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# **The responses of birds to alarm calls and predators**

by

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**Submitted in fulfilment of requirements for  
the degree of Doctor of Philosophy  
University of St Andrews**



**September 2004**

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## Abstract

Animals may communicate with predators and individuals using signals. Signals may deter pursuit by predators or may manipulate the behaviour of individuals to reduce predation on kin or a mate. Individuals may also learn from alarm calls about predators. There are many ideas about the functions of these signals but little certainty. I investigated the functions of alarm responses in birds.

Yellow-casqued hornbills *Ceratogymna elata* responded to playback of calls of crowned eagles *Stephanoaetus coronatus*, an important predator, but not those of leopards *Panthera pardus* which pose little threat to them. They also responded to the corresponding Diana monkey *Cercopithecus diana* alarm calls to the eagle but not Diana alarm calls to the leopard. They thus distinguished between these similar monkey calls and responded appropriately. They approached the playback site indicating that they might be signalling perception advertisement. Black-casqued hornbills *Ceratogymna atrata* also distinguished similarly between these predator calls and Diana monkey alarm calls as well as between the alarm calls of Campbell's monkey *Cercopithecus campbelli* which are less commonly heard. They responded more to eagle calls than primate-eagle alarm calls, perhaps because the former gives more precise information about the location of the predator.

In a second series of experiments, great tits *Parus major* were found to respond more to playback of great spotted woodpecker *Dendrocopos major* calls and more to robin *Erithacus rubecula* 'tic' alarm calls in summer than winter. This may be because it is mainly their young that are threatened by woodpeckers or by predators that elicit the tic call. Their responses to sparrowhawk *Accipiter nisus* and robin 'seeep' calls were similar in both seasons.



# Chapter 1

## General Introduction

Strong selection will act on the ability of an individual to avoid predation as being killed will almost always decrease fitness (Lima & Dill 1990). Anti-predator behaviour should therefore be a key part of an individual's behavioural repertoire to ensure survival and maximise the chance of successful reproduction. Many different forms of anti-predator behaviour have evolved and these will be strongly influenced by the mode of attack of the predator. They may take the form of defences such as weapons, or of crypsis, mimicry and aposematism that will forestall the attack of a predator (Curio 1993). Once a predator has been detected then the prey individual may employ different strategies to deter an attack. It is these secondary defences that are the focus of this thesis.

This study was greatly helped by discussions and collaboration with Klaus Zuberbühler. During his work with primates in Taï National Park, Ivory Coast (Zuberbühler *et al.* 1997; Zuberbühler 2000b, 2001), he often observed hornbills in the vicinity of his playback experiments (Klaus Zuberbühler pers. comm.). A preliminary analysis of his acoustic recordings indicated that hornbills might be responding to the playback of predator calls and primate alarm calls in Taï and this suggested some ideas for investigating the cognitive abilities of birds. In addition, there are clearly many problems and hypotheses relating to the functions of alarm calls, in particular the high-pitched 'seep' alarm call produced by so many passerine bird species. This further stimulated my work and suggested avenues of investigation.

This thesis aims to investigate how birds respond to predators and how their alarm responses might function to reduce the risk of predation to callers and other individuals. Each chapter is written to be read separately from the others and as each of the experimental chapters used different techniques I have not provided a general methods section. Chapter 2 is a review of our knowledge of anti-predator behaviour. I review how prey individuals learn about the threats that predators present to them, the function of alarm signals and their role in deterring pursuit by predators, and the evolution of alarm calls and anti-predator signals in birds. This sets out the background to the following

experimental chapters. In the work discussed in Chapter 3, I studied how yellow-casqued hornbills *Ceratogymna elata* responded to the calls of predators and the alarm calls of Diana monkeys *Cercopithecus diana*. It has been known for some time that primates can distinguish between the calls of other primate species and of birds (Seyfarth & Cheney 1980; Oda & Masataka 1996; Zuberbühler *et al.* 1997; Oda 1998; Fichtel 2004) and that some rodents can distinguish between the calls of other rodent species (Shriner 1998). Chapter 3 provides, to my knowledge, the first evidence that birds can distinguish between the different calls of a mammal or between the alarm calls of any other species. It also indicates that the responses of the birds might function to advertise the hornbills' detection of the predator. Chapter 4 investigates the responses of black-casqued hornbills *Ceratogymna atrata* to predator calls and Diana and Campbell's monkeys *Cercopithecus campbelli* alarm calls. As Campbell's monkey alarm calls are heard much less often than those of Diana monkeys in Taï National Park, this provides further evidence that there is strong selection for individuals to glean information from their environment about the presence of predators. It also indicated that the birds were responding to the precision of the information encoded in the stimuli that they heard. In Chapter 5 I switched species and studied the responses of great tits *Parus major* to predator calls and the alarm calls of robins *Erithacus rubecula*. Although birds have been shown to vary their responses to different mammal alarm calls (see Chapters 3 and 4), to date no one had shown that birds varied their responses to different bird alarm calls. I also investigated whether birds varied their responses to predators and alarm calls between seasons with the importance of the stimuli presented, i.e. the variation of the threat that the predators posed between seasons to adults and young. Chapter 6 consists of a general discussion and conclusions. I present some further ideas for research investigating communication between prey and predator and the extent to which animals make use of information in their environment to reduce the chance of predation. In the Appendix I have presented information on the variation in abundance of hornbills in Taï NP between seasons, which was collected incidentally to the analyses given in Chapter 4. This variation has not previously been described from other West African forest species and the data were obtained using a novel method.

## Hornbills and primates in the West African forests

### *Hornbills*

The selection of hornbills as the focal species for this study was based on their relative abundance within the Ivorian forests, their highly vocal behaviour and also on the possible nature of their interactions with predators and primates. Nine species of hornbills are known from the forests of Ivory Coast and, of these, four are large enough to lie within the typical prey spectra of the two main natural predators of forest monkeys in West Africa, crowned eagles *Stephanoaetus coronatus* and leopards *Panthera pardus*. However, one of the hornbill species, the black-and-white-casqued hornbill *Bycanistes subcylindricus*, is found only in the northern semi-deciduous forests, for example in Mont Péko and Marahoué National Parks, but not in the moist or wet southern forests of Taï National Park. Conversely, the black-casqued hornbill is relatively rare in Mont Péko and has probably been extirpated from Marahoué but is commoner further south. The brown-cheeked hornbill *B. cylindricus* is less vocal and rarer than the other three large species. For these reasons I felt that the largest forest species, the yellow-casqued hornbill, was the most suitable for study. However, as circumstances changed dramatically, I switched species to work on the black-casqued hornbill as it was the most abundant large hornbill in Taï where much of this work was carried out.

The yellow-casqued hornbill is found from southern Senegal to western Cameroon and is listed as near-threatened by BirdLife International (2000). It is very vocal and its nasal-sounding trumpeting calls can be heard from over a kilometre away. The male casque is very prominent and is thought to grow for some years after a male hornbill fledges (Kemp 1995). This species is often found in small groups comprising an adult male and female and one or two offspring and it may perhaps breed cooperatively as do some other hornbill species (Witmer 1993; du Plessis 1994; Kemp 1995, pers. obs.). The weight of this species is *c.* 1.5-2.1 kg (*n*=3) which is close to that of a number of diurnal primate species in West Africa (Kemp 1995; Kingdon 1997). They feed on many different tree fruits including palm nuts and they also feed on some small animals including winged ants and termites (Kemp 1995, pers. obs.).

The black-casqued hornbill is similar in many aspects of its biology to the previous species. It is smaller (0.9-1.6 kg) and has a broader range in the forests of Africa from Liberia patchily across to western Uganda. The male also has a very large casque. It is a

highly vocal species and its calls resemble a noisy baby's wail (pers. obs.). In Cameroon they make long distance movements related to seasonal availability of fruit (Whitney & Smith 1998; Holbrook & Smith 2000; Holbrook *et al.* 2002) as do other hornbills in Africa and Asia (Kalina 1988; Modse 1988; Poonswad & Tsuji 1994; Kinnaird *et al.* 1996; Anggraini *et al.* 2000; Datta & Rawat 2003).

### *Primates*

Primate behaviour in West Africa has been studied quite intensively with important studies in Ghana, Sierra Leone and Ivory Coast (e.g. Curtin & Olson 1984; Oates & Whitesides 1990; Noë & Bshary 1997; Boesch & Boesch-Achermann 2000). Studies on predator specific alarm calls and communication between primates and predators have helped shape this thesis (e.g. Seyfarth *et al.* 1980a; Hauser 1988; Cheney & Seyfarth 1990; Seyfarth & Cheney 1990; Zuberbühler *et al.* 1997; 1999b; Uster & Zuberbühler 2001). Diana *Cercopithecus diana* and Campbell's monkeys *C. campbelli* are relatively common in those few forests in West Africa where hunting is controlled. However, in many areas Diana monkeys have been exterminated by hunting and Campbell's monkeys are also scarce although still widespread (pers. obs.). This difference can be partly explained by the more obvious behaviour of the former species. The Diana monkey is much more vocal than Campbell's, calling more often in response to predator calls (Zuberbühler 2000b, 2001). It is also more colourful and has less cryptic behaviour and this may make it more vulnerable to hunting by man. The alarm calls that some cercopithecine monkeys produce are referential to specific predators (Seyfarth *et al.* 1980a; Zuberbühler *et al.* 1997; Zuberbühler 2001) and reliably indicate the presence of the corresponding predator type. Some are known to advertise detection to potential predators (e.g. Zuberbühler *et al.* 1997; Zuberbühler 2000b, 2001) whilst others do not (Seyfarth *et al.* 1980a; Cheney & Seyfarth 1990). This behavioural plasticity in closely related species suggests that the local environment, predator behaviour and perhaps social behaviour may play a role in the evolution of anti-predator responses.

## **Great tits and their anti-predator behaviour**

Great tits have a vocabulary that is ‘notorious for its variety’ and is reviewed thoroughly by Gompertz (1961). She reviewed the context in which many of their vocalisations including alarm calls were produced. She found that ‘seeep’ alarm calls (names of alarm calls in original papers have been changed to conform to those used in this thesis) were produced most commonly in response to predators and other birds flying overhead. In contrast, ‘rattle’ calls were given to terrestrial predators as well as to perched birds such as tawny owls *Strix aluco* and magpies *Pica pica*. Other studies have found that the seeep call is given by great tits and other passerines to fast-moving aerial predators such as sparrowhawks (Perrins 1968; East 1981). As great tits and other parids are very abundant in the UK and their behavioural ecology is well known, I chose to study their responses to alarm calls and predators. In particular, their anti-predator behaviour has been the focus of a number of studies (Hinde 1952; Perrins 1968; Morse 1973; Perrins 1979; Ficken *et al.* 1981; Regelman & Curio 1983; Shedd 1983; Curio *et al.* 1984; 1985; de Laet 1985; Hegner 1985; Curio & Regelman 1985; 1987; Ficken 1989; Alatalo & Helle 1990; Hogstad 1995; Hurd 1996; Krams 1998; Haftorn 2000; Radford & Blakey 2000; Krams 2001b; Baker & Becker 2002; Kullberg & Lind 2002; Rytkonen 2002; Rajala *et al.* 2003) and these aided construction of this section of my thesis.

## **Politics, migration and malaria**

This project has deviated somewhat from that originally conceived at its inception. I had planned to study hornbills in Ivory Coast for the duration of the study, but, a number of events and phenomena forced me to alter these plans. At the start of the study, I found that hornbills in Taï and Mont Péko National Parks in 2001 were abundant in both protected areas and this should have enabled me to complete the initial study (Chapter 3) in a relatively short time. This would have allowed time for further investigations into the anti-predator behaviour of hornbills (see Chapter 6). However, it was discovered that the hornbills in Taï NP apparently migrate (see Appendix), and during fieldwork from March-June they were approximately ten times less abundant than from October-December. This reduced the rate at which I was able to carry out experimental playback trials during this

period, as I encountered the birds less often. Towards the end of this period I also fell ill with malaria which further reduced the time available for data collection.

The major influence on the direction of this project, however, was the outbreak of civil war in September 2002 in Ivory Coast which prevented me from returning to the country. I therefore changed my focus somewhat and chose to investigate anti-predator behaviour in great tits around St Andrews.

## Chapter 2

### The evolution and function of anti-predator behaviour

#### The evolution of anti-predator behaviour: learning about predators

On detecting the presence of a predator, a prey individual may try to identify and localise it in order to respond appropriately (Curio 1993); without this information the individual may put itself in greater danger. Identification of the predator must include recognising that it is a threat and two main mechanisms have been suggested for development of this ability: habituation and associative learning (Curio *et al.* 1978; Vieth *et al.* 1980; Frankenberg 1981; Schusterman & Gisiner 1997; Deecke *et al.* 2002).

Habituation may be of some importance in identifying and discriminating between potential predators. Deecke *et al.* (2002) found that harbour seals *Phoca vitulina* responded little to the calls of harmless fish-eating resident killer whales *Orca orcinus* near Vancouver, but strongly to those of sympatric dangerous transient seal-eaters and also those of harmless fish-eaters from Alaska. This demonstrated conclusively that the seals had learnt that Vancouver resident killer whales were harmless. The seals had no opportunity to habituate to a harmless allopatric group with which they had no contact and also to a dangerous group, the transients which are rare and call little. What this study did not test, however, was whether the seals would originally have responded to the calls of all cetaceans. Were they selectively habituating only to those that had they learnt were not a threat or might they have originally responded only to killer whale calls (and then habituated to the non-threatening recognised groups) and not responded to the calls of other harmless sympatric cetaceans? Seychelles warblers *Acrocephalus sechellensis* show innate recognition and appropriate anti-predator behaviour to an allopatric species (female house sparrow *Passer domesticus*) resembling one of its main predators, the Seychelles fody *Foudia sechellarum*, even on islands where this predator does not occur (Veen *et al.* 2000). Only by habituation would it be possible for the warbler to lower the intensity of its innate anti-predator response to a bird resembling the fody. Thus, although there is strong evidence that animals can learn to distinguish between potential predators by

habituation, this may not be the main mechanism by which individuals learn about the threat posed by predators in general.

Seyfarth & Cheney (1980; 1986) also indicated how infant vervet monkeys *Cercopithecus aethiops* may learn the appropriate responses to conspecific alarm calls. Infants tended to look towards their mothers on hearing an alarm call and made a more accurate and quicker response when they were close to their mothers. This suggests that they learnt an appropriate response to an alarm call directly from their mother's response, i.e. by associative learning. However, the infants initially produced alarm calls to a number of different stimuli, ranging from falling leaves and non-predatory birds to actual predators. With time, they produced alarm calls more appropriately to fewer stimuli. Thus they appear to learn by association from their mothers about the threat posed by potential predators but may also habituate to those that do not pose a threat to them.

Studies across a wide range of taxa indicate that individuals can learn, by association, an appropriate response to a novel predator or to behaviour of conspecifics that reliably indicates the presence of a predator. Captive birds exhibit a rapid response to alarm calls when presented with a novel potential predator (Curio *et al.* 1978; Vieth *et al.* 1980; Frankenberg 1981). Blackbirds *Turdus merula* mobbed a bird species that they had never encountered before when they observed conspecific mobbing behaviour in conjunction with presentation of the predator (Curio *et al.* 1978). The blackbird's anti-predator behaviour, although slightly weaker, was also transferred to a plastic bottle when it was presented with mobbing behaviour (Curio *et al.* 1978). The mobbing calls of an allopatric species elicited mobbing behaviour in apostlebirds *Struthidea cinerea* (Johnson *et al.* 2003). This indicates that learning of a call may not always be necessary to elicit an alarm response and that some intrinsic characteristics of mobbing calls may explain some of the response.

The information animals can extract from observing the mobbing behaviour of other individuals can be highly specific. Conover (1987) presents strong evidence for associative learning in ring-billed gulls *Larus delawarensis* that observed conspecifics mobbing human intruders. They mobbed more at an adjacent site when the intruder was re-presented if the intruder had been holding a dead gull than if it had been empty-handed. Naïve captive-bred great tit *Parus major* fledglings showed little response to a grey partridge *Perdix perdix* and a potentially dangerous sparrowhawk *Accipiter nisus* (Kullberg & Lind 2002). Wild-bred juveniles, in contrast, did distinguish between them,



showing more distress behaviour to the sparrowhawk. This indicates that the great tit juveniles did not respond to all species as potential predators and then subsequently habituate to those that did not pose a threat. Oda & Masataka (1996) provide evidence that ring-tailed lemurs *Lemur catta* did not habituate to the two alarm calls of Verreaux's sifaka *Propithecus verreauxi*, a sympatric species. At a site where ring-tailed lemurs had previous experience of both alarm calls, they looked up to playback of the sifaka anti-raptor call and climbed trees to the sifaka anti-carnivore call. Lemurs at a second site, where they have never encountered sifakas, most often looked up on hearing either call, although a small number ran up a tree on hearing the anti-carnivore call. This implies that the experienced lemurs must have learnt an appropriate response to the anti-carnivore call (i.e. running up a tree), presumably by associating the call with the presence of a terrestrial predator.

The relatively few studies showing that habituation is of importance in distinguishing between potential predators, compared to the greater number indicating that associative learning occurs, indicates that the latter may be the most important learning mechanism for identifying predators and the most parsimonious explanation for this process. However, it is possible that habituation may be a useful learning process when distinguishing between similar potential predators (e.g. Deecke *et al.* 2002), to which initially it may be safer to produce anti-predator responses to all of them (it is better to be safe than sorry and learn more slowly, by habituation). In other situations, associative learning may be of greater value and less likely to lead to a wasteful unnecessary response. This may ensure that a prey individual learns a relatively rapid response to a novel predator by association but through habituation, to discriminate between similar potential predators, only some of which are dangerous.

Studies on captive birds have demonstrated how strong a learning stimulus alarm calls can be (see above). There are also some examples of rapid learning by primates and other mammals about predators from alarm calls in the wild. Vervet monkeys in savanna climbed up trees on approach by canids (jackals *Canis* spp. and wild dogs *Lycaon pictus*). However, in a patchy forest mosaic habitat, they did not climb trees on detecting canids (domestic dogs), as these were invariably associated with humans (although not always in close proximity to them) who often shot monkeys in trees (Kavanagh 1980). This suggests that the vervets may respond to the greater threat posed by the more dangerous predators associated with domestic dogs. Free-living golden-mantled ground squirrels *Spermophilus*

*lateralis* produced anti-predator responses to a novel neutral sound when it was presented in the presence of a predator (Shriner 1999). The responses were indistinguishable from their responses to conspecific alarm calls. Diana monkeys *Cercopithecus diana* in the centre of chimpanzee *Pan troglodytes* home range core areas were likely to respond appropriately by producing leopard alarm calls to chimp alarm calls as the chimp calls indicate leopards in the vicinity (Zuberbühler 2000a). However, Dianas at the periphery of chimp home ranges did not do so and remained cryptic as chimpanzees are a potential predator. They had not learnt that chimp alarm calls signal the presence of leopards as they rarely encounter the calls. Similarly, Diana monkeys in a fully protected area responded by calling and approaching human imitations of predator calls, whereas those Dianas subject to hunting by man did not do so (Bshary 2001). Harpy eagles *Harpia harpya* were reintroduced to a Panamanian forest and within a year of introduction, howler monkeys *Alouatta palliata* were responding to the calls of this important predator (Gil-da-Costa *et al.* 2003). By contrast, a nearby monkey population that had not been exposed to the eagles, showed no response to playback of their calls.

Prey individuals that can exploit novel information from their environment about the presence of predators and the threat that they pose will be in a strong position to reduce the chance of predation. By doing so they can benefit from the vigilance behaviour of both conspecifics and other sympatric species (e.g. Noë & Bshary 1997; Uster & Zuberbühler 2001; McGraw & Bshary 2002).

### **Pursuit deterrence**

The behaviour of some prey individuals on encountering a predator can seem counter-intuitive. Some species behave in a manner that might make them more conspicuous to a predator and would appear to put them at greater risk of predation than if they had behaved differently. This behaviour can include approaching the predator (e.g. Fitzgibbon 1994; Zuberbühler *et al.* 1997; Krams & Krama 2002), distinctive displays (e.g. Sherman 1985; Fitzgibbon & Fanshawe 1988; Cresswell 1994a) and alarm calls (e.g. Tenaza & Tilson 1977; Tilson & Norton 1981; Reby *et al.* 1999). Some behaviour in the predator context may be directed towards conspecifics and other prey individuals and can be explained by individual and kin selection as well as by investment in reproduction

(Maynard Smith 1965; Sherman 1977; Curio 1978; Klump & Shalter 1984). Reciprocal altruism is commonly given as an influence on the production of alarm calls (Trivers 1971), but much of this can be explained by other factors which will be discussed in more detail below. There is strong evidence that the behaviour of some individuals may be directed towards the predator and function to influence its behaviour by indicating to the predator that it has been detected and has a low chance of making a successful attack (Hingston 1933; Zahavi in Dawkins 1976; Sherman 1977; Curio 1978; Baker & Parker 1979). This behaviour has been termed pursuit deterrence (Woodland *et al.* 1980).

Pursuit deterrence describes the transfer of information to a predator by prey with the function of manipulating the predator's behaviour. In its most basic form this has been taken to mean 'perception advertisement': signalling to the predator that it has been detected (Hingston 1933; Smythe 1970; Curio 1978). This indicates to the predator that it has lost the element of surprise (Hingston 1933) thus reducing its chance of a successful hunt and therefore signals to the predator that it would save valuable hunting time by leaving the area (Zahavi in Dawkins 1976; Sherman 1977; Curio 1978). However, this idea makes a number of assumptions that are not fulfilled in all apparent cases of predator-prey communication. Reviews have indicated that as well as advertising perception, prey may signal other types of information (e.g. relative escape ability and individual quality) to predators (Hasson 1991; Caro 1995). Closer inspection of empirical and field data not only supports these other hypotheses but also suggests some further classes of information that may be communicated.

Despite the counter-intuitive nature of pursuit deterrence signals, their evolution may have been relatively simple. Calls given because they reduce the chance of predation on kin or a mate or may aid individual survival may have been audible or visible to predators. These may have coincidentally indicated to the predators that they had been detected and thus may halt their attack. Indeed there are a number of observations of both types of communication apparently taking place in the wild, e.g. Diana monkey and Campbell's monkey *Cercopithecus campbelli* alarm calls alert both conspecifics and predators (Zuberbühler *et al.* 1997; Zuberbühler 2001). The other important component for the evolution of pursuit deterrence signals is that the predator must observe the signal and must be able to associate it with detection by the prey. This indicates that predators may have relatively high intelligence. The cognitive abilities of some predators such as marine mammals (e.g. Bowles *et al.* 1988; Herman *et al.* 1999; Janik 2000; Deecke *et al.*

2002) and chimpanzees (e.g. Boesch & Boesch 1989; Huffman & Kalunde 1993; Boesch 1994) have been studied. However, few studies have focussed on the cognitive abilities of otherwise well studied predators, such as felids, canids and raptors that have been observed to respond appropriately to pursuit deterrence signals.

Pursuit deterrence signals have some general characteristics that are typical of all types of information transfer between prey and predators. They must be distinct and obvious and, if visual, directed at the predator. Signals may be louder or more extravagant than necessary merely to alert kin or conspecifics in close proximity (Maynard Smith 1965; Trivers 1971; Curio 1978). They should be confined to the predator context or, if produced at other times, then they should be produced concurrently with other behaviour types so that their meaning is unambiguous to the predator. I exclude aposematic signals or coloration from this analysis as they are mostly on permanent display. The signals should generally only be given at intermediate distances from the predator (Hasson 1991) and whilst the predator is still selecting its prey. However, there are exceptions to this that I will discuss below.

#### *a) Perception advertisement*

Perception advertisement, signalling to a predator that it has been detected, is a simple form of communication between prey and predator. The signal to the predator should communicate unambiguously that it has been detected, and hence may be more effective with ‘surprise’ predators that rely on remaining undetected for a successful attack, than against ‘pursuit’ predators that capture their prey after a relatively long chase. A review of relevant studies supports this view as prey individuals that give purely perception advertisement signals do so only to surprise predators (see Table 2.1). Further evidence for this is the difference in signals given by Thomson’s gazelles *Gazella thomsoni* to two different predator classes. To cheetahs *Acionyx jubatus*, a stealthy surprise predator, the gazelles often approached the predator looking directly at it (Fitzgibbon 1994), whilst on approach by wild dogs, a pursuit predator that does not rely on stealth, gazelles stotted at varying rates (Fitzgibbon & Fanshawe 1988). By approaching and looking directly at the cheetah the gazelles may indicate unambiguously that it has been detected.

A signal designed solely to advertise perception would be expected to be relatively cheap to produce and should be stereotyped and unambiguous. The gaze of prey individuals, particularly in open habitats, may be sufficient to transmit this information,

Group relatedness	Group stability	Habitat	Signal alone	Signal + group	Signal + kin	Reference
High	High	Closed	n/a	Yes	Yes	Tenaza & Tilson 1977
n/a	n/a	Variable	Yes	n/a	n/a	Yahner 1980
Unknown	Unknown	Variable	Yes	Yes	Unknown	Bildstein 1983
Low-high	High (females)	Open	Yes	Yes	Yes	Sherman 1985
Low-high	High (females)	Open	Yes	Yes	Yes	Sherman 1985
0	n/a	Open	Yes	n/a	n/a	Dial 1986
Unknown	Unknown	Open	Yes	Yes	Unknown	Caro 1986
High+Zero	Moderate-High	Variable	Yes	Yes	Yes	Lagory 1987
0	n/a	Variable	Yes	n/a	n/a	Randall & Stevens 1987
0	n/a	Open	Yes	n/a	n/a	Hasson et al 1989
0	n/a	Open	Yes	Possibly	Unknown	Holley 1993
0	n/a	Open	Yes	n/a	n/a	Butler & Roper 1994
Low	Low	Open	Yes	Yes	Unknown	Caro 1994
High	High	Closed	n/a	Yes	Yes	Zuberbühler et al 1997
Variable	Unknown	Closed	Yes	Yes	Yes	Reby et al 1999
High	High	Closed	No	Yes	Yes	Zuberbühler et al 1999
High	High	Closed	n/a	Yes	Yes	Zuberbühler 2001
High	Moderate	Closed	Yes	Yes	Yes	Rainey et al 2004
n/a	n/a	Open	Yes	n/a	n/a	Cooper et al. 2004
Low-high	Low-high	Variable	Yes	Yes	Yes	Shedd 1982
n/a	n/a	Unknown	n/a	Yes	Yes	Stone & Trost 1991
Low	Low	Open	Yes	Yes	n/a	FitzGibbon 1994
Low	Low	Open	n/a	Yes	n/a	Godin & Davis 1995
Low-high	High	Closed	No	Yes	Yes	Krams & Krama 2002
High (mate)	High	Open	Yes	Yes	Yes	Ostreiher 2003
Unknown	Unknown	Variable	Yes	Yes	Unknown	Alvarez 1993
0	n/a	Open	Yes	n/a	n/a	Ryan et al 1996
High	High	Open	Yes	Yes	Yes	Spitznagel 1996
Unknown	Unknown	Open	Yes	Yes	n/a	Woodland et al 1980
Unknown	Unknown	Open	Yes	Yes	Unknown	FitzGibbon et al. 1988
Low	Low	Open	n/a	Yes	n/a	Cresswell 1994
Low	Low	Open	Yes	Yes	Unknown	Caro 1994
Low	Low	Open	Yes	Yes	Unknown	Caro 1994
Low	Low	Open	Yes	Yes	Unknown	Caro 1994
Low-high	Unknown	Variable	Yes	Yes	Yes	Caro et al 1995
0	n/a	Variable	Yes	n/a	n/a	Leal et al 1997, Leal 1999
High	High	Variable	No	Yes	Pair	Tilson & Norton 1981
Variable	Low-high	Open	Yes	Yes	Yes	Blumstein et al 1997
0	n/a	Open	Yes	n/a	n/a	Cooper 2001

Table 2.1 (cont.)

e.g. brown hare *Lepus europaeus* (Holley 1993) and whiptail lizards *Cnemidophorus murinus* (Cooper *et al.* 2004), and the symmetrical markings on the face of some species of gazelle may reinforce the message of this directed gaze (Hasson 1991). Signals given as an animal moves away from a predator, such as tail-flicking (Woodland *et al.* 1980; Bildstein 1983; LaGory 1987), also send a strong signal that a predator has been detected and that the prey is moving away. In environments with reduced visibility, for example at night or in forest, alarm calls may be more effective in demonstrating detection than visual signals (e.g. Kloss's gibbon *Hylobates klossii*, Tenaza & Tilson 1977; European badgers *Meles meles*, Butler & Roper 1994; Diana monkeys, Zuberbühler *et al.* 1997; hornbills *Ceratogymna* spp., see Chapters 3-4, Rainey *et al.* 2004; submitted). Interestingly, although savanna living vervet monkeys (close relatives of Diana monkeys) produce referential alarm calls (Struhsaker 1967; Seyfarth *et al.* 1980a), they do not obviously function as perception advertisement signals and are apparently given to warn conspecifics about potential danger. However, as large adult male vervets are known to call less often to predators that are a threat only to smaller juvenile monkeys (Cheney & Seyfarth 1990) it is possible that there is some predator-prey communication taking place.

