitted for aerial predators. Birds were exposed to latex terrestrial snakes and mounted aerial raptors, while changes in six acoustic parameters of alarm calls were measured.

Bronze Mannikins were investigated for differences in intra-specific alarm calls between familiar and unfamiliar group members by capturing wild groups of mannikins and randomly mixing these to form assorted groups. Bronze Mannikins emitting warning calls were able to discriminate differences in predator size, and increased their calling rate and decreased the end frequency of the alarm call in response to larger predators. This may be the caller's response to increased threat or variation in frequency may obscure cues to the caller's whereabouts. Assorted group members were less aggressive to predator models than original members and panicked more during confrontations. Hence the unfamiliarity of the caller may have disrupted group cohesion.

The alarm call acoustics of the social Buff-streaked Chats and the solitary Stonechat were compared to examine the effect of group-living on alarm behaviour. Snakes elicited louder calls from both the chat species than raptors. Louder and collectively more vocal social groups might be more successful in discouraging attacks than an asocial species.

Variation in amplitude and call frequencies by the Stonechat provided some evidence that they are equally adapted to identifying predator type. Although Buff-streaked Chats increased their call rate in response to nearby predator models, Stonechats produced shorter calls in response to terrestrial predation particularly when the predators were in close proximity. Knowledge gained through direct encounters with predators or the ease with which raptors and snakes can gain access to nests may have played a part in discrimination of predator threat. Overall this study indicated strong correlations between some alarm acoustic parameters and predator size as well as the degree of threat.

PREFACE

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu Natal, Durban, from January 2000 – January 2003, under the supervision of Professors Gerard Malan and Morné du Plessis. Final submission was under the supervision of Professor Rob Slotow.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Nimmi Seoraj-Pillai (candidate)

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> “The single biggest problem in communication is
> the illusion that it has taken place.”

George Bernard Shaw

DEDICATION

This study is dedicated to

my mother
Anganee
(who despite poverty and destitution, raised me up to stand on mountains)

my beloved brother
Clint
(who passed away so young and so tragically, and who will never be forgotten)

and

my husband
Sashendra
(my best friend, my joy, my smiles, my rock)

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Chapter 1

Introduction

Why do birds use alarm vocalisations?

Due to their varied life histories and complex social structures, birds rely extensively on vocalisations as a means of social communication (Marler 1957, Bradbury & Vehrencamp 1998, Blumstein & Armitage 1998, Blumstein 2003). A variety of avian call types are produced during social interactions that serve different functions. These include flight calls to promote group cohesion (Klump & Shalter 1984), mobbing calls to discourage predator pursuit (Naguib *et al.* 1999), contact calls, to maintain contact with conspecifics during foraging or to help in locating group mates (Owings & Henessy 1984, Evans & Marler 1995, Zuberbühler 2000*a*) and alarm calls to communicate danger (Marler 1957, Sherman 1977, Bayly & Evans 2003).

Numerous hypotheses have been proposed to explain the function of warning vocalisations in birds. It has been suggested that alarm calls warn conspecifics of impending danger (Weary & Kramer 1995), let the predator know it has been detected (Blumstein & Armitage 1997*a*, Haftorn 2000, Blumstein 1999), attract attention to the predator (Hogstad 1988) and to protect close relatives (Hoogland 1983) or potential mates (Hogstad 1988). In all of these the caller is put at risk, therefore alarm calling seems to be an altruistic event associated with the caller placing itself in danger by attracting the predator's attention, allowing time for other group members to escape or seek shelter (Haftorn 2000).

Alarm calls also transmit semantic information referring to specific stimuli categories such as type of predator (Sherman 1977, Owings & Henessy 1984, Evans &

Marler *et al.* 1992, Zuberbühler 2000*a*, Baptista & Kroodsma 2001, Manser *et al.* 2002). Alarm calls also reflect the response urgency in different situations, i.e. level of threat (Klump & Shalter 1984, Macedonia & Evans 1993, Blumstein & Arnold 1995, Blumstein & Armitage 1997*a*, Greene & Meagher 1998, Manser *et al.* 2002). For example, California ground squirrels, *Spermophilus beecheyi*, emit one type of alarm call in response to a predator nearby and another call type to the same predator at a greater distance (Leger & Owings 1978, Leger *et al.* 1979).

Research into the study of animal communication has shown that many mammalian alarm calls have a high degree of input specificity (Seyfarth *et al.* 1980, Macedonia 1990, Blumstein & Armitage 1997*b*, Zuberbühler 1999*a*, Zuberbühler 2000*abc*, 2001). A study into the predator avoidance behaviour of vervet monkeys *Cercopithecus aethiops* was among the first to demonstrate high specificity in warning vocalisations that produce distinct alarm calls for their different predator types: eagles, snakes, and leopards (Seyfarth *et al.* 1980).

Belding's ground squirrel *Spermophilus beldingi* gives single-note whistles to flying raptors and multiple-note trills to terrestrial mammalian predators (Sherman 1977). These call types evoke different responses among conspecifics, e.g. the single-note whistles cause the squirrels to run for shelter. When the adaptive significance of these alarm calls was further investigated, it was found that multiple-note trills and repetitive chirps are given in response to terrestrial predators during agonistic encounters, while single-note, non-repetitive 'whistles' occur in response to raptors or nearby, fast-moving terrestrial predators (Sherman 1985).

Evidence for vocal specificity in avian alarm calls is growing. The jungle fowl *Gallus gallus* uses a long drawn out "*baaaaawk*" when a raptor flies overhead, but a "*baak-buk-buk-buk*" when it sights a ground predator, such as a raccoon (Marler & Evans 1996). Research into the alarm call system of a cooperative breeder, the Arabian babbler *Turtoides squamiceps* (Naguib *et al.* 1999), revealed that two common call types were used in different ways to communicate information about the type of predator, aerial versus terrestrial. Studies on the willow tit *Parus montanus* showed that callers identified the degree of threat posed by hawks, with more members calling when the hawk was further away (Alatalo & Helle 1990). In addition, a recent study on the white-browed scrubwren *Sericornis frontalis* indicated changes in their aerial trill alarm calls according to the distance of the approaching predator: the closer the predator, the greater the number of call elements in the call (Leavesley & Magrath 2005).

Communication, group living and alarm behaviour

Communication within the group is fundamental in achieving and maintaining cooperative relationships, with the composition of the social group having an impact on the degree of elaboration of communication that the species exhibits (Marler 1977). A social species requires inter-individual alarm signals to act as a stable and cohesive group (Bradbury & Vehrencamp 1998).

Communication can be regarded as consisting of three components: syntax (the relationship between signals and signs); semantics (the relationship between signs and their referents), and pragmatics (the relationship between signs and the responses they evoke) (Thorpe & Hall-Craggs 1976, Evans 1997). This study focused on the syntax and semantics in the warning vocalisations of social birds and examined correlations between acoustic call parameters and some predator characteristics such as type and size.

Since communication is a social action between two or more individuals, designed to influence the behaviour of listeners, the cohesiveness and stability of social groups is therefore dependant on these specialised warning calls (Marler 1957, Alatalo & Helle 1990, Blumstein & Armitage 1998, Blumstein 2003). This study investigated correlations between group living and predator information transfer.

The study comprised three investigations that examined the relationship between group-living and warning vocalisations, predator size and type, as well as distance of the predator from the group. Group living was investigated by selecting study species that show differences in social structure, i.e. a gregarious species like the Bronze Mannikin, *Spermestes cucculatus*, a pair-living or solitary species, such as the Stonechat *Saxicola torquata* and a cooperative group-living species, the Buff-streaked Chat *Oenanthe bifasciata.* Predator size and type was examined by introducing (mounted) aerial raptors and (latex) terrestrial snakes of varying size and length respectively.

The first investigation (Chapter 3) focused on the change in warning vocalisations in response to predator size and predator lethality, in a social passerine, the Bronze Mannikin. The vocalisations given in the presence of flocking members were compared to those emitted in the presence of unfamiliar members. It was predicted that conspecifics will emit more information in the presence of original group members as opposed to mixed group members. Groups of mannikins were captured with mist nets from four areas located in the Durban Metropole, South Africa i.e. original groups (flocking members). Once alarm vocalisations were recorded, the birds were randomly mixed to form assorted groups. Each group was exposed to latex terrestrial snakes and mounted aerial raptors, while changes in their alarm calls and predator response behaviours, like panic and vigilance behaviour were studied.

The second investigation (Chapter 4) compared the warning vocalisations of the social Buff-streaked Chat, to the asocial Stonechat, to determine whether these passerines could emit calls with semantic value by discriminating predator type. It was predicted that both species would either emit discrete call types for aerial and terrestrial predators or change the dynamics of the call, such a call rate or frequency to reflect response urgency. It was also predicted that the alarm calls of the social species, i.e. Buff-streaked Chats would contain more information (call elements) than that of the asocial Stonechat. Vocalisations were analysed statistically by examining acoustic parameters of alarm and territorial repertoires. Groups of Buff-streaked Chats and Stonechat pairs were captured in the Drakensberg mountain range, housed in outdoor aviaries, and exposed to five latex snakes and five perching raptors, while alarm and territorial calls were recorded.

The final investigation (Chapter 5) examined how a predator's distance from a caller influenced alarm call structure and whether these changes reflect predator threat. It was predicted that the closer the predator, the greater the number of calls emitted to evoke an urgent response. Buff-streaked Chats and Stonechats were exposed to latex snakes and perching raptors, presented at different distances from the birds.

Chapter 2

Materials and Methods

2.1 STUDY SPECIES

This study investigated the warning vocalisations and alarm call behaviour of three bird species, the Buff-streaked Chat *Oenanthe bifasciata* (Tye 1989), the African Stonechat *Saxicola torquata* (Keith *et al.* 1992), and the Bronze Mannikin *Spermestes cucullatus* (Woodall 1975). The mannikins were investigated separately for intra-specific alarm data, while the chat species were compared directly to investigate the effect of sociality on alarm vocalisations. The Bronze Mannikin was selected as they occur abundantly in the suburban gardens of the Durban Metropole (Slotow & Coumi 1999) making it practical to capture the large sample size required, while their seed diet would be easy to maintain. Apart from this, they occur in gregarious flocks year round, an ideal scenario to investigate intra-specific alarm calls between familiar and unfamiliar group members. The chat species were specifically chosen for the following: (1) their common occurrence at the Drakensberg made it relatively convenient to capture, (2) both species would acclimatise fairly well to the climatic conditions in Durban and (3) their insectivorous diet could be easily sustained by mealworms, which is very convenient and practical to house and study in captivity. Furthermore, both species although similar in structure, plumage and behaviour (Tye 1989, Keith *et al.* 1992), still possessed a distinction in their social structure: the Stonechat being solitary (Gwinner *et al* 1994) and the Buff-streaked Chat being social. Lastly, all three species are territorial and give alarm calls in response to potential predators or threat (Woodall 1975, Keith *et al.* 1992, Maclean 1993).

Bronze Mannikins

The Bronze Mannikin is a gregarious passerine, distributed throughout Sub-Saharan Africa, from Senegal to Ethiopia and south to South Africa (Hockey *et al.* 2005). Within South Africa, they are especially common in Mpumalanga, KwaZulu Natal, and the eastern Cape Province (Keith *et al.* 1992). The habitat of the Bronze Mannikin may range from woodland to savanna, depending on the availability of water. They favour grassy areas with adequate woody plants and thickets (Woodall 1975). This common, granivore (average mass 10 g) (Hockey *et al.* 2005) has successfully adapted to living in suburban gardens and may form foraging flocks of two to forty individuals, flocking in these larger groups especially in the non-breeding season (Woodall 1975, Slotow & Coumi 1999).

Recovery of ringed birds has indicated that movements are highly localized to within a radius of 1 km from the site of capture (n = 342 birds in four years) (Woodall 1975). However, in 1969, a ringed Bronze Mannikin was recaptured 9 km from the site of ringing (Woodall 1975).

The Bronze Mannikin exhibits a variety of call types ranging from feeding calls to nest calls (Woodall 1975). Contact calls and flight calls may follow warning vocalisations. These calls are emitted by members of the flock to establish contact with conspecifics and are heard just before flight or escape. Fighting calls are emitted during aggressive territorial or courtship disputes (Woodall 1975). The alarm call in particular is uttered when the birds is disturbed and is accompanied by tail and wing flickering. It comprises a series of single, short, staccato notes of uniform pitch ‘chuck, chuck’ (Woodall 1975).

Buff-streaked Chats

The systematic position of the Buff-streaked Chat is still uncertain, as it has been placed in three genera: *Myrmecocichla*, *Saxicola* and *Oenanthe* (Tye 1989, Hockey *et al.* 2005). Despite convincing argument for inclusion of this species in *Saxicola* (Tye 1989), it has been conservatively retained in *Oenanthe* (Hockey *et al.* 2005). The Buff-streaked Chat differs from most *Oenanthe* species in some morphological features, such as longer rictal bristles, shorter and flatter beaks, cinnamon-buff underparts etc., while egg colour and nest site differs from both *Oenanthe* and *Saxicola* (Hockey *et al.* 2005). It's anatomy, structure and plumage most closely resembles that of the Whinchat and Stonechat (Tye 1989).

The Buff-streaked Chat is endemic to South Africa, Swaziland and Lesotho (Harrison 1997). They usually occupy biomes > 1000 m above sea level, but have been found to inhabit areas close to sea level in KwaZulu-Natal (Clancey 1964, Harrison 1997). They have been known to move to lower altitudes in harsh winters (Harrison 1997). This insectivorous species (average mass 33 g) occupies boulder-strewn fields and rocky outcrops in montane grasslands (Clancey 1964, Harrison 1997, Hockey *et al.* 2005). They form small territorial family groups and are territorial, defending non-breeding territory by displays, song and chasing, often displacing other passerines such as cisticolas and Stonechats (Tye 1988). Buff-streaked Chats are also facultative cooperative breeders, with conspecifics or juveniles from previous broods helping to feed nestlings (Muchai *et al.* unpubl. data). Both sexes emit vocalisations or song, consisting of short, rapid phrases with penetrating whistles, trills and staccato notes (Keith *et al.* 1992). They also produce 'chaks' and 'weets' in response to threat (Keith *et al.* 1992).

Stonechats

The Stonechat is distributed throughout Sub-Saharan Africa and Madagascar (Keith *et al.* 1992, Hockey *et al.* 2005). Within South Africa they are widespread in mesic areas. They display altitudinal migration down the Drakensberg to the midlands and lowlands of KwaZulu-Natal (Keith *et al.* 1992). Stonechats live in monogamous pairs foraging within territories year-round (Gwinner *et al* 1994). These solitary nesters (average mass 15 g) (Tarboton 2001), fiercely defend territories. Their song comprises a series of repetitive piping and thrilling notes (Maclean 1993). Furthermore, they have been documented to produce sharp alarm vocalisations (Maclean 1993).

2.2 BIRD CAPTURE AND HUSBANDRY

Bronze Mannikins

Bronze Mannikins were captured with mist nets from four areas in Durban, South Africa: Durban North (31º2’23. 25’’E, 29º47’9. 03’’S), Westville (30º56’41.04’’E, 29º49’2.89’’S), New Germany (30º53’6.41’’E, 29º48’39.04’’S) and Kloof (30º48’22.51’’E, 29º49’46.08’’S). These capture sites were at least 10 km apart. Each group comprised five individuals and consisted of three adults and two juveniles, and were housed in the bird aviaries on the grounds of the University of KwaZulu-Natal (Westville Campus). Each individual was colour ringed with individual colour combinations to identify the members. Grain and seeds were available ad libitum. Fresh water was always made available.

Buff-streaked Chats and Stonechats

Free-living birds were caught between August and September 2001, and again in September 2002 in the central Drakensberg Range. Ten individual Buff-streaked Chats and ten pairs of Stonechats were captured from the central Drakensberg range, of which five individuals of Buff-streaked Chats and seven pairs of Stonechats were captured in 2002 (Table 2.1).

Table 2.1 Combination of chat species housed in aviaries during 2001 and 2002.

SITE OF CAPTURE	AVIARY	2001
1-2	1	Single Stonechat pair
3	2	Solitary Buff-streaked Chat
	3	Single Stonechat pair
4-8	4	Group of four Buff-streaked Chats
9	5	Single Stonechat pair
		2002
10	1	Single Stonechat pair
10	2	Three Stonechat pairs
10	3	Single Stonechat pair
10	4	Group of five Buff-streaked Chats
10	5	Single Stonechat pair

Capture sites for 2001 were: site 1 (29º40’28’’E, 29º15’8’’S) Northington, site 2 (29º40’34’’E 29º15’15’’S) Northington, site 3 (29º40’36’’E, 29º15’ 33’’S) Glengary farm, sites 4-8 (29º45’24’’E, 29º15’33’’S) Eversly farm, and site 9 (29º40’28’’E, 29º15’8’’S) Little falls farm. In 2002 birds were captured at site 10, (29º50’30’’E, 29º10’6’’S).

