CHAPTER 1. GENERAL INTRODUCTION

1.1 Introduction

The research for this thesis examined approach behaviour in predator encounters in two avian species and established how and why each form of approach to a predator, mobbing and predator inspection, are used and whether these derive from similar or different origins. So far, the taxa researched for mobbing and predator inspection are disparate. Mobbing behaviour has been primarily studied in birds (Caro, 2005b) although it has also been recorded in fish (Dominey, 1983; Bshary and Fricke, 2002), ungulates (Berger, 1979) and in primates (Gursky, 2003; 2005; 2006), whereas predator inspection has been primarily studied in fish (Dugatkin and Godin, 1992). There are also examples of predator inspection recorded in reptiles (Leal and Rodriguez-Robles, 1997) and mammals (Fitzgibbon, 1994; Caro *et al.*, 2004). The fact that mobbing has been studied largely in birds and predator inspection largely in fish is curious given that birds seem to undertake inspection quite readily (Koboroff, 2004; Koboroff and Kaplan, 2006). During an earlier pilot study as an undergraduate, I found that birds approached taxidermic model predators and did not vocalise or attempt to attack the model (Koboroff, 2004; Koboroff and Kaplan, 2006). This seemed so much a departure from published accounts of mobbing that it led me to investigate this further in the research presented in this thesis. I selected two avian species: the Australian magpie (*Gymnorhina tibicen tibicen*) and the zebra finch (*Taeniopygia guttata castanotis*) to consider whether mobbing and predator inspection are both expressed in birds and whether they are functionally different. I will explain in detail later why these two species were chosen (section 1.9 below).

1.2 Anti-predator strategies

Anti-predator strategies are fundamental for survival, and many strategies have evolved. Indeed, to name a few remarkable adaptations: Californian ground squirrels (*Spermophilus armatus*) chew on the skin of rattlesnakes (*Crotalus spp*.) and then lick their fur to avoid the snakes detecting their own scent (Clucas *et al.*, 2008), blue-faced honey eaters (*Entomyzon cyanotis*) approach Australian hobbies (*Falco longipennis*) performing slow summersaults (Woodall, 2005) and both fieldfares (*Turdus pilaris*) and tawny frogmouths (*Podargus strigoides*) bombard predators with faeces (Haland, 1989; Kaplan, 2007).

Anti-predator strategies are difficult to categorise because of their diversity (Ruxton *et al.*, 2004; Caro, 2005b). Some reviewers have attempted to classify anti-predator strategies as primary or secondary defences (Edmunds, 1974; Ruxton *et al.*, 2004). The definition of primary and secondary defences varies somewhat but the underlying meaning is that primary defences are those in which the animal attempts not to be detected or not to be pursued, while secondary defences are those that act after a predator has begun an attack. Although there are some advantages to such categorisations of anti-predator strategies there are also some disadvantages (Caro, 2005b). For instance, approach behaviour can be classified, as Edmunds (1974) stated, as both primary and secondary defences since approach behaviour is proactive, i.e. an individual may mob/inspect a predator that may not even be hunting (Hartley, 1950; Dugatkin and Godin, 1992) or defensive, i.e. aiding a conspecific chased or caught by a predator (Curio, 1978). Ultimately, the primary and secondary classification cannot deal with approach behaviour because, in this model, the emphasis is on the predator and what it might do. Hence, a more encompassing categorisation would be to distinguish between behavioural and morphological adaptations.

While the majority of behavioural adaptations involve potential prey attempting to avoid detection and/or increase the chance of escaping by increasing the distance between themselves and the predator (Caro, 2005b; Ruxton *et al*. 2004), animals that approach predators do entirely the opposite. When an animal approaches a predator, its presence may be noticed by the predator (Flasskamp, 1994; Godin and Davis, 1995) and it, obviously, decreases the distance between itself and the predator thereby, seemingly, decreasing the chance of escape. Hence, avoidance and approach strategies are vastly different from each other. However, the sequence of events leading to approach or avoidance strategies is similar and these will be discussed in the next section.

1.3 Predatory sequence leading to approach behaviour

Approach behaviour involves a complex process (McLean and Rhodes, 1991). An animal must, obviously, detect a predator in order to respond to it. Therefore, vigilance is an important element prior to formulating a response to a predator. Moreover, it requires an animal to recognise potential predators and, if there is more than one type of predator (as there often is), discriminate between them and then decide how to respond to the threat.

1.3.1 Predator recognition

It has been debated whether there are mechanisms for an individual to recognise a predator without having had any experience with that predator before (Caro, 2005b). For instance, hatchling brush turkeys (*Alectura lathami*), have no contact with adults and are completely independent once hatched (Goth, 2001). Therefore, they have to recognise and respond to predators without any prior experience or protection by parents and, indeed, they do recognise and flee from predators. However, they also respond to innocuous objects that do not resemble predators (Goth, 2001). Hence, it would appear that brush turkeys are fearful of any species of certain sizes and shapes (Goth, 2001).

It has also been suggested that Australian magpies may have an innate ability to recognise snakes (Brockie and Sorensen, 1998). Brockie and Sorensen (1998) found that a hand reared juvenile magpie was fearful of objects resembling snakes (i.e. a garden hose) even though the juvenile had never been exposed to a snake before. However, there is also evidence to suggest that learning is involved in anti-snake behaviour in magpies (Koboroff and Kaplan, 2006). Adult magpies tend to flee on an encounter with a snake, whereas juvenile magpies approach, mob and also inspect snakes (Koboroff and Kaplan, 2006).

The effects of learning or experience with predators on anti-predator strategies may well be substantial. There is ample evidence of learnt predator recognition. For example, in some species, young animals require some learning or exposure to predators before their response is similar to that of an experienced animal (Kullberg and Lind, 2002; Shier and Owings, 2007). Thirty day-old great tit fledglings respond to predator and non-predator species by performing freezing and producing distress calls. By contrast, adult and wild great tit fledglings discriminate between predators and non-predators. While size and shape of stimuli can be key features that elicit generalized fear behaviour, learning and/or experience may be required to discriminate between threatening and non-threatening species. Indeed, social learning about predators has been found to be the most effective means to learn about how to deal with predators (Shier and Owings, 2007). Orphaned prairie dogs (*Cynomys ludovicianus*) were presented with model predators either in the presence of an experienced adult (tutor) or without a tutor. Those that had a tutor were more wary of the predators and more of the juveniles that had been tutored survived than those that were not tutored. In other words, there is substantial evidence that recognition of predators is largely a learnt or experience-dependent behaviour.

1.3.2 Vigilance

Vigilance is one of the key factors in early detection of a predator. Presumably, the earlier an individual is able to detect a predator the more time it has to respond to the potential threat. While vigilance has been investigated primarily in single-predator systems, the majority of animals have more than one predator. For instance, Lima (1992) suggested that, in multi-predator systems, there may be predator-specific or non-predator specific vigilance. In other words, animals may have a particular vigilance behaviour for one predator or have a more generalised vigilance behaviour whereby the animal is attentive for all predators.

Predator risk can also be determined through vigilance behaviour. Chaffinches, (*Fringilla coelebs*), for instance, constantly move their heads up and down during foraging as they watch for predators. It was noted that they move their heads from side to side, as well as up and down, when they were exposed to a cat, whereas exposure to aerial predators elicited only the up/down head movements (Jones *et al.*, 2007). This shows that vigilance behaviour can also differ according to predator type. We already know that the Australian magpie is highly vigilant. Indeed, magpies have been called the 'police of the bush' but such vigilance may be directed not only at predators but also at trespassing magpies (Farabaugh *et al.*, 1992a; Kaplan, 2004; Morgan *et al.*, 2007).

However, lack of vigilance by an individual may not indicate a lack of such in a group. An individual's place in a social hierarchy can determine how vigilant it needs to be (Proctor *et al.*, 2006). Group size may also play a role in vigilance. Beauchamp (2007) found that as group size increases at night, vigilance decreases. Caro (2005b), also suggested that individual vigilance decreases as group sizes increases.

1.4 Approach behaviour

Approach behaviour in encounters with predators seems to be counter-intuitive and some researchers (Shedd, 1982; Caro, 2005b) have tried to attribute the same functions to both mobbing and predator inspection. They have done so in order to explain behavioural strategies that, at first, might appear to involve higher risk than any avoidance strategy, particularly in cases in which the potential prey has few actual defences against a predator.

At this point, I would like to clarify that the focus of this thesis is on forms of approach behaviour that do not involve the potential prey confronting a predator that has already given chase. This is known as a 'last resort' defence against a predator (Caro, 2005b, Eilam, 2005) and is neither a form of mobbing nor of predator inspection.

1.4.1 Mobbing behaviour

Caro (2005b) suggested that, once an animal detects and recognises a threat, it must take action. Mobbing behaviour has been defined in a number of ways but, actual descriptions of such behaviour are difficult to generalise because different species perform distinctly different forms and sequences of mobbing behaviour (Caro, 2005b). As a consequence, all of the definitions of mobbing behaviour have tended to be quite broad. Caro (2005b) argues that, due to the numerous potential outcomes of mobbing behaviour, any functional definition may be difficult to make. Hence, any useful definition of mobbing has to be based on the description of the behaviour of mobbing animals rather than the outcome of the mobbing event.