Although there are some instances of single individuals signalling perception (e.g. Yahner 1980; Dial 1986; Randall & Stevens 1987), there are other observations where perception is signalled by individuals when with kin, a mate or a stable group (e.g. Tenaza & Tilson 1977; Zuberbühler *et al.* 1997) (see Table 2.1). Therefore it is possible that the signals alert these individuals to the presence of the predator. However, it is likely that the information encoded by the signal is of value to both the individual itself and its kin. By signalling, a prey individual could also reduce the local density of predators by reducing their perception of the profitability of the area. This would decrease the chance of future predation of both individual and kin.

#### *b) Mobbing*

Prey individuals may mob a predator when they detect it. This is a widespread phenomenon observed in many species (e.g. Altmann 1956; Kruuk 1976; Shedd 1982; Shields 1984; Curio & Regelman 1985). Mobbing can be defined as close approach by prey individuals to a potential predator with calls or signals that are more obvious than necessary merely to signal to the predator that it has been detected. The mobbing behaviour may also include physical attacks on the predator, e.g. common terns striking

humans entering colonies (Cramp 1985) and raptors at their nests hitting humans (Newton 1979). As Bildstein (1982) points out, closely approaching a predator and physical attacks are not necessary to inform a predator that it has been detected (to advertise perception) but are necessary to drive it away, particularly if it is reluctant to leave the vicinity when resting and not hunting.

Mobbing calls and other signals (e.g. tail-flagging in squirrels and wing-flicking in blackbirds) may be made to recruit other prey to aid in the mobbing and harassment of the predator which may function to drive it from the site. Birds often approach playback of mobbing calls of sympatric species and behave appropriately, such as by participating in mobbing (e.g. Marler 1957; Curio 1978; Shalter 1979; Hurd 1996). Larger numbers of seabirds may be more effective in driving away predators (Andersson 1976). This indicates that an important function of mobbing calls and signals (e.g. wing and tail-flicking) may be recruitment of other individuals to increase the chance of driving the predator from the area. Mobbing can be stressful to potential predators and can influence time budgets. Panting and panic flights by little owls *Athene noctua* increased when mobbing calls were played to them (Flasskamp 1994). It may also encourage them to move to habitats where they are less likely to be mobbed and thus may reduce local predator density (Pettifor 1990; Pavey & Smyth 1998). It can be a dangerous activity for mobbing individuals (e.g. Denson 1979; Poiani & Yorke 1989; Sordahl 1990) but there is evidence that non-mobbing species, or groups that do not mob or approach predators, may be more likely to suffer predation (e.g. Dugatkin & Godin 1992; Godin & Davis 1995; Milinski & Boltshauser 1995; Pavey & Smyth 1998). Birds living in colonies may suffer reduced predation and this has been attributed to the protection offered by mobbing (Andersson & Wiklund 1978; Picman *et al.* 1988).

Mobbing behaviour may also allow conspecifics and other prey individuals to learn about the threat that a predator poses (Curio *et al.* 1978; Vieth *et al.* 1980; Frankenberg 1981; Gehlbach & Leverett 1995). The evolution of mobbing behaviour as an extension of perception advertisement may have been simple. Individuals that have detected the first sign of a predator's presence may gain more precise information about its location by approaching it. This approach may provide a strong indication to the predator that it has been detected. If this approach was combined with alarm calls or visual signals (e.g. Zuberbühler *et al.* 1997; Chapter 3, Rainey *et al.* 2004), then other prey individuals might be alerted to the detection of the predator and might also show an alarm response if they

also had some interest in reducing the local predator density or in protecting their kin. Such recruited individuals may travel some distance to mob or inspect the predator, e.g. yellow-casqued hornbills *Ceratogymna elata* flew more than 200 m to approach playback of crowned eagle *Stephanoaetus coronatus* shrieks and calls of mobbing hornbills (pers. obs.), so mobbing may be a powerful attracting stimulus.

### c) *Vigilance advertisement*

Although pursuit deterrence is generally taken to indicate that a prey individual has detected a predator, some species also appear to produce signals continuously as an indicator of their level of vigilance. The signal should be obvious and given towards the likely direction of attack by a predator. The signal should also be given whether or not a predator is present in the area and hence is not necessarily a form of perception advertisement. This type of behaviour appears to have been observed so far only in rails Rallidae and dippers Cinclidae (Alvarez 1993; Ryan *et al.* 1996; Spitznagel 1996). It is also possible that the clear calls produced by Diana monkeys, rates of production of which correlate with vigilance levels (Uster & Zuberbühler 2001), may transmit information to potential predators about their vigilance. The vigilance advertisement signal, in the bird species above, i.e. tail-flicking or dipping, should reliably indicate the state of vigilance of an individual (as calling does in Diana monkeys). Alvarez (1993) found that the rails *Gallinula chloropus* and *Porphyrio porphyrio* in Spain flicked their tails more when far from cover; when group-living *G. chloropus* had their tails orientated away from the group; and they flicked their tails more in the direction away from cover, the direction from which predators (e.g. marsh harrier *Circus aeruginosus*) were more likely to come but in which conspecifics would not be found. Tail-flicking was also closely correlated with individual vigilance. It is possible that this behaviour could function to recruit other conspecifics as in *G. chloropus* tail-flicking is inversely related to group size. However, the rails flick away from cover where few conspecifics would be, and as *P. porphyrio* are rarely in groups they would be unlikely to recruit other individuals.

Individuals that are vigilant and are demonstrating ‘vigilance advertisement’ may signal at higher rates than less alert individuals. Although honest signalling does not have to be costly (Maynard Smith 1994), signals advertising vigilance could be an honest and direct signal of condition. Alvarez (1993) argued that vigilant individuals may avoid wasting energy by tail-flicking only at appropriate times (i.e. when exposed or alone).



Diana monkeys also appear to produce clear calls only when there is a need to be more vigilant, e.g. when the group is spread out (Uster & Zuberbühler 2001). Non-vigilant rails might find the energetic costs of tail-flicking prohibitive as they would be poor judges of when it is safe not to signal. However, an alternative hypothesis is that vigilance signalling may interfere with other behaviour such as foraging (it may be difficult to call or tail-flick with a mouth full of food). Thus, the signal may be an honest indicator of vigilance. Chaffinches *Fringilla coelebs* that feed faster are more vigilant, as they have more time to look around them (Krams 1998) and respond more quickly to a predator than slower feeders (Cresswell et al. 2003). Vigilance signals may thus indicate the quality of a bird as this may correlate with its ability to take in food more quickly; a good quality bird may also be able to escape more easily from a predator. Indeed, dominant tits *Parus* spp. delay returning to feed after a predator attack for longer than subdominants (de Laet 1985; Hegner 1985). This may be because they are capable of displacing other individuals from feeding sites and perhaps can feed at a higher rate and thus do not need to risk returning early. Woodland *et al* (1980), in coining the term ‘pursuit deterrence’, found that rails *P. porphyrio* in Australia (a separate *P. porphyrio* subspecies) signalled more as predators approached and this correlated with alertness. By doing so they indicated not only that they had detected the predator but also the state of vigilance and the likelihood of an attack being successful. Thus, in effect, vigilance advertisement signalling may indicate indirectly the quality of an individual and the chance of an attack on it succeeding.

A number of species produce contact calls intermittently and it is possible that these may have a similar function to vigilance signalling. Diana monkeys produce ‘clear’ calls that function to indicate that the surrounding area is free of predators and extend their range of vigilance by relying on the calls of other individuals in their group (Uster & Zuberbühler 2001). Tits and chickadees produce contact calls continuously and these may serve to indicate that there are no predators in the area (e.g. Morse 1970; Sullivan 1984). These may indicate to birds in a visually restricted habitat what the overall level of vigilance is within the flock. This may allow birds to adjust their individual levels of vigilance accordingly to set optimal levels of vigilance and feeding rates. On attack by a predator, the members of a flock may cease producing contact calls and produce alarm calls. This may indicate to prey individuals that there is a predator nearby and that they should take appropriate action such as freezing and increasing vigilance (Sullivan 1984). After the departure of a predator then alarm calls may cease and contact calls may signal

all clear to birds. An alternative and non-exclusive hypothesis is that contact calls may act similarly to tail-flicking in rails; they may transfer information to a predator about the level of vigilance in a flock.

#### *d) Quality advertisement*

In theory the signals used to advertise perception to a predator should be relatively cheap to produce and unique to the predator context. However, there are a number of observations of prey individuals across a wide range of taxa advertising perception to predators by using costly signals (see Table 2.1). Woodland *et al.* (1980) found evidence that rails signalled in this manner and Klump & Shalter (1984) discussed how quality advertisement might have evolved. The first workers to demonstrate unambiguously that individuals were apparently showing 'quality advertisement' to predators were FitzGibbon & Fanshawe (1988). They showed that Thomson's gazelles that stotted (leaping off the ground with all four legs held straight and stiff) for longer were less likely to be captured by wild dogs than those that stotted for only short periods of time. Quality advertisement has so far been described in antelopes (Fitzgibbon & Fanshawe 1988; Caro 1994), deer (Caro *et al.* 1995), birds (Woodland *et al.* 1980; Cresswell 1994a) and lizards (Leal & Rodriguez-Robles 1997; Leal 1999; Cooper *et al.* 2004).

This behaviour is amongst the most counter-intuitive of all the pursuit deterrence behaviour described, since while calling or approaching a predator before an attack might appear dangerous, the type of behaviour exhibited during quality advertisement would appear more so as it is normally initiated after the predator's attack has commenced. Quality advertisement signals are apparently costly; skylarks *Alauda arvensis* frequently commence singing on being chased by merlins *Falco columbarius* (Cresswell 1994a) and the additive energetic cost of singing combined with flight may be high (Eberhardt 1994; Oberweger & Goller 2001; Gil & Gahr 2002; Ward *et al.* 2003). FitzGibbon & Fanshawe (1988) suggested that stotting in Thomson's gazelles might be an indicator of physical condition and hence relative escape ability (Zahavi in Dawkins 1976; Hasson *et al.* 1989; Hasson 1991). Gazelles were less likely to stott in the dry season when fleeing from wild dogs, perhaps because they were in poorer condition as resources were more limited (Fitzgibbon & Fanshawe 1988). This type of honest signalling indicates prey condition to the predator in a similar manner to the honest signals produced during some intraspecific displays in male-male interactions and mate attraction (Zahavi 1975; Zahavi & Zahavi

1997; Zuberbühler *et al.* 1997; Cooper 2001). Leal (1999) provides conclusive evidence that lizards *Anolis cristatellus* with high endurance capacity produced more pushup displays to predators than lower quality individuals. Endurance capacity in these lizards is related to ability to escape capture and thus numbers of pushups honestly signal escape ability. Quality advertisement signals may therefore have evolved quite separately from those signals functioning to advertise perception.

Yachi (1995) presented a model of predator-prey interactions and the development of honest signalling. He demonstrated a simple mechanism for the evolution of honest signals in the predator-prey context:

- a) Honest signals of prey individuals can only be maintained if predators prefer prey that signal weakly or not at all;
- b) A predator's preference of non-signalling prey is also a prerequisite for the evolution of honest signalling from no signalling;
- c) A predator's preference may evolve from no preference by genetic drift or pleiotropy;
- d) Once a predator's non-signalling preference is in place, honest signalling prey may invade and be more successful than non-signalling individuals;
- e) Signalling pays (i.e. signalling costs are less than the predation escape cost that must be paid for not signalling) for high escape ability prey whereas it does not for low escape ability prey.

As this behaviour is directed primarily at the predator, it is essential that predators should select their prey on the basis of the information presented to them, i.e. they should not choose high quality individuals advertising as such. Both studies observing the behaviour of prey to real predators (as opposed to a human 'predator') found that prey that signalled at high rates were chased less often (Fitzgibbon & Fanshawe 1988) and for shorter periods (Cresswell 1994a) than those that signalled at lower rates.

The factors linked to the development of quality advertisement are clear. There is good evidence indicating that quality is advertised only to pursuit predators and not to surprise predators as observed in perception advertisement (Table 2.1). These predators do not rely on surprise, followed by a relatively short successful attack. They pursue their prey for a considerable period of time and rely on stamina for success. A prey individual

that also has considerable stamina may be costly to chase and thus the rewards from it may be relatively low, even if an attack proves successful. Signals are therefore often given at the beginning of the chase to attempt to influence the predator's hunting behaviour with signal intensity rising as the predator approaches up to a minimum distance when the prey stops signalling (Fitzgibbon & Fanshawe 1988). Predators may also manipulate prey behaviour to aid initial prey selection by harassing a group to detect whether any individuals are unable to keep up with main body of the prey group. Signals may also be given by prey towards the end of a chase, perhaps when a predator may be likely to abandon its attempt (Cresswell 1994a). Both Thomson's gazelles and skylarks produced quality advertisement signals to pursuit predators but, on detecting a surprise predator, gazelles approached and stared at the predator whilst skylarks merely attempted to outdistance it but did not sing (Fitzgibbon & Fanshawe 1988; Caro 1994; Cresswell 1994a).

A major factor in this type of advertisement is that the individuals behaving in this way are not often found with kin or a mate in close proximity (Maynard Smith 1965; Curio 1978), although where the predator presents a strong threat to individual survival then this could perhaps lead to individuals with kin advertising quality (Caro *et al.* 1995). They also tend not to show fidelity to the group or range in which they are found (Trivers 1971; Krams & Krama 2002). Quality advertisement signals appear to signal to a predator that it should choose another individual that will be easier to capture. If prey individuals behaved in this way with offspring they might be counterproductively transferring the risk to them. Unlike perception advertisement signals, quality advertisement ones appear to be given mainly in open environments compared to perception advertisement. However, this may be because pursuit predators are less often found in closed environments such as forests. It may also be an artefact of the relatively few studies that have been carried out.

#### *e) Refuge advertisement*

A small number of studies have found evidence that some species reliably signal their proximity to a refuge – 'refuge advertisement'. Klipspringer antelope *Oreotragus oreotragus* produce duets to jackals when a pair reaches safety on rocks (Tilson & Norton 1981). Yellow-bellied marmots *Marmota flaviventris* produced almost all alarm calls only when within 5 m of their burrows (Blumstein *et al.* 1997). Curly-tailed lizards curled their tails more strongly when close to a refuge on approach by a human 'predator' (Cooper

2001). Rails signalled their vigilance when alert and away from cover. On approach by a predator, those rails near cover had higher signalling rates compared to those away from cover (Alvarez 1993). When a predator was not present rails signalled less near cover. These species appear to indicate their escape ability only when close to a refuge (except for rails that signal more close to cover) and this is perhaps a form of quality advertisement. They also appear to be signalling vigilance (see above). They are signalling relative escape ability (Hasson 1991), but the circumstances of this escape ability are related to a feature of the environment rather than to individual quality.

The signal produced when advertising proximity to a refuge might be expected to be similar to that produced during perception advertisement, i.e. cheap and stereotyped, and, as mentioned above, reliable signalling does not always have to be costly (Maynard Smith 1994). Thus, on detecting the signal, a predator should give up the hunt rather than deciding whether or not it is economical to continue hunting. This will allow the prey individual to resume its previous activities (e.g. feeding or mate attraction) and the predator may move on to a more productive site. Of the limited studies available, only rails vary the rate of production of signals with distance from their refuge (Alvarez 1993). It is possible that other prey species are too vulnerable to predators to benefit from signalling relative security unless they are very close to their refuge.

### **The functions of alarm calls and anti-predator signals in birds**

Studies on the function of anti-predator signals and alarm calls in birds have primarily focussed on investigating the hypotheses and predictions put forward by Curio (1978) and Klump & Shalter (1984). This has resulted in a huge amount of literature in this field but there has not been a synthesis of the subject for some time. Here I review the subject with emphasis on the literature since these two previous reviews.

#### *a) Individual selection*

Alarm signals can have both direct and indirect benefits for the signaller. By definition they are designed to signal information to other individuals, so they may benefit other related individuals but also, by manipulating the behaviour of either predators or other prey individuals in the vicinity, the individual can benefit.

Prey individuals may try to manipulate predator behaviour and deter pursuit. The pursuit deterrence hypothesis is reviewed above in greater detail (see section 2 above). Pursuit deterrence in birds has now been shown to include not only perception advertisement (see Chapter 3, Rainey *et al.* 2004), but other behaviour types including mobbing (e.g. Altmann 1956; Kruuk 1976; Curio *et al.* 1978), vigilance advertisement (Alvarez 1993; Ryan *et al.* 1996; Spitznagel 1996) and quality advertisement (Woodland *et al.* 1980; Cresswell 1994a). Refuge advertisement has yet to be observed in birds. However, this behaviour could possibly have evolved in species that can escape predators in dense or thorny vegetation, or those that nest in association with noxious insects that might harm predators (e.g. white-headed buffalo-weaver *Dinemellia dinemelli* with biting ants or chestnut-crowned sparrow-weaver *Plocepasser superciliosus* with polistine wasps, Fry & Keith 2003). It might benefit these birds to produce appropriate alarm signals on approach by a predator, when in close proximity to a refuge of this type. Individual selection may influence the production of all types of pursuit deterrence behaviour. However, signals that advertise quality, and hence may indicate to a predator that it should choose another weaker individual to pursue, are the only pursuit deterrence signals that may be produced solely because of individual selection.

Individuals may use alarm signals to manipulate the behaviour of other prey individuals around them to reduce the chance of predation on the signaller. Mobbing is a form of pursuit deterrence but it also appears to recruit other potential prey individuals (see mobbing section above). Many mobbers may attract large prey individuals that could possibly injure predators although there is no evidence for this to date in birds (Curio 1978). By attracting other individuals, mobbers may also dilute the individual risks associated with mobbing which can be considerable (e.g. Hennessy 1986; Sordahl 1990).

Alarm signals can function to coordinate appropriate escape behaviour of prey individuals under attack by predators (e.g. formation of flocks in redshank *Tringa totanus*, Cresswell 1994b). This can reduce the immediate risk of predation to the individual, for example, redshanks are more likely to escape predation in a flock (Cresswell 1993b) and this will also dilute the individual risk (Hamilton 1971). Alarm signals may also be produced when there are unlikely to be kin present (Charnov & Krebs 1975). Krams & Krama (2002) demonstrated that sedentary wintering chaffinches in stable flocks produce alarm calls despite the low likelihood of kin being present. The calls may be produced on the small chance that there are kin present and thus their survival may be aided. However,

a more likely hypothesis is that by doing so they may reduce the chance of a predator returning to a site (by lowering the predator's assessment of its profitability) and thus lower the local predator density (Klump & Shalter 1984; Sonerud 1985; Cresswell 1994b). These alarm calls may also help maintain the integrity and size of the flock which may be important in maintaining adequate vigilance levels.

The 'seep' alarm call (Figure 2.1) is produced by many different small passerines, often in the presence of a fast-moving avian predator (e.g. Marler 1955; Gompertz 1961; Perrins 1968; Charnov & Krebs 1975; Shalter 1979; East 1981; Ficken 1989). It is also produced by yellow warblers *Dendroica petechia* to brood parasitic brown-headed cowbirds *Molothrus ater* (Studd & Robertson 1985; Hobson *et al.* 1988; Hobson & Sealy 1989). Ficken (1989) demonstrated that it may be associated with the degree of urgency rather than being a referential call, like some primate ones (e.g. Seyfarth *et al.* 1980a; Zuberbühler *et al.* 1997). The seep call is high-pitched and difficult to detect and localise for both humans and birds (Marler 1955; Perrins 1968; Shalter & Schleidt 1977; Shalter 1978; Brown 1982; Jurisevic & Sanderson 1998; Wood *et al.* 2000; Jones & Hill 2001). It may be particularly difficult for predators to localise this call type (Shalter 1978; Klump *et al.* 1986) and the range at which it can be detected is much smaller for hawks than great tits (Klump & Shalter 1984). It appears to be produced more often at intermediate distances than at close range (Alatalo & Helle 1990). This suggests that birds may also be using this call to minimise the chance of predation whilst communicating information about a predator. However, at close range, where the chance of detection is elevated, the threat of predation may be too high to risk calling. Calling birds are at an increased risk of predation (Sordahl 1990; Redondo & Castro 1992; Haskell 1994; Leech & Leonard 1997; Krams 2001a), so a fundamental feature of this call may be that it is difficult to localise (Marler 1955). This would explain why it is given to both fast-moving aerial predators that are a threat to adults and also to cowbirds that are trying to locate and parasitise nests but are not a threat to adults (Gill & Sealy 2003, 2004).

The high value of the information encoded by alarm calls can sometimes be exploited by other species for their own benefit, as birds will often respond appropriately as it is better to be safe than sorry when at risk of predation (Haftorn 2000). The story of the boy who cried wolf is well known (Aesop 1484) and, similarly, white-winged tanagers *Lanio versicolor* appear to produce alarm calls if they observe a fellow flock member flushing an arthropod (Munn 1986). By doing so, they often distract the other bird and capture the

prey themselves. As the tanagers are often the first individuals to produce alarm calls to potential predators (Munn & Terborgh 1979), the other flock member may tolerate this 'cheating' as the benefits of their vigilance may outweigh the loss of prey.

*b) Kin selection*

The benefit of anti-predator signals in the presence of kin is clear (Hamilton 1964) and there is good evidence that birds do produce alarm signals more often in the presence of kin (Milinski 1978). Birds invest more in broods that are more likely to produce high quality progeny, i.e. broods that are larger in number (Williams 1966; Greig-Smith 1980; Knight & Temple 1986a; Rytkonen 2002), broods that are more costly to produce (i.e. larger sex, Wiklund 1990; Radford & Blakey 2000) and older chicks (Curio 1975; Greig-Smith 1980; East 1981; Regelman & Curio 1983; Knight & Temple 1986a; Montgomerie & Weatherhead 1988; Wiklund 1990; Halupka 1999; Pavel & Bures 2001). Although the birds should avoid committing the Concorde fallacy (Curio 1983; Windt & Curio 1986), they should invest more in those offspring (i.e. high quality young) that are more likely to survive and reproduce themselves. With increasing age and quality of chicks, there will often be less time available for breeding in temperate regions and thus a reduced opportunity of breeding successfully again. Separating variation in investment by birds in high quality older young that are more likely to survive, and variation in investment with reneating potential, is difficult. However, there are indications that more of the variance in nest defence behaviour can be explained by age of nestlings rather than the reneating potential (Weatherhead 1979; Curio 1983; Reid & Montgomerie 1985).

Alarm signals given by adult birds with vulnerable offspring are presumably usually produced because they increase offspring survival. The effects of these signals through which this is achieved may be as follows:

- i) Manipulating the behaviour of offspring, e.g. silencing begging young (Curio 1975; Greig-Smith 1980; Knight & Temple 1986a; Gill & Sealy 2003; but see Maurer *et al.* 2003) and other appropriate anti-predator behaviour such as jumping from the nest (Kleindorfer *et al.* 1996) or freezing and concealment in chicks of precocial birds (Sonerud 1985);
- ii) Cultural transmission of predator recognition (Curio *et al.* 1978; Buitron 1986); offspring may learn about the threat that a potential predator poses. There is no



direct evidence so far of offspring learning from their parents about predators, but birds are known to show rapid acquisition of information about novel predators from each other (Kruuk 1976; Vieth *et al.* 1980; Frankenberg 1981; Conover 1987) and juvenile primates are known to learn about predators from their parents (Hauser 1988; Seyfarth & Cheney 1990).

- iii) Manipulating predator behaviour. Mobbing by adults and other individuals attracted to mobbing may drive a predator from the nest site (e.g. Curio 1978; Pavey & Smyth 1998). Prey distraction behaviour may also draw the attention of a predator away from the nest (e.g. Aristotle 336 BC; Jourdain 1936).

### *c) Reproductive investment*

Production of alarm signals as a form of reproductive investment overlaps substantially with alarm call production as a result of kin selection (see above). Risk-taking by parent birds in defence of their nest has been comprehensively reviewed by Montgomerie & Weatherhead (1988). Parental characteristics that may influence the level of alarm signalling produced include: reneating potential, parental experience, sex of parent, past parental effort and parental interactions (Montgomerie & Weatherhead 1988). Offspring characteristics that may influence alarm signalling are considered above in kin selection. The greater the likelihood of offspring surviving to breed the more a parent bird may invest in their defence; if chicks in second broods are less likely to survive to the following season then adults should invest less in their defence than those from first broods (Curio *et al.* 1984; Montgomerie & Weatherhead 1988). Adults may also invest in defending their mate against predators to maximise the chance of successful reproduction (e.g. Sullivan 1985; Gyger *et al.* 1986; Hogstad 1995; Burton & Yasukawa 2001). The sex that is most abundant may invest most in mate protection as the rarer sex will be more likely to find a replacement mate (Klump & Shalter 1984). Male robins only produce the seeep alarm, perhaps to reduce the chance of the female (who does all of the incubation) being surprised at the nest (East 1981). The male may produce the seeep call to reduce the chance of her and the nest contents being predated, without giving away the location of the nest. The more essential both sexes are for successfully raising their young to independence, the more one would expect each sex to invest in the other. There is also evidence that birds will invest more in defence of an attractive (and therefore higher quality) mate (Evans & Marler 1992).