Spring-traps were baited with mealworms, ensnaring the bird when it attempted to take a worm (Forbes 2000). Buff-streaked Chat groups were trapped in boulder-strewn, montane grasslands adjacent to roads. Stonechats were captured at forest edges, especially along the road verge.

Birds were housed in aviaries (Figure 2.1) on the grounds of the University of KwaZulu-Natal, Westville Campus. Five bird aviaries were built separately, consisting of two large aviaries approximately 3 m x 3 m in dimension and three small enclosures approximately 1.2 m x 1.2 m in dimension. The Buff-streaked Chats were grouped in original territorial groups that they were captured in. At sites 4-8 (refer to coordinates), four individuals were captured. Since sociality and kin selection were being investigated, we aimed to keep flocking birds together. Hence, birds captured within the same vicinity (± 500 m^2) were assumed to be familiar to each other. Therefore, the first ‘group’ comprised a solitary bird from site 3 (male), the second group contained four individuals (two males and two females from site 1) and the third group comprised five individuals (four males and a single female, captured in 2002 from site 10). Occupation of the various aviaries are depicted in Table 2.1, however, to accommodate the large number of stonechats in 2002, aviary 2 was partitioned with hessian into three mini enclosures.

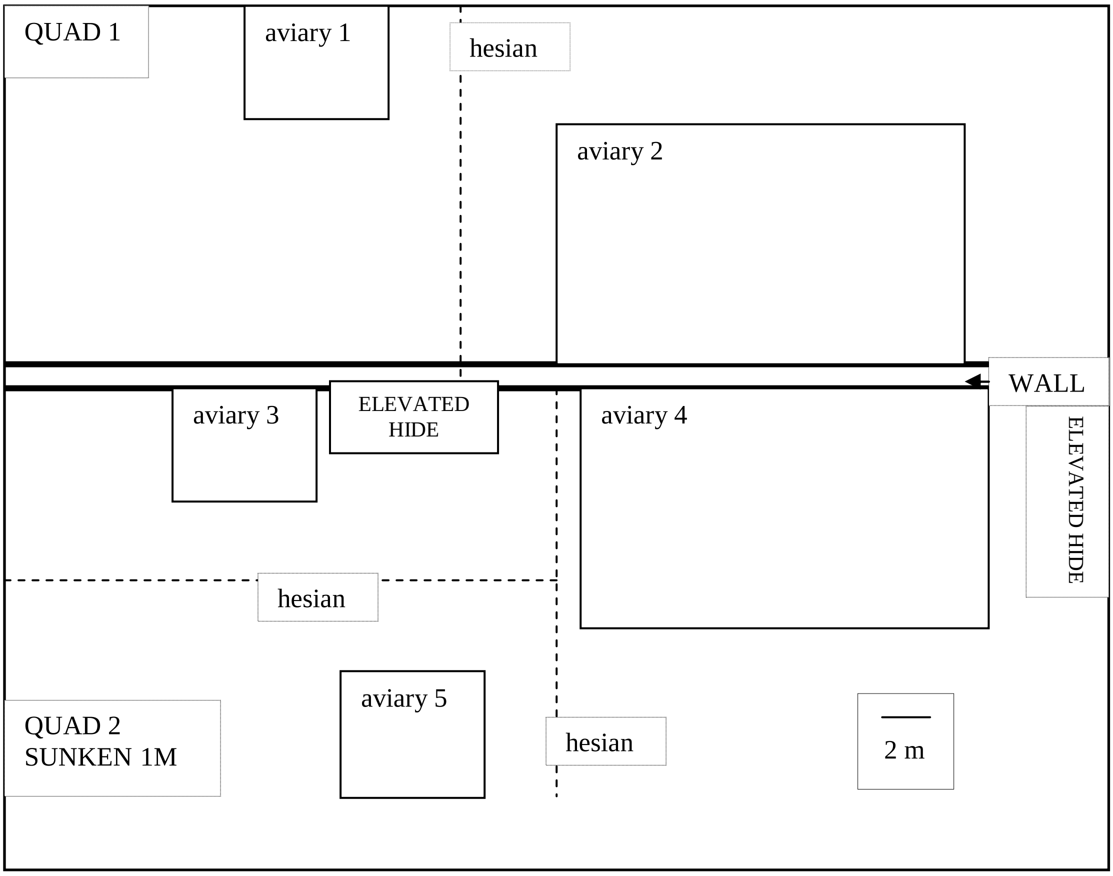

Fig. 2.1 Diagram showing experimental set-up for predator exposure to aviaries and recording of vocalisations for each investigation.

Each group was fed mealworms, the quantity of which was determined by number of individuals and body weight. Subsequently, the birds were weaned onto a mixture of mince and raisins. Three decomposing or rotten chicken breasts were also hung in each aviary to encourage maggot infestation, upon which the birds fed.

2.3 EXPERIMENTAL SET UP

Predators

Mounted raptors and latex snakes were used during experiments to simulate natural predators. The raptors consisted of a Steppe Buzzard *Buteo vulpinus* (standard wing length (SWL) = 37 cm), a Long-crested Eagle *Lophaetus occipitalis* (SWL = 47 cm), a Spotted Eagle-owl *Bubo africanus* (SWL = 30 cm), a Black-shouldered Kite *Elanus caeruleus* (SWL = 26.5 cm*)* and an African Goshawk *Accipiter tachiro* (SWL = 23.5 cm*)*. Although, the Long-crested Eagle differed in one aspect from other specimens, i.e. mounted with raised, outstretched wings, the corresponding control (non-predator) model was also mounted in this position. The wing lengths of every mounted raptor were measured using a Vernier calliper (accurate to 0.005 mm) and may differ from skin specimens. For those wings that were greater then 200 mm, string was placed along the entire length of the wing, thereafter the length of that piece of string was measured using a flat ruler and recorded. Each control was selected to resemble the test specimens in similar posture or stance. Five mounted, non-predatory control species were as follows (presented in the corresponding order): an Orange-river Francolin *Scleroptila levaillantoides* (SWL = 16.3 cm), a Red-winged Starling *Onychognathus morio* (SWL = 15 cm), a Magpie Shrike *Corvinella melanoleuca* (SWL = 14 cm), a Black-headed Oriole *Oriolus larvatus* (SWL = 14.8 cm) and a Wattled Starling *Creatophora cinerea* (SWL = 12 cm). The latex snakes comprised a long green snake (length (l) = 145 cm), a medium brown snake (l = 90 cm), a medium black snake (l = 100 cm), a medium spotted yellow snake (l = 60 cm) and a short yellow-black snake (l = 30 cm). Plastic pipes, equivalent in length and diameter to the respective snakes were employed as controls. During presentations, the snakes and pipes were puppeteered with thread, while raptors were moved on a camouflaged wheeled platform attached to a thread.

Each snake or raptor was presented individually one meter from the aviary and moved < 1 m in a neutral direction, i.e. in any direction except at or away from the aviary, in random order. This procedure was repeated for controls, also in random order.

Recordings

Alarm call responses were recorded using a SONY stereo cassette recorder (TC-DSM) and a SONY ELECTRET condenser microphone that was hung from the roof in the middle of the aviary. Each group was observed for two sessions, once in the morning between 07h30 and 10h00 and once in the afternoon between 15h00 and 16h30, when the birds were active. It was not possible to identify the specific individual/s emitting the alarm call due to the sheer speed of emission. The observer was positioned in a hide located 2 – 5 m from the cages (Figure 2.1). Each pair of Stonechat and each group of Buff-streaked Chats was presented, in random order, with each of the five raptors and snakes for a period of five minutes per predator. The procedure was repeated for the controls. Response for individual stuffed birds and latex snakes was recorded; however the raw data was pooled to study any correlation between the size of specific predator characteristics such as wing length and body length on warning behaviour.

Call structure

All calls were digitised with AVISOFT SASLAB Light and spectrograms were subsequently produced, the acoustic parameters for which, are given in the corresponding figure legend. Calls were digitized at 22.05 kHz sample frequency, while spectrograms were calculated using a Fast Fourier Transformation (FFT). The following acoustic parameters were selected for analysis:

The following six acoustic parameters were selected for analysis:

(1) the total number of calls emitted during the 5-minute sampling period

(2) the duration of the call element (sec)

(3) the pause duration (inter-call duration) between call elements (sec)

(4) the amplitude of each call element (dB),

(5) the start frequency (Hz) of each call, and

(6) the end frequency (Hz) of each call.

A detailed description of how each acoustic parameter was measured is included Chapter 4. STATISTICA (v6 Tulsa, OK) was used for analyses and two-tailed P-values are indicated.

Chapter 3

Bronze Mannikins signal predator risk threat in the presence of familiar group members

Alarm calls are emitted in response to potential predators. This chapter investigates, through experiments using surrogate predators, differences in intra-specific alarm calls between familiar and unfamiliar Bronze Mannikin *Spermestes cucculatus* group members. Four groups of Mannikins were captured with mist nets from four areas in Durban (i.e. original groups) and randomly mixed to form assorted groups. These groups were exposed to latex terrestrial snakes and mounted aerial raptors, and their alarm calls and predator response behaviours were recorded. Bronze Mannikins that emitted alarm calls were able to discriminate between predators of different sizes, by increasing their calling rate and decreasing the end frequency of the alarm call in response to larger predators. This may be the caller's response to increased threat or variation in frequency may obscure cues to the caller's whereabouts. When the alarm call structure of the original and assorted groups were compared, in response to both raptors and snakes, birds in original groups called more often, they paused longer between calls, started calling at a higher frequency and finished at a lower frequency. Callers from assorted groups were less vigilant and aggressive toward the surrogate predators and panicked more frequently. Although no playback experiments were conducted, behavioural response data also provide support that assorted groups may not have recognised the caller and therefore panicked. Hence the unfamiliarity of the caller disrupted group cohesion. The manipulated experiments carried out in this study indicated that Bronze Mannikin groups, living in year-round flocks were able to discriminate predator size risk, while unfamiliar callers in mixed groups promoted panic.

3.1 INTRODUCTION

Predation has long been implicated as a major selective force in the evolution of sociality (Lima & Dill 1990). For example, social or group-living birds can provide better protection for conspecifics through the combined effects of dilution and confusion (Hamilton 1971, Edmunds 1974), improved detection of predators (Kenward 1978) and predator deterrence (Curio 1978). Furthermore, lower individual scanning rates may free time for foraging and resting, and improved safety may make the exploitation of more exposed foraging sites possible (Bshary & Noë 1997).

When individuals in a group cooperate, assistance may range from a simple group effect, such as the simultaneous mobbing of a predator (Ligon 1991); to complex mutual dependence (Beynon & Rasa 1989). If, for example, members of a group are not familiar to each other or can interpret the finer details of each other's calls, no mutual aid occurs until they have been together for some time (Bateson 2000). Group living benefits will thus only materialise if members participate and cooperate in predator avoiding activities, such as alarm calling (Krebs & Davies 1997, Bradbury & Vehrencamp 1998).

However, the alarm call is not always a simple, clear-cut distress signal, but may contain a high degree of input specificity, i.e. distinct alarm calls are employed for different predator types such as a terrestrial snake or an aerial eagle (Seyfarth *et al.* 1980, Greene & Meagher 1998, Manser 2001). Such complex alarm calls may also refer to the degree of threat, i.e. the size of the predator (Beynon & Rasa 1989, Evans *et al.* 1993). Blue Tits *Parus caeruleus* give *seeet* calls to a small airborne model of a sparrow hawk model flying at 60 m, but scolding calls to a sparrow hawk model flying at about 4 m (Klump & Curio 1983). A study conducted on Black- capped chickadees *Poecile atricapillus* (Templeton *et al.* 2005) showed that manoeuvrability (e.g. as measured by turning radius, or radial acceleration) is extremely important in determining the outcome of predator-prey interactions and is inversely related to wing-length and body size in birds. Body size may be a good predictor of risk (Templeton *et al.* 2005), i.e. small raptors tend to be much more manoeuvrable than larger raptors and likely pose a greater threat to chickadees.

This chapter focuses on warning vocalisations in the social passerine, the Bronze Mannikin *Spermestes cucculatus.* The first objective was to, through experiments using surrogate predators, examine (i) if the alarm vocalisations for terrestrial predators should differ in acoustic structure from alarm calls emitted for aerial predators, and (ii) if these calls can discriminate the size of these two predator types. The behavioural responses of the birds to these predators are also examined to assess the context of production. The second objective was to investigate differences in intra-specific alarm calls between familiar and unfamiliar group members. To approach this issue, the following hypothesis and derived predictions were proposed. First, birds that live year round in an all-purpose flock will emit reliable information concerning predator threat to familiar group members (possibly related), but not so to non-group members (unfamiliar). Some studies have indicated that the elicitation of a vocalisation depends on both the social environment and the history of interactions between the individuals involved (Sherman 1977, Sherman 1980, Smith *et al.* 1982, Bateson 2000). For example, the study of adult female squirrel monkeys, *Samiri sciurius*, give '*chuck*' calls to one another when grooming, but only if two females involved have a long-term, stable grooming relationship (Smith *et al.* 1982). One can predict that differences in intra-specific alarm calls and alarm behaviour may indicate an increase in vigilance or defence behaviour in response to a predator, in the presence of familiar members.

3.2 METHODS

Study Species

The Bronze Mannikin was the ideal chose for this study, occurring abundantly in the suburban gardens of the Durban Metropole (Slotow & Coumi 1999) making it practical to capture the large sample size required, while their seed diet would be easy to maintain. Furthermore, they occur in gregarious flocks year round, an ideal scenario to investigate the above hypothesis.

This gregarious passerine is found in open woodland habitats of Mpumalanga, KwaZulu Natal and Eastern Cape provinces of South Africa (Woodall 1975, Keith *et. al.* 1992, Hockey *et al.* 2005). This diminutive granivore (average mass 10 g) has successfully adapted to living in suburban gardens and may form foraging flocks of up to forty individuals, in the non-breeding season (Woodall 1975, Slotow & Coumi 1999).

The Bronze Mannikin exhibits a variety of call types, ranging from feeding to nesting calls (Woodall 1975). Contact calls and flight calls may follow warning vocalisations and are emitted by members of the flock to establish contact with conspecifics and are heard just before flight or escape (Woodall 1975). Fighting calls are emitted during aggressive territorial or courtship disputes, indicating that vocalisations are frequently accompanied by changes in behaviour (Woodall 1975). Important for this study, the alarm call is uttered when the birds are disturbed and is accompanied by tail and wing flicking. The alarm call comprises a series of single, brief and staccato notes of uniform pitch, i.e. ‘chuck, chuck, chuck’ (Woodall 1975).

Recovery of ringed birds has indicated that movements are very localized to within a radius of 1 km from the site of capture (n = 342 birds over four years), although a ringed bird was once recaptured 9 km from the ringing site (Woodall 1975). In this study, the assumption was made that flocking birds were familiar to each other and that individuals are unlikely to be familiar with others living in groups further than 10 km away.

Groups

Four groups of Bronze Mannikins were captured in mist nets in Durban metropole, South Africa: Durban North (31º2’23. 25’’E, 29º47’9. 03’’S), Westville (30º56’41. 04’’E, 29º49’2. 89’’S), New Germany (30º53’6. 41’’E, 29º48’39. 04’’S and Kloof (30º48’21. 51’’E, 29º49’46. 08’’S). These capture sites were at least 10 km apart from each other. Each group comprised five individuals and consisted of three adults and two juveniles. Individual’s plumage was examined, specifically the colour of the head, breast and tail, according to Woodall (1975), to determine age. Each individual was given a unique colour-ring combination.

The above four groups of mannikins were designated the ‘original’ groups and given at least one week to become accustomed to captivity before predators were presented to them. After completion of the initial experiments (see below), the original groups were mixed randomly (using random digits), creating four ‘assorted’ groups (Table 3.1), with provision that no original group members were assigned to the same group. These assorted groups were allowed two days to become accustomed to each other before the predators were presented to them. The Mannikin groups were housed and experiments conducted in bird aviaries located the on the grounds of the University of KwaZulu-Natal (Westville campus) (Chapter 2). Each aviary contained adequate foliage provided by tall grass, dried bark and large boulders. Both predators and controls were introduced in random order to each group, for a period of five minutes (i.e. 20 x 5 = 100 min).