Hartley (1950) described mobbing behaviour as involving smaller, less powerful birds acting upon a more powerful species. Although this definition is quite broad, it does make the important point that, even though mobbers are less powerful, such species are the initiators of this confrontation. This definition lacks any description of what the birds actually do during a mobbing event. In not describing the behaviour in any great detail, Hartley (1950) does not get confounded by the variety of mobbing behaviour both within and between species (Caro, 2005b). Yet this lack of a descriptive definition has the disadvantage that it cannot shed light on patterns of behaviour that, in fact, characterise it as a mobbing event.

The definition of mobbing by Hartley (1950) was expanded by Curio (1978). He pointed out that birds gather around a predator (moving or stationary), move constantly using stereotyped movements and that this generally occurs within a minute of the discovery of the predator. He noted that mobbing birds also emit loud, broad frequency calls. Curio's (1978) definition provides a general description of some of the behaviour performed during a typical mobbing event, as I have observed in magpies. This definition is also relatively broad as he does not describe what these stereotyped movements are. Yet, there are many variations of mobbing behaviour both within and between species. Shields (1984), relying largely on descriptions similar to those of Curio (1978), added that mobbing birds often swoop at the predator and that some swoops involve a physical attack.

In summary, one may deduce from these various definitions that mobbing is an approach initiated by a group to confront a potential predator. The problem in all of these definitions is their self-imposed lack of specificity of a cycle of actions or detailed description of a singular event. The question is whether all or only some of these elements are necessary for a response to be classified as a mobbing event? Mobbing events are usually seen as anti-predator behaviour and their functions are usually described in the terms outlined below.

1.4.1.1 Functions of mobbing behaviour

The functions of mobbing behaviour were formulated by Curio (1978). In his paper, eleven non-mutually exclusive hypotheses on the function of mobbing were put forward and it is worth describing these in some detail to show that, apart from their implicitly assumed function of survival, mobbing is not so straight forward. The functions of mobbing behaviour can be subdivided into those that directly deter predators, those that reduce the risk of capture during mobbing and those that provide indirect benefits. Since my research on magpies and zebra finches set out to investigate their approach behaviour, it was essential to be aware of these interpretations of mobbing to see whether any or most could be upheld in my model species.

1.4.1.1.1 Hypotheses about deterring a predator

Three hypotheses are concerned with the question of deterring the predator from hunting. The most obvious of these hypotheses suggests that the main aim of mobbing is to deter the predators, known as the ‘move-on’ hypothesis (Curio, 1978; Flasskamp, 1994). Mobbing events, involving a number of individuals assembling around the predator while vocalising loudly, may distress the predator enough for it to move out of the area. There is some evidence that mobbing may dislodge a predator. For instance, Pavey and Smythe (1998) observed that powerful owls (*Ninox strenua*), after being mobbed whilst roosting, often chose different roost sites, seemingly as a direct consequence of mobbing. Flasskamp (1994) showed that a little owl (*Athene noctua*) and a tawny owl (*Strix aluco*) likewise chose different roosts following a mobbing event. The obvious benefit to the mobbers in this case is that the removal of the predator diminishes the threat of predation. Curio (1978) suggests, however, that the benefits of making a predator leave the area are, in fact, twofold. Not only will the predator be driven off, and all the sooner the more vigorous the mobbing, but also the predator will be denied the opportunity of gathering information about the area for future hunting attempts. Betts *et al.* (2005) provide indirect evidence to support the ‘move-on’ hypothesis. They tested whether black-throated green warblers (*Dendroica virens*) and black-throated blue warblers (*Dendroica caerulescens*) respond to playbacks of mobbing calls both inside and outside territorial boundaries. They found that there were very few instances when the birds left their territories (8.1% of trials) but they responded to all playbacks of mobbing calls within their territory. This suggests that the strategy was designed to expel the predator from the birds’ own territory, or that mobbing behaviour is constrained by territorial boundaries.

Alerting others is another proposed function of mobbing (Curio, 1978). This is closely associated with the ‘move-on’ hypothesis since mobbing calls alert others to a predator (Curio, 1978; Hurd, 1996; Forsman and Monkkonen, 2001; Templeton *et al.*, 2005; Ellis, 2008), and so recruit others to harass the predator. The Australian magpie has an unusually large number of alarm calls and quite a number of them are used during mobbing events (Kaplan *et al.,* submitted). Indeed, the Australian magpie has 27 call types that were found to attract conspecifics to the area and preceded mobbing events involving the entire group (Kaplan *et al.*, submitted). Although Zann (1996) suggests that zebra finches have two possible alarm calls, these calls are mostly emitted during a flight response and so are not mobbing calls. Lombardi and Curio (1985a; 1985b) found that zebra finches produced one call type more often during an encounter with a predator.

Hence, while we have substantial evidence that alarm calling in magpies is used to recruit others for joint mobbing attacks, zebra finches appear to use alarm calls in states of high arousal and while fleeing from predators. I will come back to this later (Ch. 3., 3.3.9 and Ch. 8, 8.8.1).

Mobbing calls may be complex signals that contain important information (Templeton et al., 2005). Stone and Trost (1991) found that mobbing calls of black-billed magpies (*Pica pica*) may contain information concerning context, relative risks and benefits to the recipient and the birds appear to take these into account before responding. Mobbing calls are not only communicated between bird species but also between other vertebrates. The Galapagos marine iguana (*Amblyrhynchus cristatus*) responds to the mobbing calls of Galapagos mockingbird (*Nesomimus parvulus*), for instance, and so may derive benefits from attending to the mobbing calls of another species (Vitousek *et al.*, 2007).

The 'perception advertisement hypothesis' argues that the purpose of this type of approach is to communicate to the predator that it has been detected (Leal and Rodriguez-Robles, 1997). Curio (1978) saw this as a signal that may deter the predator from hunting in so far as any attack relying on stealth had been thwarted. However, Hasson (1991) suggested that any communication from prey to predator was initially intended for intraspecific communication and then it evolved to communicate to the predator, thus, signalling to a predator without serving the function of 'advertisment'. A study on Arabian babblers (Ostreiher, 2003) found that babblers mob a snake and emit mobbing calls even when the bird is alone suggesting that, at least in babblers, mobbing calls may communicate to the predator as well as conspecifics.

The ‘perception advertisement’ hypothesis is closely related to the ‘move-on’ hypothesis (Curio, 1978). As suggested by Flasskamp (1994), both hypotheses state that mobbing functions to move the predator away from the immediate area. The ‘move-on’ hypothesis involves harassment of the predator until the predator leaves the area. Flasskamp (1994) describes how these two hypotheses can be distinguished: for a prey species to communicate to a predator that it is aware of its presence requires little effort. However, this may not be enough for a predator to leave the area. Perception advertisement signals may only prevent a surprise attack. Since the predator may still have an opportunity to attack later, if prey animals alert a predator that they are aware of its presence and the predator remains, a more concerted strategy may be needed to make the predator ‘move on’. As Flasskamp (1994) points out, it is of greater benefit for a prey animal to have a predator move out of its area than have it remain even though the predator may not be hunting at the time.

1.4.1.1.2 Other hypotheses

There are some indirect consequences of mobbing behaviour. For example, mobbing calls have been observed to silence offspring (Windsor and Emlen, 1975; Curio, 1978). Nestlings or fledglings tended to vocalise repetitively throughout the day usually when they caught sight of their parent birds and were expecting food. These vocalisations could easily be used by predators to locate the nest. If mobbing calls by parent birds suppress the vocalisations of the nestlings/fledglings, this may help conceal the young (Curio, 1978).

Learning to recognise and how to respond to a predator can occur through mobbing. One study by Curio *et al.*(1978) claimed to have found evidence for a 'cultural transmission' hypothesis, arguing that a juvenile or inexperienced individual may learn from the other mobbing conspecifics (a) how to recognise a predator and (b) how to respond or, at least, how to mob a predator. Curio *et al.* (1978) conditioned European blackbirds (*Turdus merula*) to mob an unnatural and seemingly non-threatening object or non-predatory bird species. By conditioning tutors to mob the stimulus and then placing inexperienced individuals with the tutors whilst mobbing, the inexperienced birds began to mob the non-threatening object. The inexperienced birds mobbed with greater intensity on the second presentation of the stimulus without the presence of a tutor. In summary, there is no lack of explanations of the outcomes of mobbing behaviour but the actual behaviour of mobbing and how it is constituted has received relatively scant attention in the literature.

There are also elements of mobbing that serve to decrease the chance of capture during a mobbing event. For instance, the 'selfish-herd effect' refers to reducing the risk to the individual associated with mobbing by attracting more mobbers to the predator (Hamilton, 1971). If there are more individuals participating in a mobbing event, there is a lower chance of capture of any one individual. The 'selfish-herd effect' is closely related to the 'confusion effect' (Curio, 1978). Mobbing behaviour usually consists of birds surrounding a predator, constantly moving and vocalising loudly and repetitively. This behaviour may confuse the predator. If there are numerous birds surrounding the predator performing similar movements, it may be difficult for the predator to single out one individual for attack.

However, currently there is no evidence to show that there is less risk of being caught by a predator if there are more mobbers present. Similarly, there is no direct evidence in avian species to suggest that the confusion effect works. However, Schradin (2000) found that leopard geckos (*Eublepharis macularius*) and common marmosets (*Callithrix jacchus jacchus*) both took much longer to capture crickets when the crickets were in groups rather than being presented singly, suggesting that predators may become confused when faced with large numbers of prey.