Alarm responses can be counter-productive, particularly if produced in response to nest predators; these alarm signals may indicate to this predator type that there is a nest in the vicinity (Smith *et al.* 1984; Craib 1994). In line with this, birds may alter their anti-predator strategies by reducing their alarm responses to predators that are most likely to attack nests but not to predators of adult birds (Arnold 2000; Nijman 2004). They also appear to respond to a predator's behaviour; small green bee-eaters *Merops orientalis* entered nests less often when a human predator was looking at the nest than when its gaze was elsewhere (Watve *et al.* 2002). Open-nesting species may also reduce visits to nests in the presence of predators but this was not observed in pied flycatchers *Ficedula hypoleuca* which, as hole-nesters, may have relatively few nest predators (Bures & Pavel 2003).

## **Conclusions**

Animals may learn about predators by habituation and association. By doing so they may have some flexibility in their responses to predators and perhaps lower the risk to themselves. Learning about predators appears to be important not only for reducing the risk of predation but also to reduce the amount of time wasted in responding to predators. By producing appropriate signals that predators may attend to, they can signal not only detection but also relative quality or escape ability. This is particularly evident in the different responses produced by Thomson's gazelles to predators (cheetahs and wild dogs) with different modes of attack (Fitzgibbon & Fanshawe 1988; Fitzgibbon 1994). The types of signals produced may be influenced by the hunting behaviour of the predator but also the social system of the prey species and the presence of kin in the vicinity.

Anti-predator behaviour in birds may be influenced by individual or kin selection or by levels of investment in reproduction. Alarm calls function to communicate information to other individuals and thus are of obvious importance for kin selection or investment in reproduction. They may, however, be of importance in individual selection by reducing the chance of an individual being predated in a flock and the predator's assessment of the profitability of returning to a site.

## Chapter 3

### Yellow-casqued hornbills can distinguish between primate alarm calls

#### Introduction

Some mammals have been found to obtain information from the vocalisations of other species. Thus, various primates distinguish between and respond appropriately to the alarm calls of other primate species and of birds, as well as those of conspecifics (e.g. Seyfarth *et al.* 1980a; Seyfarth & Cheney 1990; Zuberbühler 2000b). Some other mammal species have also been shown to respond appropriately to the calls of potential predators (e.g. Zuberbühler 2000a; Deecke *et al.* 2002) and of birds (e.g. Rasa 1983; Isack & Reyer 1989). Equivalent studies on birds have been more limited. While some have been found to respond appropriately to other species' alarm calls (e.g. Vieth *et al.* 1980; Nuechterlein 1981; Sullivan 1984), there have been no studies of the abilities of wild birds to distinguish between the different alarm calls of another species.

Diana monkeys *Cercopithecus diana* produce different alarm calls to two of their main predators in West African forests: crowned eagles *Stephanoaetus coronatus* and leopards *Panthera pardus* (Zuberbühler *et al.* 1997). Yellow-casqued hornbills *Ceratogymna elata* are sympatric with both Diana monkeys and these two predators in many parts of their range. They are amongst the largest birds in the forest ((mass ca. 2 kg, Kemp 1995) and may be vulnerable to similar predators to Diana monkeys ((mass 2.2-7.5 kg, Kingdon 1997). Crowned eagles prey on hornbills, although they feed mostly on primates and small ungulates (Keith 1969; Mitani *et al.* 2001; Shultz 2002). However, leopards feed almost entirely on mammals (Hoppe-Dominik 1984; Ray & Sunquist 2001; Zuberbühler & Jenny 2002). While leopards do sometimes climb up to the canopy where hornbills spend much of their time (Bshary & Noë 1997), and hornbills occasionally feed on the ground (pers. obs.), these are rare events.

As eagles prey on hornbills, I predicted that hornbills would respond to their calls. Similarly, as leopards are not thought to prey on hornbills, the birds should not respond to their calls. An appropriate response to a predator, including production of alarm calls,

may produce benefits to the individual calling and to its relatives (e.g. Maynard Smith 1965; Charnov & Krebs 1975). Conversely, it would be of no benefit to hornbills to respond to leopard vocalisations if they are not subject to predation by leopards, and could even be costly if their response reveals their presence to another predator (Sordahl 1990; Redondo & Castro 1992; Haskell 1994; Leech & Leonard 1997; Mougeot & Bretagnolle 2000; Krams 2001a) or reduces the time available for feeding (Caraco *et al.* 1980).

The most appropriate response of a prey species to the presence of a predator depends on the hunting behaviour of the predator. Eagles and leopards use surprise during an attack (Zuberbühler *et al.* 1999b; Shultz 2001). I predicted that hornbills would respond to the presence of a surprise predator by attempting to locate it and monitor its movements thereby removing the element of surprise and the chances of a successful attack (e.g. Curio 1978; Klump & Shalter 1984; Gautier-Hion & Tutin 1988). Hornbills in Ivory Coast mob crowned eagles by calling and approaching the predator (S. Shultz pers. comm.). I also predicted that hornbills would produce alarm calls to alert others to the presence of the predator (Frankenberg 1981) or to signal that it has been detected: the perception advertisement hypothesis (Curio 1978). Zuberbühler *et al.* (1999b) showed that primate alarm calls deterred leopards from hunting and caused them to leave the area. There is also some evidence that crowned eagles are deterred from hunting on hearing Diana monkey alarm calls (Shultz 2001).

As hornbills are often found close to Diana monkeys, sometimes feeding in the same trees, they are likely to hear each other's calls frequently. They may therefore, associate the two different Diana monkey alarm calls with the presence of the corresponding predator and thus come to respond appropriately. As eagles (but not leopards) are predators of hornbills I predicted that hornbills would respond to the Diana monkey-eagle alarm call but not the Diana monkey-leopard alarm call.

## Methods

### *Study site*

I carried out the field work in Taï and Mont Péko National Parks, Ivory Coast between October 2001 and May 2002 inclusive. In Taï, the work was based in two areas: c. 70 km<sup>2</sup> around the Centre de Recherche en Ecologie (CRE) (5°50'N, 7°21'W); and c. 25 km<sup>2</sup> near

the Ecotel at Guiroutou (5°24'N, 7°15'W). In Mont Péko, the area covered was c. 15 km<sup>2</sup> in the north of the park near Goenié (7°06'N, 7°16'W).

### *Selecting hornbill flocks*

I located yellow-casqued hornbills during systematic searching by listening for their vocalisations, noisy wingbeats and occasionally by direct observations (both forests are dense and visibility is limited). To maximise independence for each playback trial, playbacks were separated spatially by at least 500 m or, if within 500 m, temporally by at least four months to reduce the chance of hornbills becoming habituated to a particular stimulus type. This is a realistic separation as natural predators such as the crowned eagle can attack a single monkey group several times in a day (Zuberbühler *et al.* 1997). I worked at three different sites and hornbills range and migrate widely both within and between seasons (Poonswad & Tsuji 1994; Holbrook *et al.* 2002) so, although the hornbills could not be recognised individually, it is highly unlikely that any two trials involved the same individual.

### *Playback protocol*

Pilot work in Mont Péko found that hornbills have low calling rates, reduced activity and low response rates before 0700 hours and after 1300 hours, so all the experiments took place between these times. When a flock was located, I approached to within 50 m so that the vocalisation played back was close enough to be of immediate importance to the birds. The speaker was placed at a height of c. 2 m above ground to reduce attenuation of the sound. Both species of predator and Diana monkeys can be found at ground level (pers. obs.). The experiment was only begun if there was no predator present and if alarm calls had not been produced by hornbills, primates or other animals in the area within 10 min of the start of recording and if the birds had not responded to my approach. If hornbills noticed me they often flew off.

Once a hornbill flock had been approached, an adult individual in each flock, usually a male, was located and notes were taken of its behaviour. Adult females were only selected if they could be distinguished clearly from immatures using both vocal behaviour and plumage (Kemp 1995, pers. obs.). I focussed on adult individuals, as they were more likely to have experienced interactions between Diana monkeys and predators. Yellow-casqued hornbill flocks consist of small family groups containing at least one adult male

Campbell's-eagle calls (Wilcoxon signed rank test:  $Z=154$ ,  $n=77$ ,  $P=0.003$ ) (Fig. 4.4c). They did not increase the numbers of calls they made to leopard growls (Wilcoxon signed rank test, one tailed:  $Z=259.5$ ,  $n=196$ ,  $P=0.521$ ) (Fig. 4.4d), to Diana-leopard calls (Wilcoxon signed rank test:  $Z=83.0$ ,  $n=100$ ,  $P=0.931$ ) (Fig. 4.4e) or to Campbell's-leopard calls (Wilcoxon signed rank test:  $Z=27.0$ ,  $n=75$ ,  $P=0.625$ ) (Fig. 4.4f).

Finally, call rates of hornbills when hearing the predator calls were compared to call rates on hearing the associated monkey alarm calls. Within the eagle-related stimuli (Fig. 4.5a) I found that hornbills increased their call rates more often to eagle shrieks than to Diana-eagle alarm calls (Fisher's exact test:  $n=84,60$ ,  $P=0.006$ ). They also increased their call rates more often to eagle shrieks than to Campbell's-eagle alarm calls (Fisher's exact test:  $n=84,77$ ,  $P=0.006$ ). No significant changes were observed when I compared the hornbills' responses to leopard growls (Fig. 4.5b) with Diana leopard (Fisher's exact test:  $n=196,100$ ,  $P=1.000$ ) or Campbell's leopard alarm calls (Fisher's exact test:  $n=196,75$ ,  $P=1.000$ ). Given the large numbers of playback trials when there was no change in response or no birds calling I excluded the no change category from Fig. 4.5 to demonstrate more clearly the variation in responses. There were no cases when birds called and made equal numbers of calls before and after playback.

## Discussion

### Hornbill responses to predators

Our data suggest that in about half of all cases one or several black-casqued hornbills were within the range of a playback stimulus. This is because in about 48 % of all trials involving eagle shrieks, the most powerful stimulus in eliciting vocal responses in hornbills, one or several birds vocalised in the 5 min period before and after the playback (Fig 4.3a). The overall response rate to leopards was much weaker (17%) and in most cases, no calls were given even though it is quite likely that birds were present. As I predicted, our data showed that black-casqued hornbills distinguished between the calls of the two predators, similar to other hornbill species (Hauser & Wrangham 1990; Chapter 3, Rainey *et al.* 2004). Given that all these playback trials were carried out in the presence of primate species, it is conceivable that as the primates often responded to these stimuli, the

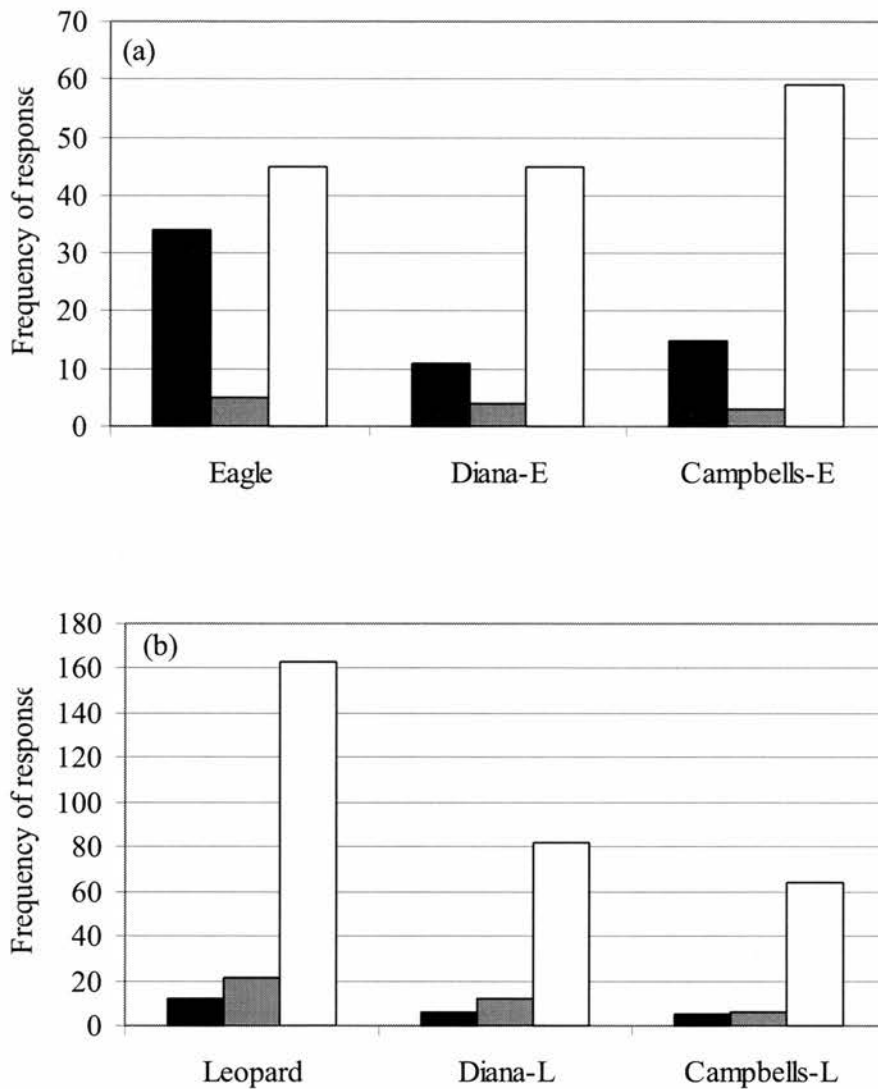


Figure 4.5. Frequency of hornbill response types to playback of different stimuli: (a) hornbills increased the calls they produced more often to eagle shrieks than to Diana-eagle calls ( $P=0.006$ ) and to Campbell's-eagle calls ( $P=0.006$ ); (b) there was no difference in the numbers of calls produced between leopard growls and Diana-leopard calls ( $P=1.000$ ) or Campbell's-leopard calls ( $P=1.000$ ). Black bars: increased calls; hatched bars: decreased calls; white bars: no change.

hornbills could be responding to the primate alarm calls rather than the predator stimuli. However, as there was a much stronger response to the eagle stimulus rather than to the primate-eagle stimuli (Fig. 4.3) this suggested that the birds were responding to the experimental playback of the predators' calls.

### **The effect of functionally referential primate alarm calls**

Black-casqued hornbills were able to distinguish between the two different alarm calls produced by each monkey species. They responded to the Diana monkey eagle alarm call by increasing call rates, but not to the similar sounding Diana monkey leopard alarm calls (Fig. 4.3b). An analogous response pattern was found in response to the Campbell's monkey alarm calls (Fig. 4.3c). In this sense, our results go beyond previous studies, in suggesting that black-casqued hornbills are able to acquire extensive knowledge of other species' communication systems. The ability of hornbills to distinguish between not only Diana monkey alarm calls, but apparently also between Campbell's monkey alarm calls, is particularly remarkable. In comparison to the loud and conspicuous Diana monkeys, Campbell's monkeys are generally very cryptic in their overall behaviour, both visually and acoustically, and they produce alarm calls much less frequently (Wolters & Zuberbühler 2003), suggesting that there may be many fewer learning opportunities for the birds.

### **Predator presence: the effect of spatial information**

The data further showed that hornbills increased their call rates more often after playback of eagle shrieks than after either Diana-eagle calls or Campbell's-eagle calls (Fig. 4.5). This supported the hypothesis that hearing a predator provided more accurate information about the location of a predator than did primate alarm calls, as alarm calls might only signal that a particular predator was in the vicinity, but not its exact location. Most probably, the hornbills behaved more cautiously when responding to monkey alarm calls, as these calls did not provide any information about the location of the predator (Chapter 3, Rainey *et al.* 2004). Similarly, experimental evidence on yellowhammers *Emberiza*



*citrinella* showed that birds that had heard nearby conspecifics' alarm calls to a sparrow-hawk model were more alert and resumed foraging later than birds that saw the actual sparrow-hawk model (van der Veen 2002). A similar phenomenon had been observed in primate anti-predator behaviour: Diana monkeys produced fewer vocalisations in response to Campbell's monkey eagle alarm calls than to eagle shrieks, further suggesting that behaving conspicuously while the location of the predator is unknown is not an adaptive strategy (Zuberbühler 2000b).

### **The evolution of avian cognition**

The ability to take advantage of environmental information regarding the type of predator present is relatively well described for non-human primates (e.g. Seyfarth *et al.* 1980a; Oda & Masataka 1996; Zuberbühler 2000b). Here, I have provided further evidence that this ability is not restricted to mammals, by showing that hornbills can distinguish between the different referential alarm calls of non-human primates (see Chapter 3, Rainey *et al.* 2004). Interestingly, hornbills are exceptional amongst birds in that they exhibit a number of behaviours that are often considered as indicators of more sophisticated cognitive capacities, including social interactions with members of other species. Rasa (1983) found that savanna hornbills *Tockus deckeni* and *T. flavirostris* and dwarf mongooses *Helogale undulata* have a mutualistic relationship relating to predator detection and foraging. The birds are often first to detect and respond to dangerous raptors and they are capable of distinguishing between different species or raptor. This includes those that pose a threat only to the mongooses but do not prey upon the hornbills, not, however, to raptors that are not mongoose predators (Rasa 1983). Moreover, hornbills have relatively large brains and, unlike most other bird species, they exhibit social play (Diamond & Bond 2003). Many large frugivorous hornbills are not territorial as they require large numbers of ephemeral fruiting trees (Kemp 1995, pers. obs.). Defending a territory containing sufficient trees to maintain a family group throughout the year would be uneconomical and they appear to defend only a small area around the nest site. Hornbills are long-lived, indulge in allo-preening and many species breed cooperatively, including the *Ceratogymna* species (Kemp 1995, pers. obs.). Pairs of hornbills remain together for years and nest repeatedly with the same mate with young from previous years

helping at the nest (Kalina 1988; Kemp 1995). These observations combine to suggest that there are similarities between the social systems of some hornbills and those of primates and that this may be conducive to the development of sophisticated cognitive abilities.

Future work will have to determine whether the hornbills' ability to recognise their predators by their vocalisations and to respond appropriately to the alarm calls of the sympatric primates are unique amongst the numerous species of forest birds. The evidence suggests that hornbills do have sophisticated cognitive abilities (Rasa 1983; Kemp 1995; Diamond & Bond 2003) but as predation acts so strongly on future fitness (Lima & Dill 1990) it might be expected that other bird species may be capable of discriminating between the alarm calls of sympatric species.

## Chapter 5

### Seasonal variation in responses of great tits to alarm calls and predators

#### Introduction

The responses of an animal to a potential predator are influenced by the hunting behaviour of the predator and the threat that it poses (e.g. Owings & Leger 1980; Seyfarth *et al.* 1980a; b; Cresswell 1993a). The methods of attack by different predators present threats requiring varying escape responses. Thus, some species vary their alarm responses with the predator type and this appears to reduce the risk of predation (e.g. Fitzgibbon & Fanshawe 1988; Pereira & Macedonia 1991; Cresswell 1993a; Zuberbühler *et al.* 1999b). It might also be expected that, if the threat that a predator poses to a prey individual or its kin varies over a period of time (e.g. between breeding and non-breeding seasons), then the response of the individual to its presence should also vary. Similarly, environmental cues, such as alarm calls of sympatric species, that reliably indicate the presence of a predator that varies in threat over time, may also elicit variable responses in the individual.

#### (1) Variation in responses of birds to different predators

Alarm responses may be produced as a form of investment in reproduction (e.g. Maynard Smith 1965; Sherman 1977; Curio *et al.* 1978; Klump & Shalter 1984, see Chapter 2). Birds have been found to vary their responses to a potential predator over the breeding cycle and in the presence or absence of their mate (e.g. Greig-Smith 1980; East 1981; Hogstad 1995). Some workers have shown that birds have variable responses to different predator types. East (1981) showed that robins *Erithacus rubecula* with nestlings produced one alarm call to corvids and a different one to grey squirrels *Sciurus carolinensis*. These two predators have different modes of attack and thus require different escape strategies. Cresswell (1993a) showed that redshanks *Tringa totanus* took

flight more often to an attack by sparrowhawks *Accipiter nisus* than to peregrine falcons *Falco peregrinus* to which they often crouched or submerged themselves. Buitron (1983) found that magpie *Pica pica* responses to different predator types appeared to change throughout the breeding season; however, she used  $\alpha$  levels of 0.1 to assess significance. In Chapters 3-4 (Rainey *et al.* 2004; submitted), I have not demonstrated that hornbills *Ceratogymna elata* and *C. atrata* have variable responses to different predators but that they responded to one potential predator and not another. Other studies have not compared variation in responses to more than one predator type. East (1981) found that adult robins produced a 'seep' alarm call in the presence of a human when young were immobile (in the nest or only recently fledged). The seep call is high-pitched and difficult to localise (Marler 1955; Perrins 1968). The 'tic' alarm call, however, was given more often when the young were older (East 1981). The tic call may possibly have the advantage of being more audible at greater distances and therefore mobile and dispersed offspring may be alerted earlier to the presence of a predator and could take appropriate evasive action. Magpies also showed a similar response to predators; they increased the production of some alarm calls and decreased others as the breeding season progressed (Stone & Trost 1991). Greig-Smith (1980) found that the 'whit' and 'chack' alarm calls of adult stonechats *Saxicola torquata* in response to a human 'predator' varied through the breeding season, although they both varied in the same way unlike the two robin alarm calls (East 1981). Kleindorfer *et al.* (1996) also found that moustached warbler *Acrocephalus melanopogon* chicks had variable responses to models of different predators; leaving the nest or ducking into it equally for snakes and ducking only into the nest to harriers. Some evidence suggests that great tits *Parus major* vary their responses to different predator classes, producing a seep call to fast-moving avian predators and a rattle call to slow-moving terrestrial predators (Gompertz 1961). What has not so far been demonstrated is whether birds have variable motivation to produce alarm calls and respond to predators because they have vulnerable offspring, or whether they are responding to the increased threat that different predators pose to their young. Many experiments use humans as 'predators' but Knight & Temple (1986b) point out that birds may reduce their response or habituate to such a predator through the breeding cycle with repeated presentation of this predator. This may explain part of the observed variation and increase in alarm responses over the breeding cycle of birds.

Alarm calls or mobbing behaviour may function to warn young and to teach them which predators are dangerous and also for them to practise mobbing predators (e.g. Rand 1941; Sherman 1977; Curio *et al.* 1978; Vieth *et al.* 1980; Frankenberg 1981; Buitron 1983; Klump & Shalter 1984; Sherman 1985). The benefits of alarm calling and the types of alarm calls produced depend on the presence of an appropriate receiver (Hogstad 1995). As young birds in the nest may be more vulnerable to some predators than others and this vulnerability may change over time, it is likely that adults will produce calls to these predators only when their young are vulnerable. Birds are known to vary the rate at which they produce alarm calls with the age of the young in the nest. Both robins and stonechats tend to produce alarm calls more often with increasing age of nestlings and a decline shortly after fledging (Greig-Smith 1980; East 1981). This may correspond to the most vulnerable period in the life of a young bird. Variation in the types of alarm calls produced between the breeding and non-breeding seasons has not been well studied. By studying alarm call production through the year it is possible to investigate whether adult birds produce alarm calls appropriately to different predators based on the threat that they pose.

Responses by great tits and blue tits *Parus caeruleus* to sparrowhawks have been reasonably well documented. Tits are known to mob sitting hawks by diving at the predator and calling. An attacking hawk may cause a bird to produce alarm calls and fly down to cover (Hinde 1952; Gompertz 1961; Morse 1973; Cramp & Perrins 1993, pers. obs.). If a hawk flew overhead without attacking, the immediate response of the tits was similar (Morse 1973). However, the birds resumed their previous activity more quickly after an attack than if the hawk had merely flown overhead. This might indicate that hawks do not return immediately to a site that they have recently attacked, presumably because they have lost the element of surprise. However, a hawk passing overhead may be prospecting for potential prey and could return in the near future. Responses to great spotted woodpeckers *Dendrocopos major*, a potential nest predator, have not been so well documented, but I have observed adult birds mobbing woodpeckers close to their nests and these observations are presented in the results section.

I attempted to answer the following question: do birds have variable responses to different predator classes and do these responses vary seasonally in relation to the threat that these predators represent to adult birds and their offspring? Specifically I was interested in testing whether or not great tits showed variable responses to predators with

different attack modes: sparrowhawks and woodpeckers. I was also interested in observing whether responses to these predators varied seasonally as the woodpecker is only a threat to great tit nestlings. Thus, it could be predicted that the great tits would respond to the woodpecker only when they have eggs or young in the nest. It is possible that they will also respond more to the sparrowhawk during the breeding season as they will produce alarm responses to protect both kin and mate.

## **(2) Variation in responses of birds to different alarm calls**

Few studies have investigated the abilities of birds to distinguish between the different calls produced by other species. Sullivan (1984) showed that the downy woodpecker *Picoides pubescens* produced different responses to an alarm call and a contact call of another bird species but not between two different alarm calls of another species. Hornbills have been found to distinguish between the alarm calls of primates (Chapters 3-4, Rainey *et al.* 2004; submitted). However, no one has yet investigated the abilities of birds to distinguish between the alarm calls of another bird species although mammals have been shown to distinguish between the different alarm calls of both birds (Hauser 1988; Seyfarth & Cheney 1990) and other mammal species (Oda & Masataka 1996; Oda 1998; Shriner 1998; Zuberbühler 2000b). Shalter (1979) presented some limited evidence that blue tits responded appropriately to the alarm calls and mobbing behaviour of sympatric species, however, the results were not conclusive as there was no control.

I investigated responses of great tits to the different alarm calls of robins, a common sympatric species whose calls they should hear frequently. The hypothesis is that robin seep calls are given to fast-moving avian predators and that robin tic alarm calls are given in response to slower-moving non-volant predators (Gompertz 1961; Ficken 1989). The seep calls should therefore be of relevance to great tits throughout the year. The latter call types, although likely to indicate the presence of a predator throughout the year may be of greater importance when the tits have chicks in the nest that are vulnerable to slow-moving predators. I tested whether great tits varied alarm responses appropriately between seasons in relation to the vulnerability of their offspring. I also investigated whether responses to great tit alarm calls were similar to those to robin alarm calls.

It has been observed that producing alarm calls is a form of reproductive investment (e.g. Maynard Smith 1965; Curio *et al.* 1978; Klump & Shalter 1984) and therefore birds may call more in the presence of a mate or offspring, particularly if they are of high quality (e.g. Stefanski & Falls 1972; Robertson & Biermann 1979; Biermann & Robertson 1981; Regelmann & Curio 1983; Curio *et al.* 1984; Gyger *et al.* 1986; Curio & Regelmann 1987; Montgomerie & Weatherhead 1988; Evans & Marler 1992; Hogstad 1995; Radford & Blakey 2000). To assess whether adult great tits might respond more to predator and alarm calls in the presence of kin or mate, I noted whether or not other great tits were present during each experimental trial.

## Methods

### *Study species*

I studied great tits as they are vulnerable to predation by different predators; sparrowhawks prey on adults and fledged young; and predators such as great spotted woodpeckers and squirrels prey on great tit chicks despite great tits nesting in holes (Perrins 1979). Great tits are amongst the best studied of bird species although their anti-predator behaviour (see Chapter 1) is not as well studied as their behavioural ecology (e.g. Perrins 1968; 1979; McGregor *et al.* 1981). They breed in nest boxes and this makes them relatively easy to study.