A detailed account of the type of raptor and snake surrogate used, their controls and the procedures used to introduce the surrogate predators is included in the experimental set up (section 2.3).

Table 3.1 Assorted group membership after original Bronze Mannikin groups was mixed randomly.

Group A	**Group B**	**Group C**	**Group D**
Adult - Durban North	Juvenile - New Germany	Juvenile – Westville	Juvenile - Durban North
Adult – Kloof	Adult - Durban North	Adult - New Germany	Adult - New Germany
Juvenile – Westville	Adult - Westville	Adult – Kloof	Adult - Westville
Juvenile - Durban North	Juvenile - Kloof	Adult - Durban North	Juvenile - New Germany
Adult - New Germany	Adult - Westville	Juvenile – Kloof	Adult - Kloof

Calls

Two levels of acoustic structure of the Bronze Mannikin ‘chuck, chuck’ alarm call were analysed, i.e. the single call element and the entire call series. All calls were digitised with AVISOFT SASLAB Light and spectrograms were subsequently produced. The following six acoustic parameters were selected for analysis: (1) the total number of calls emitted during the 5-minute sampling period, (2) the duration of the call element, (3) the pause duration (inter-call duration) between call elements, (4) the amplitude of each call element (dB), (5) the start frequency (Hz) of each call, and (6) the end frequency (Hz) of each call.

Firstly, the treatment (snake and raptor) data of each group were compared to its control (passerine and piping) using the Wilcoxon Signed Ranks Test. Secondly, to determine whether alarm behaviour was influenced by group composition, the behavioural data generated by the original and assorted groups were compared separately for raptors and snakes (see below) employing Kruskal-Wallis Tests. Thirdly, the snake and raptor data were pooled and the acoustic parameters compared between original and assorted groups.

To investigate whether mannikins can distinguish predator type, the acoustic data for original and assorted groups were combined for each parameter and compared between snakes and raptors.

To investigate whether mannikins can distinguish predator size, a linear regression analyses was conducted, using the six acoustic parameters listed above as dependent variables, and snake length and raptor wing length size as independent variables. Snake size (i.e. length) and raptor size (wing length) were used as indices of threat that may influence call rate, call duration and other acoustic parameters. These indices were subjected to the Kolmogorov-Smirnov one-sample test for normality. When the distribution was not found to be normal, non-parametric tests were used.

SPSS 11.0 for Windows and STATISTICA (v6 Tulsa, OK) were used for the calculation of statistical tests and indicated two-tailed P values.

Predator response behaviour

During the 5 min presentations, the scan sampling method (Altmann 1974, Dunbar 1976) was used, and the following behavioural responses were identified: foraging, social interactions, cringing/ hiding, panic, and vigilant postures (Table 3.2). Each act was noted if a particular behaviour was performed (observed) by one of the group members during each presentation. To investigate whether mannikins were able to discriminate between predators and non-predators, chi-square tests were performed to measure if sample distributions deviate from theoretical distributions (Siegel & Castellan 1988). Original and assorted group data were tested for differences in their behavioural responses to raptors and snakes. When no differences were found the data were pooled for the two predator types. Lastly, for original and assorted groups combined, the behavioural responses were similarly tested for predator type, i.e. compared between snakes and raptors.

Table 3.2 An ethogram for the Bronze Mannikin behaviour showing the various acts exhibited by members of the groups.

Behaviour category	**Description (developed by observer)**
Foraging	The bird is standing with its head held down. Bird scrapes substratum with toes. Its head or beak is in contact with forage material.
Social Interactions	Includes play and agonistic (aggressive/submissive) behaviours.
Hiding	Bird seeks refuge, crouching behind plants/grass or rocks.
Panic behaviour	Bird panics by flying aimlessly into mesh/perches.
Vigilant Posture	Bird is standing with it head and back erect, scanning the horizon usually from prominent perches.
Aggressive displays	Bird repeatedly nods or bobs head, flicks tail and wings in a confrontational position. Beak gapes open.

3.3 RESULTS

3.3.1 Acoustic parameters

Treatment versus control

For original groups, the treatment samples (snakes and raptors combined) differed from the control samples (pipes and non-predatory birds) in that no alarm calls were recorded in the latter (Table 3.3). In assorted groups, the birds responded significantly differently to treatment vs. control samples for all acoustic parameters (Table 3.3).

Table 3.3: Comparison between the treatment (snakes and raptors combined) and control (pipes and non-predatory birds combined) presentations for original (n = 20) and assorted groups (n = 20) (Wilcoxon Signed Ranks Test only for Assorted comparison). Means and are presented for the different acoustic parameters

Parameter	**Original groups**		**Assorted groups**		**Wilcoxon Signed Rank Test**
	Control	**Treatment**	**Control**	**Treatment**	
Number of calls/5 min	0.00	81.48	0.42	61.48	5.51***
Amplitude (dB)	0.00	7.98	-0.35	-8.45	5.49***
Duration of call (s)	0.00	0.16	0.01	0.13	5.51***
Pause duration (s)	0.00	0.24	0.03	0.63	5.43***
Peak frequency start (kHz)	0.00	4.59	0.17	4.10	5.50***
Peak frequency end (kHz)	0.00	4.69	0.16	4.12	5.52***

*** = $P < 0.001$

Original vs. Assorted groups

Original and assorted groups responded differently to mounted raptors for all acoustic parameters, except for duration of call (Table 3.4). Birds in original groups called more often, the calls were louder (i.e. amplitude of -7.54 dB is louder than –8.60 dB), they paused longer between calls, and started calling at a higher frequency while ending at a lower frequency. For latex snakes, original and assorted groups responded differently for all acoustic parameters, except amplitude (Table 3.5). Again, original groups called more, the calls were longer in duration, they paused longer between calls, and each call started at a higher frequency but ended at a lower frequency.

Table 3.4 Comparison of acoustic parameters between the original and assorted Bronze Mannikin groups in response to mounted raptors. (Means ± SD).

Parameter	**Original Group (n = 20)**	**Assorted Group (n = 20)**	**Mann- Whitney Test U-value**
Number of calls/5 min	95.95 ± 18.99	75.9 ± 12.05	81.50*
Amplitude (dB)	-7.54 ± 0.11	-8.60 ± 0.50	85.00*
Duration of call (s)	0.16 ± 0.04	0.44 ± 0.39	170.00
Pause duration (s)	0.23 ± 0.02	0.63 ± 0.11	0.00***
Peak frequency end (kHz)	4.56 ± 0.35	3.93 ± 0.26	42.00*
Peak frequency start (kHz)	4.60 ± 0.38	4.12 ± 0.18	66.00*

* = $P < 0.05$, *** = $P < 0.001$

Table 3.5 Comparison of acoustic parameters between original and assorted Bronze Mannikin groups in response to latex snakes. (Means ± SD).

Parameter	**Original Group (n = 20)**	**Assorted Group (n = 20)**	**Mann- Whitney Test U value**
Number of calls/5 min	67.00±23.36	47.05 ± 13.03	95.00*
Amplitude (dB)	-8.43 ± 0.92	-8.22 ± 1.15	187.00
Duration of call (s)	0.16 ± 0.04	0.09 ± 0.04	49.50*
Pause duration (s)	0.24 ± 0.02	0.63 ± 0.32	49.50*
Peak frequency end (kHz)	4.62 ± 0.36	3.96 ± 0.26	40.50*
Peak frequency start (kHz)	4.67 ± 0.41	4.10 ± 0.21	58.00*

* = $P < 0.05$

Snakes vs. raptors

Mannikins called significantly more frequently when exposed to models of raptors compared to snakes (Table 3.6), but no differences were detected for the other acoustic parameters.

Table 3.6 Comparison of acoustic parameters given by Bronze Mannikins in response to snakes and raptors. Data for original and assorted groups were combined (Means ± SD).

Parameter	**Snakes (n = 20)**	**Raptors (n = 20)**	**Mann-Whitney Test U value**
Number of calls/5 min	57.00 ± 21.23	85.93 ± 18.70	245.5***
Amplitude (dB)	-8.35 ± 1.04	-8.07 ± 1.01	757.5
Duration of call (s)	0.13 ± 0.05	0.16 ± 0.09	667.0
Pause duration (s)	0.44 ± 0.29	0.43 ± 0.22	786.5
Peak frequency start (kHz)	4.27 ± 0.44	4.25 ± 0.44	795.5
Peak frequency end (kHz)	4.39 ± 0.43	4.36 ± 0.39	678.5

* = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$

Regression analyses

Original group members increased their call frequency and amplitude in relation to raptor size, whereas the end and start frequencies of the calls decreased (Table 3.7, Figure 3.1). On average, the larger raptor elicited a 50% increase in alarm call rate compared to the smallest raptor. In assorted groups, the pause duration increased with an increase in raptor size (Table 3.7).

Table 3.7 Regression analysis results (R^2 values provided) for comparisons between acoustic parameters and predator size.

Indices of threat	Parameter	Original Group R^2	Assorted Group R^2
Snake Length	Number of calls/5 min	0.9025***	- 0.0529
	Amplitude (dB)	0.2025*	0.1296
	Duration of call (s)	- 0.0064	0.1521
	Pause duration (s)	0.1296	- 0.0625
	Peak frequency start (kHz)	- 0.0400	- 0.0256
	Peak frequency end (kHz)	- 0.2809*	- 0.2704*
Raptor Wing Length			
	Number of calls/5 min	0.6241***	- 0.0676
	Amplitude (dB)	0.4096**	0.0529
	Duration of call (s)	0.1849	0.0441
	Pause duration (s)	- 0.1521	0.2704*
	Peak frequency start (kHz)	- 0.6241***	- 0.1296
	Peak frequency end (kHz)	- 0.6889***	- 0.0196

* = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$

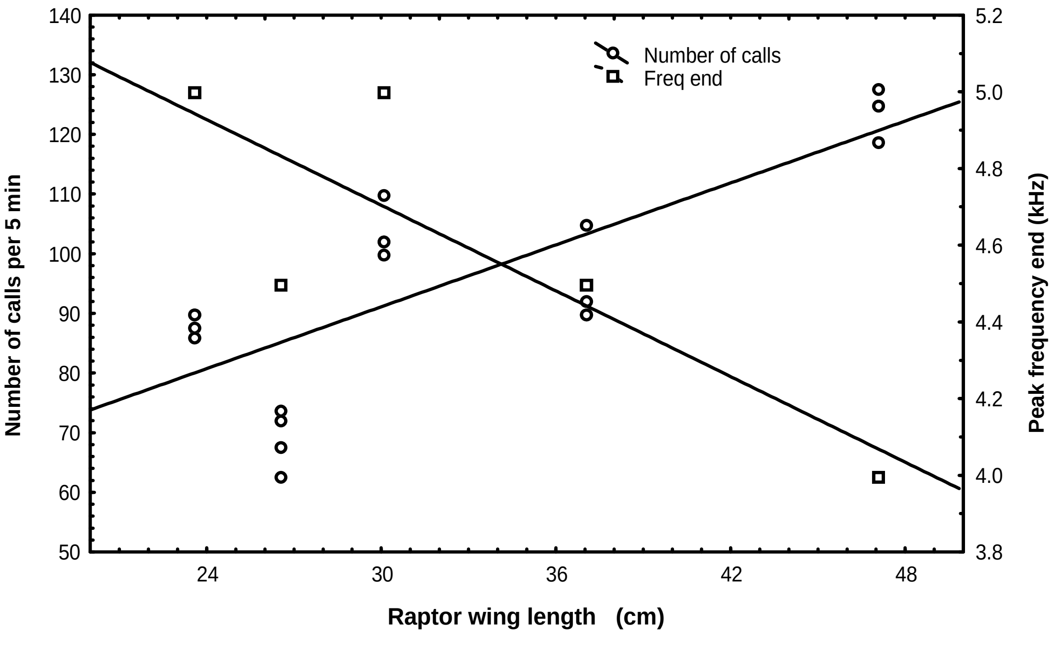

Fig. 3.1 The linear relationships between raptor wing lengths, alarm call frequency and duration for original groups.

When exposed to snakes with increasing body lengths, original group members increased their call frequency and amplitude, and decreased the end frequency of the call (Table 3.7, Figure 3.2). On average, the long snake elicited almost three times the rate of alarm calls compared to the short snake. Assorted group members only decreased the end frequency of the alarm calls in response to snakes, but not to raptors (Table 3.7).

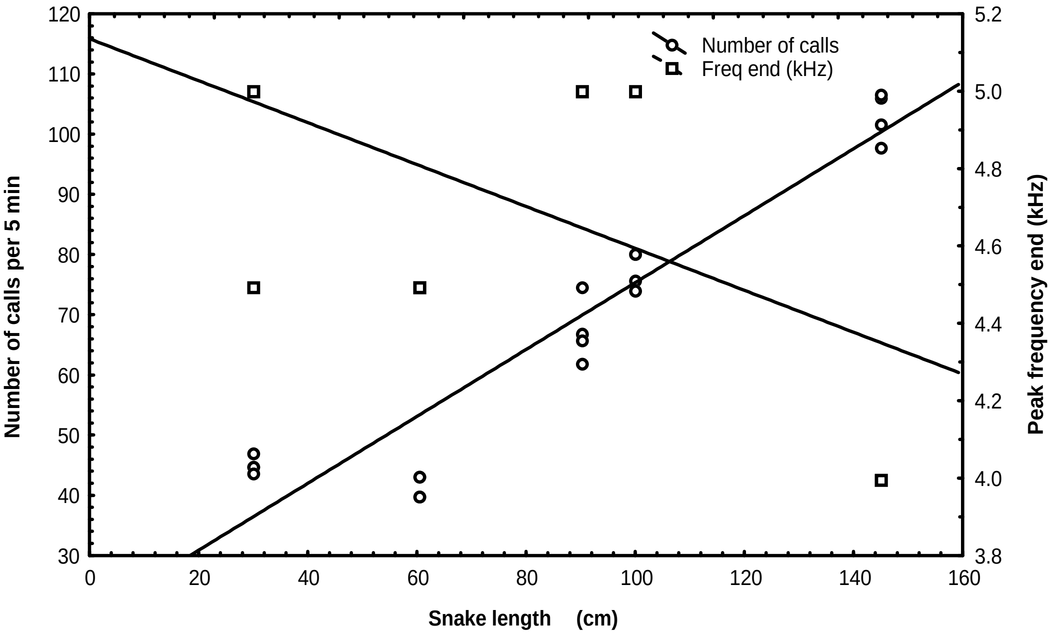

Fig. 3.2 The linear relationships between snake lengths, alarm call frequency and call rate for original groups.

3.3.2 Analyses of behavioural data

Predators vs. controls

The original groups behaved significantly differently when exposed to the predators (snakes and raptors combined) than when exposed to the controls (pipes and non-predatory birds) (χ^2 tests with Yates correction, all $p < 0.001$). Similarly, treatment versus control samples differed significantly (χ^2 tests with Yates correction, all p <

0.001) for the assorted groups. Both the original and assorted groups foraged and socialised less, but took flight and behaved both, more vigilantly and aggressively when exposed to predator models (Table 3.8).

Original vs. Assorted groups

Assorted and original groups generally did not behave differently when exposed to raptors (Table 3.8), but assorted group members took flight more and original group members behaved were more aggressively towards the raptors. When exposed to snakes, original groups behaved very aggressively towards these predators, whereas assorted groups did not (Table 3.8).

Table 3.8 Comparison of behavioural acts between original and assorted Bronze Mannikins when exposed to mounted predators and latex snakes. Chi square tests with Yates correction are shown.

Predator	**Behavioural act**	**Response**	**Original**	**Assorted**	χ^2
Raptors	Foraged	Yes	0	2	0.53
		No	20	18	
Raptors	Social interactions	Yes	3	2	0.00
		No	17	18	
Raptors	Panic behaviour	Yes	11	18	4.51*
		No	9	2	
Raptors	Vigilant posture	Yes	20	16	2.50
		No	0	4	
Raptors	Aggressive displays	Yes	14	3	10.23**
		No	6	17	
Snakes	Foraged	Yes	0	2	0.53
		No	20	18	
Snakes	Social interactions	Yes	2	1	0.02
		No	18	19	
Snakes	Panic behaviour	Yes	13	17	1.20
		No	7	3	
Snakes	Vigilant posture	Yes	20	17	1.44
		No	0	3	
Snakes	Aggressive displays	Yes	18	6	12.60***
		No	2	14	

* = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$

When the behavioural data for the snakes and raptors were combined (after no differences were found), mannikins from original groups took flight less often than birds in the assorted groups ($\chi^2 = 6.46$, $P < 0.05$, Table 3.9). The opposite trend was observed for vigilance behaviour. Aggressive displays were performed significantly more frequently in original groups compared to assorted groups ($\chi^2 = 24.22$, $P < 0.001$, Table 3.9).