1.4.2 Exploration

The second major form of approach behaviour that is relevant to my own research is inspection behaviour. Indeed, it was one of the main tasks of my study to analyse whether and how the two types of approach to a potential predator differ and what functions can be ascribed to them. Before discussing predator inspection, I thought it pertinent to elaborate on other forms of inspection behaviour, usually called exploration, given that there may be important similarities between predator inspection and exploration. Exploration is the way in which animals learn about their environment (Greenberg and Mettke-Hofmann, 2001). Exploration has an important role to play, since it leads to discoveries, for instance of a new food sources, and possibly even to the occupation of a new ecological niche (Greenberg and Mettke-Hofmann, 2001).

Ecological factors may affect a species' tendency to explore its environment. Invading species are assumed to be more neophilic (i.e. approach novel stimuli) than established species since invading species have to adapt to a new environment (Martin and Fitzgerald, 2005). Indeed, house sparrows (*Passer domesticus*) that have only recently invaded an area show a greater propensity to try a novel food than sparrows that are established within an area (Martin and Fitzgerald, 2005). However, both invading and established sparrows approach novel objects with the same propensity (Martin and Fitzgerald, 2005). This suggests that neophilia is not entirely lost once a species has been established within an environment. Furthermore, there is evidence to suggest that resident species are more likely to approach novel objects than nomadic species (Mettke-Hofmann *et al.*, 2005). Resident or established species require information about their environment which may alter according to the time of year. Mettke-Hofmann *et al.* (2006) found that garden warblers (*Sylvia borin*) increase their propensity to explore their environment during the breeding season.

The propensity to explore the environment may also be influenced by conspecifics. Ravens (*Corvus corax*) showed varied latency to approach a novel object depending on the conspecifics that accompanied them (Stowe *et al.*, 2006; Stowe and Kotrschal, 2007). Individual ravens were classified as either "slow" or "fast" explorers and paired in slow/fast pairs. Latency to approach the novel object significantly decreased for the slow ravens but significantly increased for fast ravens meaning that social interactions influenced willingness and speed of exploration (Stowe and Kotrschal, 2007). Exploration behaviour of great tits (*Parus major*) was also influenced by conspecifics but, in their case, fast great tits were not affected by a slow conspecific, whereas slow conspecifics readily approached the novel object in the company of a fast great tit (van Oers *et al.*, 2005).

Latency to approach may also have to do with experience. In an experiment using garden warblers (*Sylvia borin*), birds were presented with a simple and a complex novel object (Mettke-Hofmann *et al.*, 2006). Experienced birds (i.e. birds that had been exposed to different novel objects earlier) took longer to approach both objects than inexperienced birds. This suggests that experience may enhance exploration in future encounters with novel objects, possibly because the experienced individuals may be categorising objects more rapidly (Mettke-Hofmann *et al.*, 2006).

Exploration behaviour may well also be correlated with other personality traits. Beauchamp (2000) found that zebra finches that are more active and explore their environment more than others were always the first to reach a feeding patch, termed as leadership by the author. Dingemanse & de Goede (2004), in investigating hierarchy and exploratory behaviour in great tits, first determined a linear dominance hierarchy based on interactions between individuals while feeding and then correlated this with exploration behaviour. They found that individuals that were higher in the hierarchy explored new environments after shorter latency than individuals that were lower in the hierarchy. This complemented a study by Verbeek *et al.* (1996) which had shown that great tits that are more aggressive (i.e. initiate more fights) explore new environments after shorter latency. However, there is also evidence to suggest the contrary; namely, that in some species, subordinates explore environments more readily than dominant individuals. Subordinate barnacle geese (*Branta leucopsis*) are found in the “explorative front position” of the flock for finding potential feeding sites. Subordinates reach new food sources before dominant individuals. However, once a feeding site has been discovered, the dominant individual then expels the subordinates (Stahl *et al*., 2001). This may not necessarily be an example of subordinates showing a greater propensity to explore their environment than dominant individuals. Instead, individuals at the front of the flock may be at more risk of predation while the dominant individual may be privileged to be more protected within the flock.

If exploration or inspection is needed to learn about the environment, presumably, younger and inexperienced individuals ought to perform more exploratory behaviour than adults. Indeed, Heinrich (1995) found that juvenile ravens readily explore novel objects. This study demonstrated that, once a juvenile had experience with an object, it required no further examination.

Play behaviour may also be a form of exploration. Indeed, magpies are one of only a few songbird species in which play behaviour has been reported (Pellis, 1981a; 1981b; Pozis-Franscois *et al.,* 1999). Play behaviour is most prevalent in juveniles (Pellis, 1981a; 1981b) but adults also play (Brown and Veltman, 1987; Kaplan, 2004, Pozis-Franscois *et al.,* 1999). Most play involves interaction between individuals such as play fighting (Pellis, 1981b; Kaplan, 2004, Pozis-Franscois *et al.,* 1999). However, magpies also manipulate a number of objects (Pellis, 1981b; Brown and Veltman, 1987; Kaplan, 2004) similar to young ravens

(Heinrich, 1995). While a major function of play behaviour seems to be acquire social skills (Kaplan, 2004), play behaviour is also a form of exploration that may involve food or even potential predators (Pellis, 1981b). It would seem that play may later be adapted to other forms of exploration (see Chapter 8).

There is some evidence that exploratory behaviour may relate to anti-predator behaviour. Hollander *et al*. (2008) investigated whether nest defence is associated with an individual's propensity to explore and found that great tits that had scored higher on 'exploration' also defended the nest with greater intensity. Overall, there are many factors (i.e. age, play behaviour, experience, time of year and social context) that have been shown to influence an individual's propensity to explore its environment.

1.4.3 Predator inspection

How exploration differs from predator inspection is not always clear or easy to determine and it is often even less clear whether predator inspection is undertaken to learn about a new predator or to view closely a known predator.

George (1960) first described in fishes the phenomenon of potential prey approaching predators. However, it was not until Pitcher *et al*. (1986) that the term 'predator inspection' was used to describe this behaviour (Dugatkin, 1997). Pitcher *et al*. (1986) described predator inspection in minnows (*Phoxinus phoxinus*) when confronting a pike (*Esox lucius*). The behaviour they observed concerned a small group of minnows that left their shoal, approached the stalking predator, halted briefly, and then returned to the group (Pitcher *et al*., 1986). This description of inspection applies to most species of fish that undertake predator inspection and it is also similar to inspection cited in other vertebrates, mainly mammals (Fitzgibbon, 1994).

Fish have also been documented as mobbing predators (Dominey, 1983; Bshary and Fricke, 2002) but there is no indication that inspecting fish may then mob the predator. Dominey (1983) describes mobbing by fish as “assemblages of individuals around a potentially dangerous predator”. Pitcher (1992) points out that mobbing fish attack predators while the majority of inspection events involve only small groups or individuals and no attacks. Pitcher (1992) then made a clear distinction between the predator inspection and mobbing events. It follows that the functions ascribed to mobbing behaviour, therefore, may not apply to predator inspection, at least not as far as research on fish has revealed.

As there is little evidence available in the literature describing predator inspection in birds, let alone ascribing any separate function to it, I will rely primarily on evidence provided by studies with fish and mammals in the following sections.

1.4.3.1 Function of predator inspection

If a predator has been detected, it does not necessarily mean that the predator is in hunting mode at that particular time; as a result, any anti-predator behaviour such as a flight response may not be needed and may even be disadvantageous (i.e. flight responses may trigger chase responses in the predator). Hence, there is the possibility that animals can monitor and assess a predation threat and judge whether or not to engage in an anti-predator behaviour or resume feeding or some other activity. Predator inspection may thus be used to monitor and assess the level of threat posed by a predator (Dugatkin and Godin, 1992). Increased perceived threat can elicit a more cautious approach by fish. Three studies have observed the effects of the predator's diet on inspection behaviour by fish (Brown *et al.*, 2001b; Brown and Schwarzbauer, 2001; Brown and Dreier, 2002). In these studies, the predatory fish were fed either individuals of the prey species or other food sources. If a predator had been fed on a diet of the prey species, there was an increase in the latency of inspection behaviour by the prey species. Also, the rate of inspection was lower and the group size was smaller compared to inspection of predators that had been fed on a different diet.

In addition, prey fish also avoid the head region of predators that have been fed the prey species, a behaviour that does not occur as often when the predator has been fed other food (Brown *et al.*, 2001b; Brown and Schwarzbauer, 2001; Brown and Dreier, 2002). Avoiding the head region has been termed 'attack-cone avoidance' (George, 1960) and it seems to be another form of risk assessment, in so far as potential prey avoids the body region from which the strike is most likely to occur (i.e. the around the head of the predator). The higher the risks associated with the inspection behaviour, the greater the attack cone avoidance observed (Brown *et al.*, 2001b). To some extent this will become relevant later when discussing predator inspection in magpies (Chapter 5).

Alerting others may be another function of predator inspection behaviour, as is the case for mobbing behaviour (Dugatkin and Godin, 1992; Pitcher, 1992). After gathering information about the predator, animals may then transfer this to other conspecifics or heterospecifics. Pitcher *et al.* (1986) also showed 'information transfer' from inspecting minnows to other non-inspecting group members. Once returning to a feeding area following an inspection event, the non-inspecting minnows foraging in the area ceased to forage and were more active. Here the behaviour of inspecting fish alerted non-inspecting fish of a potential threat. Magurran and Higham (1988) also found that minnows were able to transfer information of a predation threat. One minnow (transmitter) was able to view the predator whilst a second minnow (receiver) could view only its conspecifics and not the predator. The behaviour of the receiving minnow changed dramatically after observing the transmitting minnow that had just inspected the predator. The receiving minnow ceased foraging and sought a nearby refuge. The overall outcome may be that an entire shoal leaves the feeding area completely (Pitcher *et al.*, 1986).