### *Study dates*

Fieldwork for this experiment took place in the non-breeding (winter) (13 February-18 April 2003) and breeding (summer) seasons (15 May-10 June 2003). The breeding season was defined as the date of completion of the clutch and the start of incubation to the time that the young left the nest. Great tits do not commence incubation until the clutch is complete (Perrins 1979). As I was intending to carry out playback experiments to birds at the nest and as the birds do not remain in the vicinity of the nest until incubation, this phase of the project could not be commenced until after completion of the clutch. Date of completion of the clutch was determined by observation of birds at the nests and by frequent checking of the size of the clutches.

### *Study sites*

During the non-breeding season experiments took place at 13 seed feeders at three sites (Kippo Wood, Strathtyrum Estate and Tentsmuir Forest) and during the breeding season at the nest sites in which birds were breeding at four sites (Kippo, Strathtyrum, Craigtoun Park and Tentsmuir). Minimum separation of feeders was 400 m so that playback of stimuli at one site could not be heard at other sites. Birds may move between sites so it is possible that they may be exposed to stimuli more than once. However, the separation between feeders will reduce the likelihood of birds moving between sites. Also, predators may attack a group of prey individuals more than once in a day (Zuberbühler *et al.* 1997, pers. obs.), so they are unlikely to become habituated to the stimuli. All but one of the great tit pairs was using a nest box for breeding. The natural territorial behaviour of great tits would normally result in the separation of nests being great enough to ensure that playback at one site would be unlikely to be heard at an adjoining site. However, at Craigtoun, there are few large trees with nest holes, and here several great tit pairs used nest boxes within 10 metres of each other. This problem is discussed further below.

### *Stimuli*

The different exemplars of the playback stimuli were obtained from the National Sound Archive, London, from Roche (1996), or from personal recordings made during pilot work for this study. To reduce the possibility of pseudoreplication (Kroodsma 1989; McGregor *et al.* 1992) I used multiple exemplars of each playback stimulus (Table 5.1). All stimulus types can be heard naturally from February to June in Scotland.

(1) Three different predator stimuli were used: calls of sparrowhawks, great spotted woodpeckers and as a control, woodpigeon *Columba palumbus*. Each of the predators has distinctive calls (Fig. 5.1). All exemplars of sparrowhawk calls were natural recordings of series of 3-5 groups of calls. Woodpecker exemplars consisted of 8-19 calls compiled from natural recordings and had extra calls spliced in to lengthen the recordings to 15 s. Woodpigeon calls were continuous calls lasting 15 s with extra phrases spliced in to lengthen the recordings to 15 s.

(2) Three different alarm call stimuli were used: robin seeep and tic alarm calls and song as a control (Fig. 5.1). Robin seeep alarm call exemplars were made from different



Stimulus type	No. of exemplars	No. of trials		Figure
		- winter	- summer	
Sparrowhawk	4	11	12	5.1a
Woodpecker	3	9	10	5.1b
Woodpigeon	8	10	14	5.1c
Robin seep	7	10	11	5.1d
Robin 'tic'	7	10	13	5.1e
Robin song	4	10	11	5.1f

Table 5.1. Details of playback stimuli.

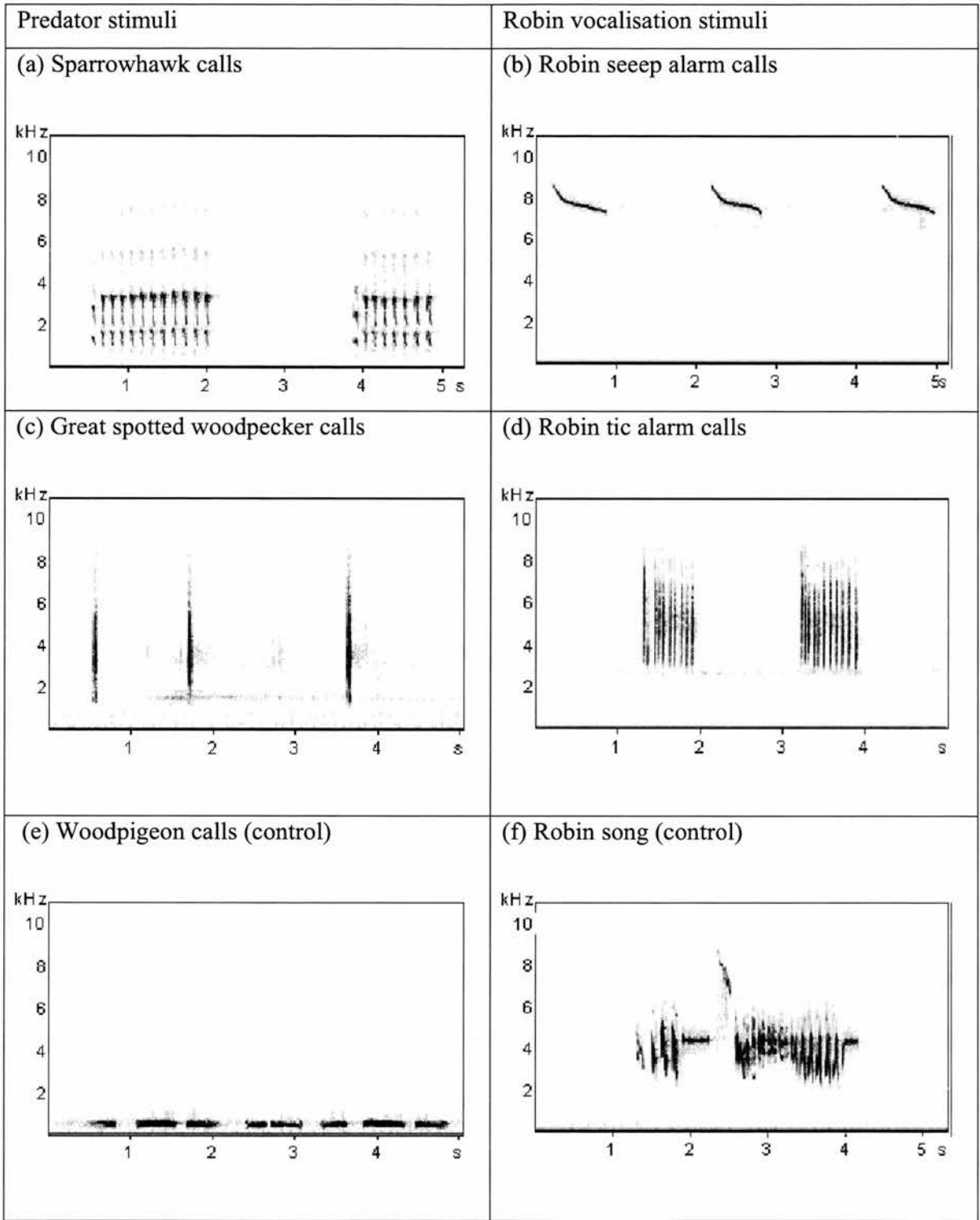


Figure 5.1. Spectrograms of typical vocalisations in each playback stimulus.

recordings and consisted of 6-7 calls. Robin tic alarm calls consisted of 22-35 calls and were compiled from natural recordings and had extra calls spliced in to lengthen the exemplars to 15 s. Robin song exemplars were made from natural song recordings with extra phrases spliced in to lengthen the exemplars to 15 s.

#### *Playback and experimental protocol*

Playback protocol at both feeders and nests was similar. On arrival at each site, the playback equipment and microphone were set up *c.* 5 m from the feeder or nest. I wore disruptive pattern material clothing and concealed myself with the recording equipment up to 15 m from the feeder or nest (usually under a bush). After waiting 5 mins to ensure that there had been no predation event (predator attack or alarm calls) and that the birds had recovered from the disturbance during setting up (i.e. the birds had returned to visiting the feeder or nest box), tape recording was started once a subject bird arrived at the feeder or nest box. This bird became the focal bird throughout that experimental trial and was the only bird on which data (calls and behavioural notes) were taken. After 1 min the stimulus was played back. The position of the bird when the stimulus is presented at the nest could have influenced the response. For example, a bird may be safer to remain within the nest box if there is a predator outside. The stimulus was therefore played back when it was outside the nest box. The recorded calls were played back for 15 s and tape recording continued for 5 mins after presentation of the stimulus. If large numbers of other birds were present during playback to flocks in winter then the experiment was delayed. They could have increased the chance of focal individuals being influenced by calls of other birds. Notes were also taken of the numbers and species of other birds present during the trial.

#### *Repetition of playback trials*

Each feeder or nest was the site of a maximum of 6 playback trials (each trial using different stimuli). However, as 13 feeders were in place and 21 nest boxes were occupied, the number of experiments repeated at each feeder or nest box was often less than this. The order of playback of stimuli at each site for each season was chosen using a randomised block design (randomly generated numbers were used to select the next stimulus type for playback at each site). This minimised the possibility of habituation of the birds to any of the stimuli. At Craigtoun, some nests were in close proximity to each

other (see above). To control for neighbouring individuals responding to experimental stimuli or vocalisations from an adjacent territory, I did not carry out playbacks if neighbours were nearby or at their nest. I also separated playbacks at closely adjoining sites by at least 2 hours. I could not separate them further as this would have increased the number of journeys and time spent travelling between sites. Playback of each stimulus once per feeder and per nest box was planned so that the experiments would have sufficient power to reduce the chance of committing Type II errors. However, these totals were not attained in some cases because of time constraints; the great tit breeding season lasts approximately a month and travel between sites reduced time available.

### *Data collection*

I noted tit behaviour before and after presentation of each stimulus. Scanning behaviour was identified as when birds stopped their previous activity (e.g. feeding or preening) and began looking around them, either in the direction of the playback loudspeaker or elsewhere. I noted movements with respect to the stimulus, to cover (nearest dense vegetation) or towards the feeder or nest box, although in practice very few birds flew towards the loudspeaker. Presentation of movement observations are thus of birds that moved towards cover. Movement or scanning behaviour was deemed to have occurred if the birds behaved in this way during the 15 s of the playback. Tape recordings were analysed by noting call types in the 30 s after the start of playback using spectrograms of the calls on Avisoft-SASLab Pro 3.9. This short time period for comparison was considered sufficient after observing responses to attacks by natural predators (sparrowhawks and great spotted woodpeckers) and to these playback trials. Few alarm vocalisations were made more than 30 s after a natural attack or presentation of the stimulus. Call types were compared between stimuli within and between seasons. Other birds that called or responded were also recorded in order to assess whether the focal bird was responding to these other individuals and also to distinguish the recordings of the vocalisations of the different birds.

### *Equipment*

The stimuli were played back from a Goodmans GCD506R CD-player through a Nagra DSM loudspeaker-amplifier. Peak amplitudes of each stimulus were standardised at c. 75-80 dB for hawk calls and c. 70-75 dB for all other calls with a Tenma Sound Level Meter

72-6604, A-weighting, at 1 m from the speaker. The stimuli were played back at standardised volumes at amplitudes similar to natural levels that had been estimated from pilot trials and observations. Vocal responses were recorded using a Marantz CP430 cassette recorder with a Sennheiser ME66 microphone. Recordings of calls were displayed as spectrograms with Avisoft-SASLab Pro 3.9. I used SPSS 11.5.0 to calculate Fisher's exact tests. The sequential Bonferroni technique was used *a posteriori* to minimise group-wide Type I errors (Rice 1989) and I set  $\alpha$  at 0.017 (for multiple comparisons in groups of three tests) and 0.025 (for two).

## Results

Great tit responses to predator calls were varied but often took the form of scanning, moving to cover or vocalising. Scanning and moving to cover were the most common responses and I compared the number of different playback trials to which birds scanned or moved to assess the effects of the different stimuli. I also assessed vocal responses to playback, and rattle and seep calls were the most common of these (although relatively few vocal responses were recorded over all). To control for the possible presence of the mate influencing the likelihood of birds calling to the different stimuli I tested birds with or without their mate. Although parids often maintain pair bonds for years (Ficken *et al.* 1981; Hogstad 1995) I could not be sure in winter if birds found together were pairs, I simply assessed whether tits observed with conspecifics scanned more. Birds did not scan more to the stimuli in the presence of another great tit in winter (Fisher's exact test:  $n=10,21$ ,  $P=1.000$ ) or in summer (Fisher's exact test:  $n=4,42$ ,  $P=1.000$ ) (comparison using responses to sparrowhawk, woodpecker, robin seep and tic calls) (Fig 5.2). However, they did scan more in summer than in winter (Fisher's exact test:  $n=40,46$ ,  $P<0.001$ ) (Fig 5.3) (comparison using responses to sparrowhawk, woodpecker, robin seep and tic calls). Here I was assessing the seasonal variation in the likelihood that birds would show an alarm response to the stimuli indicating the presence of a predator. I therefore did not use control stimuli as one would not expect them to elicit alarm responses.

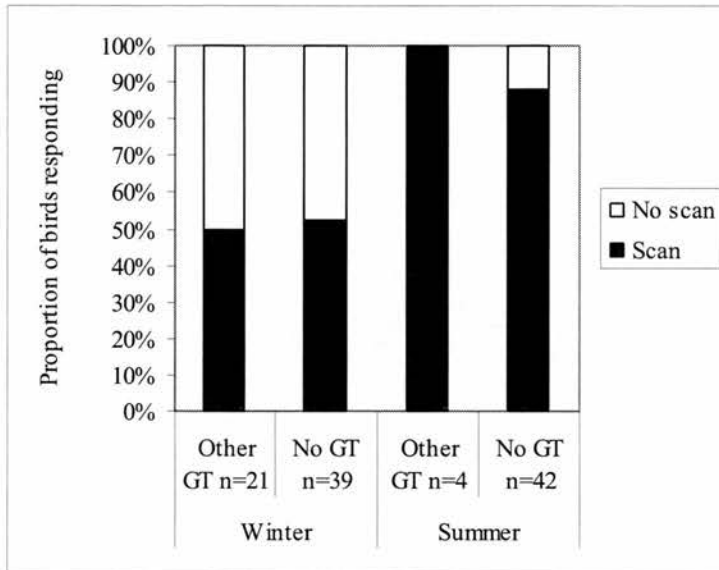


Figure 5.2. Proportion of birds scanning in the presence or absence of conspecifics (GT) (winter) or mates (GT) (summer) to predator calls and robin alarm calls.

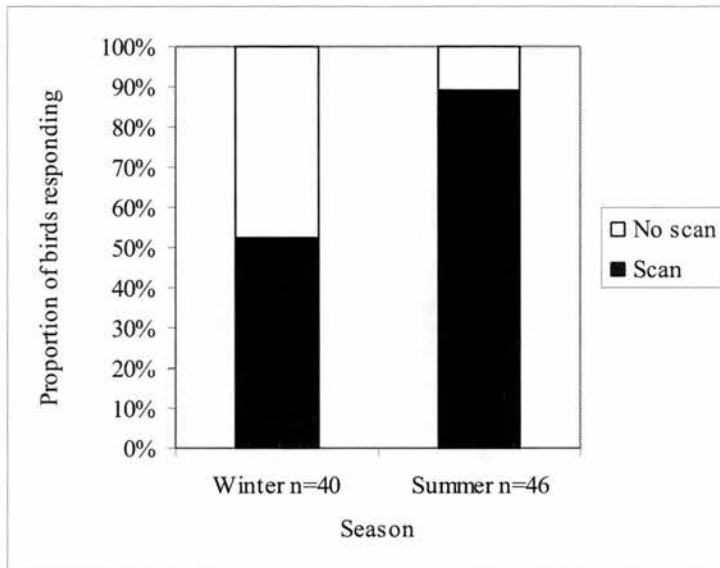


Figure 5.3. Proportion of birds scanning in winter and summer to predator calls or robin alarm calls.

and one adult female with one or two immatures. Occasionally individual birds or pairs were located and on one occasion a flock of more than thirty birds was encountered feeding on flying ants or termites. In all but six playback tests an adult male was present in the flock and targeted for observations.

The following four categories of vocalisations were used as playback stimuli:

- (i) Crowned eagle shrieks – 15 s of continuous recording;
- (ii) Leopard growls – 15 s of continuous recording;
- (iii) Diana monkey alarm calls in response to a crowned eagle – 15 s of recordings containing three calls;
- (iv) Diana monkey alarm calls in response to a leopard – 15 s of recordings containing four calls; this call consists of fewer syllables than the Diana-eagle alarm call (Zuberbühler *et al.* 1997).

Crowned eagle shrieks were obtained from commercial recordings (Chappuis 2000) and leopard growls from the National Sound Archive, London. Diana monkey alarm calls of both types were originally recorded in Taï (spectrograms of all four stimuli are presented in Fig. 3.1). Exemplars of eagle shrieks and leopard growls were natural sequences from different individuals and each lasted 15 s. I used alarm call sequences from six different male Diana monkeys, three of which were eagle alarm calls and three were leopard alarm calls. Three or four calls (see above) from an individual calling sequence were selected for each playback exemplar. I used three different exemplars of each category to reduce pseudoreplication (Kroodsma 1989; McGregor *et al.* 1992). I carried out a total of 34 playback trials: four in Mont Péko and 30 in Taï. One recording was corrupted and could not be used for analysis although observational data were obtained from this trial. After 5 min of tape recording and behavioural observations, one of the stimuli was played back for a total of 15 s followed by a further 5 min of recording and observations.

#### *Observational notes*

I noted the times at which the focal individual called and this allowed me to separate its calls from those of other individuals. Yellow-casqued hornbill calls often have resonant harmonics and are nasal in tone (see Fig. 3.2). As hornbills have noisy wingbeats it was



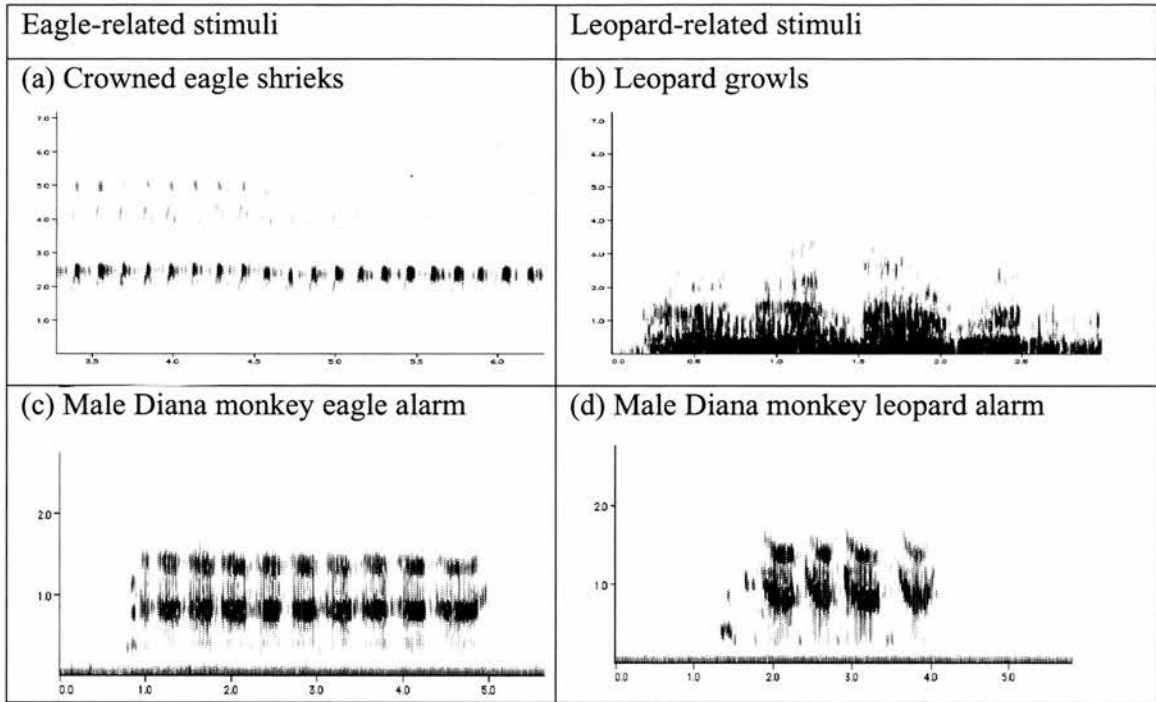


Figure 3.1 Spectrograms of typical calls of each four playback stimulus.

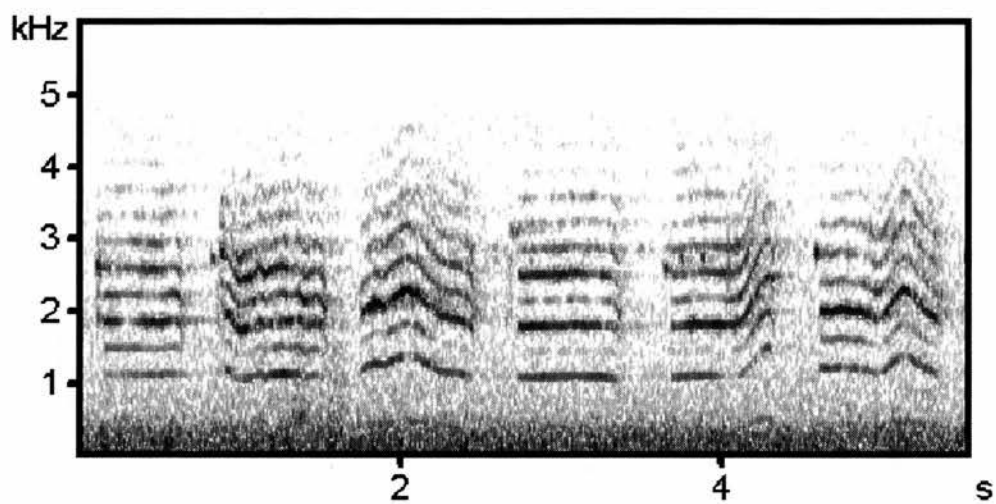


Figure 3.2. Spectrogram of typical yellow-casqued hornbill calls.

possible to follow their movements even when dense vegetation limited visual observation. I noted the focal bird's behaviour before and after playback and its movements with respect to the playback site. Classification of movement as being towards or away from the playback site was based on the first movement between branches or trees (rather than along a branch) with respect to the playback site. The rationale for this was that, as greater effort is generally needed to move between branches than along a branch, such movement would be more likely to relate to the stimulus. The direction of movement was classed as being in the 180° segment towards or away from the playback site. In fact, almost all movements were at a narrow angle to the playback.

### *Equipment*

The stimuli were played back from a Goodmans GCD506R CD-player through a Nagra DSM loudspeaker-amplifier. Peak amplitudes of each stimulus were standardised at about 95 dB with a Tenma Sound Level Meter 72-6604, A-weighting, at 1 m from the speaker. Audible responses were recorded using a Sony WMD6C Professional Walkman with a Sennheiser ME66 microphone. Minitab 12 was used for statistical analysis. Recordings of calls were displayed as spectrograms with Avisoft-SASLab Pro 3.9 from which individual calls could be counted.

## **Results**

### **Vocal behaviour**

The difference in the total number of calls in the 5 min before and after playback indicated that hornbills called significantly more after some playback types than others (Kruskal-Wallis test:  $H_3=8.6$ ,  $p=0.035$ ) (Fig. 3.3). Post hoc nonparametric multiple comparison (Zar 1999) showed that hornbills called significantly more after playback of eagle shrieks compared to playback of leopard growls ( $Q_4=8.22$ ,  $n=11,7$ ,  $p<0.001$ ). Similarly, hornbills called significantly more after playback of Diana-eagle alarm calls than after playback of Diana-leopard alarm calls ( $Q_4=8.39$ ,  $n=8,7$ ,  $p<0.001$ ).

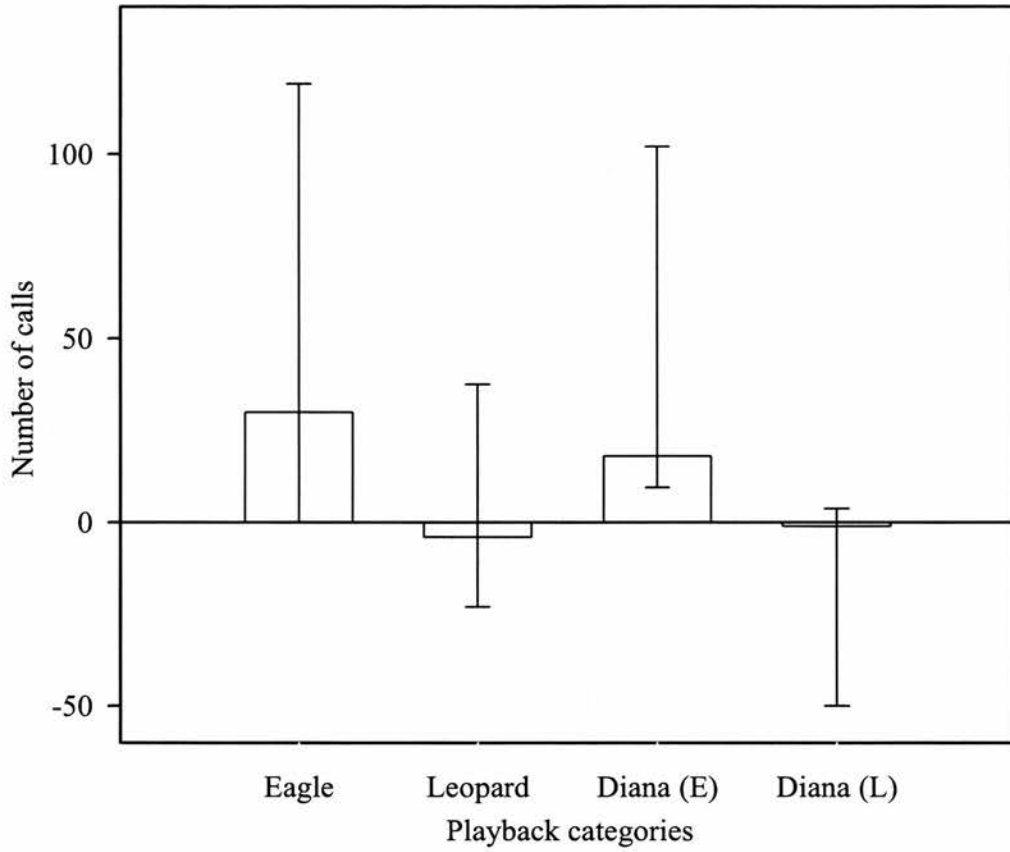


Figure 3.3. Median and inter-quartile ranges of differences between the numbers of calls hornbills made before and after playback of different stimulus types. Hornbills increased the differences between the numbers of calls after eagle playback than after leopard playback,  $p < 0.001$ ; and hornbills increased the differences between the numbers of calls more after Diana-eagle playback than after Diana-leopard playback,  $p < 0.001$ .