Table 3.9 Comparison of behavioural acts between original and assorted Bronze Mannikin groups exposed to predators (raptors and snakes combined). Chi square tests with Yates correction are shown.

Behavioural act	**Response**	**Original**	**Assorted**	χ^2
Foraged	Yes	0	4	2.37
	No	40	36	
Social interactions	Yes	5	3	0.14
	No	35	37	
Panic behaviour	Yes	24	35	6.46*
	No	16	5	
Vigilant posture	Yes	40	33	5.64*
	No	0	7	
Aggressive displays	Yes	32	9	24.22***
	No	8	31	

* = $P < 0.05$, *** = $P < 0.001$

Predator type

Bronze Mannikins in original groups, apparently did not differentiate between raptors and snakes for any of the behavioural responses (χ^2 tests, all $P > 0.23$). Similarly, members of assorted groups did not differentiate between raptors and snakes for any of the behavioural responses (χ^2 tests, all $P > 0.45$).

3.4 DISCUSSION

Living in groups has the primary benefit that group members may share information about the presence and nature of predators (Sherman 1977, Weary & Kramer 1995, Bateson 2000). However, this is only the case if group members are familiar with each other and can recognise and interpret each other's calls (Smith *et al.* 1982, Bateson 2000). Furthermore, within a group of cooperating individuals, the alarm calls may signify the size and type of predator (Beynon & Rasa 1989, Marler & Evans 1996, Greene & Meagher 1998).

In the wild, snakes are a common threat to birds (particularly when breeding). Due to their ingenious tree-climbing abilities and slender, flexible bodies, snakes can easily access bird nests located either on the ground or in vegetation (Wiles *et al.* 2003). Raptors also pose a lethal threat as they ambush birds at feeding sites, catch them in flight or eat their young (Woodall 1975).

In the Durban Metropole where Bronze Mannikins were caught and held in aviaries, bird-eating snakes and raptors are abundant. The aviaries were located within territories of one pair of Little Sparrowhawks *Accipiter minullus,* African Goshawks and Black Sparrowhawks *A. melanoleucus* respectively (G. Malan pers. obs.), while the Boomslang *Dispholidus typus* and the Vine snake *Thelotornis capensis* are also located within this vicinity (A.J.L. Lambiris pers. obs.). The mannikins, especially the adults, would thus have been exposed to these predators. This eliminated the potential problem of the prey animals being unfamiliar with the predators and thus providing unnatural responses to their presence (Leavesley & Magrath 2005). Furthermore, our experimental controls demonstrated that Bronze Mannikins were able to identify mounted raptors and latex snakes as potential predators.

Furthermore, the Bronze Mannikins' strong behavioural responses to predators, providing further confidence in the interpretation of the experiments. However to conduct a full study of communication (as mentioned in the introductory chapter) it is necessary to examine both the alarm call and the response (Leavesley & Magrath 2005).

To study the behavioural response of birds to the presence of predators, playbacks are used and the actual flee alarm call is played to individual birds (Manser 2001). Since this study examined the behavioural response of five birds in the presence of the predator, the reactions of the mannikins might have been independent replies to the presence of the predator, or individuals actually responding to the caller rather than to the predator. Because of possible pseudoreplication of calls and the above audience effect (Marler & Evans 1996), the behavioural responses must be viewed within the context of the predator exposures: in this case, a group of Bronze Mannikins being exposed to a surrogate predator one metre from their aviary. Conclusions can thus only be drawn regarding the context under which the alarm calls were made, rather than its meaning (Leavesley & Magrath 2005).

In this study, Bronze Mannikins apparently perceived the larger predators as more intimidating than smaller predators, although they might not necessarily impose a greater risk of depredation. However, mannikins increased their call frequency with predator size, and for larger raptors, their alarm-call amplitude and duration. The employment of this alarm-call strategy for larger predators has been associated with an increase in predation risk and threat (Evans *et al.* 1993, Le Roux *et al.* 2001, Bayly & Evans 2003). Since it may be difficult for larger predators to catch diminutive manikins (G. Malan pers.obs.), the threat may derive from being confronted, in the experimental situation, by a larger predator. Larger predators are detected more easily and the longer, higher amplitude and more frequent calls have the potential to notify group members and other potential prey species in the immediate vicinity (Bayly & Evans 2003). Overall Bronze Mannikins apparently perceived the larger predators as more intimidating than smaller predators, although they might not necessarily impose a greater risk of predation. Although the Long-crested Eagle was mounted with raised outstretched wings, which may have inflated some results, the reaction elicited from this particular raptor still reinforces the theory that larger birds appear more intimidating. Although these eagles have been reported to raise their wings before strike (Brown *et al.* 1982), they rarely predate upon small birds (Hall 1979). Overall the results pertaining to raptor size should be treated with some caution.

The fact that mannikins respond to larger predators by decreasing the start and end frequencies of their calls, is in accordance with other studies that found that prey species adapt their acoustic signalling, in response to increased predation threat, to decrease the conspicuousness of the flock and to prevent the predator from using the call location to pinpoint the prey (Niko'skii *et al.* 1994; Blumstein & Armitage 1997*a*, Bayly & Evans 2003). Introductory and end pulses are potentially costly at they are readily localized by predators, therefore the manipulation of frequency allows the birds to manage short-term predation risk by making it difficult to localise, while continuing to signal to companions (Bayly & Evans 2003).

Secondly, Bronze Mannikins may have used alarm calls to provide information to group members about the type of predator. A higher call rate in response to aerial models might indicate that mannikins perceived a raptor perching outside the cage (three-dimensional) as a more formidable threat than snakes slithering past (two-dimensional), also as an aerial predator can potentially move faster that a terrestrial one.

Animals have been known to increase their call frequency, employing the simple pulses to encode referential information about the increase in predator threat (Blumstein 1999, Bayly and Evans 2003), and Bronze Mannikins may have employed this simple strategy to alert group members to the presence of the potentially more dangerous raptors.

Group cooperation

Apart from communicating the degree of danger, Marler (1977) suggests that it would be advantageous for groups to evolve means of discriminating members from others, or refraining from interacting with non-members, or even repelling them aggressively from the social group. In this study, original Bronze Mannikin groups appear to identify and communicate warning signals accurately and effectively. Assorted groups, although incorporating two members from the original group, appear not to conform to the stable social group. They panicked more frequently and were less vigilant than the original birds. Panic-stricken individuals are symptomatic of a high predation threat (Lima and Dill 1990) and increased vigilance is indicative of a stable social group (Rasa 1989, Curio 1978). More importantly, assorted groups decreased their aggressive behaviour (i.e. tail and wing flicking, head bobbing) towards the predator, perhaps because they did not trust their conspecifics to behave cohesively in an attack to force the predator to leave.

Differences were not only found in the anti-predator behaviour of assorted vs. original groups, but also in the alarm call structure. The presence of known group mates may influence whether additional contextual cues are used to interpret a call’s meaning (Blumstein 1999). In original groups, caller identity may be such a cue that conspecifics in assorted groups may not recognise. Furthermore, in assorted groups, the majority of individuals might not have learnt these individual-specific associations and this simple lack of understanding between birds might have caused the message transferred to get lost. When either survival is at stake, due to the immediate presence of a predator or ultimately due to the trade-off between foraging and vigilance, selection would favour individuals who responded reliably to alarm calls (Sherman 1985, Bachman 1993, Hare and Atkins 2001). By calling less frequently, pausing shorter between calls and producing calls with a lower start frequency but a higher end frequency, Bronze Mannikins in assorted groups might have transferred the predation threat information inadequately to the other group members, causing these members, in turn, not to respond reliably to alarm calls. The breakdown in communication between group members might have caused the decrease in aggressive displays and vigilance, and the increase in panic behaviour.

The captive Bronze Mannikins exposed to surrogate predators in this study demonstrated that their alarm calls carried a degree of input specificity, i.e. the birds were able to distinguish predator size and type. They communicated this threat effectively through their call structure and some changes in anti-predator behaviour (vigilance and aggressive displays). By participating and cooperating in predator avoidance and deterrence activities, group members can potentially gain fitness benefits, while group members not familiar with the caller identity and the contextual cues of one another’s calls may fail to respond.

Future studies should investigate groups in their natural habitat and exposed to live predators, through the technique of playbacks, to assign meaning to alarm behaviour and calls. Different size groups exposed to an array of predators (and controls) will reveal how a group will communicate and react when confronted by a potential predator. Only then can the fitness costs and benefits associated with group living be measured.

Chapter 4

Warning your mates of danger: does degree of sociality make a difference?

Alarm calls transmit semantic information referring to specific stimuli categories such as predator type. This study examined the effect of group living on alarm vocalisations by comparing the alarm calls of the social Buff-streaked Chat, *Oenanthe bifasciata* to that of the asocial Stonechat, *Saxicola torquata*. In addition we investigated if these passerines produced vocalisations of semantic value that discriminate predator type. Three groups of Buff-streaked Chats and ten pairs of Stonechats were captured with spring traps from the Drakensburg range, and housed separately in groups in outdoor aviaries. Groups or pairs of these passerines were sequentially exposed to five latex snakes and five mounted raptors, while alarm and territorial calls were recorded respectively. The largest group of Buff-streaked Chats increased their aerial-alarm call rate (39 calls in five minutes) and dropped their end pulses (for both predators) by 0.6 kHz. Several theories may explain these outcomes: (1) larger and louder groups of Buff-streaked Chats present a more formidable mob to discourage attack; (2) softer end pulses emitted by Buff-streaked Chats may minimize cues of the callers' location and; (3) high call rates are implemented by Buff-streaked Chats during high risk situations to reflect the response urgency required to escape aerial predation. Furthermore, the social species behaved conversely, which may be due to the species' habitats (signal attenuation), or a strategy to dissuade predator attack.

4.1 INTRODUCTION

Many species form social groups to better protect themselves from predators. The advantage of living in groups is that vigilance by the group as a whole increases (Bradbury & Vehrencamp 1998). Vigilance is predominantly communicated through warning vocalisations that may divert the predator's attention to other prey, discourage predator pursuit or alert relatives of impending danger, hence reducing the likelihood of later attacks by the same predator and warning others likely to reciprocate (Marler 1957, Trivers 1971, Sherman 1977, Sherman 1980). Although a predator will more easily detect a larger group, predation rates per individual decrease with group size, not only because of more effective vigilance, but also because of the confusion and dilution effects (Marler 1957, Sherman 1977, Bradbury & Vehrencamp 1998).

The alarm calls provide information on the presence and location of the predator (Sherman 1977), as well as the type of predator (Cheyney & Seyfarth 1988, Beynon & Rasa 1989). Some species produce a single invariable call containing little information, while others produce multiple types of calls. Blumstein (2003) suggested that complex communication coevolved with complex sociality because more social species have more to communicate about. Blumstein & Armitage (1997*b*, 1998) defined ‘more social species’ according to a demographic metric of the social group, i.e. they quantified variation in the number, sex, reproductive condition, and age of group members as indices of sociality. Stemming from this theory, one can predict that a social species will display inter-individual alarm communication as opposed to an asocial species, which has a reduced need for inter-individual alarm communication.

Similar warning and defence behaviour is displayed through territoriality. Territories are defined as defended areas, maintained by aggressive displays and territorial song or vocalisations to defend boundaries (McGregor 1993). Territorial behaviour encompasses group and nest defence, features fundamental to social organisations (McGregor 1993). Larger repertoires and increased territorial defence maybe associated with increased survival of offspring and good mate quality (Bradbury & Vehrencamp 1998). Group-living birds thus make good subjects in which to investigate the ability to modify antipredator and territorial vocal behaviour according to predation threat. To test this, I compared the warning vocalisations of a social species, the Buff-streaked Chat *Oenanthe bifasciata,* with the solitary, Stonechat

Saxicola torquata. These species were specifically chosen for various reasons: both species are commonly found at the foothills of the Drakensberg range (Keith *et al.* 1992) which made it convenient to conduct capture expeditions, both species would acclimatise fairly well to the climatic conditions in Durban and their insectivorous diet could be easily catered for, making it very practical to study in captivity. In addition, both species shared similar structure, plumage, habitat and behaviour (Tye 1989, Keith *et al.* 1992) yet still possessed a distinction in their social structure, the Stonechat being solitary and the Buff-streaked Chat being social making them the ideal choice.

It should be noted that group size alone is an inadequate metric of the level of sociality (Blumstein 1997), because social behaviour involves a diversity of relationships between individuals. Social behaviour includes the nature of the relationship, the stability and persistence of the relationship, a species mating or grouping system, by a series of ecological factors and by life-history variables (Blumstein 1997). If one considers these factors, the Buff-streaked Chat fulfils these relationships far more consistently than the Stonechat.

Buff-streaked Chats are endemic to southern Africa and especially common in the KwaZulu-Natal Drakensberg (Keith *et al.* 1992). This insectivorous species (average mass 33 g) occupies boulder fields and rock outcrops in montane grasslands. An insectivorous diet influences social dispersion of group members such that they forage in groups tracking a clumped food source (Knight 1988). They form small territorial family-groups (Tye 1988). During territorial defence and alarm encounters, Buff-streaked Chats emit a ‘chack’ and a short squeaky whistle (Keith *et al.* 1992).

The Stonechat is a diminutive, predominantly insectivorous passerine (average mass 15 g). They inhabit open grassland, especially with scattered shrubs to montane forest edges of the Drakensberg range. In South Africa, Stonechats live in monogamous pairs, foraging within defended territories. They regularly perch on fences and telegraph wire along road verges. Breeding Stonechats emit a mixed sequence of two calls (‘whits’ and ‘chacks’) in response to territory and nest defence respectively (Greig-Smith 1980). They also share similar habitats and during unfavourable conditions, their niches may overlap and they may compete for food and resources (especially insects during winter) (pers. obs.).

In order to compare the warning signals emitted by the Buff-streaked Chat and Stonechats, the following questions were addressed:

(1) Do the alarm calls of Buff-streaked Chats contain more information than that of the Stonechat, i.e. more call elements within a sample period of 5 minutes?

(2) How do the territorial repertoires of these two species differ and what are the implications for vigilance behaviour?

4.2 METHODS

Study Species

Free-living birds were caught between August and September 2001, and again in September 2002 in the central and northern Drakensberg Range. Buff-streaked Chat groups were trapped in boulder-strewn, montane grasslands adjacent to roads. Stonechats were captured at forest edges, especially along the road verge. Spring-traps (Forbes 2000) were baited with mealworms, ensnaring the bird when it attempted to take a worm.

Ten individual Buff-streaked Chats and ten pairs of Stonechats were captured in total. The Buff-streaked Chats were mixed randomly into the following ‘groups’. The first ‘group’ comprised a solitary bird (male), the second group contained four individuals (two males and two females) and the third group comprised five individuals (four males and a single female).

A detailed account of the type of raptor and snake surrogate used, their controls and the procedures used to introduce the surrogate predators is included in the experimental set up (section 2.3).

Vocal repertoire

The vocal repertoire of the Buff-streaked Chat comprised a number of acoustically distinct, but simple calls (Gibbon 1991) (Figure 4.1):

(a) Territorial call, as a series of multi-syllable notes that was far ranging and audible by humans up to 500m distances (Gibbon 1991);

(b) Calls emitted exclusively in the presence of raptors were referred to as raptor alarm call. It is low in frequency and characterized by fast but short elements,

(c) Calls emitted exclusively in the presence of snakes were referred to as snake alarm call. They occurred as single, staccato calls repeated at regular intervals and

(d) Begging call, used for short-range communication, and uttered by all members of the group. They were high-pitched, repetitive whistles emitted in conjunction with the presentation of mealworms at feeding time.