While alerting others seems to be a function of both mobbing and predator inspection, there is perhaps one fundamental difference between alerting others during mobbing and during inspection behaviour. Alerting others during mobbing behaviour is usually associated with loud and continuous vocalisations, as seen in Australian magpies that repeatedly vocalise and alert group members during an encounter with the predator (Kaplan *et al.* submitted, Kaplan, 2004). These vocalisations are not only signals to conspecifics but a signal to the predator as well (Ostreiher, 2003). Alternatively, information transfer during predator inspection does not seem to be a signal to the predator as the individual retreats to its group before signalling (Pitcher *et al.*, 1986). The role of alarm calling is, therefore, a variable that may aid in discriminating mobbing and predator inspection (see Chapter 5).

If an ambush predator is approached by its prey, this obviously foils a surprise attack. Indeed, one study on fish has shown that inspecting guppies are less likely to be attacked and killed than non-inspecting guppies perhaps due to perception advertisement (Godin and Davis, 1995). In a study on the Thompson's gazelles, it was found that cheetahs that were inspected moved further between rests and hunts (Fitzgibbon, 1994). As feline predators rely, to some degree, on a surprise attack, monitoring by the prey of a predator that is stalking or beginning to hunt removes the possibility of an ambush and of any advantage the predator might have had over its quarry. This is important since Gazelles are agile and fast-moving animals, perhaps more so than their predators. Thus, perception advertisement may not just be a function of mobbing and it may also be a function of predator inspection (Dugatkin and Godin, 1992; Pitcher, 1992).

One could conceive of the possibility that inspection behaviour is associated more with exploration than with anti-predator behaviour (Dugatkin and Godin, 1992). Animals may simply approach a novel stimulus that, by chance, happens to be a predator. If this were so, however, they should inspect novel unfamiliar stimuli just as often as they inspect predators. Indeed, inspection behaviour does occur when animals are presented with a novel stimulus, yet inspection/exploration of novel objects tends to decline rapidly, whereas inspection of predators remains relatively consistent (Pitcher, 1992). In this thesis, experiments were conducted specifically to test naïve and experienced zebra finches in their response to model predators and novel objects (see Chapter 8).

As argued in the previous section, experience may well influence the occurrence or frequency of predator inspection. In this case it would be argued that, presumably, more experienced animals should respond differently to predators (i.e. should need less inspection) than naïve animals. Using wild caught three-spine sticklebacks (*Gasterosteus aculeatus*) from areas either containing or not containing predators, Walling *et al.* (2004) showed a distinct difference between the two populations. Fish that were taken from a habitat with predators were considered experienced fish and the other populations from habitats without predators were considered to be predator naïve. The experienced fish inspected more often than the naïve fish. Age in the experienced population of sticklebacks had no effect on the results. Unexpectedly, these results showed that experience with predators increased predator inspection behaviour instead of reducing it.

In addition, the experienced fish responded more often to models that were increasingly realistic. This was not so in the naïve fish (Walling *et al.*, 2004). Further evidence to support the role of inspection in predator recognition comes from Magurran and Girling (1986). Here, inspecting minnows habituated rapidly to unrealistic models. The more realistic the model was, the longer it took for the minnows to habituate. It thus seems unlikely that inspection behaviour is merely a characteristic of the behaviour of a novice or naïve animal, nor is it solely dependent on curiosity. Hence, there must be a better explanation as to why inspection behaviour has evolved since there is little evidence to support the view that the purpose of inspection is solely to gather experience.

1.5 Selection of study species

This research project used two native Australian avian species, the Australian magpie (*Gymnorhina tibicen tibicen*) and the zebra finch (*Taeniopygia guttata castanotis*). It was important for this study to use two species that contrast with each other in a variety of characteristics. This was considered important because it is possible that the type of approach behaviour performed, be it mobbing or predator inspection, may have to do with specific biological or ecological characteristics of the species, such as social organisation, territoriality, size or ecology. Any species similar with regard to some of these specific variables (including the ecological niche occupied) may use similar approach behaviour strategies.

One of the important criteria for selecting the magpie is that this species is territorial (Carrick, 1972; Farabaugh *et al.*, 1992a) and the zebra finch was selected because it is locally nomadic (Zann, 1996). As there was no published evidence that predator inspection is used as an anti-predator strategy in birds (with the possible exception of Kruuk, 1976), it was not possible to base any selection of the species for this study on approach behaviour alone. Hence, I searched the literature to see whether there were reported differences in social behaviour between species that mob and those that inspect. To my knowledge, there has been no systematic study of the relationship between territoriality and approach behaviour. However, it is clear that the research has identified both similarities and differences between mobbing and predator inspection. In researching approach behaviour, I soon noticed a relationship between territoriality and approach behaviour and thus have presented evidence that ecological factors may also play a role in the type of anti-predator strategies used. It seems as though species that perform mobbing behaviour tend to occupy permanent territories (for example; birds: Curio *et al.*, 1978; fish: Dominey, 1983; and primates: Gursky, 2005) whereas animals that are locally nomadic and may or may not occupy home ranges tend to perform predator inspection (e.g. in fish Pitcher *et al.*, 1986; and mammals, such as Thompson's gazelles, Fitzgibbon, 1994). I have already mentioned (see section 1.4.1.1 above) a study by Betts *et al.* (2005) showing that mobbing is constrained by territory boundaries. In fact Betts *et al.* (2005) concluded that at least the move-on hypothesis appears to be clearly linked to territoriality. If territoriality is an important variable in mobbing behaviour then one would expect that mobbing events decline in species that are locally nomadic or migratory. Using this information, the two species that were selected reflecting these differences.

We know that the magpie has some potential predators and most of these are raptors (Baker-Gabb, 1984). Potential raptor predators of magpies include the wedge-tailed eagle, *Aquila audax*, (Leopold and Wolfe, 1970; Brooker and Ridpath, 1980), the little eagle, *Hieraetus morphnoides*, (Debus, 1984) and the brown goshawk, *Accipter fasciatus*, (Bravery, 1970). However, there is little information about the anti-predator behaviour of magpies to these predators, presumably because it depends on sightings in the field and this happens infrequently and unpredictably. There are a number of studies that have anecdotal evidence of magpie responses to predators and these will be discussed in Chapter 3. However, the alarm calls of magpies have been researched. Magpies have an extensive vocal repertoire (Sanderson and Crouche, 1993; Kaplan, 2006b) and their alarm vocalisations are used even as warning signals by heterospecifics (Kaplan, 2004). Magpies also have a complex social structure. They occupy territories and defend them vigorously (Farabaugh *et al.*, 1992b).

There is relatively little information available on anti-predator behaviour of zebra finches (Zann, 1996). However, many predators of the zebra finch are known. Zann (1996) suggests that zebra finches must be particularly vulnerable around watering holes since flock sizes were larger as the birds approach a watering hole compared to flock sizes of birds that were flying away from it. Zann (1996) states that black kites (*Milvus migrans*), brown goshawks (*Accipiter fasciatus*), collared sparrowhawk (*Accipter cirrhocephalus*), black falcons (*Falco subniger*), Australian hobbys (*Falco longipennis*), brown falcons (*Falco berigora*) and pied butcherbirds (*Cracticus nigrogularis*) are the main predators of zebra finches around watering holes. Furthermore, Evans *et al.* (1985) found brown goshawks, blue-winged kookaburras (*Dacelo leachii*) and pied butcherbirds were the major predators of zebra finches in the Kimberely region (north-west tropical region of Australia). Mulga snakes (*Pseudechis australis*) and dingoes (*Canis familiaris dingo*) have also been seen hunting zebra finches (Zann, 1996). Zebra finches are also vulnerable to nest predation with 66% of nests suffering predation and 80% of juveniles are lost before they reached the age of 80 days (Zann, 1996).

It was predicted that magpies, as a territorial species, would mob more frequently than the zebra finch, and that the zebra finch would perform predator inspection more so than magpies. However, it was possible that magpies may approach predators without also mobbing the potential predator at that particular time. In previous studies, magpies have been observed to approach predators and were seemingly not mobbing them (Koboroff, 2004; Koboroff and Kaplan, 2006). Experiments investigating the behaviour of magpies were conducted in the field, where groups that occupied a permanent territory could be tested.

Working with magpies had one drawback; they cannot be kept easily in captivity and, as a native species, are also protected. Hence, experiments that required controlled conditions in captivity could not be applied to magpies. The zebra finch, also a native Australian species but excluded from the protected species act for commercial purposes, offered a useful contrast to the territorial magpie as they could be held and reared in aviaries thus provided an opportunity to test also whether age and experience influence approach behaviour, as was found in other studies (Caro, 2005).

As zebra finches do not occupy territories, it was predicted that they would primarily perform predator inspection behaviour, even though they have been reported to mob predators (Lombardi and Curio, 1985a; 1985b) if they approached them at all (Zann, 1996). Lombardi and Curio (1985a; 1985b) measured the number of “excited” behaviours exhibited by the zebra finches, wing and tail flicks, monocular fixations of the stimulus, elongation of the bird’s body, flights toward the stimulus and rate of certain vocalisations. With the exception of vocalisations that may indeed be specific mobbing calls and the movements toward the stimuli, none of the other behaviour scored necessarily indicated mobbing behaviour but rather arousal. Therefore, I was quite confident that the zebra finches would show predator inspection and perhaps mobbing.

1.6 Aims of the study

The aim of this research project was to determine whether predator inspection and mobbing are completely different forms of approach strategies, in terms of actual behaviour and function, and this was addressed predominantly in experiments involving free-ranging magpies. I was particularly interested in the role of variations and sequences in mobbing events and inspection behaviour.