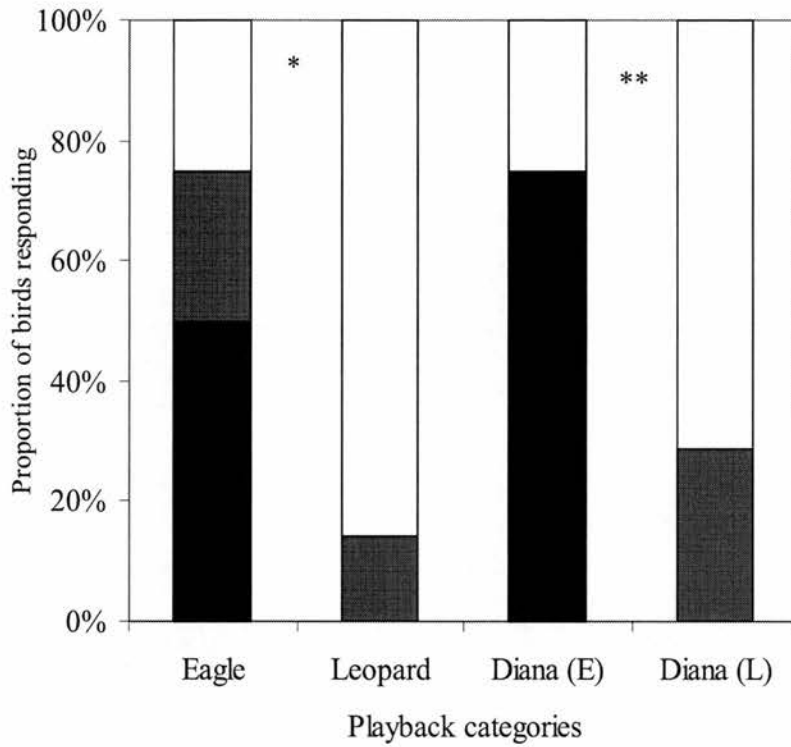


Figure 3.4. Proportion of hornbills approaching, departing from and not moving in relation to the playback site in response to different playback stimuli. Black bars, approach; cross-hatched bars, depart; open bars, no movement. \*Hornbills approached eagle playback more often than leopard playback,  $P=0.03$ . \*\*Hornbills approached Diana-eagle playback more often than Diana-leopard playback,  $P=0.006$ .

## Locomotor behaviour

As Fig. 3.4 shows, hornbills approached the playback site significantly more often in response to playback of eagle shrieks than playback of leopard growls (Fisher's exact test,  $n=12,7$ ,  $p=0.03$ ). Hornbills also approached the playback site more often in response to playback of the Diana-eagle alarm call than the Diana-leopard alarm call (Fisher's exact test,  $n=8,7$ ,  $p=0.006$ ). No significant differences between approaches to eagle shrieks and Diana-eagle alarm calls were found (Fisher's exact test,  $n=12,8$ ,  $p=0.26$ ) nor between approaches to leopard growls and Diana-leopard alarm calls (Fisher's exact test,  $n=7,7$ ,  $p=1$ ) (Fig. 3.3).

## Discussion

My results indicate that yellow-casqued hornbills distinguish between predator vocalisations and between the corresponding alarm calls of the sympatric Diana monkey. Both vocal and locomotor responses of hornbills to playback of eagle shrieks and Diana-eagle alarm calls were significantly different from the responses to playback of leopard growls and Diana-leopard alarm calls. This is the first time to my knowledge that a bird has been shown to distinguish between the alarm calls of any other species and the first time that they have been found to distinguish between mammal calls of any type. The result is particularly intriguing as the two Diana alarm calls are acoustically very similar (see Zuberbühler *et al.* 1997).

My sample sizes were small and the statistical analyses may have had low power to detect significant results (Thomas & Juanes 1996). However, I had matched controls (eagle to leopard and Diana-eagle to Diana-leopard), which also had small sample sizes, yet the effects were still significant. This indicates that, despite this low power, the responses varied between the different playback categories. Sample sizes were too small to test for the influence of hornbill gender on variation in responses to the different stimuli. However, both sexes exhibited all types of response so it is probable that they respond similarly. The general pattern of results observed in Mont Péko was similar to that observed in Tai and this indicates that despite the small sample size, the responses here were representative.

The 'perception advertisement' hypothesis (Curio 1978) suggests that animals may produce alarm calls when they detect a predator because this indicates to the predator that it has been detected and that it has lost the element of surprise. An attack would therefore probably fail and the predator would best abandon the attack. This may explain the tendency of hornbills, and of primates (Gautier-Hion & Tutin 1988; Zuberbühler *et al.* 1997), to approach the predator as it demonstrates more clearly to the predator that it has been located. There were indications that hornbills tended to approach the playback site more often after playback of Diana-eagle alarm calls than after playback of eagle shrieks (Fig. 3.3). This difference was not significant but could indicate that because alarm calls unlike predator calls do not indicate the precise location of the predator (van der Veen 2002), the hornbills may best locate the predator by approaching the alarm call. This may help the bird to decide in which direction to flee or whether or not to mob the predator. It is therefore possible that hornbills are advertising perception to the predator (Curio 1978) and that the alarm signals may not be directed at kin (Maynard Smith 1965).

How do hornbills acquire the ability to distinguish between the four different types of vocalizations? Animal learning theory offers a number of mechanisms that may be responsible for the birds' knowledge. First, many mature birds will have experienced attacks by crowned eagles, either directly or indirectly by observing other nearby individuals being attacked. Since both eagle shrieks and Diana-eagle alarm calls reliably predict the presence of a crowned eagle in the immediate vicinity both stimuli will quickly become associated with eagle presence through associative learning. Second, young birds may learn to respond to the eagle shrieks and Diana-eagle alarm calls by observing other, more experienced, flock members reacting to these calls, even in the absence of direct contact with the predator. Observing other individuals engaging in anti-predator behaviour is a powerful stimulus and a reliable source for rapid learning (e.g. Curio *et al.* 1978; Vieth *et al.* 1980; Frankenberg 1981). Since leopards do not attack hornbills, no such learning will take place, and consequently both leopard growls and Diana-leopard alarm calls will not come to elicit responses in hornbills. An alternative hypothesis states that hornbills will call spontaneously to any loud stimulus, but through individual experience they selectively habituate to those stimuli that do not predict the presence of a species that preys on them (i.e. leopard growls and Diana-leopard alarm calls) (see Deecke *et al.* 2002).

My findings suggest that eagle shrieks and Diana-eagle alarm calls are functionally equivalent for hornbills (Schusterman & Gisiner 1997), in the sense that they both predict the presence of a crowned eagle. In primates it has been claimed that they linked to a mental representation of the predator (Zuberbühler *et al.* 1999a). It is not yet possible to comment on the mental processes that underlie the birds' responses. What is remarkable is that although the acoustic differences between the two types of Diana monkey alarm calls are subtle to human ears, the hornbills respond differently to them, demonstrating how sensitive these animals are in their pursuit of important information, to the extent of eavesdropping on signals that are not intended for them. Indeed it would be surprising if they did not eavesdrop on signals in their environment.



## Chapter 4

### **Information accuracy: variation in black-casqued hornbill responses to predators and primate alarm calls**

#### **Introduction**

Various species of birds, rodents, carnivores, and primates produce acoustically distinct alarm calls to different classes of predators, or to the kinds of threats associated with them (e.g. Slobodchikoff *et al.* 1991; Naguib *et al.* 1999; Zuberbühler 2003). In addition, some mammal species are able to discriminate between alarm calls of other species and to respond appropriately to them (e.g. Seyfarth *et al.* 1980a; Seyfarth & Cheney 1990; Evans *et al.* 1993; Oda & Masataka 1996; Zuberbühler 2000b; Manser *et al.* 2001; Zuberbühler 2001). In Chapter 3 I demonstrated that this ability is not restricted to mammals as yellow-casqued hornbills *Ceratogymna elata* distinguished appropriately between vocalisations of leopards, *Panthera pardus*, and crowned eagles, *Stephanoaetus coronatus*, as well as between the predator-specific alarm calls of sympatric Diana monkeys *Cercopithecus diana*. Eagle-related stimuli caused a significant increase in vocal behaviour and approach, but this was not observed for leopard-related stimuli.

The fact that hornbills behaved conspicuously in the presence of predatory eagles seems somewhat counterintuitive and requires further explanation. Conspicuous behaviour in the presence of a predator may be adaptive if it alerts nearby kin and other reproductively relevant conspecifics (Maynard Smith 1965). This explanation may apply to pairs of or mated hornbills that are often accompanied by their own offspring. However, solitary hornbills sometimes increased their call rates and approached the stimuli, implying that this behaviour is not solely directed at kin or conspecifics (Chapter 3, Rainey *et al.* 2004). A second line of argument suggests that conspicuous behaviour is adaptive if it negatively manipulates the predator's hunting behaviour, for example by signalling detection (Curio 1978), and there is some empirical evidence suggesting that predators do respond to these signals (Tilson & Norton 1981; Caro 1995; Zuberbühler *et al.* 1999b). Detection signalling (or perception advertisement) could be an adaptive

strategy in response to both eagles and leopards since both of them rely on surprising their prey (Zuberbühler *et al.* 1999b; Shultz 2001). In the forests of Taï National Park, monkey alarm calls deterred leopards from hunting and caused them to leave the vicinity (Zuberbühler *et al.* 1999b). There is also some evidence that crowned eagles are deterred from hunting on hearing Diana monkey alarm calls (Shultz 2001), suggesting that conspicuous vocal behaviour is an adaptive strategy in response to these predators. No systematic data are available for hornbills interacting with predators, although S. Shultz (pers. comm.) has made direct observations of hornbills approaching and calling in the presence of crowned eagles.

The ability to recognise and distinguish other species' alarm calls is clearly an adaptive trait as it provides individuals with information about the type of predator present without having seen it. Although monkey alarm calls have the capacity to encode information about predator type, there is currently no evidence that these calls can encode information about the predator's exact spatial location (Zuberbühler 2003). Not knowing the predator's whereabouts, however, might have important implications about the best anti-predator strategy to pursue. In particular, it might not be adaptive for individuals to engage in highly conspicuous behaviour until the predator's location is determined (Chapter 3, Rainey *et al.* 2004). There is evidence that some bird species produce alarm calls at a lower rate if they do not know the exact location of the predator (Curio 1978; Conover 1987; van der Veen 2002).

### *Hypotheses and predictions*

During field experiments on primates in Ivory Coast involving playback of predator calls and primate alarm calls, Klaus Zuberbühler found that hornbills were often in the vicinity of the experiments. There was some indication that they were calling in response to the stimuli and their calls were often tape-recorded concurrently with the primate calls. Accordingly and in light of my findings in Chapter 3, I decided to assess the ability of hornbills to distinguish between different predator and primate calls. Black-casqued hornbills, *Ceratogymna atrata*, in Taï National Park live sympatrically with Diana monkeys, Campbell's monkeys, *C. campbelli*, crowned eagles, and leopards. They are amongst the largest forest birds ((mass 0.9-1.6 kg, Kemp 1995) in West Africa and, as such, are vulnerable to the same predators as the monkeys ((Diana mass 2.2-7.5 kg, Campbell's mass 3-5.8 kg, Kingdon 1997). Crowned eagles are known to prey on

hornbills (Keith 1969; Mitani *et al.* 2001; Shultz 2002). Leopards prey almost entirely on mammals although bird remains have been found in their faeces (Hoppe-Dominik 1984; Ray & Sunquist 2001; Zuberbühler & Jenny 2002). Leopards can climb up to the canopy where hornbills spend much of their time (Bshary & Noë 1997), and hornbills may feed on the ground (pers. obs.), but these are rare events.

Because of this and because of our previous results on yellow-casqued hornbills, I predicted that the closely related black-casqued hornbills would increase the number of calls in response to eagle shrieks, but show little or no change in response to leopard growls. Both monkey species produce acoustically distinct alarm calls in response to crowned eagles and leopards (Zuberbühler *et al.* 1997; Zuberbühler 2000b). My first prediction here was that black-casqued hornbills would increase the number of calls in response to Diana eagle alarm calls, but show little or no change in response to leopard alarm calls. Second, the same response pattern was predicted when the birds were exposed to the alarm calls of Campbell's monkeys to these two predators (Zuberbühler 2000b). Third, based on the previous considerations I predicted that hornbills might produce higher rates of alarm calls in response to eagle shrieks compared to Diana or Campbell's monkey eagle alarm calls, due to the uncertainties concerning the predator's location in the latter two cases. However, I predicted no difference in call rates between their response to leopard growls and monkey leopard alarm calls.

## Methods

### *Study site and species*

Recordings were made by Klaus Zuberbühler between June 1994 and June 2002 in Tai National Park, Ivory Coast, in *c.* 100 km<sup>2</sup> of forest around the Centre de Recherche en Ecologie (CRE; 5°50'N, 7°21'W). Black-casqued hornbills are common throughout Tai but as canopy species they can be difficult to locate visually. Black-casqued hornbills sometimes forage in small flocks in the vicinity of monkey groups, including Diana and Campbell's monkeys. Occasionally, they have been observed in larger groups, especially when several individuals were feeding on a large food source, for example at *Raphia* palms or on flying termites (pers. obs.). In this study, no attempts to locate and observe individual birds were made. Instead, playback experiments were conducted independently

of the presence or absence of birds. Each recording was separated from other recordings spatially by at least 500 m or temporally by one year thus ensuring independence between them.

### *Playback protocol*

All playback experiments were carried out in the vicinity of a monkey group, whose behaviour was the main focus of other studies (e.g. Zuberbühler *et al.* 1997; Zuberbühler 2001). The following six categories of vocalisations were used as playback stimuli (a) crowned eagle shrieks; (b) leopard growls; (c) Diana monkey eagle alarm calls; (d) Diana monkey leopard alarm calls; (e) Campbell's monkey eagle alarm calls; (f) Campbell's monkey leopard alarm calls. Leopard growls were purchased from the National Sound Archive, London. All other calls were recorded in the study area. All stimuli lasted for circa 15 s. Monkey alarm calls consisted of recordings of natural call series given by various adult males in response to crowned eagles or leopards. From the various master recordings the following 87 playback stimuli were made: eagle shrieks  $n=22$ ; leopard growls:  $n=27$ ; Diana monkey eagle alarm calls:  $n=10$ ; Diana monkey leopard alarm calls:  $n=11$ ; Campbell's eagle alarm calls:  $n=9$ ; Campbell's leopard alarm calls:  $n=8$ . Fig. 4.1 illustrates the various playback stimuli used in this study.

Throughout the eight-year study period, a total of 592 playback trials were carried out: 84 crowned eagle trials, 196 leopard trials, 60 Diana-eagle alarm call trials, 100 Diana-leopard alarm call trials, 77 Campbell's-eagle alarm call trials, and 75 Campbell's-leopard alarm call trials. Stimuli were played back at natural amplitudes varying from 88-110 dB. Each trial consisted of a 5 min pre-playback recording, followed by the playback stimulus, followed by a 5 min post-playback recording.

### *Acoustic observations*

Most hornbill flocks consist of an adult male and female pair and one or two offspring with age- and sex-related differences in casque sizes (Kemp 1995, pers. obs.). I screened all 592 10 min recordings for the presence of black-casqued hornbill vocalisations. The casque grows until the birds are adult and casques are sexually dimorphic, as the casque is likely to be involved in amplification and resonance of calls (Alexander *et al.* 1994; Kemp 1995), individuals of different ages and sexes within a small flock can be distinguished relatively easily. Whenever calls of black-casqued hornbills could be identified, I noted

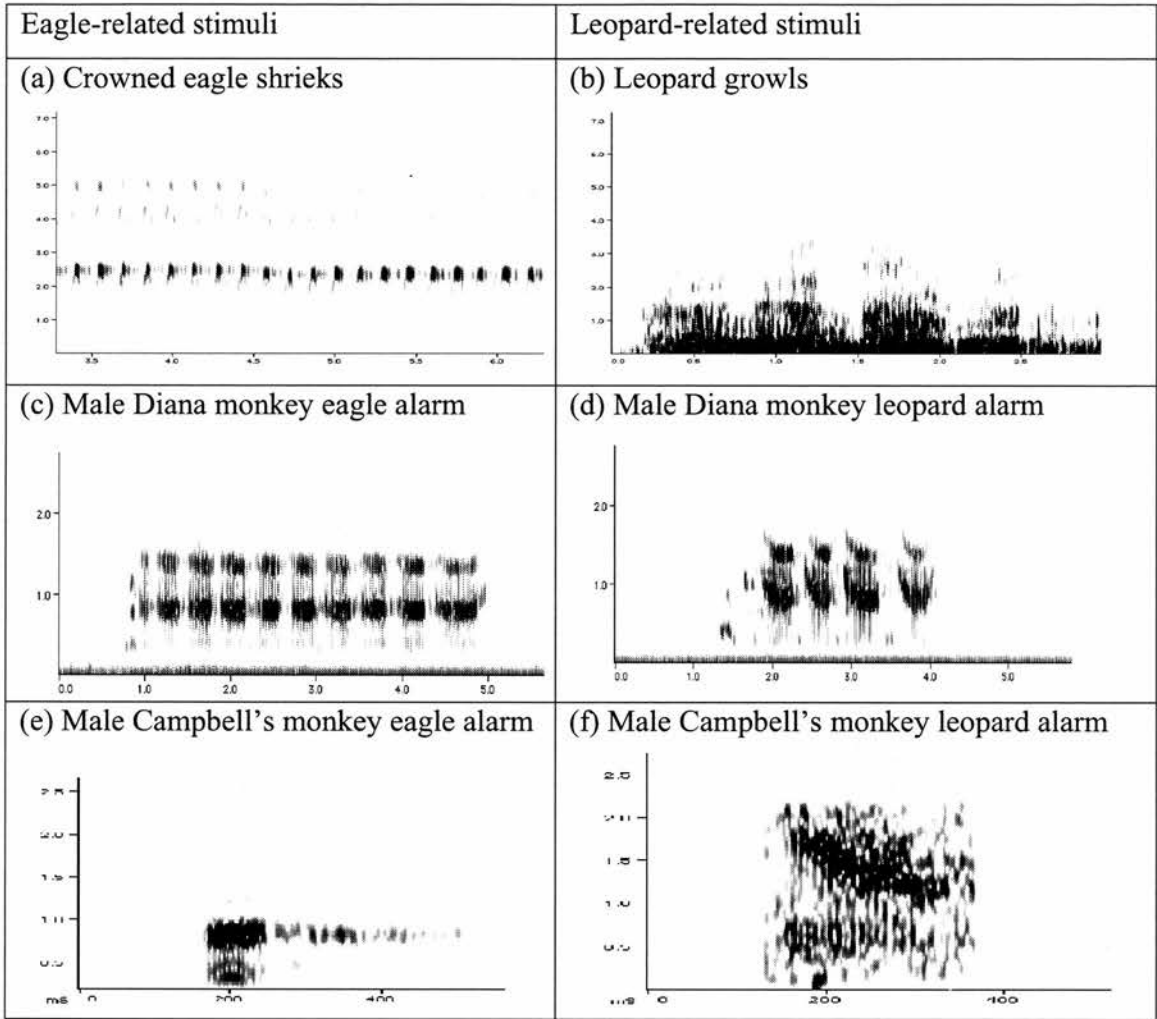


Figure 4.1. Spectrograms of typical calls of each playback stimulus.

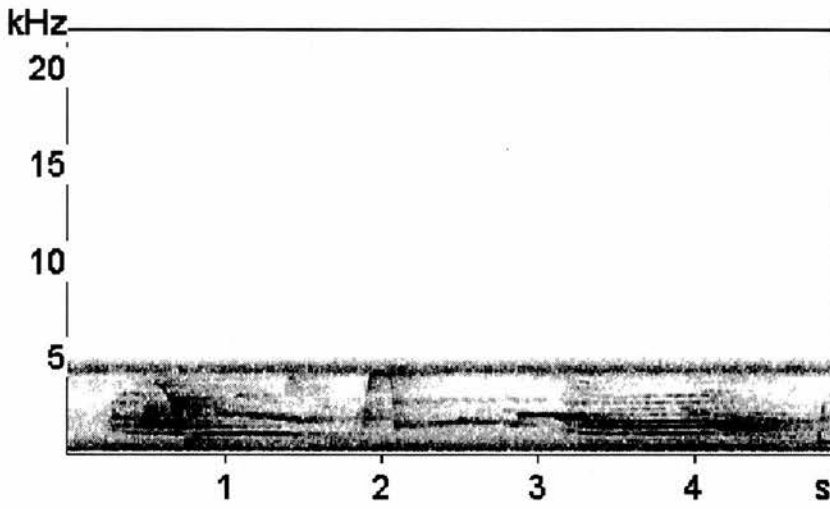


Figure 4.2. Spectrogram of typical black-casqued hornbill calls.

the number of calls made by the first individual to call during the recording. I then compared the numbers of calls made before and after a playback stimulus across the different stimuli. Fig. 4.2 illustrates typical black-casqued vocalisations.

### *Equipment*

Playback stimuli were played back from a Sony WMD6C Professional Walkman through a Nagra DSM loudspeaker-amplifier. Peak amplitudes of each stimulus were standardised with a Radio Shack sound level meter 33-2050, C-weighting, at 1 m from the speaker. Recordings were made using a Sony TCM5000EV cassette recorder and a Sony WMD6C Professional Walkman with a Sennheiser ME66 directional microphone. Statistical analysis was carried out with SPSS 11.5.0 and Minitab 13. Recordings of calls were displayed as spectrograms with Avisoft-SASLab Pro 3.9, allowing us to count individual calls.

## **Results**

Black-casqued hornbills increased call rates significantly more often in response to playbacks of eagle shrieks than leopard growls (Fisher's exact test:  $n=84,196$ ,  $P<0.001$ ; Fig. 4.3). As predicted they also increased call rates significantly more often to Diana-eagle than to Diana-leopard alarm calls (Fisher's exact test:  $n=60,100$ ,  $P=0.018$ ; Fig. 4.3) as well as to Campbell's-eagle alarm calls than to Campbell's-leopard alarm calls (Fisher's exact test:  $n=77,75$ ,  $P=0.029$ ; Fig. 4.3).

In a second analysis, I compared the actual call rates before and after a playback stimulus for those trials where I recorded at least one individual's calls. I found that all three eagle-related stimuli caused a significant increase in call rates, compared to the leopard-related stimuli where no significant changes were observed (Fig. 4.4). As the playback trials for this study were carried out independently of the presence or absence of hornbills, I adjusted for the large numbers of trials on which no calls were recorded by analysing the change in numbers of calls produced between the 5 min before and after playback for each stimulus. I found that hornbills increased the numbers of calls they made to eagle shrieks (Wilcoxon signed rank test:  $Z=799$ ,  $n=84$ ,  $P<0.001$ ) (Fig. 4.4a), to Diana-eagle calls (Wilcoxon signed rank test:  $Z=97.5$ ,  $n=60$ ,  $P=0.036$ ) (Fig. 4.4b) and to

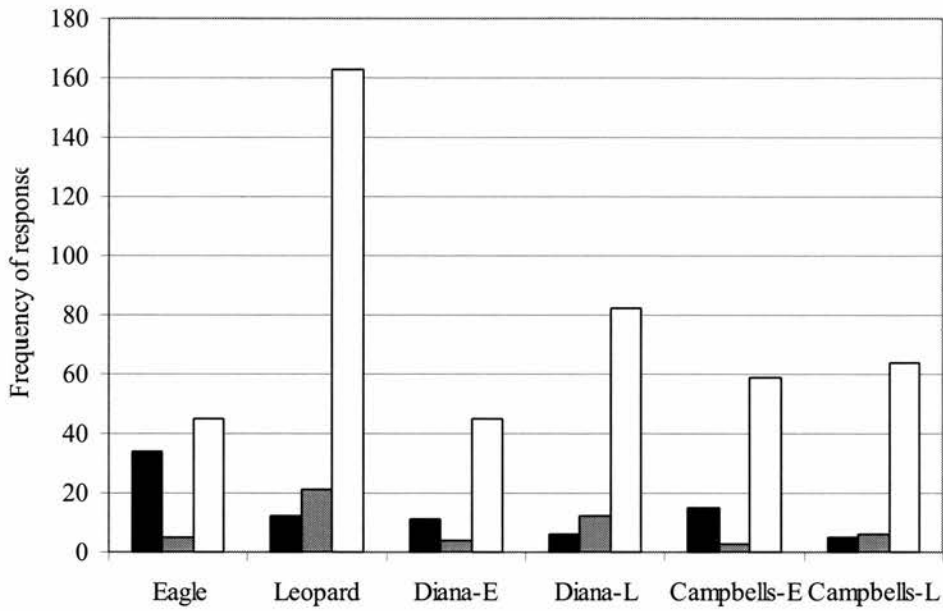


Figure 4.3. Frequency of hornbill response types to playback of the different stimuli. Comparison of the change in numbers of calls they produced in the 5 min period after playback compared to the 5 min before playback. Hornbills increased the number of calls they produced more often to: eagle shrieks than to leopard growls ( $P < 0.001$ ); to Diana-eagle calls than to Diana-leopard calls ( $P = 0.018$ ); and to Campbell's-eagle calls than to Campbell's-leopard calls ( $P = 0.029$ ). Black bars: increased calls; hatched bars: decreased calls; white bars: no change.