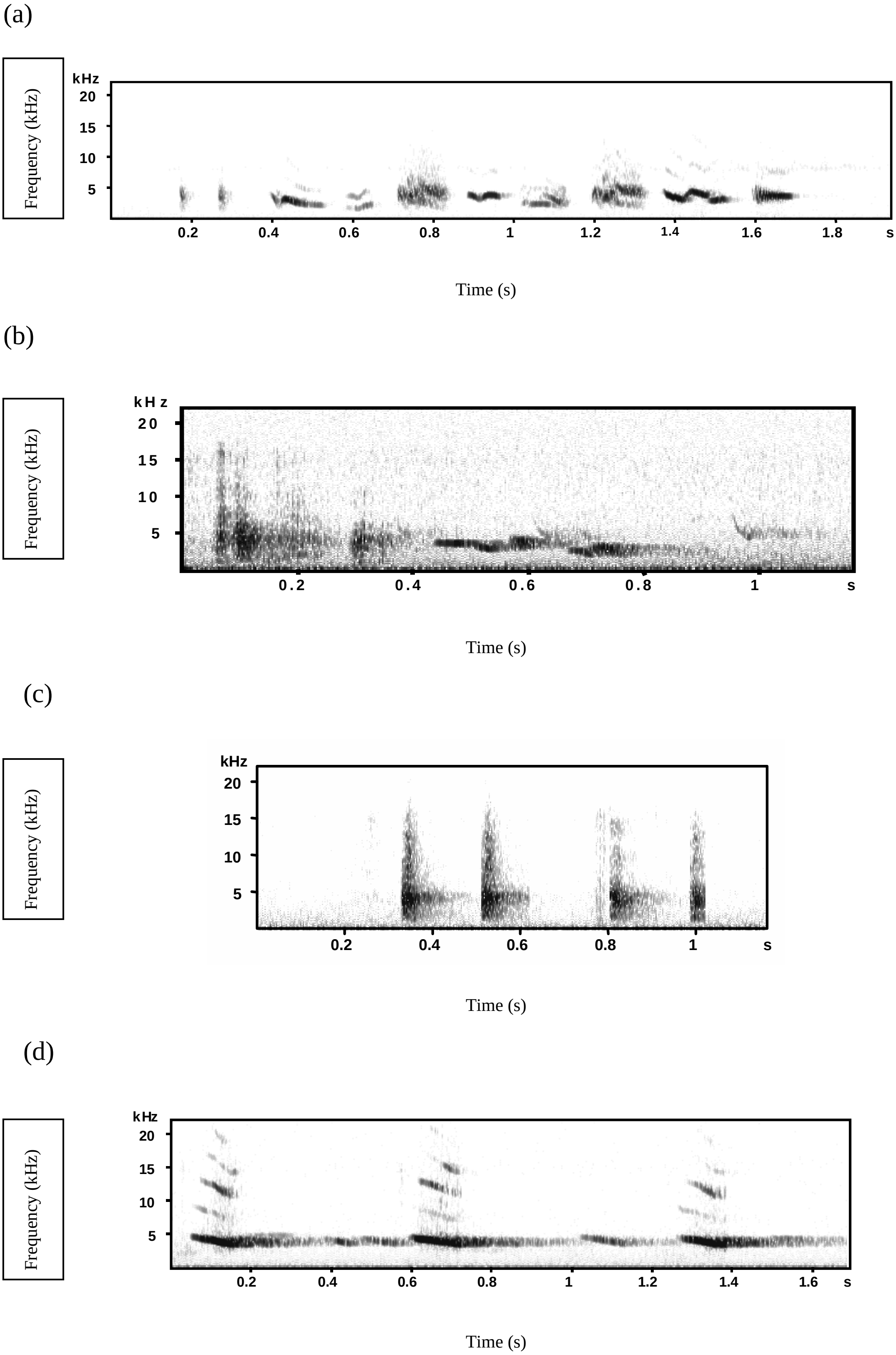

Fig. 4.1 Spectrograms of call types emitted by the Buff-streaked Chats; (a) Territorial call, (b) Raptor alarm call, (c) Snake alarm call, (d) Begging call. Sonagrams were made with AVISOFT SASLAB LIGHT recording parameters: 22.05 kHz sampling frequency, 16 bit sampling. Analysis parameters: FFT, hamming window analysis; frequency resolution 345.1/64 points filter bandwidth.

The vocal repertoire of the Stonechat consisted of a series of distinct calls uttered by both male and female (Gibbon 1991) (Figure 4.2):

(a) Territorial calls, as a high-pitched, repetitive, multi-syllable call (Gibbon 1991)

(b) Calls emitted exclusively in the presence of snakes were referred to as snake alarm call: a simple, single note '*chat'* that was in low frequency

(c) Calls emitted exclusively in the presence of raptors were referred to as raptor alarm call and comprised a single-note '*whit*".

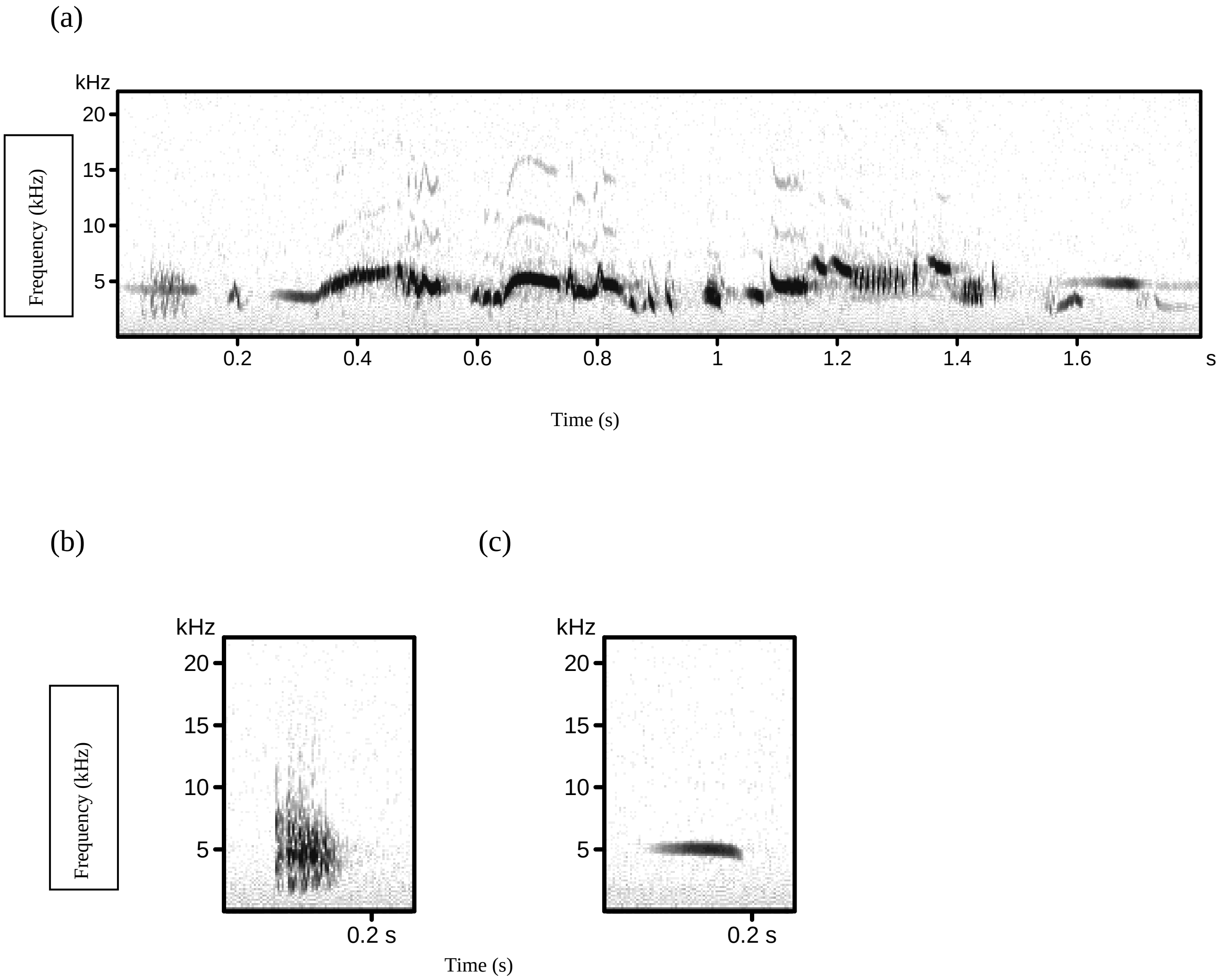

Fig. 4.2 Spectrograms of call types emitted by the Stonechat; (a) Territorial call, (b) Snake alarm call, (c) Raptor alarm call. Sonagrams were made with AVISOFT SASLAB LIGHT recording parameters: 22.05 kHz sampling frequency, 16 bit sampling. Analysis parameters: FFT, hamming window analysis; frequency resolution 345.1/64 points filter bandwidth.

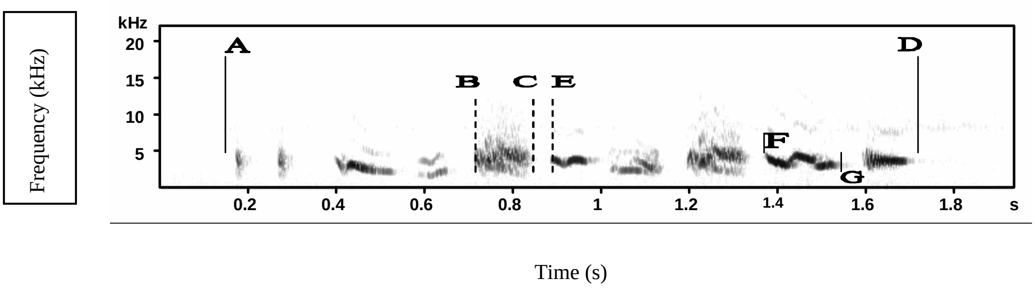

Fig. 4.3 Parameters used in the acoustic analysis of Buff-streaked Chat Territorial calls. A-D call duration; B-C syllable duration; C-E pause duration (inter syllable duration); F peak frequency start, G peak frequency end). Sonagrams were made with AVISOFT SASLAB LIGHT recording parameters: 22.05 kHz-sampling frequency, 16 bit sampling. Analysis parameters: FFT, hamming window analysis; frequency resolution 345.1/64 points filter bandwidth

Alarm calls

Inter-individual communication was defined by calls emitted by group members to whom other conspecifics reacted to by an increase in the alarm call rate or an increase in call duration. It was not possible to identify the specific individual/s emitting the alarm due to the sheer speed of emission. Further, it was postulated that in order to accommodate these signals, the call structure would be manipulated accordingly; hence, the Stonechat should display a much smaller alarm call repertoire than the group-living Buff-streaked Chat.

The following six (alarm) acoustic parameters (Figure 4.3) could be measured with AVISOFT SASLAB Light and spectrograms were subsequently produced. (1) The total number of calls emitted during the 5 minute sampling period, (2) the duration of the call element, (3) the pause duration (inter-call duration) between call elements, (4) the amplitude of each call element (dB), (5) the start frequency (kHz) (start pulse) of each call, and (6) the end frequency (kHz) (end pulse) of each call. The acoustic data for all three Buff-streaked Chat groups were initially compared for differences, and thereafter combined (when no differences were found) for each acoustic parameter and analysed separately for snakes and raptors. This procedure was repeated for the Stonechat data.

To investigate the influence of group size on alarm vocalisations, a linear regression was employed with the six acoustic parameters listed above as dependent variables and Buff-streaked Chat ‘number of individuals’ as the independent variable. ‘Number of individuals’ or group size was considered as an indicator of the level of inter-individual communication that may influence linear changes in call rate, call duration and the other acoustic parameters. The acoustic signals emitted by the two species were compared for raptors and snakes separately.

Territorial calls

The territorial calls of Buff-streaked Chats and Stonechats were analysed at two levels of acoustic structure: the single call syllable and the entire call series (Figure 4.3). The following parameters were analysed: number of calls per 5 minutes, amplitude, duration of syllable, peak start frequency syllable, the end frequency syllable, pause duration (inter call duration).

A linear regression was employed with the six acoustic parameters listed above as dependent variables and ‘number of individuals’ as the independent variable. Furthermore, the Mann-Whitney U test was used to compare the territorial calls emitted by the Buff-streaked Chats to those of the Stonechat. STATISTICA (v6 Tulsa, OK) was used to perform the statistical tests and indicate two-tailed P values.

4.3 RESULTS

4.3.1 Alarm calls

Group Size

When exposed to snakes, Buff-streaked Chats responded by increasing the amplitude, emitting louder calls, with an increase in group size (Table 4.1, Figure 4.4). The smallest group (the solitary Buff-streaked Chat) produced, on average, amplitudes of –5.8 dB, while the five member group (largest group) produced amplitudes of –4.4 dB (louder) ($R^2 = 0.3481$, $P < 0.05$, Table 4.1, Figure 4.4). In addition, when exposed to snakes, larger Buff-streaked Chat groups decreased their end frequencies (Figure 4.4). The solitary Buff-streaked Chat emitted on average, end pulses of 6.2 kHz, while the largest group produced end frequencies of 4.75 kHz ($R^2 = 0.3249$, $P < 0.05$, Table 4.1, Figure 4.4).

Table 4.1 Results of the linear regression (R^2 values indicated below) to investigate the relationship between Buff-streaked Chat group size and acoustic alarm call parameters.

Parameter	**Snakes** **R^2**	**Raptors** **R^2**
Number of calls/5 min	0.0625	0.5476^{**}
Amplitude (dB)	0.3481^{*}	0.0361
Duration of call (s)	0.1521	0.0441
Pause duration (s)	0.0576	0.1089
Peak frequency start (kHz)	0.0016	0.0049
Peak frequency end (kHz)	$- 0.3249^{*}$	$- 0.6084^{***}$

*$P < 0.05$, ** $P < 0.005$, *** $P < 0.001$

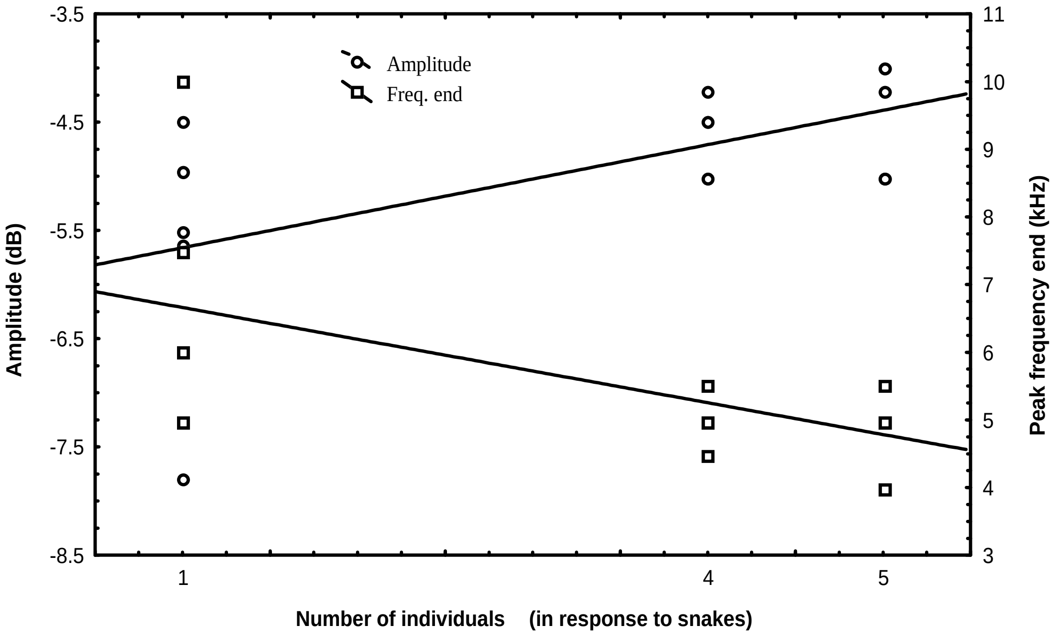

Fig. 4.4 The effect of group size on amplitude and peak frequency end emitted by Buff-streaked Chats in response to snakes

In response to raptors, the call rate increased significantly with an increase in group size (R^2 = 0.5476, P < 0.005, Table 4.1, Figure 4.5). The solitary Buff-streaked Chat called on average 24 times in 5 min, while the largest group produced 39 calls in 5 min (Figure 4.5). The peak frequency end decreased from 5.10 kHz (solitary Buff-streaked Chat) to 4.5 kHz (largest Buff-streaked Chat group) (R^2 = 0.6084, P < 0.001, Table 4.1, Figure 4.5). It is also evident that larger groups emitted louder calls in response to snakes, however calling more often in response to raptors. Other variables showed no significant trends (Table 4.1).