Chapters 3-7 investigated mobbing and predator inspection in magpies. Chapter 3 established an ethogram of the anti-predator behaviour performed by magpies on the basis of field observations. This was an obvious and essential first step in this study since there is little detailed description of the response of magpies to predators. Once the ethogram was established, three experiments testing magpie responses were conducted in the field (309 trials).

Experiment 1 investigated whether time of year and/or predator species influenced approach behaviour, using a total of 21 groups of magpies (Chapter 4). This experiment yielded a considerable data set and resulted in three chapters. Chapter 4 examined the responses of the magpies to aerial and ground predators, and it concentrated on mobbing behaviour. In Chapter 5, the same data set was examined for evidence of predator inspection in magpies. Here, functional differences between predator inspection and mobbing were considered. Chapter 6 investigated the eye used by the magpies to fixate a model predator, as a measure to determine which hemisphere of the brain was used to process the visual information (i.e. lateralisation). This was one of only four other studies to investigate laterality in a species in its natural habitat.

Experiments 2 and 3 are presented in Chapter 7. Experiment 2 investigated whether predator inspection could be elicited by presenting the magpies with model predators in different postures or contexts. This second experiment consisted of 32 trials. Eight magpie groups were presented with model predators in either a natural and unnatural postures in order to determine whether unfamiliar presentations of predators increased inspection behaviour. Experiment 3, in the same Chapter, was a replication of a study by Kruuk (1976) in which he presented to gulls a dead conspecific together with a predator and scored the response of conspecific gulls. It was replicated since this study has been thought to present the only evidence of predator inspection in birds (Pitcher, 1992; FitzGibbon, 1994; Leal and Rodriguez-Robles, 1997). This third experiment also involved eight magpie groups and 32 trials.

Experiments 4 and 5 are presented in Chapter 8, both conducted using zebra finches. In Experiment 4, seven experienced zebra finch pairs, which had been raised commercially in outdoor aviaries, were presented with a novel object and a model predator (56 trials). The aim here was to determine whether inspection of a predator differed from inspection of a novel object. In the final experiment (Experiment 5), six adult zebra finch pairs (raised in an outdoor aviary and thus considered to be 'experienced' with predators) and six adult zebra finches pairs that had been raised indoors by the experimenter (thus considered to be predator 'naïve') were presented with two model predators and a novel object (288 trials). The 'experienced' finches were compared with the 'naïve' finches to determine whether experience influenced predator inspection behaviour.

CHAPTER 2. GENERAL METHOD: FIELD EXPERIMENTS (AUSTRALIAN MAGPIES)

2.1 Introduction

This research project has been divided into fieldwork and laboratory work. The fieldwork was conducted observing groups of Australian magpies in their natural environment, and the laboratory experiments were conducted in captively bred zebra finches housed in the Animal House facility of the University of New England. The criteria for selecting these two species were discussed in the previous chapter. There are obvious advantages and disadvantages in conducting experiments solely in the field or in the laboratory (Martin and Bateson, 1993). Subjects held in captivity are constrained, in both their movements and behaviour. In the field, subjects are able to move about freely and demonstrate their full suite of behaviours (Martin and Bateson, 1993). However, fieldwork does have the disadvantage of unpredictability of events and of not knowing what experiences an animal has had over its lifespan prior to any observation or experiments. Moreover, it can often not be ascertained whether a specific event just prior to an experiment may have influenced the results. In the laboratory, experience and conditions can be controlled and this thus eliminates extraneous factors that may influence the behaviour of interest. By conducting both, field and laboratory experiments, it was possible to ask different questions about anti-predator behaviour. Laboratory experiments were essential to control experience and exposure to threatening stimuli. This is important since experience is known to influence anti-predator behaviour and predator inspection in particular (Fitzgibbon, 1994; Brown and Dreier, 2002; Kelley and Magurran, 2003; Walling *et al.*, 2004). Thus, in the laboratory, the relationship between experience and approach behaviour could be investigated whereas, in the field, this could not be examined with any accuracy since level of experience could not be assumed or known.

The methods used in the laboratory experiments (zebra finches) will be addressed in Chapter 8. Methods that will be described here exclusively concern the overall general methodology for the preliminary observations (Chapter 3) and for the three fieldwork experiments involving magpies reported in Chapters 4, 5, 6 and 7.

A number of criteria were used to select the magpie groups. These criteria were to identify the type of magpie group (i.e. permanent territory or otherwise), identify the number of group members, identify territorial boundaries and evaluate certain aspects of a territory (i.e. how accessible it was to the experimenter). In total, field work using magpies consisted of the preliminary trials for the ethogram and three main experiments totalling 345 trials. Specific methodologies, when these involve design variations, will be described in the respective chapters. However, the rationale for group selection, sites, basic procedure, the stimuli presented and the scoring methods remained the same for all these experiments.

2.2 Study sites

All groups of magpies were located on the Northern Tablelands of New South Wales, (Australia) within the city limits of Armidale and on campus of the University of New England, (30˚32`S, 151˚40`E inland, between Sydney and Brisbane at an altitude of 1000m). Both, the layout of the university and the city (population of approximately 20, 000) includes spacious parks and individual properties have generously large backyards often with lawns and some native shrubs and trees. It is an environment in which magpies appear to thrive and have plenty of opportunity to establish suitable territories.

2.2.1 Selection of magpie groups

The magpie groups were initially selected according to two main criteria: (1) the social organisation of magpie groups, and (2) specific landscape features of the territories. I selected groups that occupied permanent territories and territories that were easily accessible to the experimenter. Methodologically, this proved to be very important in order to achieve comparability of behaviour across groups.

Magpies may form one of four types of territorial groups, these are (1) permanent, (2) marginal (to permanent territories), (3) mobile and (4) open groups, as Carrick (1972) concluded in an extensive study of magpie groups in the Canberra region. According to Carrick (1972), not all magpie groups may occupy permanent territories while those groups that do breed do so consistently from year to year (Carrick, 1972). Marginal groups may also breed but are not usually successful and do not breed from year to year (Carrick, 1972). Breeding usually fails for mobile groups, and open groups do not attempt to breed at all (Carrick, 1972). Hence, for this project, only groups that occupied permanent territories were tested. This was important for two reasons. First, territoriality may be an important factor in approach behaviour since territorial animals seem to mob (see Ch. 1, 1.5 and Chapter 8). Second, Experiment 1 (to be described fully in Chapter 4) examined whether anti-predator behaviour is influenced by the developmental stage of juvenile magpies. As only magpie groups that occupy permanent territories tend to breed successfully, these were also the only groups reliably consisting of both juveniles and adults from one year of this research to the next.

Figure 2.1. Typical magpie territory.

Within Armidale and the campus of the University of New England, 44 groups with nestlings/fledglings were identified. All of these groups occupied sporting fields or parklands in areas known to be excellent for magpies to establish permanent territories (Jones, 2002) by providing suitable resources. Figure 2.1 shows a typical magpie territory used in this study. Further, each territory had to be easily accessible and provide a clear view for the experimenter to observe the entire, or at least the majority, of the group members in order to be able to evaluate whether the magpies fled, avoided or approached the stimulus once an experiment was conducted. Finally, the territory also needed to have little human traffic. The behaviour of the magpies can be affected by sudden appearances and movements of humans (Jones and Thomas, 1999) and this, in turn, could have influenced the results.

From the 44 groups that bred successfully, 23 satisfied all of the criteria. The number of groups and which groups were used in each experiment will be described in detail in the respective chapters.

Selection of the groups occurred between August and September 2005, prior to any experimentation, and in the breeding season, including the late nestling and early fledgling stage (see 2.2.3.2). This period was selected specifically in order to ascertain more accurately which groups had produced offspring, i.e. were occupants of permanent territories.

2.2.2 Location of groups

Eight groups were located on the extensive campus of the University of New England and 15 occupied parklands in Armidale (see Figure 2.2).