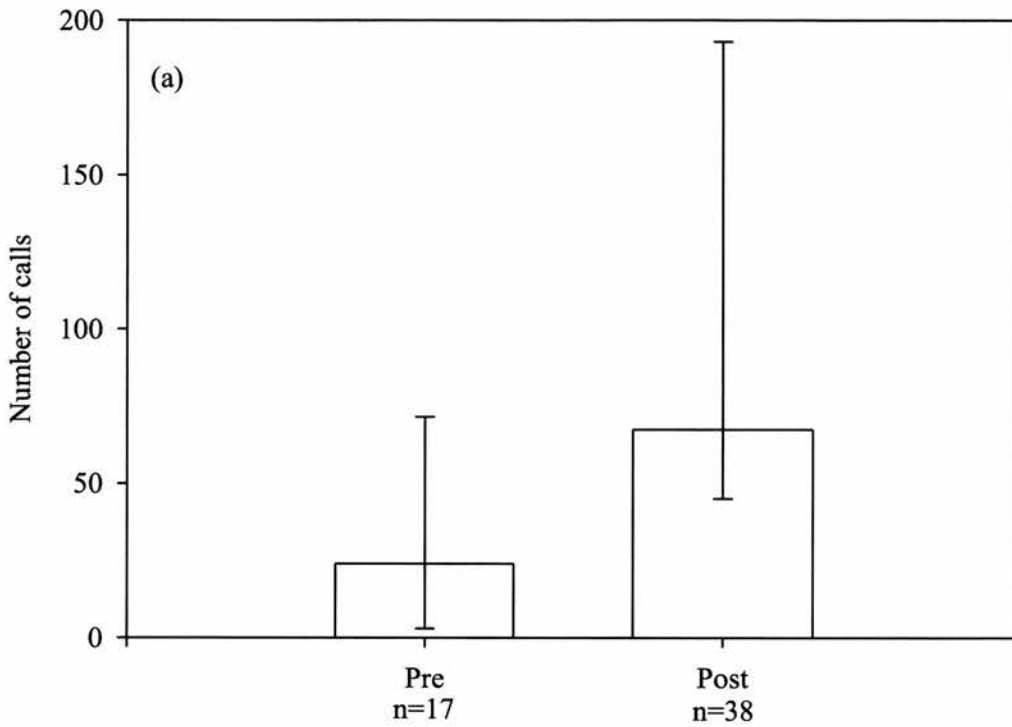
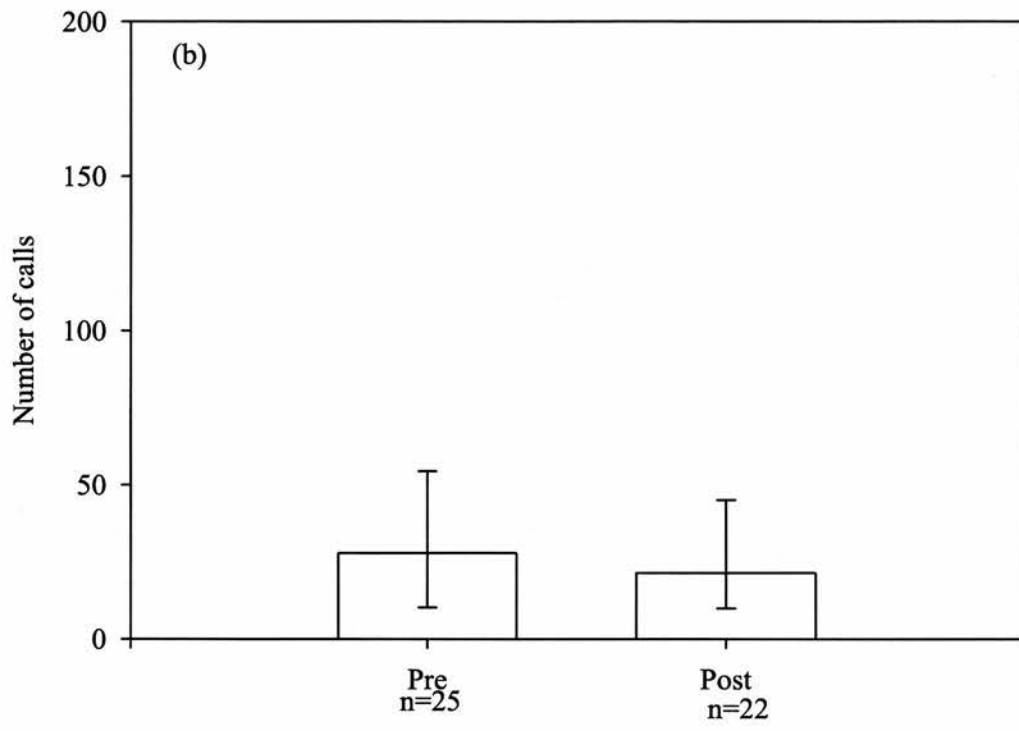
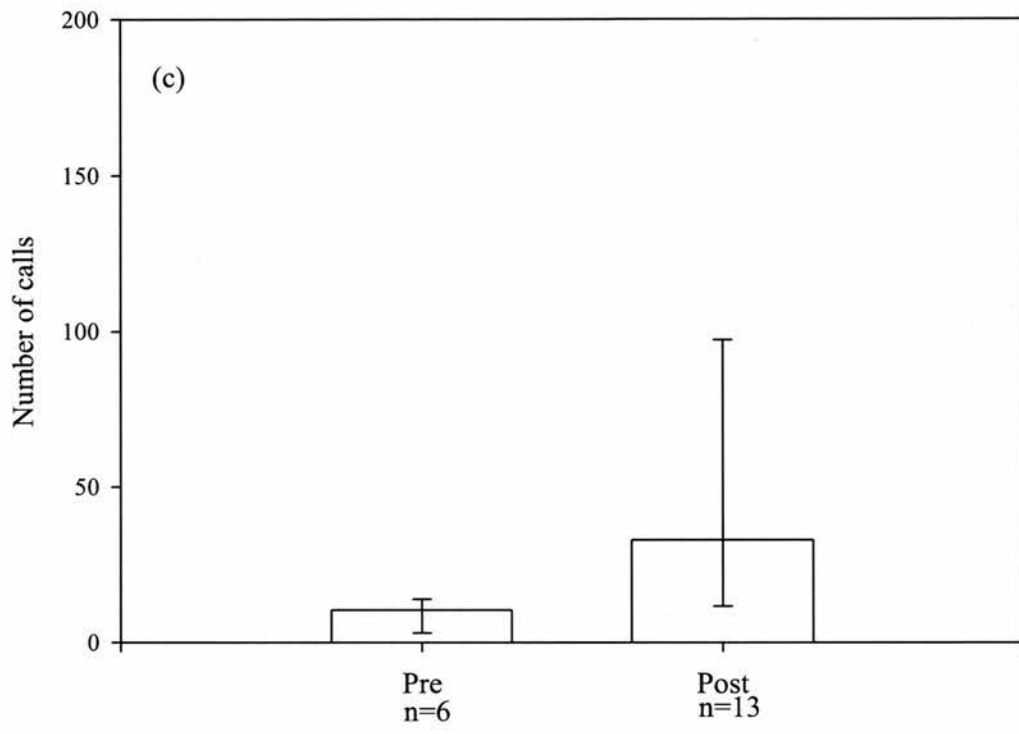
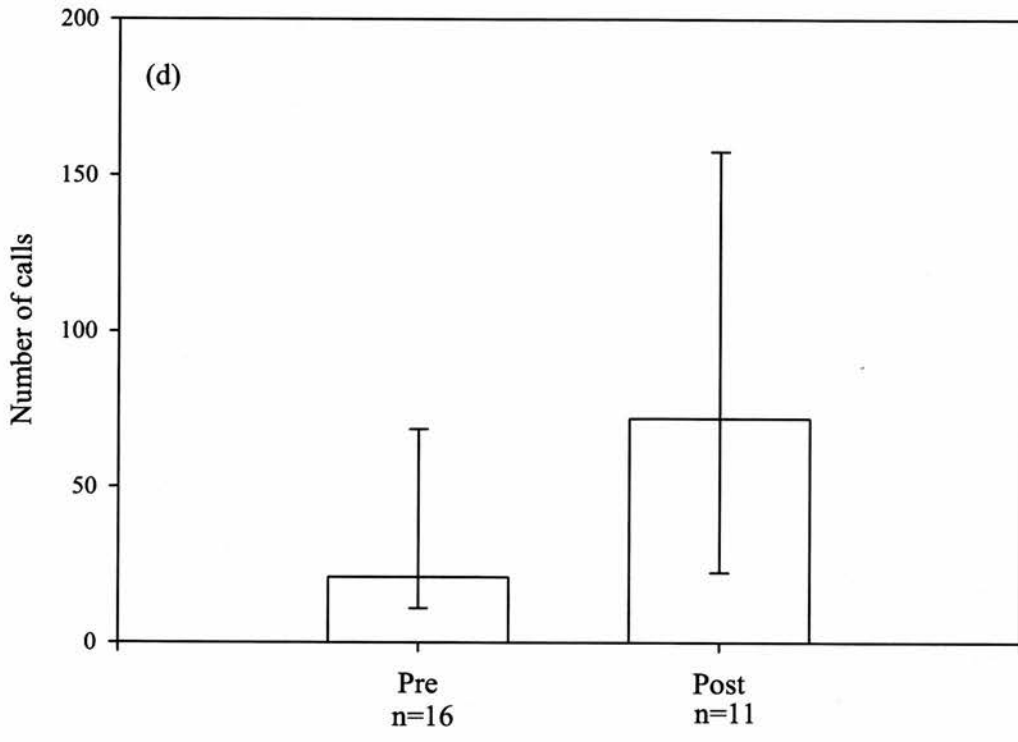
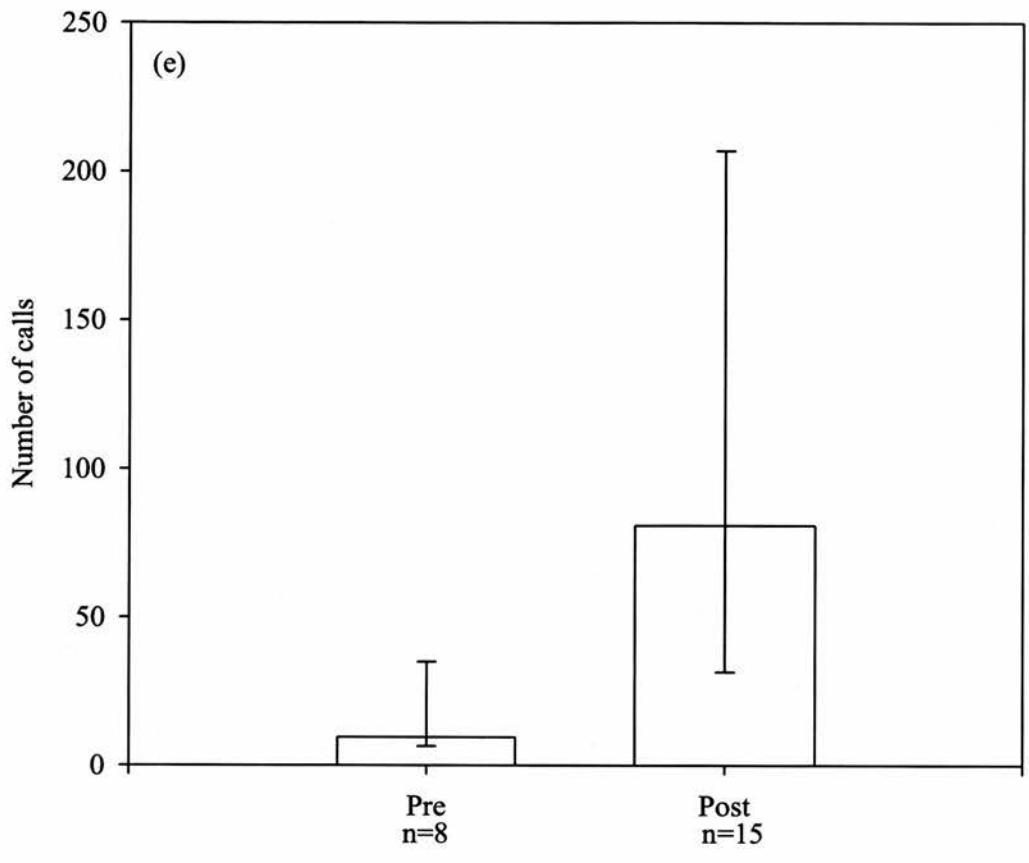


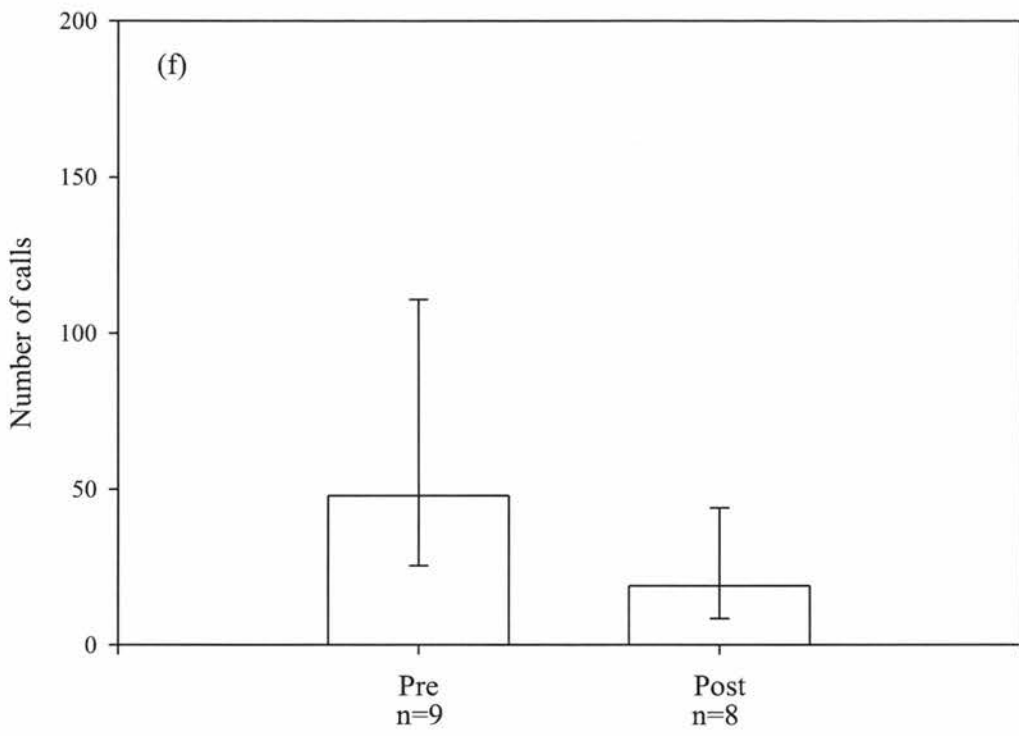
Figure 4.4. Median and interquartile ranges of numbers of calls produced before and after playback of each stimulus: (a) eagle shrieks; (b) leopard growls; (c) Diana-eagle calls; (d) Diana-leopard calls; (e) Campbell's-eagle calls; (f) Campbell's-leopard calls. Sample size refers to the numbers of recordings on which there were changes in call rates, i.e. those used in Wilcoxon statistical tests.











## **(1) Responses to predator calls**

### *Winter*

Great tits in winter did not respond significantly more by scanning to either of the predator calls or the control (Fisher's exact test:  $n=11,9,10$ ,  $P=0.129$ ) (Fig. 5.4a). Relatively few vocalisations were produced in response to playback in either season. No significant differences were found between seep responses (Fisher's exact test:  $n=11,9,10$ ,  $P=0.091$ ) (Fig. 5.4b) or rattle responses to the different predator stimuli in winter (Fisher's exact test:  $n=11,9,10$ ,  $P=0.562$ ) (Fig. 5.4c). No significant differences were found between movement responses to the different predator stimuli in winter (Fisher's exact test:  $n=11,9,10$ ,  $P=0.621$ ) (Fig. 5.4d).

### *Summer*

Great tits in summer responded significantly more by scanning to some calls than others (Fisher's exact test:  $n=12,10,14$ ,  $P<0.001$ ) (Fig. 5.4a). They scanned more to hawk calls than to pigeon calls (Fisher's exact test:  $n=12,14$ ,  $P<0.001$ ) and scanned more to woodpecker calls than to pigeon calls (Fisher's exact test:  $n=10,14$ ,  $P<0.001$ ). Scanning responses did not differ between hawk and woodpecker calls (Fisher's exact test:  $n=12,10$ ,  $P=1.000$ ). Great tits also showed significant variation between seep responses to the different predator stimuli in summer (Fisher's exact test:  $n=12,10,14$ ,  $P=0.012$ ) (Fig. 5.4b). However, there were no significant differences between pairs of stimuli when the sequential Bonferroni correction was used (Rice 1989). Great tits showed variation in their rattle responses to the different predator stimuli in summer (Fisher's exact test:  $n=12,10,14$ ,  $P=0.018$ ) and there was significant variation in rattle responses between hawks and pigeons (Fisher's exact test:  $n=12,14$ ,  $P=0.012$ ) (Fig. 5.4c). There were significant differences between movement responses to the different predator stimuli in summer (Fisher's exact test:  $n=12,10,14$ ,  $P=0.004$ ) (Fig. 5.4d). There was no variation in movement responses between hawks and woodpeckers (Fisher's exact test:  $n=12,10$ ,  $P=0.691$ ) but there was between hawks and pigeons (Fisher's exact test:  $n=12,14$ ,  $P=0.004$ ) and between pigeons and woodpeckers (Fisher's exact test:  $n=10,14$ ,  $P=0.020$ ).

I observed a number of interactions between great spotted woodpeckers and great tits in the breeding season at Craigtoun Park. On three occasions woodpeckers landed on the nest boxes. Twice they looked into the nest hole but no chicks were seen to be eaten by

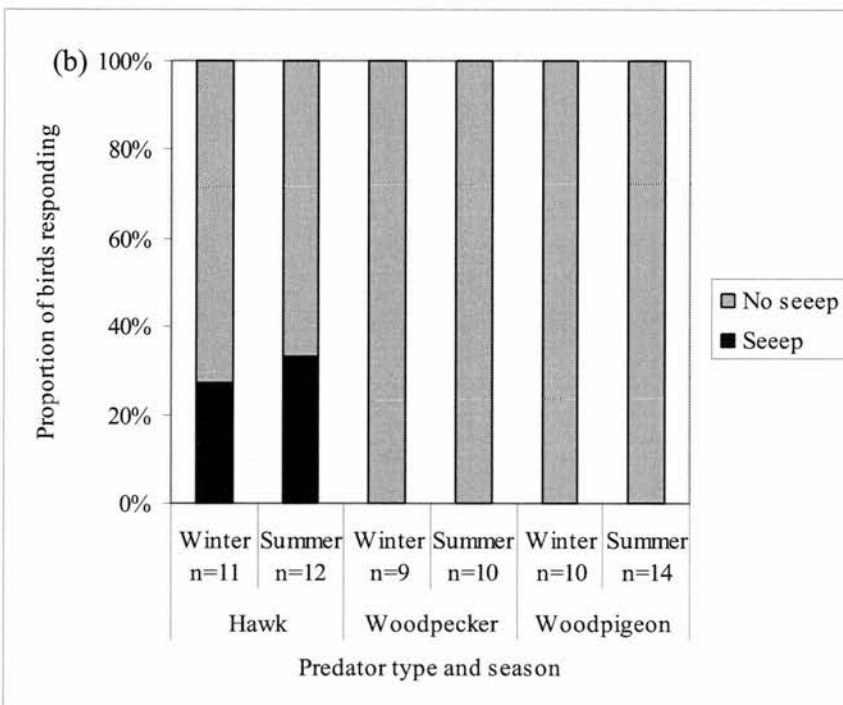
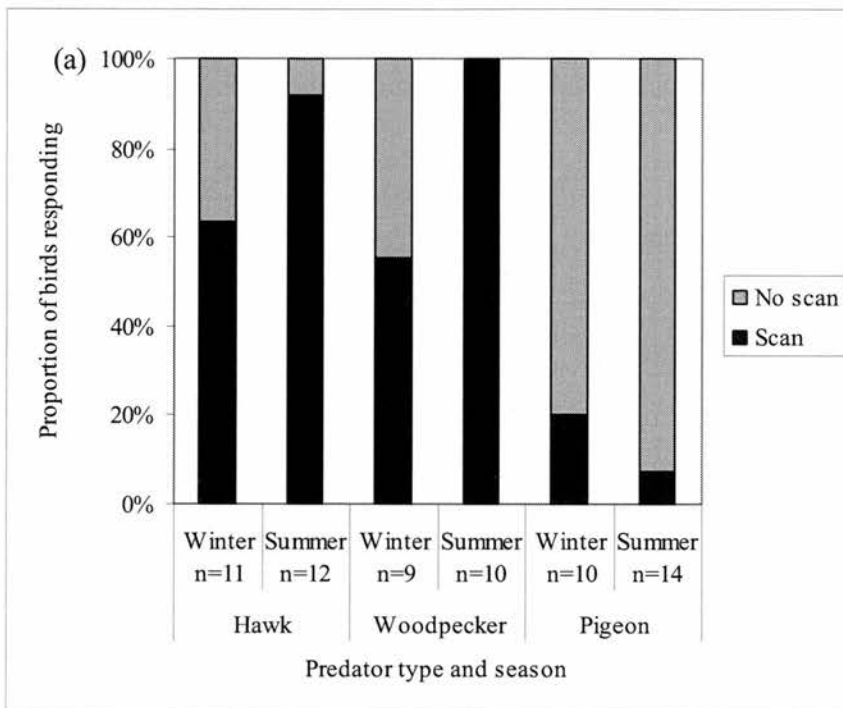


Figure 5.4. Responses of great tits to predator calls. Proportion of birds: (a) scanning; (b) producing seep calls; (c) producing rattle calls; and (d) moving towards cover ((c) and (d) overleaf).



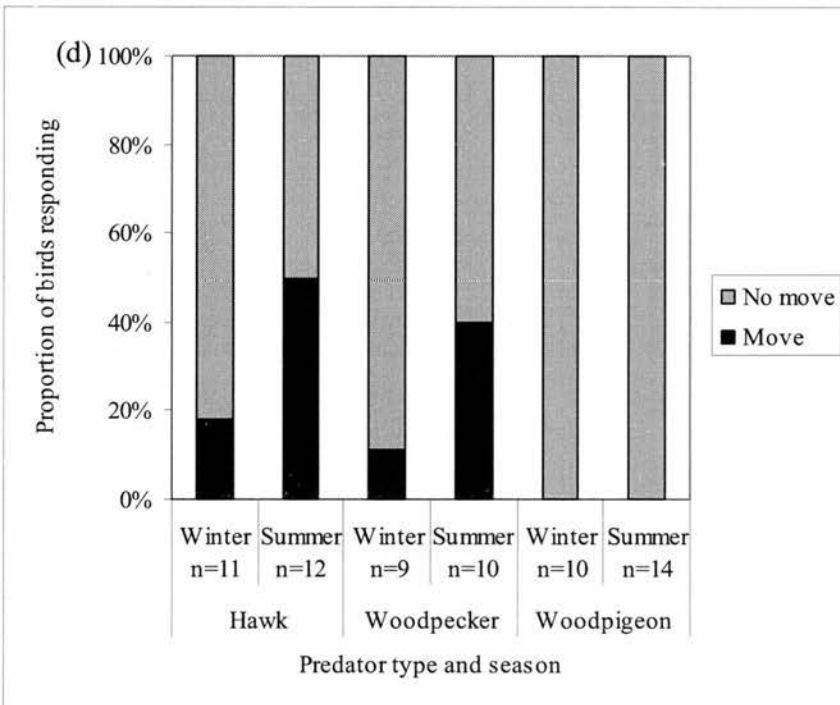
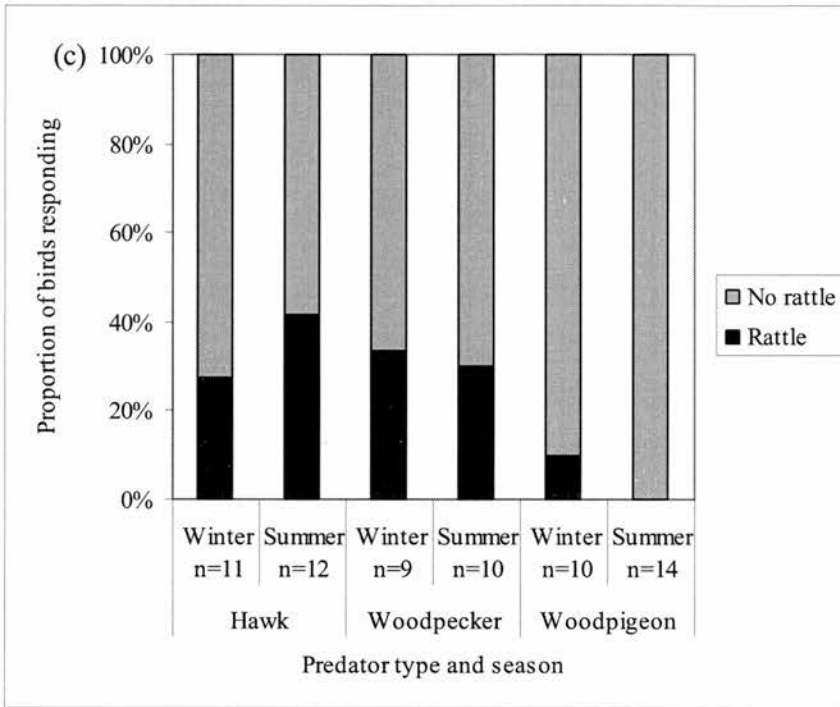


Figure 5.4. (cont.).

woodpeckers. However, the number of chicks in one nest declined from 6 to 2 (and no dead chicks were found in the nest) and the lining was completely removed from the box, almost certainly by a woodpecker. Adult tits were observed mobbing the woodpeckers on two occasions. They approached the woodpecker to a distance of *c.* 1 m, produced rattle calls and made many short movements between branches. They did not physically attack the woodpeckers and this suggests that the woodpeckers may pose some threat to the adults at close range.

### *Between seasons*

As there was apparent variation in some great tit responses to stimuli between winter and summer (Fig. 5.4) I analysed these differences. There were significant differences in scanning responses to woodpecker calls between winter and summer (Fisher's exact test:  $n=9,10$ ,  $P=0.033$ ) but not between seasons to hawk calls (Fisher's exact test:  $n=11,12$ ,  $P=0.155$ ) or to woodpigeon calls (Fisher's exact test:  $n=10,14$ ,  $P=0.550$ ) (Fig. 5.4). There were no significant differences in movement responses to hawk (Fisher's exact test:  $n=11,12$ ,  $P=0.193$ ); to woodpecker (Fisher's exact test:  $n=9,10$ ,  $P=0.303$ ); or to pigeon calls between seasons (Fisher's exact test:  $n=12,10,14$ ,  $P=1.000$ ).

## **(2) Responses to alarm calls**

### *Winter*

As Fig. 5.5a shows, great tits in winter scanned more in response to some robin calls than others (Fisher's exact test:  $n=10,10,10$ ,  $P=0.001$ ). They scanned more in response to robin seep calls than they did to either robin tic calls (Fisher's exact test:  $n=10,10$ ,  $P=0.005$ ) or robin song (Fisher's exact test:  $n=10,10$ ,  $P=0.005$ ). There were no differences between responses to robin tic and song (Fisher's exact test:  $n=10,10$ ,  $P=1.000$ ). There was no variation in seep responses between stimulus types (Fisher's exact test:  $n=10,10,10$ ,  $P=1.000$ ) (Fig. 5.5b). There was apparent variation in rattle responses to the different stimuli in winter (Fisher's exact test:  $n=10,10,10$ ,  $P=0.023$ ) but there were no differences in responses between pairs of stimuli (Fig. 5.5c). In winter there were no differences between moving responses to the different stimuli (Fisher's exact test:  $n=10,10,10$ ,  $P=0.075$ ) (Fig. 5.5d).