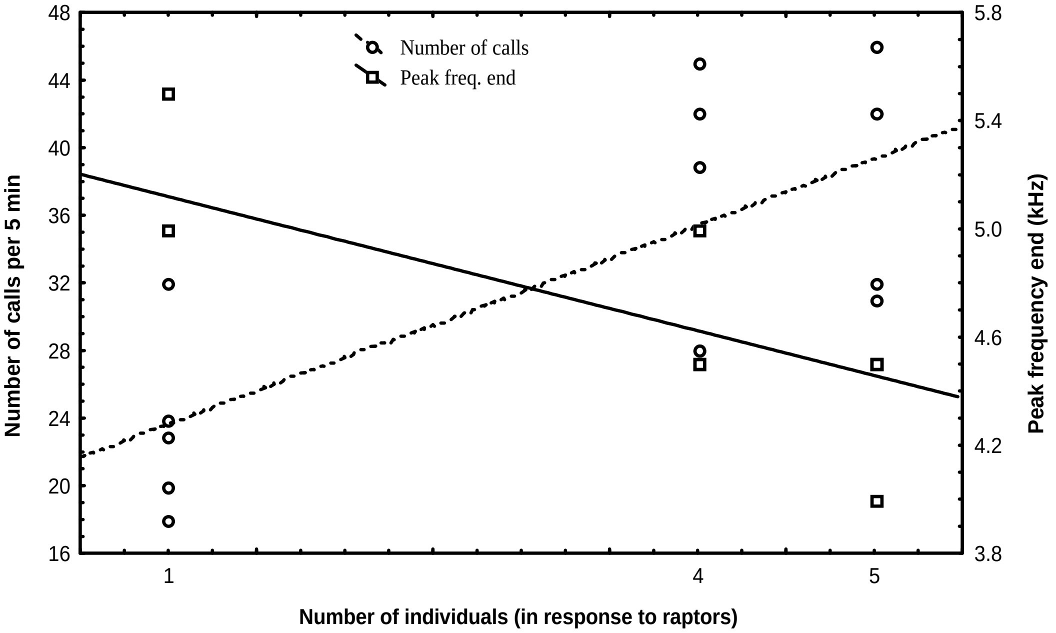

Fig. 4.5 The effect of group size on the number of calls and peak frequency end (kHz) emitted in five minute sample session by Buff-streaked Chats in response to raptors. Peak frequency end values appear missing however, one data point represents more than one value (i.e. values overlap).

Sociality vs. asociality

Similarly, when exposed to snakes, significant differences were found between the alarm calls of Buff-streaked Chats and Stonechats for all acoustic variables, except duration of call (Table 4.2). The Buff-streaked Chat called more frequently (27 calls in 5 min) than the Stonechat (15 calls in 5 min, $P < 0.005$). The Buff-streaked Chat emitted a softer call (amplitude –5.16 dB) than the Stonechat (amplitude –4.68 dB, $P < 0.001$). The start (14.95 kHz) pulses produced by Buff-streaked Chats were louder than the pulses emitted by Stonechats (11.19 kHz, $P < 0.001$), while the end pulses of *Saxicola torquata* (6.12 kHz, $P < 0.005$) proved to be louder than that of *Oenanthe bifasciata* (5.90 kHz). Furthermore, Stonechats paused longer (22.00 sec) between alarm calls than Buff-streaked Chats (5.64 sec, $P < 0.001$).

Table 4.2 Results of Mann-Whitney U tests to compare Buff-streaked Chat alarm data to that of the Stonechat in response to snakes. (Mean ± SD, n = 15)

Parameter	**Buff-streaked Chat**	**Stonechat**	**Mann- Whitney Test - U value**
Number of calls/5 min	27.20 ± 8.04	15.20 ± 6.83	27.00**
Amplitude (dB)	- 5.16 ± 1.03	-4.00 ± 0.00	15.00***
Duration of call (s)	0.15 ± 0.03	0.16 ± 0.01	102.50
Pause duration (s)	6.54 ± 1.25	22.15 ± 12.37	8.00***
Peak frequency start (kHz)	14.95 ± 0.37	11.19 ± 0.26	0.00***
Peak frequency end (kHz)	5.90 ± 1.66	6.12 ± 0.21	35.50**

** $P < 0.005$, *** $P < 0.001$

When exposed to raptors, significant differences were found between Buff-streaked Chats and Stonechats, for all acoustic parameters, except for duration of call (Table 4.3). In response to aerial predators, the solitary Buff-streaked Chat emitted an average of 29 calls in 5 minutes, while the Stonechat emitted 16 calls in 5 minutes ($P < 0.001$, Table 4.3). In addition, Buff-streaked Chats emitted softer calls (amplitude -4.68 kHz) than Stonechats (amplitude –4.00 kHz, $P < 0.001$, Table 4.3). Buff-streaked Chat paused longer between calls (7.10 seconds) compared to the Stonechat (5.40 seconds, $P < 0.001$). The peak frequency start and end produced by the Stonechats were louder than that produced by the Buff-streaked Chats ($P < 0.001$, Table 4.3).

Table 4.3 Results of the Mann-Whitney test to compare Buff-streaked Chat alarm data to that of the Stonechat in response to raptors. (Mean ± SD, n = 15)

Parameter	**Buff-streaked Chat**	**Stonechat**	**Mann- Whitney Test U value**
Number of calls/5 min	29.20 ± 9.37	16.30 ± 1.89	3.50***
Amplitude (dB)	-4.68 ± 0.34	-4.00 ± 0.00	22.50***
Duration of call (s)	0.18 ± 0.48	0.20 ± 0.04	437.00
Pause duration (s)	7.10 ± 1.56	5.40 ± 0.21	6.00***
Peak frequency start (kHz)	4.56 ± 0.28	8.34 ± 3.00	6.00***
Peak frequency end (kHz)	4.90 ± 0.32	5.23 ± 0.50	1.00***

*** $P < 0.001$

4.3.2 Territorial calls

For territorial calls, no significant relationship was found between the acoustic variables and Buff-streaked Chat group size (Table 4.4).

Table 4.4 Results of the linear regression (R^2 values indicated below) to investigate the relationship between Buff-streaked Chat group size and acoustic parameters of territorial calls.

Parameter	**Snakes** R^2	**Raptors** R^2
Number of calls/5 min	0.0049	0.0225
Amplitude (dB)	0.0000	0.0000
Duration of syllable (s)	0.0049	0.0000
Pause duration of call (s)	0.0441	0.0256
Peak frequency start syllable (kHz)	0.0000	0.0000
Peak frequency end syllable (kHz)	0.0000	0.0000

Further, no significant differences were found in territorial acoustic parameters response to snakes (Table 4.5). Peak start frequency emitted by Stonechats, increased in response to raptors (Table 4.6).

Table 4.5 Results of Mann-Whitney test to compare Buff-streaked Chat and Stonechat territorial calls in response to Snakes. (Mean ± SD, n = 15)

Parameter	**Buff-streaked Chat**	**Stonechat**	**Mann- Whitney Test - U value**
Number of calls/5 min	1.27 ± 1.75	1.13 ± 1.25	85.50
Amplitude (dB)	-1.60 ± 1.66	-2.13 ± 2.06	97.50
Duration of syllable (s)	0.68 ± 0.16	0.83 ± 0.81	108.50
Pause duration of call (s)	15.00 ± 21.89	66.20 ± 91.37	80.50
Peak frequency start syllable kHz)	2.00 ± 1.86	2.67 ± 2.58	97.50
Peak frequency end syllable (kHz)	1.80 ± 1.86	1.63 ± 2.39	108.00

Table 4.6 Results of Mann-Whitney test to compare Buff-streaked Chat and Stonechat territorial calls in response to raptors. (Mean ± SD, n = 15)

Parameter	**Buff-streaked Chat**	**Stonechat**	**Mann- Whitney Test- U value**
Number of calls/5 min	0.67 ± 1.5	1.00 ± 1.36	83.00
Amplitude (dB)	-4.00 ± 1.66	-2.13 ± 2.06	75.00
Duration of syllable (s)	0.30 ± 0.16	0.83 ± 0.81	67.50
Pause duration of call (s)	9.13 ± 21.89	134.67 ± 145.15	112.50
Peak frequency start syllable (kHz)	0.90 ± 1.86	2.67 ± 2.58	63.00*
Peak frequency end syllable (kHz)	0.90 ± 1.86	1.57 ± 2.29	94.50

$* P < 0.05$

4.4 DISCUSSION

Larger groups of *O. bifasciata* produced louder calls in response to snakes. These louder calls may indicate that larger groups have more individuals available to emit warning calls, thereby increasing the signal amplitude. Owing to the combined vigilance of all group members, the probability of detecting a predator also increases with group size (‘group-size effect’ Krebs & Davies 1997). Secondly, larger and louder groups present a formidable mob encouraging a predator to ‘move on’ (predator deterrence; Klump & Shalter 1984). In addition, the individual risk of being caught decreases with group size because of dilution and confusion effects (‘predation-risk effect’ Krebs & Davies 1997. Larger groups dropped their end frequency in response to snakes and raptors. These decreasing end pulses minimised cues to the caller’s location and prevented a larger group from being detected through reduced conspicuousness. The manipulation of end pulses may be an antipredator device, where Buff-streaked Chats lowered their end frequency below the auditory threshold or range of the predator. This is also consistent with several studies where, for example, aerial alarm calls were not detectable by raptors since they were produced in a frequency range where songbirds have greater sensitivity (Klump *et al.* 1986, Jurisevic & Sanderson 1998, Bayly & Evans 2003).

Larger social groups also increased their calling rate (but with softer calls) in response to raptors. An increased warning rate may be implemented in high-risk situations (Blumstein 1999). This is especially necessary since raptors are fast and agile aerial predators, providing a more dangerous threat than a slower, terrestrial predator (Templeton *et al.* 2005). The calling rate reflects this response urgency clearly by escalating. In addition, increased calling may also deter or discourage the predator from attack (Sherman 1977, Wood *et al.* 2000) as it has already been detected, and the element of surprise no longer exists. In summary, there are correlations between group size and call rate, larger groups possessing heightened vigilance in anticipation of raptors.

Stonechats emit fewer but louder alarm calls than the Buff-streaked Chat for both predator types. Higher call rates contain more calls in a five-minute period. This provides some evidence that larger social groups emit comparatively more information than pair-living or asocial individuals. However, these results may also be linked to the type of habitats that these two species occupy (M. A. du Plessis pers. comm.). The boulder fields and rocky outcrops occupied by Buff-streaked Chats pose physical barriers that may affect signal attenuation, i.e. change in the intensity of signals suffered by sound travelling through a medium. Buff-streaked Chats increased their start pulses but decreased their end pulses in response to snakes, while Stonechats did the opposite.

These changes in acoustic parameters may also reflect each species' individual predator labelling mechanism. In a study conducted on Diana Monkeys *Cercopithecus* *diana*, the calls frequent at syllable onset and subsequent transition provided reliable information about the type of predator present (Zuberbülher 2000*a*).

Buff-streaked Chats emitted softer start and end pulses in response to raptors, which they frequently encountered in their natural habitats (pers. obs.) (Bayly & Evans 2003). Stonechats, on the other hand, increased both start and end pulses, which is consistent with findings of Wood *et al.* (2000). They gave evidence that aerial alarm calls that are audible to raptors discourage attack by informing the predator that it has been sighted and the prey have sought shelter.

The comparison of changing call rate of the two species alone is not sufficient evidence to conclusively support the hypothesis that social species communicate more information to conspecifics than asocial species. The variation in amplitude and changes in frequencies displayed by the Stonechat provide some evidence that they are equally adapted to identifying predator type. Playback experiments are necessary to determine if these signals are emitted to elicit an escape action from conspecifics or reciprocate warning information to potential mates within eavesdropping range. A number of mammals, e.g. the elephant shrew *Elephantulus rufescens* exhibit long term bonds in which protection of mates may provide direct fitness benefits to compensate for the costs of alarm signals (Faurie *et al.* 1996).

Buff-streaked Chats and Stonechats emitted territorial calls of similar acoustic structure; however, Stonechats emitted start pulses about 2 kHz louder than the Buff-streaked Chats.

Stonechats are known to defend territories either as heterosexual pairs or as single birds (Gwinner *et al.* 1994). Pairs were found to be aggressive (wing- and tail-flicking and alarm calls) towards both conspecific intruders and stonechat dummies, particularly during autumn when territories are established (Gwinner *et al.* 1994). These pairs could therefore be aggressively territorial to either reduce their defence costs associated with the maintenance of a territory; or to increase the net vigilance by reducing the risk of attacks by competitors or predators (Gwinner *et al.* 1994).

Chapter 5

Vocal response to predator’s distance from the group: does the degree of sociality have an effect on rate, duration or complexity of alarm calls?

Alarm calls reflect the response urgency in different situations. This study investigated the effect of a predator’s distance from a caller on alarm call structure, and whether the caller can encode information regarding predator proximity from the group. Further, the complexity of alarm calls given by closely related species living in pairs as opposed to those living in permanent groups was compared, under the assumption that a social species would emit comparatively more complex information than an asocial species. The warning vocalisations of three groups of the social Buff-streaked Chat, *Oenanthe bifasciata*, were compared to that of ten pairs of asocial, Stonechat, *Saxicola torquata*. The birds were captured from the Drakensberg, and housed separately in groups in outdoor aviaries. They were then exposed to five latex snakes and five perching raptors, presented individually at 1 m, 5 m and 10 m respectively, while alarm calls were recorded. Analyses of the acoustic variables revealed that both call rate and call duration decreased when the predator was further away. High call rates have been associated with heightened vigilance especially when predation risk is high. The correlation between some acoustic parameters and predator’s distance provide some evidence that both species can discriminate response urgency and predation threat. Buff-streaked Chats called comparatively more often than the Stonechat in response to aerial predation, a strategy to reduce conspicuousness of the group, or to indicate increased predation risk. Sociality may therefore influence the perception of threat, where group living birds perceived aerial predation as a direct threat, while terrestrial predation evoked a direct threat to pair living species.

5.1 INTRODUCTION

Alarm calls signal the presence of predators and the potential danger to conspecifics (Marler 1957, Seyfarth *et al.* 1980, Weary & Kramer 1995, Fichtel & Kappeler 2002). These calls serve to warn, and thereby protect close relatives (Hoogland 1983), to deter a predator from attack (Blumstein & Armitage 1997*a*, Blumstein 1999, Zuberbühler 1999*a*) and signal predator identity (Struhsaker 1967, Seyfarth *et al.* 1980, Zuberbühler 1999*a*, 1999*b*). Apart from warning relatives, predator deterrence and identification, alarm calls also signal predator location or the predator's proximity to the group (Sherman 1977, Owing & Henessy 1984, Evans & Marler 1995, Zuberbühler 2000*a*, Leavesley & Magrath 2005).

The distance or proximity of the predator from the group is thought to be encoded in a signal by changes in length and rate of calling, or the number of individuals vocalizing (Seyfarth *et al.* 1980, Beynon & Rasa 1989, Leavesley & Magrath 2005). This category of alarm communication is referred to as response urgency vocalisations, which may require quick escape action (Leger & Owings 1978 Leavesley & Magrath 2005,) or increased vigilance (Blumstein 1999). Beynon & Rasa (1989) found that the dwarf mongoose, *Helogale undulata* decreased the rate and duration of calls as the predator moved further away. They defined the predator's proximity from the group as an indicator of the degree of 'threat' or 'dangerousness', i.e., the closer the predators, the better the chance of a successful kill. California ground squirrels, *Spermophilus beecheyi*, emit one type of alarm call in response to a predator nearby and another call type to the same predator at a greater distance (Leger & Owings 1978, Leger *et al.* 1979). When Richardson's ground squirrel, *Spermophilus richardsonii*, was exposed to model predators at distances ranging from 1-8 m, the call rate was inversely correlated with the distance between the model and the caller (Warkentin *et al.* 2001).

Studies investigating the effect of a predator's proximity on acoustics of potential avian prey are limited. This study investigates how a predator's distance from a caller influences alarm call structure and whether the caller can encode information regarding predator's proximity from the group. Further, the information complexity of alarm calls given by closely related species living in pairs as opposed to those living in permanent groups was examined, under the assumption that a social species would emit comparatively more complex information than an asocial species. Beynon and Rasa (1989) defined 'complex information transfer' as the ability to relay specific predator-related information by the use of recombinable codes and frequency changes in a form compatible with the criteria for language. That is to say that: the vocalisations must be symbolic, consist of discrete call types, and refer to distant objects. The warning vocalisations of a social species, the Buff-streaked Chat *Oenanthe bifasciata*, were compared to the pair-living, Stonechat *Saxicola torquata*. As discussed in the previous chapter, the Buff-streaked Chat fulfils the criteria for a social species far more consistently than the Stonechat (see Chapter 4). Furthermore, it has already been established that both the Stonechat and Buff-streaked Chat emit discrete and distinct call types for aerial and terrestrial predators (see chapter 4). Therefore, one can predict that, individuals living in families to emit either longer calls (containing more information), or call more often than pair living subjects.