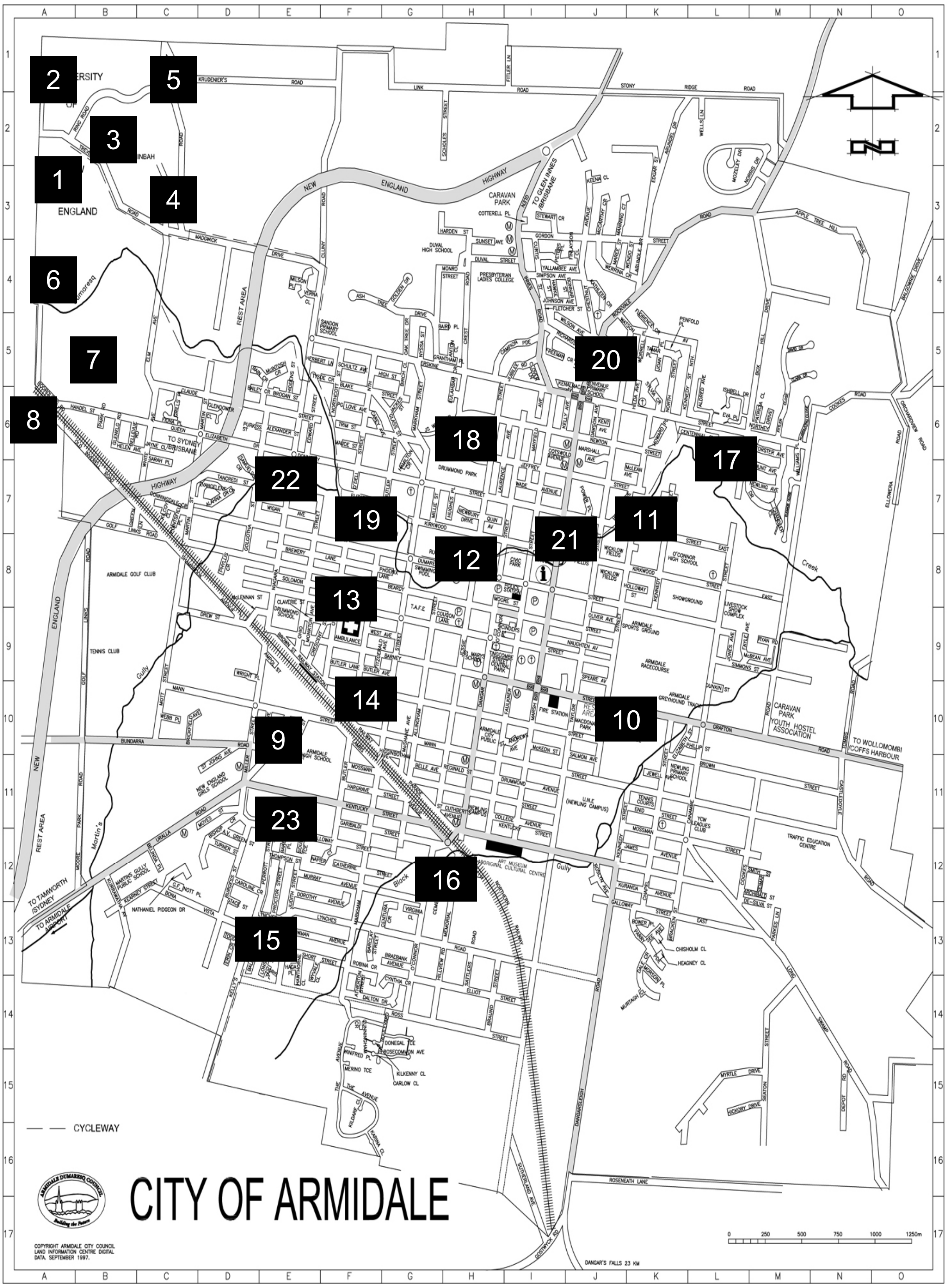


Figure 2.2. Map of Armidale showing the location of all groups (numbered 1-23).

2.2.3 Identifying groups

Following the selection of the groups, further observations were conducted in order to identify the group composition, group size and the age of each of the group members. Each group was observed for 6 hours across 6 days prior to any experimentation. During these initial observations, the number of adults and juveniles was recorded and an estimation was made of each group's territorial boundaries. The following sections explain the details for determining group members and territory boundary estimates.

2.2.3.1 *Identification of individuals and number of magpies per group*

The number of magpies in each group was determined. Knowing that it is relatively rare that intruders within a permanent territory are tolerated (Kaplan, 2004), the group composition could be determined by observing the number of magpies within close proximity to each (and not performing agonistic displays). The number of magpies within each group was recorded for the three experiments (see below). This included the number of adults and juveniles per group.

Adult and juvenile magpies are easily distinguished from each other. Adult magpies have distinct black and white plumage, whereas juveniles have a mottled, brown-grey plumaged (Figure 2.3). Magpies also have sex differences in their plumage. The females have a partially grey nape while the male's nape is white (Kaplan, 2004).

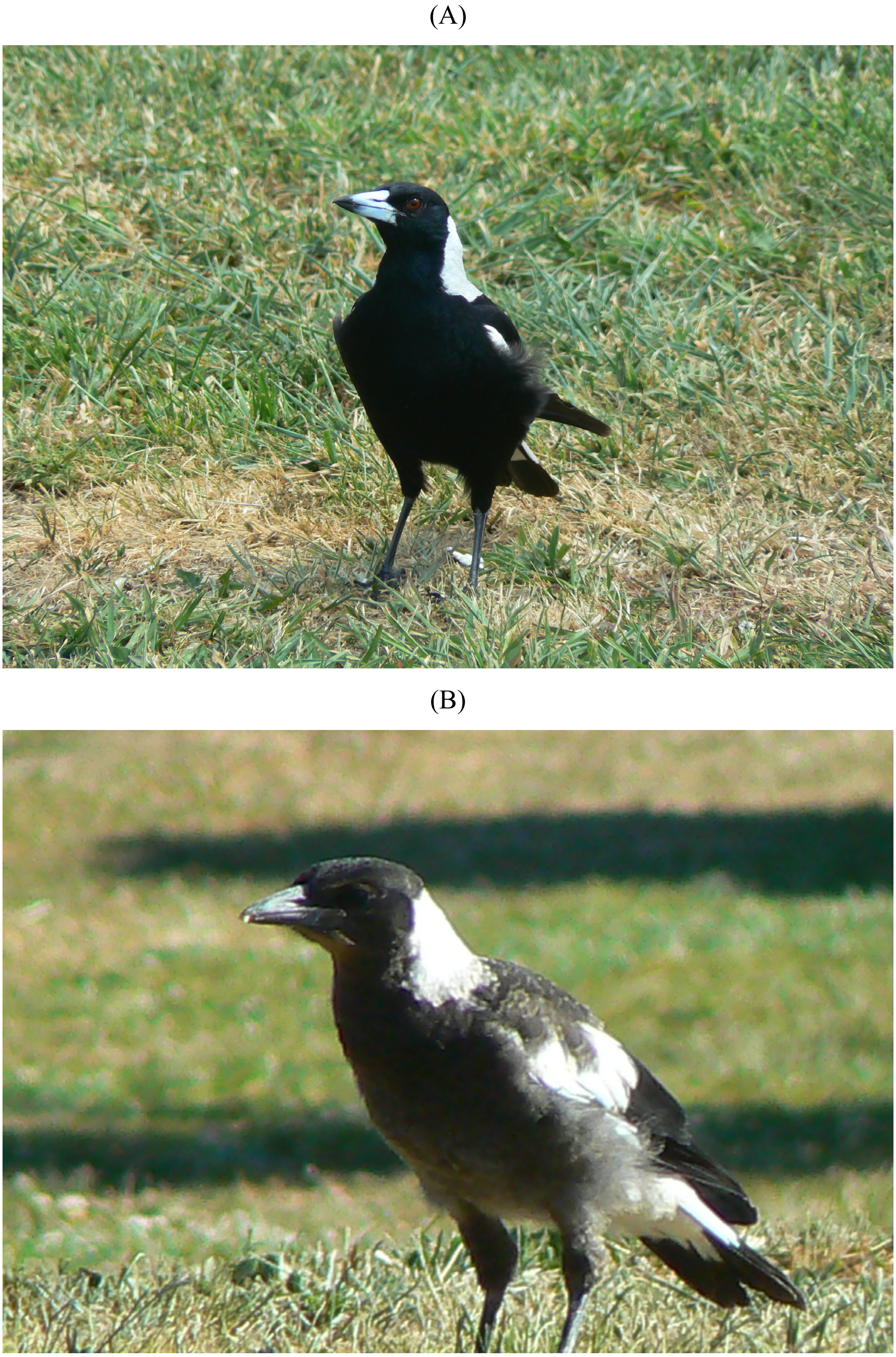


Figure 2.3. Photographs of an adult magpie (a) and a juvenile magpie (b). Adult magpies are distinctly black with white markings. Juvenile magpies have mottled, brown-grey plumage and a darker beak than adults. Also different eye colours: adults have reddish brown eye colour and juveniles have dark brown eyes.

(A)

(B)

Figure 2.4. Photographs of wing marking of two individuals. Note how individual (A) has a small and thin white marking on the wing while individual (B) has a much broader white marking on its wing and a smaller white marking on the edge of the wing.

Individual magpies can also be identified because they have distinct wing markings that are individually distinct one from another magpie (Kaplan, 2004) see Figure 2.4.

2.2.3.2 Seasons

This field study was conducted over one and half years across all seasons, including two breeding seasons (September 2005 to August 2007). The Australian magpie has an extended breeding season and, across Australia, has been recorded to breed in all months of the year (Barrett *et al.*, 2003). In the area of this project, breeding generally occurs between August (egg laying) to December (fledglings) (Higgins *et al.*, 2006). However, the breeding times varied a little during this project. In the first year of the project, juveniles fledged in September 2005 and dispersed in July-August 2006. In the second year, juveniles fledged between late October and early November 2006 but still dispersed in July/August 2007.

The research was undertaken at four distinct time periods. Throughout these periods the number of magpies per group was monitored continuously (see Table 2.1). Experiment 1 was conducted from September 2005 to August 2006 and it was subdivided into three separate stages: (1) September 2005-January 2006, (2) February-April 2006 and (3) June-August 2006. The selection of these stages will be discussed in Chapter 4. The choices were mainly based on the different stages of juvenile development in magpies. Experiments 2 and 3 were conducted between May-August 2007 and are presented in Chapter 7.