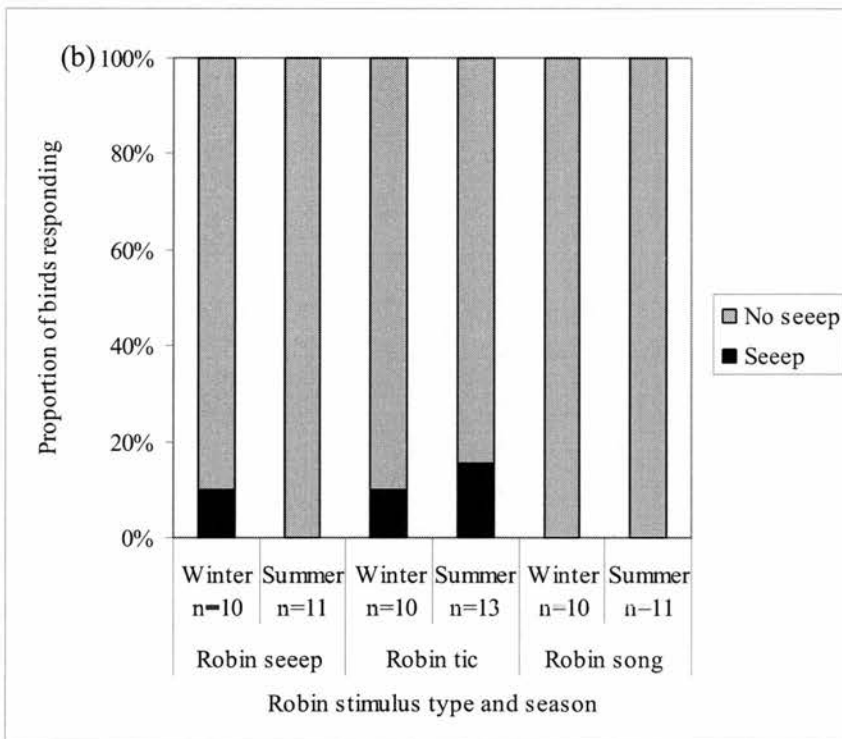
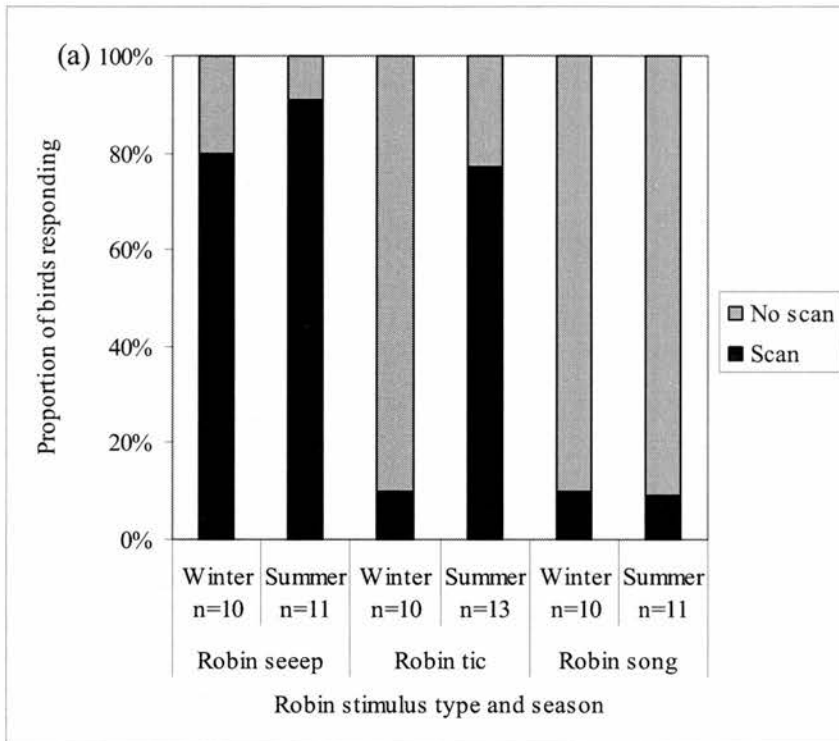


Figure 5.5. Responses of great tits to robin vocalisations. Proportion of birds: (a) scanning; (b) producing seep calls; (c) producing rattle calls; and (d) moving towards cover ((c) and (d) overleaf).

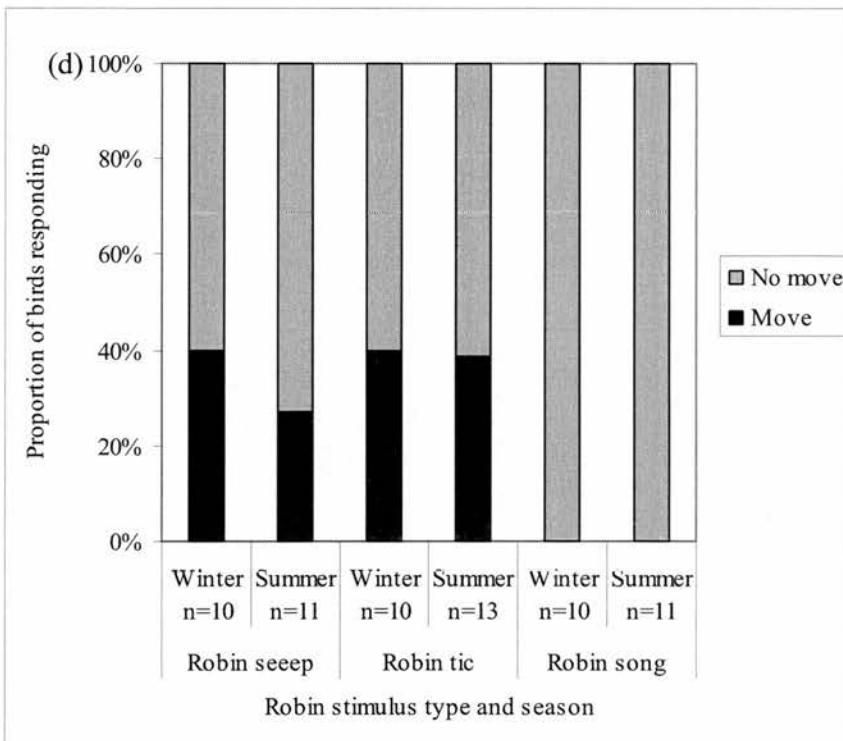
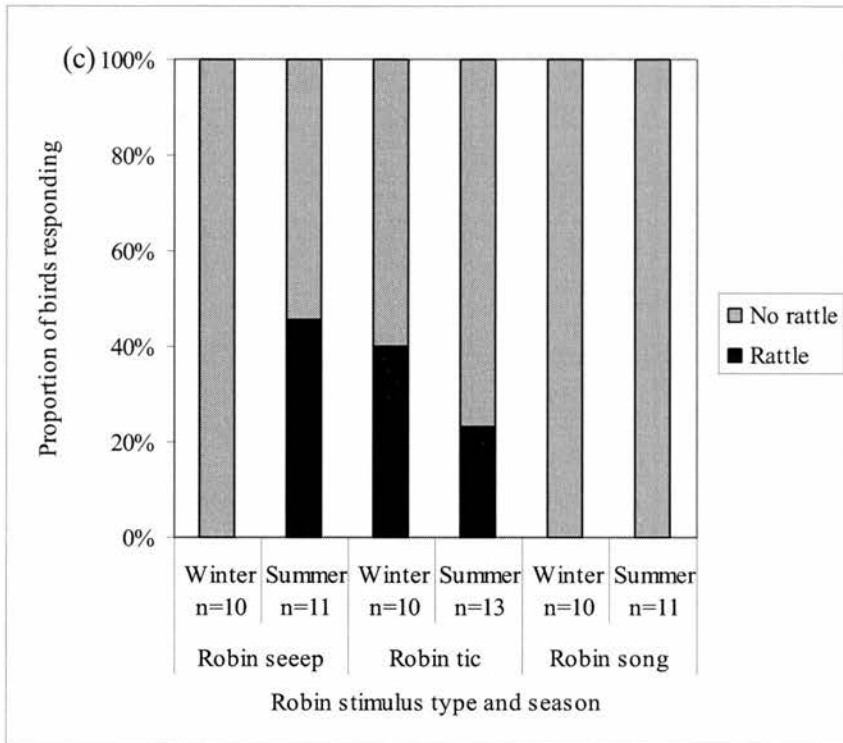


Figure 5.5. (cont.).

### *Summer*

Great tits in summer responded more by scanning to some robin calls than others (Fisher's exact test:  $n=11,13,11$ ,  $P<0.001$ ) (Fig.5.5a). There were no differences in scanning responses between robin seep and robin tic calls (Fisher's exact test:  $n=11,13$ ,  $P=0.596$ ) (Fig. 5.5b). They responded more to seep calls than to the control robin song (Fisher's exact test:  $n=11,11$ ,  $P<0.001$ ) and more to tic calls than robin song (Fisher's exact test:  $n=13,11$ ,  $P=0.001$ ). Great tits in summer did not apparently vary their seep responses to playback of robin calls (Fisher's exact test:  $n=11,13,11$ ,  $P=0.316$ ) (Fig. 5.5c). There was variation in rattle responses between the three robin stimuli (Fisher's exact test:  $n=11,13,11$ ,  $p=0.044$ ) but there was no variation in responses between pairs of stimuli after the Bonferroni correction (Rice 1989). In summer there were no differences between moving responses to the different stimuli (Fisher's exact test:  $n=11,13,11$ ,  $P=0.070$ ) (Fig. 5.5d).

### *Between seasons*

As there was apparent variation in some great tit responses between winter and summer I analysed these differences. Great tits scanned significantly more to tic calls in summer than in winter (Fisher's exact test:  $n=10,13$ ,  $P=0.003$ ) but not to seep calls (Fisher's exact test:  $n=10,11$ ,  $P=0.586$ ) nor to the control robin song (Fisher's exact test:  $n=10,11$ ,  $P=1.000$ ) between winter and summer (Fig. 5.5). Great tits were more likely to produce rattle calls after playback of robin seep calls in summer than in winter (Fisher's exact test:  $n=10,11$ ,  $P=0.035$ ). Great tits showed no differences in rattle responses between seasons to tic calls (Fisher's exact test:  $n=10,13$ ,  $P=0.650$ ) nor to robin song (Fisher's exact test:  $n=10,11$ ,  $P=1.000$ ).

## **Discussion**

I found no tendency for great tits to scan more on hearing all stimulus types in the presence of conspecifics or mates in either winter or summer. This may have been because birds were not with their mates in winter, and thus would not be motivated to call and in summer, few focal birds were seen with their mates at the nest. However, there was

strong evidence that tits scanned more to woodpecker calls and robin tic alarm call stimuli in the summer than in the winter. As there were few occasions when focal birds were observed with their mates at the nest, it is likely that the tendency of birds to scan was influenced by the presence of young and chicks in the nest.

### **(1) Responses to predator calls**

In winter there was no variation in the number of great tits scanning in response to playback of the different predator calls. In contrast, great tits in summer scanned more to hawk calls and woodpecker calls than to pigeon calls. There was no difference between responses to hawk and woodpecker calls. Great tits only varied their responses between seasons to woodpeckers but not to hawks or pigeons. This indicates that great tits may show plasticity in their responses to different predator types, depending on the threat that they pose to their kin. There was some variation in seep responses to predator calls in summer but there were no differences between pairs of stimuli. There were no differences between seep responses between seasons. They produced seep calls to playback of hawk calls although the evidence was not conclusive (Figs. 5.4-5.5). It is possible that tits produce this call mainly on detecting the presence of a fast-moving predator such as a sparrowhawk. It may not be so important to produce further seep calls on hearing a seep alarm call as this might not convey any further useful information. Tits varied production of rattle calls in the summer to predators. The rattle call is particularly obvious and easy to localise and it is possible that helps nestlings to learn about the threats that predators pose (Curio *et al.* 1978). Great tits often produce this call type when mobbing (Gompertz 1961, pers. obs.) and it may be particularly important for transmitting information about predators in this context. The birds moved more often to cover to the hawk and woodpecker stimuli than the pigeon stimulus in the summer, but there is no obvious explanation why this should differ between seasons as it would not assist offspring learning about predators.

I predicted that birds may respond to predator calls by attempting to locate the predator and by producing alarm signals (cf. Seyfarth *et al.* 1980b). The great tits responded by scanning and this may help to locate the predator. Movement responses to the different predator stimuli did not show consistent variation and the birds did not

approach the playback site. I did not specifically note whether birds attempted to conceal themselves by remaining still as I only noted whether they exhibited active behaviour. It is possible that freezing may be the safest strategy in response to some predator types such as the fast-moving sparrowhawk. Relatively few birds produced alarm calls. As I used audible stimuli during this experiment it might be predicted that the tits would have a reduced requirement to vocalise in response if they were attempting to warn kin: calling increases the predation rate on tits in winter (Alatalo & Helle 1990; Krams 2001b). However, it could be predicted that in the summer, when the adult birds might be expected to be teaching their offspring about the threat that predators pose, they would be more likely to vocalise on hearing a predator.

Great tits respond to hawk calls in both winter and summer as this predator poses a threat to adult birds. Woodpeckers are a threat only to chicks in the nest but not to adults and in winter are, therefore, of little relevance to adult birds. The adults may be investing in offspring survival by producing alarm responses to woodpeckers in summer as they do to hawks year round as a form of reproductive investment (Maynard Smith 1965; Curio *et al.* 1978; Klump & Shalter 1984). The birds would thus be displaying some plasticity in their anti-predator behaviour as they vary their responses to woodpeckers between seasons. The exact point at which they start to respond to woodpeckers was not ascertained but might be predicted to be with the onset of laying, as great spotted woodpeckers are known to take eggs (Cramp 1985).

Variation in responses by birds to different predator types has been reported before (see chapter introduction, East 1981; Cresswell 1993a) and my data indicate that great tits may also do so. In contrast, my results do not show that great tits produce different types of response (although it is likely that they may do so), rather that the tendency to respond to the differing predator types varies between seasons. East (1981) also showed that birds varied their responses to a human 'predator' through the breeding cycle. However, her study did not investigate temporal variation in responses to different predator types, i.e. she did not control for robins exhibiting similar variation in their responses to all predator types over time. Nijman (2004) found some evidence that drongos *Dicrurus* spp. mobbed Javan hawk-eagles *Spizaetus bartelsi* more, and the nest predatory black eagle *Ictinaetus malayensis* less, in the breeding season compared to the non-breeding season (perhaps because mobbing might signal to a nest predator that a nest was in the vicinity). However,

the data did not produce significant results and so do not show conclusively that drongos showed variable responses to predators over time.

## **(2) Responses to alarm calls**

### *Robin calls*

Great tits in winter were more likely to scan to robin seep calls than robin tic calls or robin song and they did not differentiate between robin tic calls and song. In summer, great tits responded more to seep calls and tic calls than to robin song but the scanning response to both calls was similar. There was no variation in responses to robin seep calls between winter and summer, nor any variation to robin song. However, responses to tic calls did vary between seasons. Great tits do appear to distinguish between the two robin alarm calls and also vary their responses to the alarm calls between seasons perhaps because of the vulnerability of their offspring. The adults may be investing in offspring survival by scanning to the robin tic call in summer as they do to the robin seep call year round (Maynard Smith 1965). There were indications that tits were varying production of rattle calls to the different robin stimuli but the results were not consistent between seasons.

The great tits appear to distinguish between the alarm calls of robins as the number of birds scanning varies differentially between seasons. Scanning responses to predators are also similar (Fig. 5.5) although their responses to robin vocalisations are not entirely consistent with this. The ability of great tits to vary their responses to alarm calls between seasons would appear to be impressive as it demonstrates that like hornbills (see Chapters 3-4, Rainey *et al.* 2004, submitted), these birds are capable of extracting important information by eavesdropping on the calls of other species about the presence of different predator types.

The association of a robin call with the presence of a predator that is only a threat when young are in the nest, implies that the great tits are either showing rapid associative learning of the robin call with the predator or that they have experience of it from previous seasons. Great tit survival between years is low (Cramp & Perrins 1993) but, as both woodpeckers and robins are common, and alarm calls given in the predator context



are a strong learning stimulus (Curio *et al.* 1978; Vieth *et al.* 1980), it is possible that both hypotheses hold.

## Conclusions

This study provides some evidence that birds can vary their responses to predators and alarm calls appropriately, as in the breeding season their offspring may be vulnerable to slower-moving predators that would not threaten the adults. However, the results between treatments are somewhat inconsistent making it difficult to draw clear conclusions from these results. These may be a result of natural behaviour of the tits but two main problems may have limited some aspects of this study and the conclusions that can be drawn from it:

- i) Sample sizes were small as time was limited and the power of statistical tests to find effects in this study may be low. Power analysis of nonparametric data is complicated and thus was not attempted retrospectively. However, a relatively modest increase in sample size could have increased the chance of finding significant effects. I analysed my data with an artificial 50% increase in the sample size with the same proportionate responses. This appeared to increase the power of statistical tests sufficiently to produce significant seep responses to predator calls and rattle and movement responses to robin calls in both winter and summer. This has important implications as I must be cautious in stating that there were no differences between responses to reduce the chance of committing a Type II error.
- ii) I did not record freezing as a specific response. This behaviour has been observed before in response to predators but I assumed that other alarm responses would be more commonly observed. I did observe some birds freezing and it is possible that it might have been a reasonably common alarm response. However, compared to the limitations of sample size, this may not have been a significant problem.

One of the most interesting observations of this study was how few vocalisations were produced in response to alarm calls. This may indicate that, as producing alarm calls may be costly (Alatalo & Helle 1990; Krams 2001b), and as the stimulus indicating the

presence of the predator is audible to the prey individual, its kin or mate there may be a reduced requirement for an individual to produce alarm calls. Alarm calls would not provide any extra information which was not already in the public domain. This argument assumes that the birds are not producing the calls to transfer information to the predator. A number of species are known to produce alarm calls to manipulate the behaviour of a potential predator (see Chapter 2). These calls are produced to predator stimuli and to alarm calls that reliably indicate the presence of the predator (e.g. Zuberbühler *et al.* 1997; Zuberbühler 2000c, 2001; see Chapter 3-4, Rainey *et al.* 2004; submitted). The great tits studies here, however, produced one alarm response to a sparrowhawk stimulus and a different less vocal response to robin seep alarm calls, which denote the presence of a hawk (East 1981). This variation in responses between those given to a predator and those to an alarm call has been observed before in primates (Zuberbühler 2001), hornbills (see Chapters 3-4, Rainey *et al.* 2004; submitted) and chaffinches (van der Veen 2002) and is thought to be related to the accuracy of the information available; a predator call indicates the location of a predator, an alarm call indicates only that a predator is in the vicinity. Adult great tits may not be responding to the precision of the information but to the requirement to transmit information to their kin. Thus if information signalling the presence of a predator has already been made available, because the primary goal of an adult great tit is likely to be alerting or teaching its kin, there will be little motivation for it to produce the same type of signal again.

## Chapter 6

### General Discussion and Conclusions

The results of this thesis show that birds are capable of exploiting specific information available in their environment about the threat that predators pose to them. They can sometimes respond appropriately to the alarm calls of other species, both of birds and mammals. Alarm calls provide less accurate information than the calls of the predators eliciting the calls, and the birds studied appeared more cautious in their responses to alarm calls than to predator calls. Their alarm responses may, in some situations, communicate information to predators or other prey individuals. The information transmitted to a predator may contain information signalling that the signaller has detected the predator, or advertising its vigilance, quality or proximity to a refuge. Alarm signals may also communicate information to kin, to a mate or to other group members. This may aid individuals in escaping predation, driving off predators or reducing the chance of a predator returning to that site. It may increase their chances of successful reproduction by aiding mate survival or reducing the chance of nest predation. Production of alarm signals may also aid the survival of kin by enabling them to engage in appropriate anti-predator behaviour and by teaching naïve offspring about the threat that predators pose.

Most work on communication of pursuit deterrence signals has focussed on the responses of conspecifics or other prey species to the signals. A small number of studies have investigated responses of predators to alarm calls (Fitzgibbon & Fanshawe 1988; Cresswell 1994a; Zuberbühler *et al.* 1999b). Some studies have shown how predators learn the meaning of aposematic signals of prey (e.g. Lindstrom *et al.* 1999; Gamberale-Stille 2000). However, no work has yet focussed on understanding how predators learn appropriate responses to alarm calls. How, for example, do young and naïve predators learn about information transmitted to them by prey in alarm calls? How long does it take them to learn that they may waste effort and time if they continue with a hunt after prey detect them and produce alarm calls? Similarly, if predators encounter novel prey, how do they learn to respond to the alarm calls of that prey species?

Predators are also believed to make use of the quality advertisement behaviour of prey to manipulate prey behaviour and this may allow them to detect weaker prey individuals in a group (e.g. Kruuk 1972; Curio 1976). This behaviour has been observed in some species, particularly in large mammals but this does not appear to have been studied in birds.

Many bird species produce alarm calls specific to the predator context and to individual predator types (e.g. Gompertz 1961; East 1981). However, although yellow-casqued hornbills may produce long calls more commonly after playback of predator calls, this accounted for a small proportion of the overall variation in total calls produced after playback. Further study of hornbill responses to predators would indicate if they do have alarm calls for specific predators. Playback of different hornbill calls to conspecifics and observation of responses would provide some indication of their function and the information they communicate. Comparison of responses between playback of hornbill calls and predator calls would provide data on the precision of the information encoded in the hornbill calls. Can they encode information indicating distance to the predator or possibly direction of threat? Do they and other species such as great tits produce more calls to an immediate threat compared to a distant threat as has been observed in black-capped chickadees *Poecile atricapilla* (Baker & Becker 2002)? Can primates and other sympatric species use this information? So far, some studies have found that animals can communicate whether a predator is above or below (e.g. Seyfarth *et al.* 1980a; Seyfarth & Cheney 1990; Oda & Masataka 1996; Oda 1998), but none so far have shown that alarm calls communicate direction in the horizontal plane. What mechanism could lead to the evolution of this type of communication? There is evidence that the position of a predator can be monitored by listening to the wave of alarm calls through the area or movement of a 'patch' of silence (McGregor & Dabelsteen 1996). Silence occurs as birds halt production of alarm calls and other vocalisations when in close proximity to a predator.

I found that great tits produced few alarm calls or other vocalisations in response to playback of predator calls or robin alarm calls. This may be because the stimuli presented were acoustic and thus, as information was already in the acoustic environment, the birds did not need to communicate further acoustic information to other birds in the vicinity. Comparison of responses between presentation of model predators and of predator calls could indicate whether great tits called less if information about predators was already available in the acoustic environment. As birds vocalising can suffer increased predation

rates (e.g. Endler 1993; Krams 2001b; Bayly & Evans 2003) there may be a strong incentive to avoid producing alarm calls if at all possible.

Hornbills are very vocal and their calls are commonly heard in the West African forests. It might be expected that the sympatric primate species in the same forests would listen to their calls and extract information from them concerning the presence of predators. Diana monkeys respond to crested guineafowl *Guttera pucherani* calls as if they indicate the presence of a leopard (Zuberbühler 2000d). However, when these calls are preceded by human vocalisations the monkeys remain silent. Using the same technique it might be possible to test whether Diana monkeys respond to hornbill calls as if they indicated the presence of a crowned eagle.

The complexity of their behaviour suggests that hornbills are thought to be relatively intelligent amongst bird species (e.g. Kemp 1995; Diamond & Bond 2003) and this may explain their ability in responding to only those primate calls that indicate the presence of relevant predator. However, as predation is such a strong selective force and alarm calls are a strong learning stimulus (Curio *et al.* 1978; Vieth *et al.* 1980; Lima & Dill 1990), other bird species may be capable of distinguishing between alarm calls of primates. The learning ability of guineafowl may be more limited than that of hornbills and they are more likely to be vulnerable to leopards than eagles as guineafowl are terrestrial. Playback to guineafowl of the calls of these two predators and the two associated alarm calls of Diana monkeys could provide further evidence that strong selective pressure acts on individuals to obtain information about predators from their environment.

White-crested *Tockus albocristatus* and black hornbills *Anthracoceros malayanus* are known to associate with primates and appear to benefit by feeding on the insects that they disturb (Brosset & Erard 1986; Kemp 1995; Galetti & McConkey 1998). Is there any evidence that primates benefit by associating with hornbills? It has been observed in some forest primates that there are anti-predator benefits of associating with other primate species (e.g. McGraw & Bshary 2002; Wolters & Zuberbühler 2003; Eckardt & Zuberbühler 2004). As hornbills fly above the canopy and may therefore be the first to detect eagles, monkeys found in association with them may show decreased vigilance and may also be able to expand their ecological niche into higher strata within the forest. If primates do make use of hornbill vigilance and calls to detect predators, are their foraging and ranging patterns and vigilance affected by the absence of most large hornbills from Tai NP from March to June?

Refuge advertisement (see Chapter 2) has been described in an antelope and in lizards and marmots but not yet in birds. Although there are few birds that make use of refugia, it is possible that those in close proximity to a refuge may produce alarm calls when threatened by a predator indicating that the predator would have more success hunting elsewhere. It would be possible to test this in birds that nest close to noxious insects or in the nest of a large predator. In Chapter 2 I indicated that a number of different types of pursuit deterrence behaviour and signals may be produced but many of these need to be tested further. A glance at the list of authors in Table 2.1 indicates that there have been few long term studies in this area and that much may remain to be learnt.

Although birds are known to be capable of learning about the threat that predators pose to them and juvenile primates can learn about predators from their parents, no studies have tested whether juvenile birds learn specifically from their parents about different predators (see Chapter 2). This could be tested relatively easily with captive or wild individuals.

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## Appendix

### Seasonal variation in hornbill abundance in Taï National Park, Ivory Coast estimated from acoustic recordings

#### Summary

Distance sampling, line transects and radio-tracking have previously been used to estimate population abundances and movements of hornbills. I used a large dataset of audio recordings made over 10 years to estimate seasonal variation in abundance of three species, black-casqued hornbill *Ceratogymna atrata*, yellow-casqued hornbill *C. elata* and brown-cheeked hornbill *Bycanistes cylindricus*, in Taï National Park, Ivory Coast. The latter two species are near-threatened. Recordings of hornbill wingbeats were used to control for potential seasonal variation in call production. Yellow- and black-casqued hornbill calls were ten times as abundant from July to February as they were from March to June. Brown-cheeked hornbills showed little variation in abundance between seasons. The significance of these findings is discussed with consideration to the fragmentation and regeneration of the Upper Guinea forests and the relatively small size of the remaining forest habitat.

#### Introduction

A number of Asian and African hornbill species are known to make local and long-distance movements depending on available fruit resources (e.g. Kalina 1988; Modse 1988; Poonswad & Tsuji 1994; Kinnaird *et al.* 1996; Anggraini *et al.* 2000; Datta & Rawat 2003). In Cameroon, hornbills vary in abundance with fruit resources (Whitney & Smith 1998; Holbrook & Smith 2000) and Holbrook *et al.* (2002) have found that they make long-distance movements linked to seasonal variation in environmental conditions. Previously, there have only been indications that forest hornbills in Côte d'Ivoire varied in abundance throughout the year (Thiollay 1985; Gartshore *et al.* 1995).

Observations during collection of data on hornbill behaviour (see Chapter 3, Rainey *et al.* 2004) in Taï National Park (NP), Ivory Coast indicated that both yellow-casqued *Ceratogymna elata* and black-casqued hornbills *C. atrata* were encountered less often in some months than others. I encountered 3-4 flocks of yellow-casqued hornbills per day from November-December 2001 compared to one flock every 4-5 days from March-May 2002. In Chapter 3 (Rainey *et al.* 2004) I concentrated on yellow-casqued hornbills, other observations made simultaneously indicated that black-casqued hornbills may also have become less common during the same period (pers. obs.). Methods of studying hornbill movements and variation in abundance have included radio-tracking (e.g. Holbrook & Smith 2000; Holbrook *et al.* 2002) and point counts, line transects and Distance sampling (e.g. Gartshore *et al.* 1995; Kinnaird *et al.* 1996; Whitney & Smith 1998; Marsden 1999). Plans to estimate the seasonal variation in abundance of hornbills in Taï NP using distance sampling (Buckland *et al.* 2001) were thwarted by the outbreak of civil war in Ivory Coast in September 2002. However, Klaus Zuberbühler had a large dataset of audio recordings made during fieldwork on primate behaviour between 1991 and 2002 (see Zuberbühler 1993; Zuberbühler *et al.* 1997; Range & Fischer 2004). This presented me with a unique opportunity to investigate hornbill abundance by studying their vocal behaviour.

I aimed to assess the seasonal variation in abundance of three of the hornbill species found in Taï NP. Eight species are known from the park (Gartshore *et al.* 1995) not including black-and-white-casqued hornbill *Bycanistes subcylindricus* which may be found in the semi-deciduous forest in the north of the park. It has recently been found in Cavally Forest Reserve (FR) (6°11'N, 7°47'W) to the north-west of Taï NP (Demey & Rainey in press). I focussed on the three largest species: black-casqued hornbill, yellow-casqued hornbill and brown-cheeked hornbill *B. cylindricus*; the latter two are of global conservation concern and classified as near-threatened (BirdLife International 2000). These three species are also the most vocal and frequently observed in closed forest (pers. obs.) and hence were most likely to provide me with sufficient data to investigate variation in abundance from vocalisations.