5.2 METHODS

Study Species

Free-living birds were caught in August and September 2001, and in September 2002, in the central and northern Drakensberg Range. Buff-streaked Chat groups were trapped in boulder-strewn, montane grasslands adjacent to roads. Stonechats were captured at forest edges, especially along the road verge. Spring-traps (Forbes 2000) were baited with mealworms, ensnaring the bird when it attempted to take a worm.

Ten individual Buff-streaked Chats and ten pairs of Stonechats were captured. The Buff-streaked Chats were divided into the following groups. The first group comprised a solitary bird (male), the second group contained four individuals (two males and two females) and the third group comprised five individuals (four males and a single female).

A detailed account of the type of raptor and snake surrogate used, their controls and the procedures used to introduce the surrogate predators is included in the experimental set up (section 2.3).

In addition to methods described in section 2.3 each snake and raptor was presented individually at 1 m, 5 m and 10 m respectively, from the aviary and moved < 0.5 m in a neutral direction, i.e. in any direction except at or away from the birds.

Alarm calls

The following six (alarm) acoustic parameters were measured with AVISOFT SASLAB Light and spectrograms were subsequently produced. These parameters consisted of: the total number of calls emitted during the 5 minute sampling period, the duration of the call element, the pause duration (inter-call duration) between call elements, the amplitude of each call element (dB), the start frequency (kHz) (start pulse) of each call, and the end frequency (kHz) (end pulse) of each call. The acoustic data for the three Buff-streaked Chat groups were initially compared for differences, and thereafter combined (using the Wilcoxon Signed Ranks Test), and if no differences were found, combined for each acoustic parameter and analysed separately for snakes and raptors.

To investigate the influence of predator distance from caller on alarm vocalisations, a linear regression was performed with the six acoustic parameters listed above as dependent variables and ‘predator distance from caller’ as the independent variable. I defined the predator’s proximity from the group as an indicator of the degree of ‘dangerousness’, under the assumption that the predator’s close proximity to the caller increased the chances of a successful kill. Furthermore, an ANCOVA (analyses of co-variance) was incorporated to increase the sensitivity of results. The acoustic data emitted by the Buff-streaked Chat and Stonechat, the species being the independent variable and predator distance, the co-variate, using STATISTICA (vs. 6 Tulsa, OK), ANCOVA. This test computes significant differences between the two species by provided adjusted means for the data. Only acoustic parameters that reported significant relationships with distance (positive or negative) for both species were included in the analyses. The acoustic data emitted by the Buff-streaked Chat and Stonechat was analysed separately (for raptors and snakes).

5.3 RESULTS

5.3.1 Alarm calls

Buff-streaked Chats

When exposed to raptors at various proximities (viz. 1 m, 5 m and 10 m) from the aviary, Buff-streaked Chats responded by emitting 24 calls per 5 min at 1 m, decreasing their call rate to 16 calls at 5 m and thereafter dropping the call rate to 3 calls per 5 min at 10 m (Table 5.1). Call duration also shortened from 0.21 sec at 1 m to 0.10 sec at 10 m (Table 5.1). In contrast, amplitude became louder (-4.76 dB at 1 m to –2.40 dB at 10 m), while peak end frequency became softer, dropping from 5.20 kHz at 1 m to 2.60 kHz at 10 m (Figure 5.1). Furthermore, Buff-streaked Chats paused for lengthier intervals at (33.05 sec) 10 m as opposed to the 12 sec interval at 5 m and the 8.27 sec interval at 1 m (Figure 5.2). All the parameters listed above, showed a significant linear relationship with the raptor's distance from the group.

Table 5.1 Buff-streaked Chat's response to raptors at various distances from caller (Means ± SD, n = 15).

Parameter	**Predator at 1 m**	**Predator at 5 m**	**Predator at 10 m**
Number of calls/ 5 min	23.60 ± 6.88	15.60 ± 6.88	2.60 ± 2.61
Amplitude (dB)	-4.76 ± 0.25	-4.10 ± 0.22	-2.40 ± 2.19
Duration of call (s)	0.21 ± 0.03	0.20 ± 0.29	0.10 ± 0.10
Pause duration (s)	8.26 ± 1.96	12.39 ± 2.68	33.05 ± 30.82
Peak frequency start (kHz)	4.60 ± 0.22	4.60 ± 0.22	2.80 ± 2.56
Peak frequency end (kHz)	5.20 ± 0.28	4.30 ± 0.45	2.60 ± 2.41

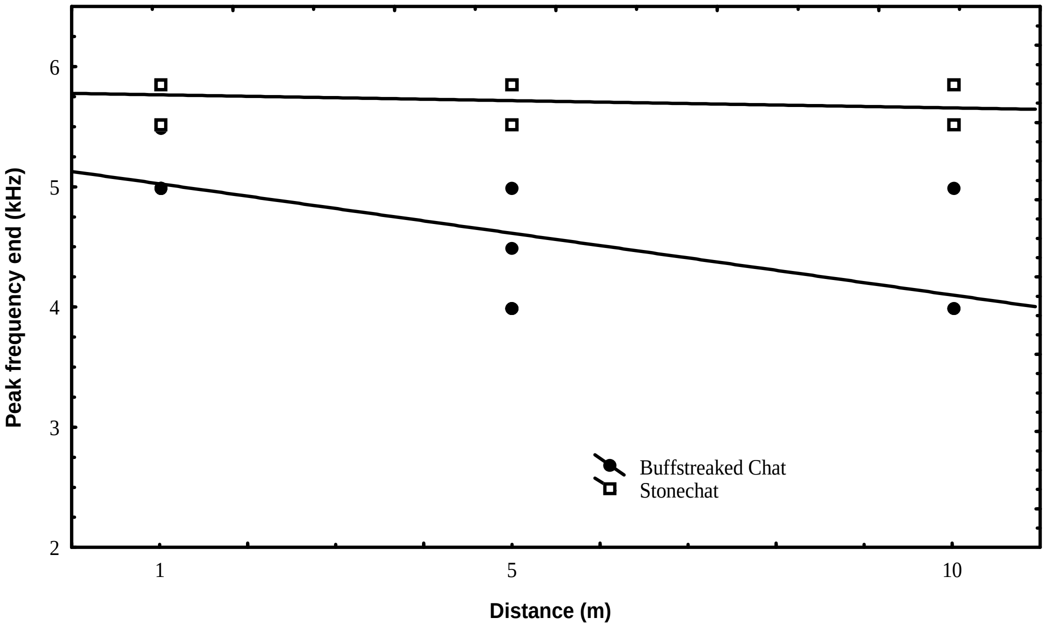

Fig. 5.1 The effect of the predator's distance from the caller on peak frequency end, in response to raptors.

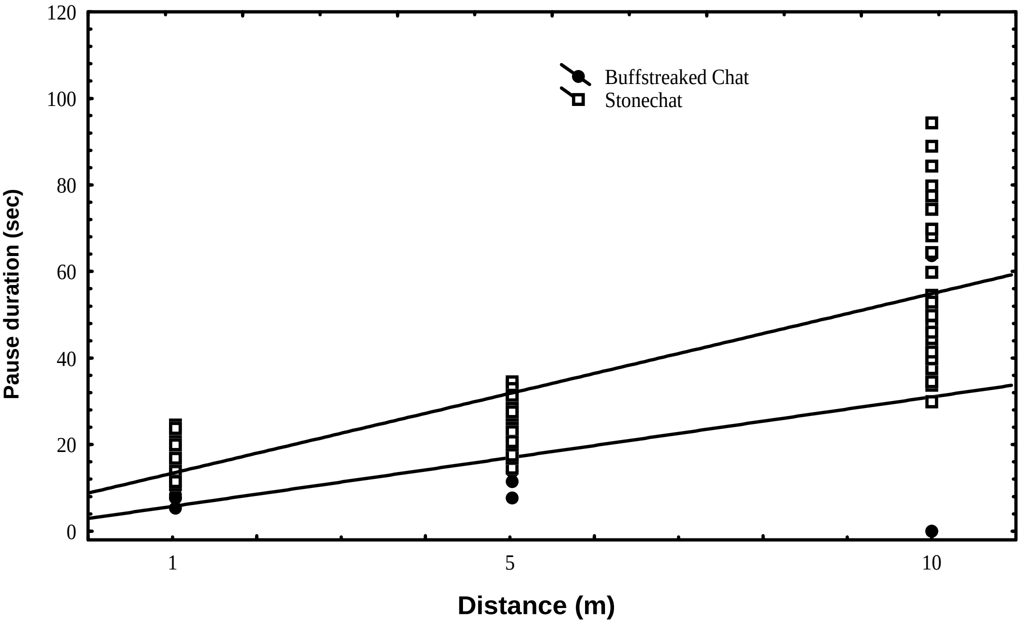

Fig. 5.2 The effect of the predator's distance from the caller on pause duration, in response to raptors.

Identical experiments performed with snakes produced virtually identical results (Tables 5.2 and 5.3, Figure 5.3), where call rate and duration were negatively correlated with distance from the predator. Similarly, amplitude and pause duration showed positive correlation to distance from predator, while peak start frequency became softer as the predator moved further away (15.40 kHz at 1 m to 3.70 kHz at 10 m).

Table 5.2 Buff-streaked Chat's response to snakes at various distances from caller (Means ± SD, n = 15).

Parameter	Predator at 1 m	Predator at 5 m	Predator at 10 m
Number of calls/ 5 min	22.60 ± 4.22	13.80 ± 4.76	1.80 ± 1.48
Amplitude (dB)	-5.68 ± 1.27	-4.90 ± 0.42	-3.20 ± 1.79
Duration of call (s)	0.14 ± 0.01	0.15 ± 0.16	0.09 ± 0.06
Pause duration (s)	7.18 ± 1.46	8.87 ± 1.96	53.14 ± 32.24
Peak frequency start (kHz)	15.40 ± 0.65	15.40 ± 0.55	3.70 ± 2.08
Peak frequency end (kHz)	5.00 ± 0.00	5.20 ± 0.27	4.00 ± 2.24

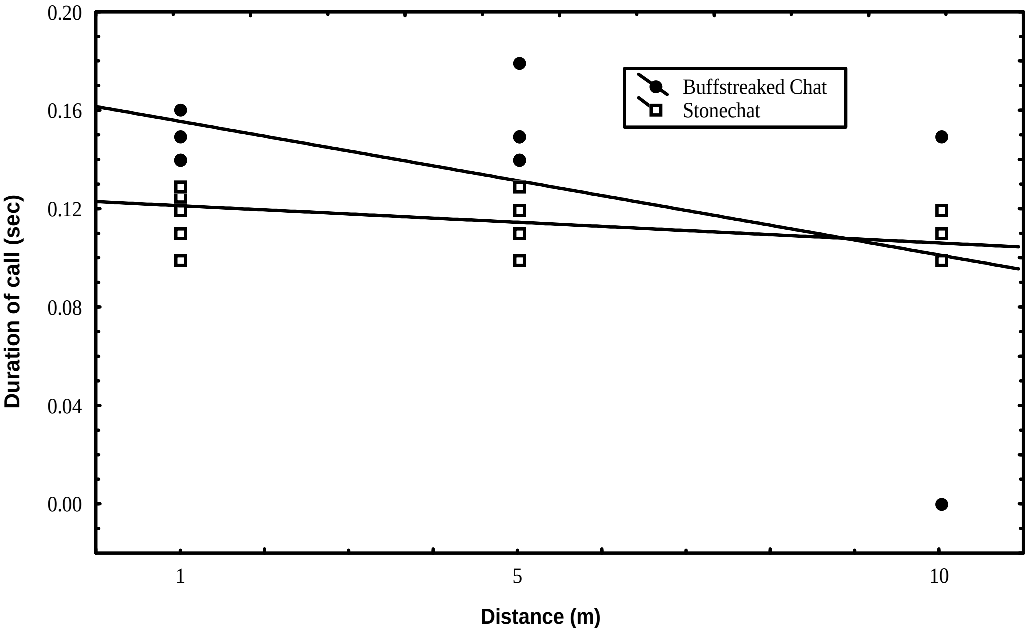

Fig. 5.3 The effect of the predator's distance from the caller on call duration, in response to snakes in Buff-streaked Chats and Stonechats.

Table 5.3 Results of the linear regression (R^2 values indicated below) to investigate the relationship between predator's distance from Buff-streaked Chat group and acoustic parameters of alarm calls.

Parameter	**Raptors** **R^2**	**Snakes** **R^2**
Number of calls/ 5 min	-0.7225^{***}	-0.8649^{***}
Amplitude (dB)	0.4096^{*}	0.4356^{*}
Duration of call (s)	-0.3721^{*}	0.3025^{*}
Pause duration (s)	0.2916^{*}	0.5184^{*}
Peak frequency start (kHz)	0.2304	-0.7744^{***}
Peak frequency end (kHz)	-0.4096^{*}	-0.1156

$^{*}P < 0.05$, $^{***} P < 0.001$

Stonechats

When exposed to raptors at various distances (viz. 1 m, 5 m and 10 m) away from the aviary, Stonechats responded by emitting 17 calls per 5 min at 1 m, decreasing their call rate to an average of 11 calls at 5 m and finally dropping the call rate to approximately 5 calls per 5 min at 10 m (Table 5.4). Call duration also shortened from 1.51 sec at 1 m to 1.49 sec at 10 m. In addition, amplitude became increasingly louder

(-4.00 dB at 1 m to –3.52 dB at 10 m), while peak end frequency softened from 5.31 kHz at 1 m to 5.15 kHz at 10 m (Table 5.4). Stonechats also paused for lengthier periods at 10 m (58 sec) as opposed to the 25 sec interval at 5 m away and the 17 sec interval at 1 m. All the parameters listed above showed a significant linear relationship with the raptor's distance from the birds (Table 5.5).

Table 5.4 Stonechat's response to raptors at various distances from caller (Means ± SD, n = 50).

Parameter	Predator at 1m	Predator at 5m	Predator at 10m
Number of calls/ 5 min	16.84 ± 2.90	10.82 ± 2.67	4.74 ± 2.83
Amplitude (dB)	-4.00 ± 0.00	-3.62 ± 0.49	-3.52 ± 0.50
Duration of call (s)	1.51 ± 0.04	1.50 ± 0.03	1.49 ± 0.02
Pause duration (s)	17.39 ± 0.41	24.64 ± 5.47	58.06 ± 17.31
Peak frequency start (kHz)	5.50 ± 0.00	5.50 ± 0.00	5.50 ± 0.00
Peak frequency end (kHz)	5.31 ± 0.03	5.37 ± 0.22	5.15 ± 0.23

Identical experiments performed with snakes produced virtually identical results (Tables 5.5 and 5.6) where call rate and duration were negatively correlated with distance from the predator. The start pulse dropped from 11.65 kHz at 1 m to 10.58 kHz at 10 m), while the end pulse similarly softened from 6.13 kHz at 1 m to 5.50 kHz at 5 m away, finally dropping to 5.22 kHz at 10 m. Furthermore, Stonechats increased their pause duration at 10 m (44 sec) as opposed to the inter-call duration of 26 sec at 1 m (Figure 5.4).

Table 5.5 Results of the linear regression (R^2 values indicated below) to investigate the relationship between predator's distance from Stonechat group and acoustic parameters of alarm calls.