Table 2.1. Number of adult and juvenile magpies per group across all study periods. The grey cells in the table indicate that these groups were no tested during that particular stages

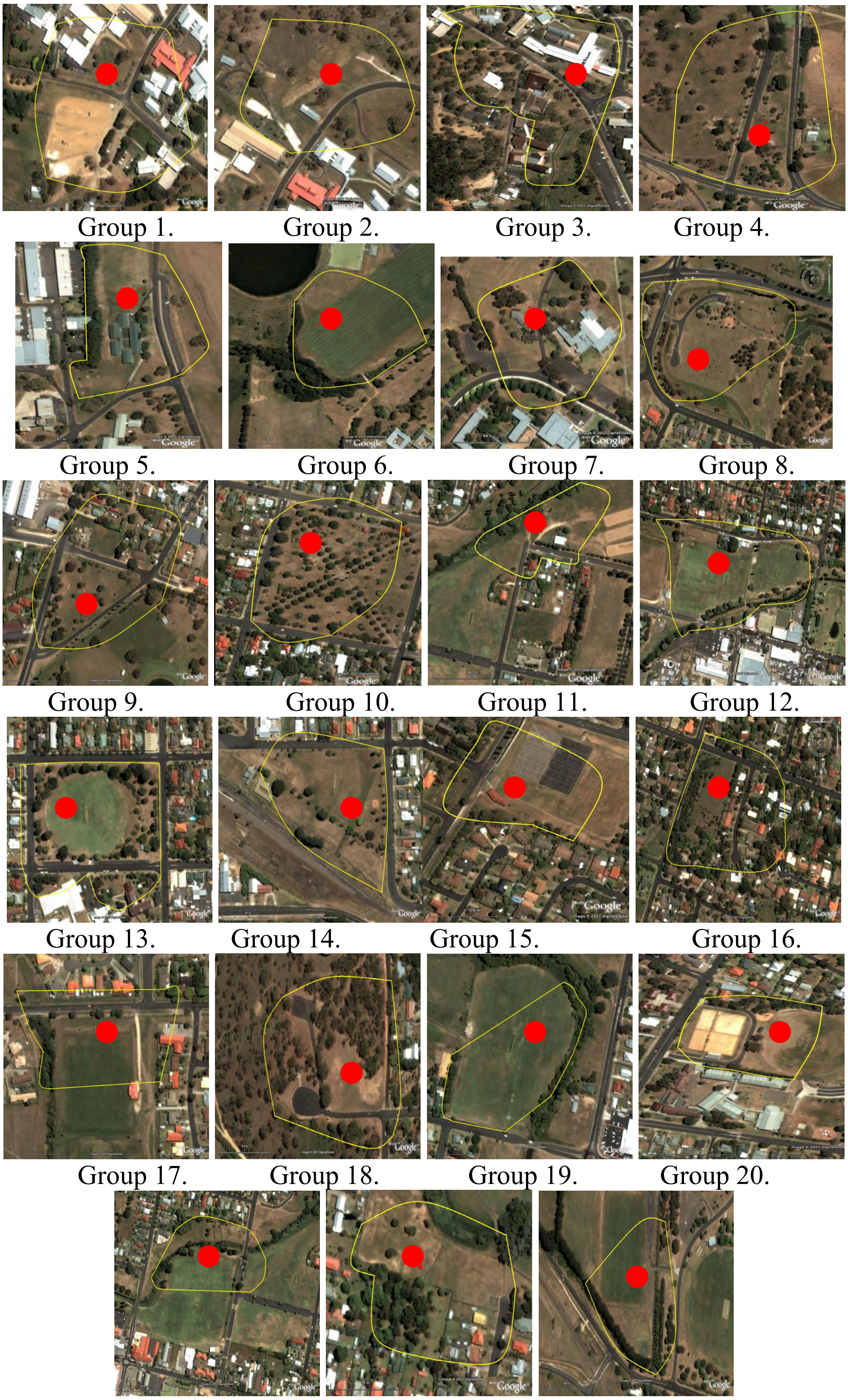
	September-January 2005-2006			February-April 2006			June-August 2006			May-August 2007		
Group	Adults	Juveniles	**Total**	Adults	Juveniles	**Total**	Adults	Juveniles	**Total**	Adults	Juveniles	**Total**
1	4	2	**6**	4	0	**4**	4	0	**4**	5	2	**7**
2	2	0	**2**	2	2	**4**	2	2	**4**	3	2	**5**
3	6	2	**8**	6	1	**7**	6	0	**6**	10	2	**12**
4	4	2	**6**	4	2	**6**	4	2	**6**			
5	5	2	**7**	5	2	**7**	5	2	**7**			
6	7	3	**10**	7	2	**9**	7	2	**9**			
7	6	2	**8**	6	2	**8**	6	1	**7**			
8	4	2	**6**	4	2	**6**	4	0	**4**	4		**4**
9	4	1	**5**	2	0	**2**	2	0	**2**	2	3	**5**
10	4	2	**6**	4	2	**6**	4	2	**6**	3	1	**4**
11	3	2	**5**	3	2	**5**	3	2	**5**	4	2	**6**
12	8	2	**10**	8	2	**10**	8	2	**10**	8	3	**11**
13	2	2	**4**	2	1	**3**	3	0	**3**			
14	4	0	**4**	4	0	**4**	4	0	**4**			
15				6	2	**8**				4		**4**
16				5	0	**5**				3	2	**5**
17				8	4	**12**				8	2	**10**
18				4	0	**4**						
19				6	2	**8**				4		**4**
20				3	2	**5**				3	2	**5**
21				4	2	**6**						
22										6	2	**8**
23										6	2	**8**
Mean	4.5	1.7	**6.2**	4.6	1.5	**6.1**	4.4	1.1	**5.5**	4.9	2.1	**6.5**
SEM	0.5	0.2	**0.6**	0.4	0.2	**0.5**	0.5	0.3	**0.6**	0.4	0.1	**0.5**

2.2.3.3 Territorial boundaries

Identifying territorial boundaries was essential for several reasons. This was important to ensure accuracy of testing the same groups in repeat trials. Subsequent checks were made prior to commencing a new experiment just in case groups had been changing in size or territorial dimensions, by knowing the extent of a group's territory, the experimenter could locate a group relatively easily. Second, identifying the territory boundaries was critical for determining where the stimuli were to be placed (see below, 2.3.2).

The main method used to estimate territory boundaries was achieved by observing the extent of a group's movement. Whilst observing each magpie group, the location of all magpies within the vicinity (and not defending a territory) was noted. Gradually, over a 6 hour observation period per group, both the number of magpies within a group and the extent of a group's movements were identified and the boundaries could be determined. It was only in exceptional circumstances (i.e. chasing intruders or mobbing predators) that magpies were observed to move beyond these boundaries.

To verify these results, observations of agonistic displays were also noted. Magpies that occupy permanent territories are known to defend their territories vigorously and do so using a variety of methods (Farabaugh *et al.*, 1992; Kaplan, 2004). Interactions between groups generally occur at the boundary locations; hence they helped to confirm the boundaries (Robinson, 1956; Farabaugh *et al.*, 1992; Rollinson, 2003).



Group 1. Group 2. Group 3. Group 4.

Group 5. Group 6. Group 7. Group 8.

Group 9. Group 10. Group 11. Group 12.

Group 13. Group 14. Group 15. Group 16.

Group 17. Group 18. Group 19. Group 20.

Group21. Group 22. Group 23.

Figure 2.5. Satellite pictures of each groups' territory. The yellow line is the estimate of the territory boundary. The red circle is the location of presentation of the stimuli.

Thus, in the pre-experimental observational phase of this research, agonistic interactions were recorded and such records were maintained throughout the fieldwork stages in order to confirm boundaries or document boundary shifts. In total, 55 agonistic displays were observed across all groups.

Scores were separated into four territorial display types (Kaplan 2004), two of which made the borders very clear. In (1), the most commonly observed display (N=38), one or two magpies, defending against conspecific intruders walked back and forth along the boundary. Eventually, this culminated in carolling (Kaplan 2004). In (2) the entire group flew down to the territorial boundary to face the neighbouring group. Again, carolling ensued (N=4). The final two types of territorial displays involved aerial manoeuvres. These involved either an individual (N=0) or the entire group (N=13) performing aerial displays near the boundaries (Kaplan, 2004). Hence, by observing the extent of foraging and flight movements, combined with the locations of agonistic displays, boundaries could be identified quite accurately. The results of these observations are presented in Figure 2.5.

2.3 Experiments

Experiments conducted between September 2005 and August 2007 were in accordance with the NSW *Animal Research Act 1985*, approved by the Animal Ethics Committee of the University of New England and licensed under the Australian Government National Parks and Wildlife Services.

2.3.1 Stimuli

Taxidermic models of five known aerial and ground predators of magpies were used during this study. It was important to test magpies using aerial as well as ground predators. Since birds have the obvious advantage of being able to escape from ground predators more easily than aerial predators, aerial predators could represent a more immediate threat and this might affect anti-predator behaviour. Hence, both predator types were represented and three out of five models chosen were aerial predators: taxidermic models of the wedge-tailed eagle (*Aquila audax*), little eagle (*Hieraetus morphnoides*) and brown goshawk (*Accipter fasciatus*). For ground predators a taxidermic model of a monitor lizard (*Varinus varnus*) and a non-descript model of a snake were selected.

The five predator models were chosen according to a number of ecological factors. They had been identified as part of the local wildlife within the study site area and having home ranges in and around the city of Armidale. Further, they were known to prey upon birds locally and there is evidence that most of them might occasionally prey upon magpies, particularly on nestlings and juveniles (see details per species below).