Some bird vocalisations, most often those of species in the most seasonal environments, are known to occur only in certain seasons (e.g. Keith *et al.* 1992; Catchpole & Slater 1995), therefore it was important to be certain that the hornbills were genuinely absent from the study area and were not simply varying their call rates. There is highly seasonally variable rainfall in the Upper Guinea forests (Fig. A.1). Hornbills lack

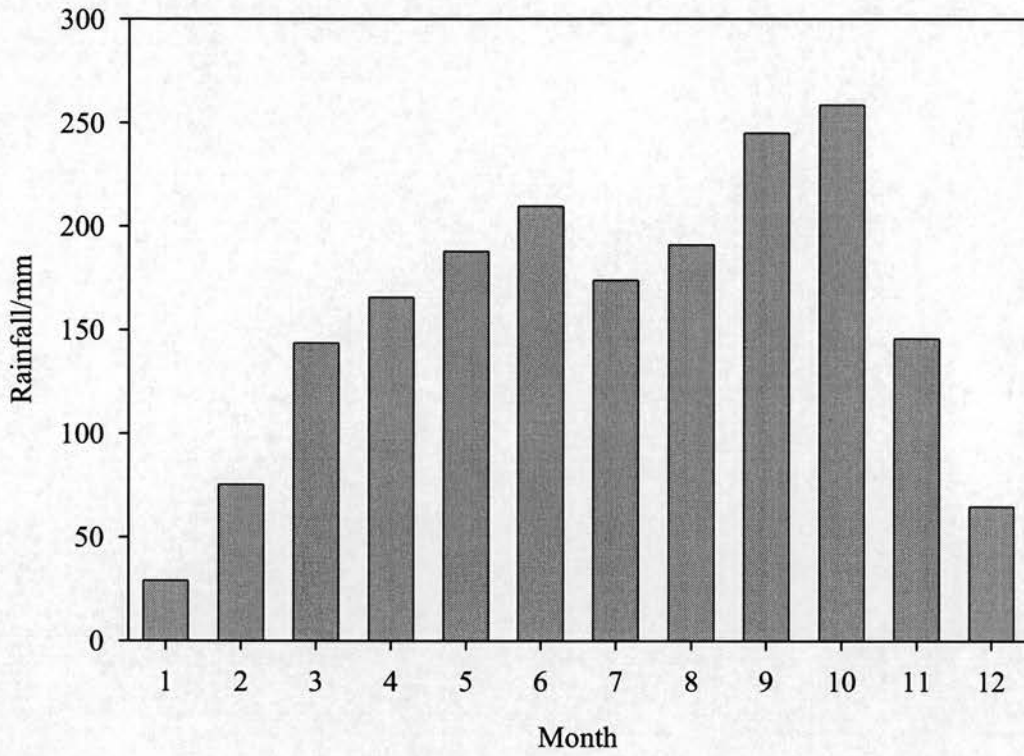


Figure A.1. Average monthly rainfall 1995-99. Recorded at CRE, Tai NP, (Klaus Zuberbühler unpubl. data).

some underwing coverts on their wings and have noisy wingbeats that can be heard from up to 500 m away (Kemp 1995; Kinnaird *et al.* 1996; Rainey *et al.* 2004). The birds fly year round, although females seal themselves into their nest hole during incubation of the eggs and young. Thus the noisy wingbeats of the birds can be heard if they are active in an area. To assess whether or not an index of variation in hornbill abundance could be estimated from vocalisations, I compared variation in wingbeat noise throughout the year against variation in vocalisations. The three large hornbill species in Taï all have noisy wingbeats. Brown-cheeked hornbills (mass: 0.9-1.4 kg, wing length: 276-330 mm) have more rapid and lighter wingbeats and are smaller than black-casqued (mass: 0.9-1.6 kg, wing length: 330-440 mm) and yellow-casqued hornbills (mass: 1.5-2.1 kg, wing length: 344-415) (ranges are maxima, Kemp 1995). The wingbeats of large male yellow-casqued hornbills are often lower pitched and slower than those of black-casqued hornbills and thus they can be distinguished but generally it is difficult to distinguish between the wingbeats of these two species audibly or by visual inspection of spectrograms.

## Methods

Klaus Zuberbühler had made audio cassette recordings during experimental trials on the acoustic behaviour of primates (*Cercopithecus diana*, *C. campbelli*, *C. nictitans*, *Cercocebus torquatus* and *Colobus polykomos*). The recordings were of high quality and other calls in the forest environment were also recorded coincidentally. They were made when primates were present irrespective of the presence or absence of hornbills. Primates were located by systematic searching of the research area. Hornbills do feed on some of the same fruit species as primates but the extent of overlap is low (Poulsen *et al.* 2002). It is therefore unlikely that any seasonal variation in associations of hornbills and primates will have had a strong influence on the results. Hornbills have very loud calls and occasionally these can be heard from over 1 km away (Kemp 1995; Rainey *et al.* 2004) so most calls made within a few hundred metres of the microphone would have been recorded. Each recording lasted 5 min and was separated from other recordings spatially by at least 500 m or temporally by one year thus ensuring independence between them. A total of 667 recordings (3,335 min) were analysed varying from 33 to 101 recordings per month (Table A.1). All available recordings were used. From preliminary observations,

Month	No. of recordings	Month	No. of recordings
Jan	52	Jul	54
Feb	101	Aug	43
Mar	33	Sep	34
Apr	50	Oct	70
May	71	Nov	39
Jun	70	Dec	50

Table A.1. Number of recordings in each month.

both yellow- and black-casqued hornbills were thought to be less abundant between March and June compared to November and December. Using limited data from Gartshore *et al.* (1995), I estimated that hornbills would be relatively abundant from July to February. I therefore split the year into two periods, 'high' (July-February) and 'low' seasons (March-June) to allow comparisons of presence/absence.

The limited available data suggest that yellow-casqued hornbill breeds in most months of the year in the Upper Guinea region (Grimes 1987; Gartshore *et al.* 1995; Kemp 1995, pers. obs.). Therefore it is unlikely that the variation in vocalisations or in activity (and thus wingbeat noise) is related directly to the breeding season in Taï NP. Brown-cheeked hornbill has been found in breeding condition in January and August (Kemp 1995). A nestling black-casqued hornbill was found in Ghana in November by Grimes (1987).

### **Variation in occurrence of wingbeats**

To control for potential seasonal variation in call production by hornbills, I compared the proportion of recordings in each calendar month in which I noted wingbeats against the proportion of recordings in each month that hornbills called for both black- and yellow-casqued hornbills combined and for each species separately. Brown-cheeked hornbill wingbeats, although noisy, are less obvious and were excluded from this analysis. Their wingbeats are faster and less deep and can thus be distinguished from those of the other two species (pers. obs.)

### **Variation in occurrence of vocalisations**

As the recordings were made in every month of the year at the study site, I was able to assess the abundance of all three species from the proportion of recordings in which the call of each species was found in each month. The means for each month were used to estimate mean numbers of calls per recording for the high (July to February) and low seasons (March to June).

### *Study site and dates*



The recordings were made in Taï NP around the Centre de Recherche en Ecologie (CRE) (5°50'N, 7°21'W) covering an area of *c.* 100 km<sup>2</sup>. This work was carried out from March to June 1991 and June 1994 to June 2002 inclusive (although not in every month of all years, Table A.1).

### *Equipment*

Vocalisations and wingbeats were recorded using a Sony WMD6C Professional Walkman with a Sennheiser ME66 microphone. Recordings of calls were displayed as spectrograms with Avisoft-SASLab Pro 3.9. Statistical analysis was carried out with Minitab 12. I took coordinates of different forests using a Garmin GPS 12. Taxonomy and nomenclature follow Borrow and Demey (2001).

## **Results**

### **Variation in wingbeat abundance**

The proportion of recordings in which wingbeats of black- and yellow-casqued hornbills combined were recorded was closely correlated with the prevalence of calling by these two species combined ( $r^2(\text{adj})=0.748$ ,  $P=0.0002$ ) (Fig. A.2a), the calls of black-casqued hornbills alone ( $r^2(\text{adj})=0.721$ ,  $P=0.0003$ ) (Fig. A.2b) and yellow-casqued hornbills alone ( $r^2(\text{adj})=0.436$ ,  $P=0.012$ ) (Fig. A.2c) but not to the calls of brown-cheeked hornbills ( $r^2(\text{adj})=0.041$ ,  $P=0.252$ ) (Fig. A.2d). Variation in wingbeats throughout the year was found to be highly distinctive with a peak from September to January and a trough from March to June (Fig. A.3). The difference between the proportion of recordings in which wingbeats were heard in the high season (wingbeats on 19.4% of recordings) (July-February) compared to the low season (0.8%) (March-June) was highly significant (Fisher's exact test:  $n=224,443$ ,  $P<0.001$ ).

### **Variation in vocalisation abundance**

As calls were produced in proportion to the abundance of black- and yellow-casqued hornbills (prevalence of wingbeats indicating hornbill abundance) I then assessed

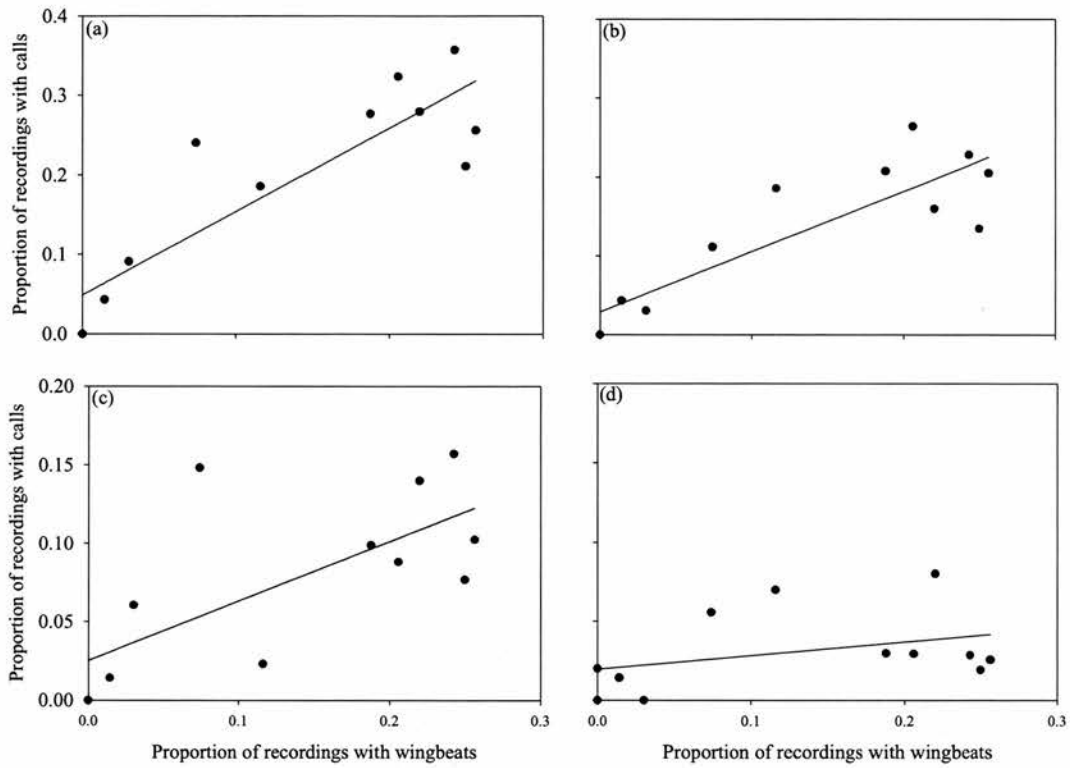


Figure A.2. Regression of proportion of recordings each month in which calls of (a) black- and/or yellow-casqued hornbills ( $y=1.05x+0.049$ ,  $P=0.0002$ ); (b) black-casqued only ( $y=0.768x+0.029$ ,  $P=0.0003$ ); (c) yellow-casqued only ( $y=0.379x+0.025$ ,  $P=0.012$ ); and (d) brown-cheeked hornbills ( $y=0.086x+0.020$ ,  $P=0.252$ ); were heard against proportion of recordings on which wingbeats were recorded.

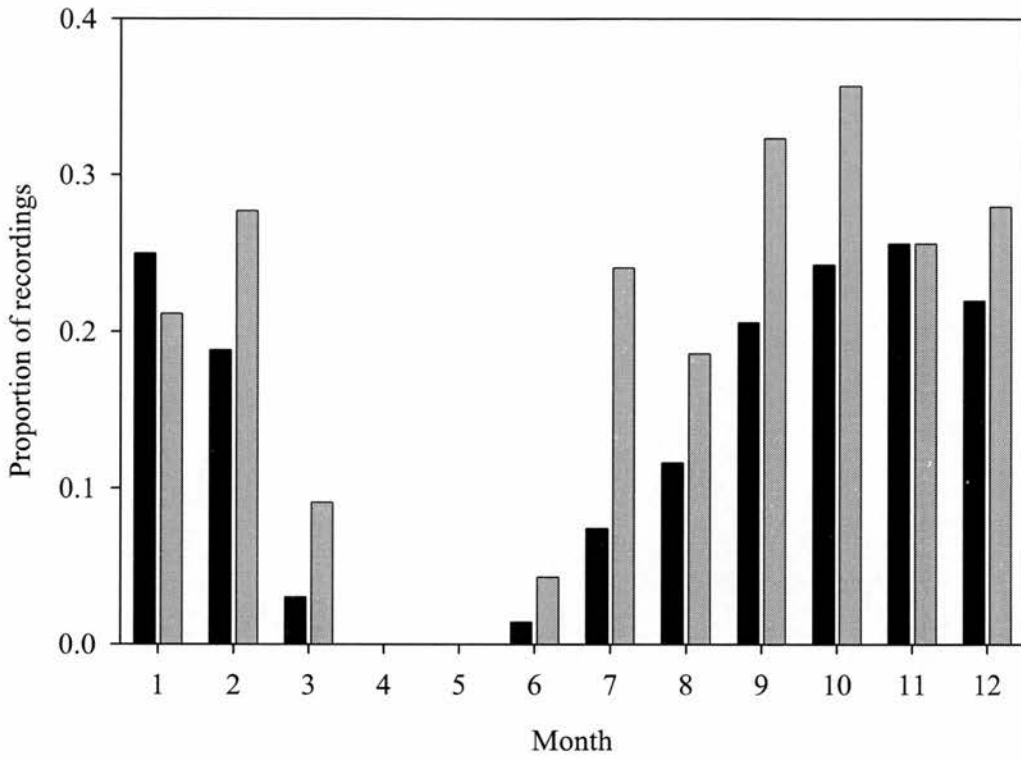


Figure A.3. Proportion of recordings per month in which wingbeats (black bars) and calls (grey bars) of black-casqued and/or yellow-casqued Hornbills were recorded.

variation in abundance of these species and brown-cheeked hornbill. The seasonal variation in the number of recordings on which calls of either black- or yellow-casqued hornbills were recorded was also highly distinctive (Fig. A.4). The difference between the number of recordings on which calls of black- and/or yellow-casqued hornbills were heard in the high season (black- and/or yellow-casqued calls on 27.1% of recordings) (July-February) compared to the low season (2.7%) (March-June) was highly significant (Fisher's exact test:  $n=224,443$ ,  $P<0.001$ ). Black-casqued calls were recorded significantly more often in the high season (18.7%) compared to the low season (1.8%) (Fisher's exact test:  $n=224,443$ ,  $P<0.001$ ) (Figs. A.4 and A.5). Yellow-casqued calls were recorded significantly more often in the high season (10.8%) compared to the low season (0.8%) (Fisher's exact test:  $n=224,443$ ,  $P<0.001$ ) (Figs. A.4 and A.5). Brown-cheeked calls showed no significant variation in abundance between the high season (4.1%) compared to the low season (1.3%) (Fisher's exact test:  $n=224,443$ ,  $P=0.062$ ) (Figs. A.4 and A.5).

## Discussion

I found that the prevalence of hornbill wingbeats was closely correlated with the variation in abundance of the calls of black- and yellow-casqued hornbills for both species combined and for both species separately. Black- and yellow-casqued hornbills showed significant seasonal variation in abundance being almost ten times more common from July to February compared to March to June (Fig. A.5). Brown-cheeked hornbills showed less consistent variation in abundance between seasons. Statistical analysis may have had low power to detect any seasonal trends in abundance for this latter species, as it makes fewer and quieter vocalisations than the other two species (pers. obs.). Thus it will be detected over a smaller area than the two *Ceratogymna* species and may have its relative abundance underestimated if vocalisations are used to detect it compared to the other species.

The variation in prevalence of wingbeats reliably indicated call variation. The seasonal variation of wingbeats is most probably explained by either reduced activity of black- and yellow-casqued hornbills from March to June or by their departure from Tai NP. The most likely hypothesis is that they leave the park. It is unlikely that they show reduced

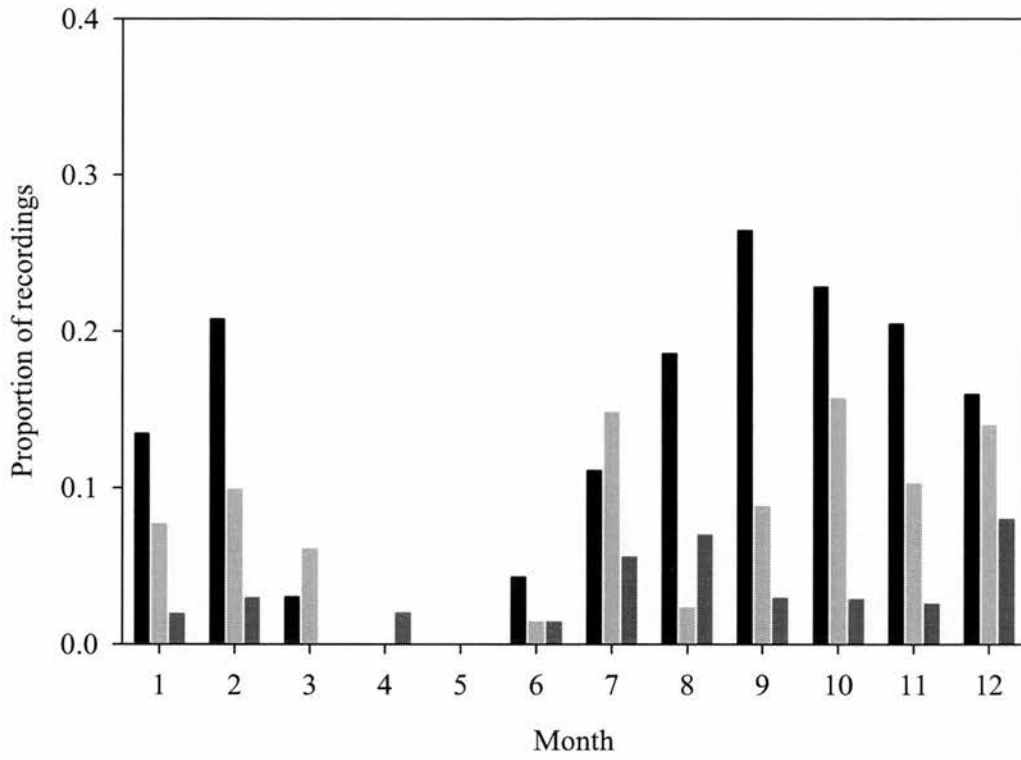


Figure A.4. Proportion of recordings per month in which calls of black-casqued (black bars), yellow-casqued (light grey bars) and brown-cheeked hornbills (dark grey bars) were recorded.

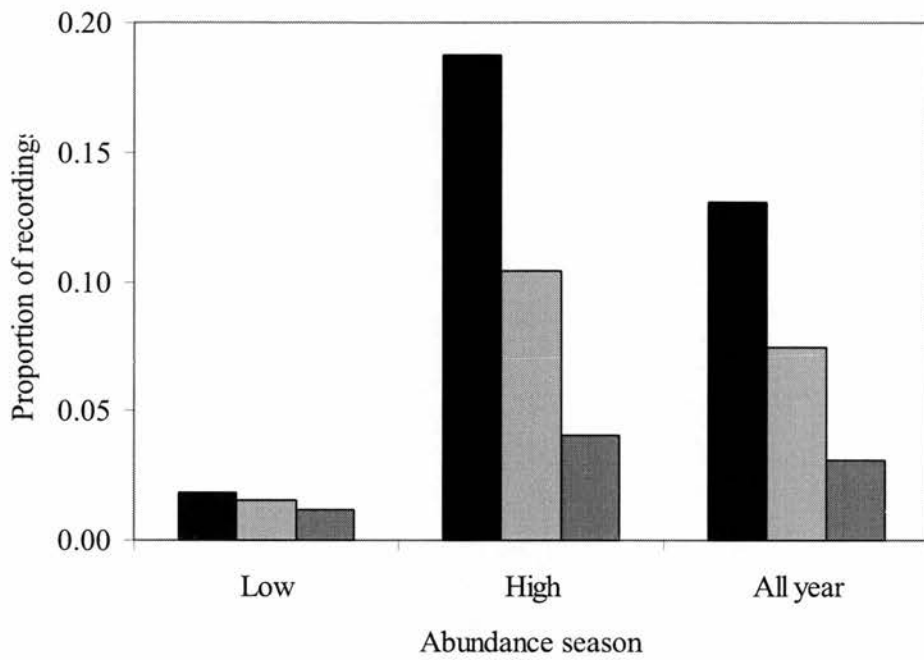


Figure A.5. Average proportion of recordings for low (March-June) and high seasons (July-February) in which calls of black-casqued (black bars), yellow-casqued (light grey bars) and brown-cheeked hornbills (dark grey bars) were recorded.

activity, as they do not apparently have fixed breeding seasons (Grimes 1987; Gartshore *et al.* 1995; Kemp 1995, pers. obs.), breeding in both dry and rainy seasons (Fig. A.1). They are also highly mobile and can move nomadically between ephemeral fruiting sources (e.g. Leighton 1986; Poonswad & Tsuji 1994; Kinnaird *et al.* 1996; Holbrook & Smith 2000; Holbrook *et al.* 2002) and it would be difficult for such species, which do not maintain territories, to obtain sufficient food without travelling between distant feeding sites. Thus their wingbeats would be heard year round if they were present in Taï NP. The latter hypothesis therefore, that the birds leave the park, would appear to be the most likely. It is possible that moult could make their wingbeats less noisy but as the noise is created by the absence of underwing coverts in hornbills, this is unlikely.

Are black- and yellow-casqued hornbills engaging in nomadism or migration? Nomadism would imply that the birds are tracking available resources on an *ad hoc* basis with no seasonal bias. This study is composed of data collected from ten different years. If the birds were nomadic it would be unlikely that I would have detected seasonal bias in their variation in abundance. However, as I did observe this seasonal bias, the birds are more likely to be migrating regularly. There are few observations of any forest stenotopic species migrating in the West African forests (Elgood *et al.* 1973; Thiollay 1985; Grimes 1987) and black- and yellow-casqued hornbills may be amongst the few species that migrate.

Previous studies investigating the relationship between variation in hornbill abundance and environmental factors have studied fruiting phenology in their forest habitats (e.g. Kinnaird *et al.* 1996; Whitney & Smith 1998; Holbrook & Smith 2000; Holbrook *et al.* 2002). Our knowledge of hornbill diet in the Upper Guinea forests is poor and the fruiting phenology of their food species is unknown. The diets of black-casqued and white-thighed hornbills *Bycanistes albotibialis* (the latter a sister species of brown-cheeked hornbill) in Cameroon have been better studied (Brosset & Erard 1986; Whitney & Smith 1998; Holbrook & Smith 2000; Holbrook *et al.* 2002). However, few of these tree species occur in Upper Guinea and phenology data are only available in Taï for fruit species that are the main ones consumed by primates (A. Korstjens pers. comm.). Although there is some overlap in the species consumed by hornbills and other frugivores such as primates and elephants, there is little overlap in the proportion of the total number of individual fruits of each tree species consumed by hornbills and other frugivores (Clark *et al.* 2001;

Poulsen *et al.* 2002). Therefore these data may explain little of the variation in hornbill abundance in Taï NP.

The variation in abundance of black- and yellow-casqued hornbills and their probable movement to areas outside Taï NP have some important consequences:

- 1) It is likely that they require a larger area of forest than is available to them in Taï NP alone. They probably do not migrate southwards in the low season as they were uncommon in Haute Dodo FR (4°54'N, 7°19'W) south of Taï NP in March 2002 (Demey & Rainey in press). It is possible that they migrate latitudinally into the northern semi-deciduous forest (which has a different rainfall regime than the southern moist forest, Thiollay 1985) in, for example, Mont Péko (6°58'N, 7°12'W) and Mont Sangbé NPs (8°00'N, 7°12'W). Although there are hornbills present year round in these parks, they do appear to vary in numbers throughout the year (R. Demey pers. comm.). The consequence of this is that these species may require very large tracts of forest to maintain their populations at current levels, as has been observed in Asia by Datta & Rawat (2003). It has previously been suggested that, in the process of estimating minimum reserve size, the critical habitats used throughout the annual cycle of a species should be identified and protected (Powell & Bjork 1995). This is a problem that has not yet been addressed in Upper Guinea.
- 2) The reduction in forest area in Upper Guinea, and particularly in Côte d'Ivoire, over the last 25 years (Sayer *et al.* 1992) has resulted in widespread fragmentation of the remaining forests. This may have reduced the hornbill population through loss of forest habitat but also some local populations may have become isolated and reduced in numbers or locally extinct because of this. For example, the black-casqued hornbill has not been observed in Marahoué NP (7°08'N, 5°56'W) for over 20 years (Thiollay 1985, pers. obs.), and this may be related to the park's recent isolation from other areas of forest. Hornbills are known to be excellent dispersers and are some of the few remaining species that can disperse seeds to isolated forest fragments (e.g. Jensch & Ellenberg 1999; Chapman *et al.* 2003). However, it is possible that very large expanses of non-forest habitat may exclude hornbills from the more isolated fragments. Smaller fragments may also not support sufficient fruiting trees to enable populations of some species to survive (Shankar Raman & Mudappa 2003). This isolation may have important consequences for forest regeneration from dispersed seeds.



3) Hunting of all large wildlife species for meat is the greatest threat to their survival in most of forested Central and West Africa (Barnes 2002; Milner-Gulland & Bennett 2003). Large hornbills are also hunted by the Oubi and Guéré people in south-western Côte d'Ivoire for use in traditional ceremonies (pers. obs.). As hornbills must fly across areas of non-forest habitat to reach more distant forest fragments, it is possible that they may suffer an increased risk of mortality from hunting than if they were sedentary in closed forest.

Few studies have estimated the abundance of birds or other species from acoustic recordings. The fortuitous availability of so many high quality acoustic recordings does mean that this study may be unique. However, it is possible that other sets of recordings are available which may provide an insight into seasonal variation in relative abundance of a species. Given the relatively low cost of obtaining the data it would be worthwhile searching for these recordings as they may contain such important information.