Parameter	Raptors R^2	Snakes R^2
Number of calls/ 5 min	-0.7569***	-0.4624***
Amplitude (dB)	0.1764***	0.0100
Duration of call (s)	0.0729***	0.2809***
Pause duration (s)	0.6724***	0.3364***
Peak frequency start (kHz)	0.0196	-0.3600***
Peak frequency end (kHz)	0.0784***	-0.5041***

***$P < 0.001$

Table 5.6 Stonechat's response to snakes at various distances from the group (Means ± SD, n = 50)

Parameter	Predator at 1 m	Predator at 5 m	Predator at 10 m
Number of calls/ 5 min	15.60 ± 5.66	12.68 ± 3.90	5.08 ± 2.93
Amplitude (dB)	-4.00 ± 0.00	-4.00 ± 0.00	-4.00 ± 0.00
Duration of call (s)	0.12 ± 0.00	0.11 ± 0.00	0.11 ± 0.01
Pause duration (s)	22.12 ± 1.60	25.70 ± 1.49	44.44 ± 15.95
Peak frequency start (kHz)	11.65 ± 0.08	11.31 ± 0.08	10.58 ± 0.62
Peak frequency end (kHz)	6.13 ± 0.04	5.50 ± 0.06	5.22 ± 0.31

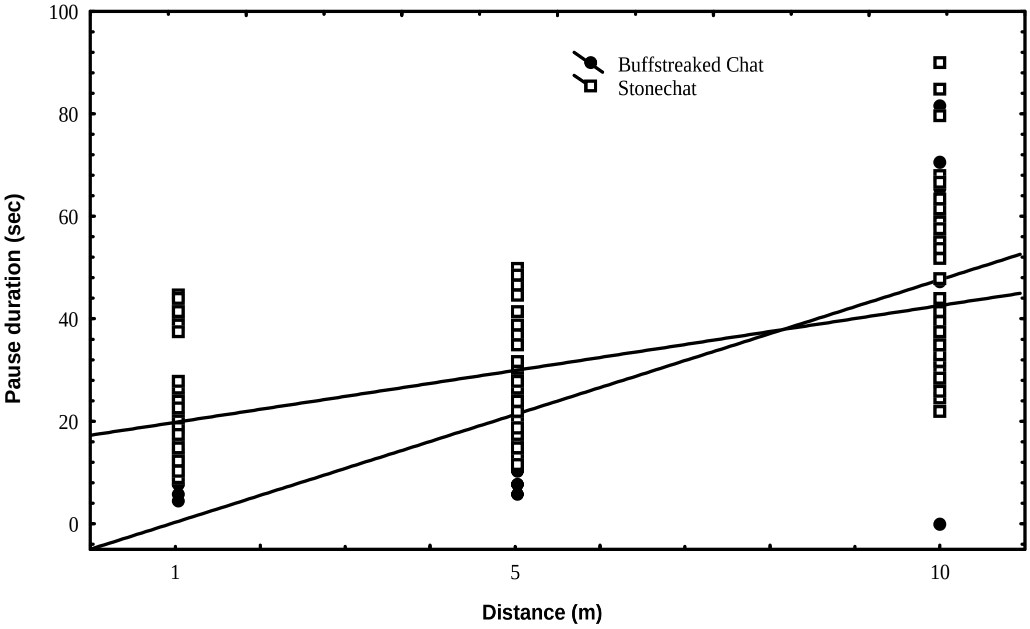

Fig. 5.4 The effect of the predator's distance from the caller on pause duration, in response to snakes in Buff-streaked Chats and Stonechats.

The analyses of co-variance revealed that Buff-streaked Chats called more often than Stonechats in response to aerial threat, incorporating shorter (0.17 sec), softer calls (lower end pulses) than the latter (1.49 sec) (Table 5.7). In response to terrestrial threat, Stonechats emitted shorter calls with longer intervals (30.75 sec) between calls than *Oenanthe bifasciata* (23.06 sec) (Table 5.8). Other parameters showed no significant trends.

Table 5.7 Results of the ANCOVA (analyses of covariance) to investigate the relationship between raptor's distance from group and acoustic parameters that showed significant difference between calling variable and distance for Buff-streaked Chats and Stonechats.

Parameter	**Buff-streaked Chat**	**Stonechat**	**Main effect $F_{(1,162)}$**
	Adjusted Means		
Number of calls/5 min	13.93	10.80	12.28^{***}
Amplitude (dB)	-3.75	-3.79	0.66
Duration of call (s)	0.17	1.49	17343.00^{***}
Pause duration (s)	17.89	33.36	21.08^{***}
Peak frequency end (kHz)	-4.03	5.28	73.04^{***}

*** $P < 0.001$

Table 5.8 Results of the ANCOVA (analyses of covariance) to investigate the relationship between snake's distance from group and acoustic parameters that showed significant difference between calling variable and distance for Buff-streaked Chats and Stonechats.

Parameter	**Buff-streaked Chat**	**Stonechat**	**Main Effect $F_{(1,162)}$**
	Adjusted Means		
Number of calls/5 min	12.73	11.12	1.77
Duration of call (dB)	0.13	0.11	14.80^{***}
Pause duration (s)	23.06	30.75	4.05^{**}
Peak frequency start (kHz)	11.50	11.18	0.52

**$P < 0.005$, *** $P < 0.001$

5.4 DISCUSSION

Analyses of the acoustic variables revealed that both call rate and call duration decreased with increasing distance between the caller (Buff-streaked Chat) and the predator (both raptors and snakes). High call rates have been associated with heightened vigilance (Macedonia & Evans 1993, Warkentin *et al*. 2001), especially when predation risk is high. Buff-streaked Chats thereafter dropped the rate as the predator moved away, signalling that the threat had passed. These correlations were consistent with Warkentin *et al*. (2001) study on juvenile Richardson's ground squirrels *Spermophilus richardsonii*, who were presented with a predator model at distances ranging from 1-8 m. Warkentins' study showed that the rate of calling was inversely correlated with the distance between the model and the caller (Warkentin *et al*. 2001). The correlation of the current study may reveal response urgency, where predators at close ranges elicit high call rates.

Results or call duration were however inconsistent with the findings of Beynon & Rasa (1989), who reported that *H. undulata* increased their call duration from 616 ms (milliseconds) at 10 m to 900 ms at 25 m from the predator. In contrast, Buff-streaked Chats, gave the shortest call when the predator was furthest away, which may signify a drop in predator threat.

Furthermore, both the amplitude and pause duration increased when the predator was further away from the group (both raptors and snakes). These louder calls interspersed by long pauses may signify that the threat has moved on. In addition, both the end frequency (for raptors) and the start frequency (for snakes) decreased when the predator was further away. This, as in the instance of amplitude, may signify a drop in vigilance. These results conform to the study by Leavesley & Magrath 2005, who found that Scrubwrens, *Sericornis frontalis*, decreased their frequency (pitch) as the predator moved away.

Analyses of Stonechat vocalisations revealed similar trends to the Buff-streaked Chat, i.e., a decrease in both call rates and call duration when the predator was further away (both raptors and snakes). Again, this may signify reduced vigilance and indicate that the threat has passed on. These findings correspond to marmot studies where *Marmota caudata* that showed variations in call rate according to extent of threat (Blumstein 1995*a*, Blumstein & Arnold 1995).

The amplitude (in response to aerial predators only) and pause duration (in response to both snakes and raptors) increased as the distance between caller and predator increased. Stonechats therefore gave softer calls when predation was imminent or high, to reduce conspicuousness, thereby simultaneously warning conspecifics of impending danger without being detected. These variations may reflect a long evolutionary adaptation to reduce conspicuousness from predators with good auditory acuity (Bayly & Evans 2003), especially raptors, and to communicate warning information beyond the sensitivity of the predator. Although, increasing amplitude (and emitting louder calls) is readily localised and hence relatively costly, it is emitted when the predator is further away, and hence assumed to be less dangerous.

The peak start frequency (for snakes) and the peak end (for both raptors and snakes) dropped as the predator moved further from the caller, a trend seen for Buff-streaked Chats as well as Stonechats. Since, the structure of the pulse or start and end frequency is consistent with an alerting function (Endler 1993, Bayly & Evans 2003), these parameters have been manipulated to become softer, presumably to evoke a decrease in alertness or vigilance when the predator moves away.

In summary, these results are consistent with Macedonia & Evans' (1993) study, which indicated that ground-dwelling squirrels use alarm call systems based upon response urgency. It also corresponds to reports of rodents that vary the call rate according to the extent of threat (golden marmots, *Marmota caudata aurea*, Blumstein 1995*b*, alpine marmots, *Marmota marmota*, Blumstein & Arnold 1995, eastern chipmunks, *Tamias striatus,* Burke de Silva *et al*. 1994).

Comparisons between the Buff-streaked Chat and Stonechat revealed the following: In response to aerial threat, the Buff-streaked Chat seems to be comparatively more vigilant than the Stonechat. Evidence of this is reflected in the higher call rate produced by Buff-streaked Chats. Further, the results of the ANCOVA revealed that Stonechats paused comparatively longer than Buff-streaked Chats during both predatory encounters. An increase in silence between alarm vocalisations may signify a drop in vigilance, implying that Buff-streaked Chats may be comparatively more vigilant than Stonechats.

In addition, the shorter, softer calls of Stonechats may indicate a strategy to reduce conspicuousness, especially so for group-living birds. It is more likely that a social species, living in larger groups, will be more conspicuous to raptors than pair-living birds. A larger group will therefore be more vulnerable to predation in this sense. This is consistent with the findings of Chapter 4, that larger groups depict heightened vigilance for raptors. Hence, it is costly for the Buff-streaked Chat to emit louder end pulses that would give cues to the group's location, placing conspecifics and nestlings in danger. Buff-streaked Chats are reported to be facultative cooperative breeders, helping to provision nestlings (Hockey *et al.* 2005).

In contrast, terrestrial predators elicited calls of shorter duration from Stonechats, consistent with Niko'skii's study (1994), which showed that call duration was reduced in response to increasing predation risk. The Stonechat may regard the snake as a greater threat than the raptor, therefore giving shorter calls to reflect response urgency. The Buff-streaked Chats can give comparatively longer calls, having the added benefit of group members to mob the terrestrial predator or deter the snake from attack (Klump & Shalter 1984). Playback experiments in nature would be required to confirm this theory.

The findings of this study are consistent with the hypothesis that the distance of the predator from the caller influences the call structure by triggering variations in acoustic parameters. The variation in acoustic parameters provide mixed evidence that the Buff-streaked Chat and Stonechat can discriminate a predator's proximity to the group. The variation in acoustic parameters corresponds directly to the spacial proximity of a predator to the caller and may serve as an adaptive strategy to evoke vigilance responses in the face of potential danger. Although there seems to be some evidence to indicate that the Stonechat and Buff-streaked Chat differ in their strategy of communicating predator-related information, the findings of this study cannot conclusively establish that Buff-streaked Chats transfer 'more complex information' than Stonechats. It can be tentatively put forth, however, that the perception of threat may be directly related to group living or sociality, where social group-living birds fear aerial predation, whilst the asocial species fear terrestrial threat. However, the prediction that 'individuals living in families emit longer calls (containing more information) to alert their group members than pair living subjects’ therefore requires further study, with larger sample sizes and acoustic software for micro-call element analysis.

Chapter 6

Conclusions

The aim of this study was to investigate whether the alarm calls of three passerine species, viz. the Buff-streaked Chat, the Stonechat and the Bronze Mannikin, contained semantic information about predator type and distance from the caller. The study comprised three investigations that examined the differences in intra-specific alarm calls between familiar and unfamiliar group members, the effect of group-living on warning vocalisations, and the caller's ability to recognise the predator model's proximity to the group.

Key results:

(1) The experiments concerning the Bronze Mannikins (Chapter 3) showed that these granivores appear to communicate reliably predator-size risk in the presence of familiar group members only, in response to both aerial and raptor predator models. Naturally occurring social groups of Bronze Mannikins called more often than mixed groups. Birds in original groups manipulated the start and end frequencies of their warning vocalisations, to either reduce the conspicuousness of the group or minimize cues to the caller's whereabouts. Assorted group members are less aggressive to predator models than original members. By participating and cooperating in predator avoidance and deterrence activities, group members can potentially gain fitness benefits, while group members not familiar with the caller's identity and the contextual cues of one another's calls may fail to respond.

(2) Group-living Buff-streaked Chats (Chapter 4) gave louder calls for snake models whereas raptor models elicited calls of softer amplitude. These changes in acoustics may signify predation risk. Variation in predation risk may encompass both behavioural and physical characteristics of predators, therefore prey species might be expected to categorise their predators along behavioural and morphological dimensions. On the other hand, larger and therefore collectively more vocal groups of Buff-streaked Chats, might be more successful in discouraging attacks than smaller groups or asocial, pair living species.

(3) Softer end frequencies given by Buff-streaked Chats compared to Stonechats (Chapter 5) are difficult to localise, minimizing conspicuousness of the group and locality cues of the caller. Hence, softer end pulses may be beneficial to Buff-streaked Chats and help balance the costs of living in larger (and more conspicuous) groups.

(4) Aerial predation elicited an increase in calling rate by Buff-streaked Chats. Since high-risk situations or a higher intensity of predation has been associated with increased call rate, the Buff-streaked Chat may have evolved these referential calls to transfer information to familiar group members. Furthermore, the encoding of this information in call rate might increase response urgency to escape aerial predation. However playback experiments are required to confirm this.

(5) The Stonechat may initially appear to transfer comparatively less information than the Buff-streaked Chat as indicated by the lower call rate of *Saxicola torquata* (Chapter 4). However this is not sufficient evidence to conclusively support the hypothesis that

social species communicate more information to conspecifics than asocial species. The variation in amplitude and changes in frequencies displayed by the Stonechat provided some evidence that they are equally adapted to identifying predator type (and perceiving raptorial acuity).

(6) Both Buff-streaked Chats and Stonechats can discriminate a predator model's distance from the group (Chapter 5). Correlations between call rate and distance are apparent, although Buff-streaked Chats maintained a higher call rate than Stonechats. This is a strategy to perhaps indicate high-risk situations, e.g. aerial predation. Stonechats showed equally competent predator-proximity discrimination, by producing shorter calls in response terrestrial predation at close proximity, to communicate increased threat. These two passerines differ in their perception of degree of threat, and utilize different changes in acoustic parameters to survive (Chapter 5). It is therefore unconvincing that the degree of sociality alone influenced the Stonechat's perception of threat. Instead past encounters with natural predators or the ability of raptors and snakes to access nesting sites and subsequent predation upon individuals, group members and nestlings may have influenced the perception of threat (Young 2003).

Potential shortcomings of the current study

Experimental design

It should be noted that no playback experiments were investigated in this study. Communication is a process of information exchange between sender and receiver. To demonstrate the meaning of an alarm call it is necessary to consider both signal production and response (Evans 1997, Blumstein 1999). On the production side, it is necessary to show that an alarm call is given more in the presence of predators than non-predators (which this study shows); however on the response side, without playbacks it is unknown whether any apparent response to an alarm call may be the result of an animal independently seeing the predator or observing the actions of the caller. It is stated in the introductory chapter that the approach of this study due to limitations of a Master's thesis, concentrates on the syntax and semantics of communication and not pragmatics, hence some evidence of communication is provided but remains incomplete.

Study species and sample sizes

The small sample size of this study, enforced by the physical difficulty of capturing and caring for larger number of individuals, may have influenced the results and conclusions of this study. Further acoustic analyses with larger sample sizes may be necessary. Since the Buff-streaked Chat is an endemic South African species, relatively difficult to capture (pers. obs.), I was reluctant to keep more birds in captivity due to the warm, low altitude and humid climatic conditions of Durban that made life in temporary captivity uncomfortable for the birds. The analysis of natural-predator elicited alarm vocalisations should be explored in the future, in the natural habitat of the study animal.

Surrogate predators

The elicitation of alarm calls and response behaviour by live predators may differ from the results derived from predator models. This should in future be properly verified.

Group members as kin

In this study, the relatedness of group members of the Buff-streaked Chat and Bronze Mannikin in particular, was not known. Therefore, subtle differences in the call responses between relatives (kin), as opposed to known, but unrelated group members could not be investigated. Future study should thus examine if closely related group members transfer more information, regarding predator type, size and proximity, to each other. If so, a further study should then examine the costs and benefits of advances communication transfer to relatives.

Group versus solitary living

The results of this study provide some evidence that group-living, in response to predation evolved in groups without long-term stable membership. In these groups, conspecifics developed sufficient familial-cooperative bonds, in order to successfully avoid or deter predation attack, by means of reliable warning vocalisations and cooperative vigilance behaviour. In addition, the formation of groups might have provided increased pressure to reduce conspicuousness of the flock, through the manipulation of start and end frequencies of alarm calls. Group-living also made it possible for social species to engage in mobbing or aggression as a means to discourage predator attack. However, the degree of sociality alone did not influence the ability of a solitary species to discriminate predator type, threat and proximity.

The coevolution of communication and complex sociality

Blumstein (2003) proposed that sociality may promote the evolution of complex communication, as species that are more social have more to communicate about (Maynard Smith 1965, Marler 1977, Blumstein & Armitage 1997*b*). In the context of alarm calls, more socially complex species may gain more than solitary species by precisely specifying the degree of risk or predator type to group mates who are likely to be relatives (Blumstein & Armitage 1997*b*).

Kin selection and altruistic signalling in the face of predation risk

Several authors have implicated kin selection as a mechanism to explain alarm calling (e.g. Sherman 1977, Hoogland 1983, Blumstein 2003). Kin selection includes that fitness that individuals gain by helping their descendant kin (i.e. direct fitness) and non-descendant kin (indirect fitness). By invoking kin selection, researchers imply that indirect fitness benefits are an important driving force behind the apparently altruistic behaviours such as alarm calling. Since the degree of relation between the individual birds in the experimental groups was unknown, the importance of kinship could not be assessed. Sherman (1977) proposed that warnings are only given when sufficiently related kin are nearby, i.e. these need not be descendant kin like offspring to justify emitting warning calls.

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