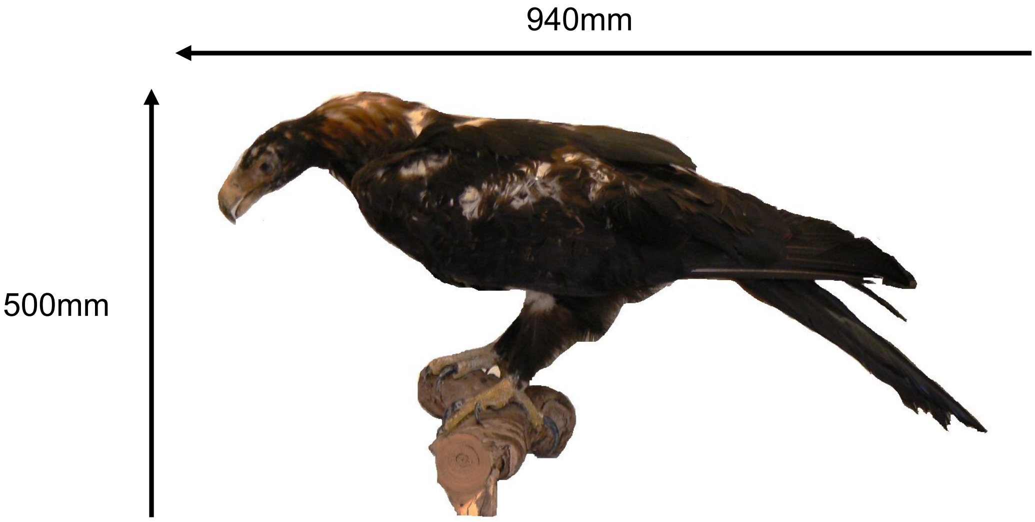


Figure 2.6. Wedge-tailed eagle (*Aquila audax*)**.** The wedge-tailed eagle is 85-107cm in length. Its wingspan is 185-230cm and males weigh 3.2kg (±0.5kg) and females 4.5kg (±0.8kg) (Marchant and Higgins, 1993). The main hunting techniques of a wedge-tailed eagle are glide attacks, direct-flying attacks or tail-chasing with the majority of prey being captured on the ground (Marchant and Higgins, 1993). Birds make up 10% to 28% of the wedge-tailed eagle's diet depending on the region (Baker-Gabb, 1984; Sharp *et al.*, 2002) and magpies consists of 0.6%-3.5% of the overall diet (Leopold and Wolfe, 1970; Brooker and Ridpath, 1980). The wedge-tailed eagle is relatively common in Armidale, at least two breeding pairs being observed within close proximity of Armidale and the university campus during the study period. The territories of some of these pairs encompassed Armidale and the University of New England.

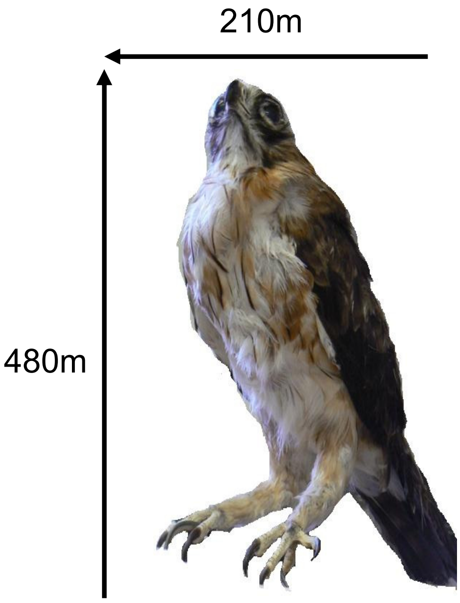


Figure 2.7. Little eagle (*Hieraetus morphnoides*). The little eagle is 44-45cm in length has a wingspan of 110-135cm. Male weighs 630g (±70g) and females 1000g (±200g) (Marchant and Higgins, 1993). The hunting methods of this species mainly consist of high soaring flights or attacks from perches (Debus, 1984). The majority of the little eagle's diet consists of mammals, primarily rabbits (Marchant and Higgins, 1993), However, when there are few rabbits available, the diet switches to birds representing up to 77% of the total diet (Debus, 1984). The magpie represents 6% of its diet outside the breeding season, rising to 18% when the magpie's offspring fledge 5.7% (Debus, 1984). A number of breeding pairs were identified to have home ranges near Armidale and the University of New England throughout this study. There were also a number of non-breeding little eagles in the area.

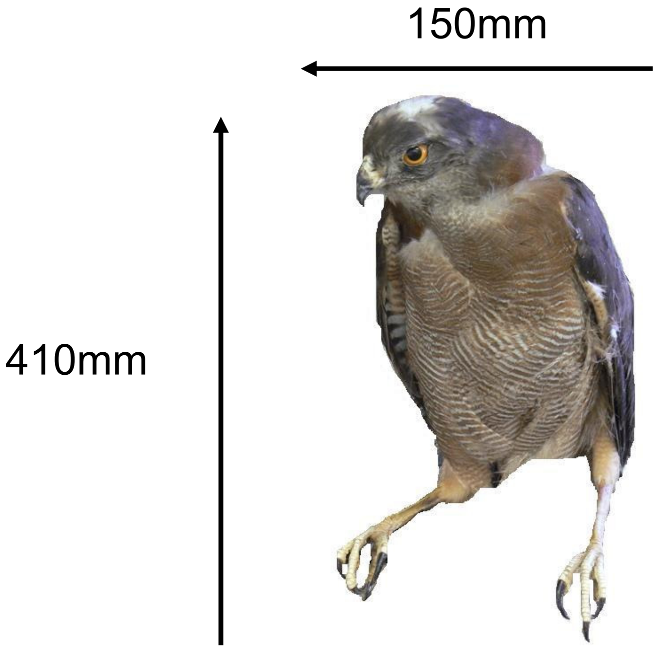


Figure 2.8 Brown goshawk (*Accipter fasciatus*). The brown goshawk is 40-55cm in length, has a 75-95cm wingspan and males weigh 310g and females 570g (Marchant and Higgins, 1993). The brown goshawk is an ambush hunter mainly hunting from a perch and flushing out prey, with the majority of attacks relying on stealth and surprise (Marchant and Higgins, 1993). The diet mainly consists of birds which varies from 37-67% in its diet (Marchant and Higgins, 1993). Magpies make up 0.8-4.3% of the brown goshawk's diet (Bravery, 1970). Brown goshawks are observed in Armidale but to a lesser extent than the two species of eagle described above.

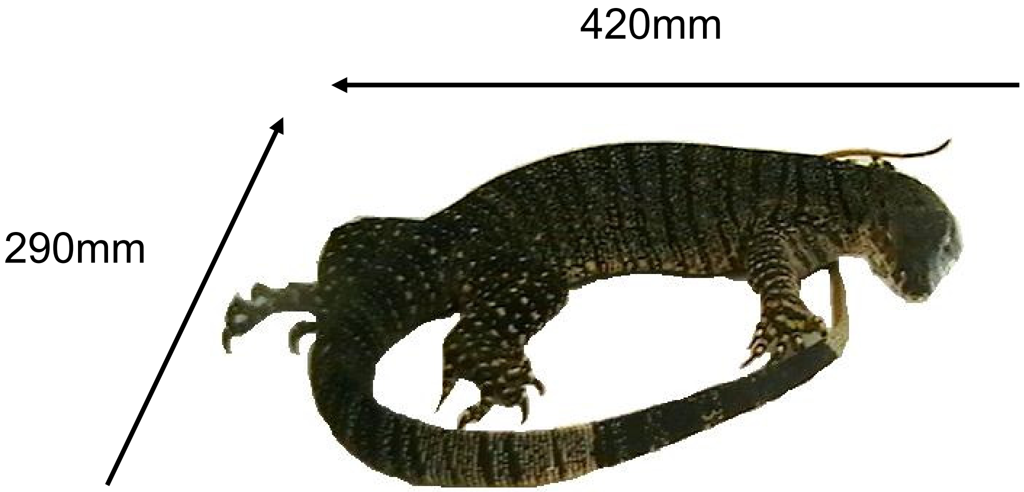


Figure 2.9. Lace monitor lizard (*Varinus varnus*). The lace monitor lizard is the second largest indigenous carnivore in Australia (Weaver, 1989). The diet of the lace monitor consists mainly of mammals and insects however, 16% of the diet consists of birds (Weaver, 1989). In Weaver's study (1989), most samples were unidentifiable but a juvenile pied currawong (*Stepera graculina*), a closely related species of the magpie, was found in the stomach contents and this would suggest that magpies may well be preyed upon by this species. It is known that they raid nest of eggs and nestlings of many avian species (King and Green, 1999).

Figure 2.10. Model snake. The model snake was 130cm in length and 6cm in circumference (taken 5cm from the tip of the mouth). The snake was dull in colour and resembled three species of snake that are relatively similar in size, shape and colour: a young brown snake (*Demansia textilis*), a copperhead (*Austrelaps superbus*) or even a small tiger snake (*Notechus scutatus*). This model was used in an earlier study on magpies (Koboroff and Kaplan, 2006) but then presented by moving it along the ground near magpie groups. In this current project, the snake, as every other model species, was presented in a stationary way for consistency of presentation.

2.3.2 Determining stimulus presentation area

The area, where stimuli were presented to each group, was chosen to be as close as possible to the centre of the territory and in an area known to be visited frequently by the magpies. This was done to ensure that neighbouring groups would not be attracted to the area and less ambiguity would arise as to whether any different levels of attention were or were not due to edge-effects of territory (Brown *et al.*, 1993) rather than to the predator itself.

Even though three of the five predators presented were aerial predators, all stimuli were presented on the ground. Apart from experimental consistency, this procedure also reflects natural circumstances since these specific aerial predators capture their prey on or near the ground. In other words, the trials aimed to test response to the predators rather than location of the stimulus.

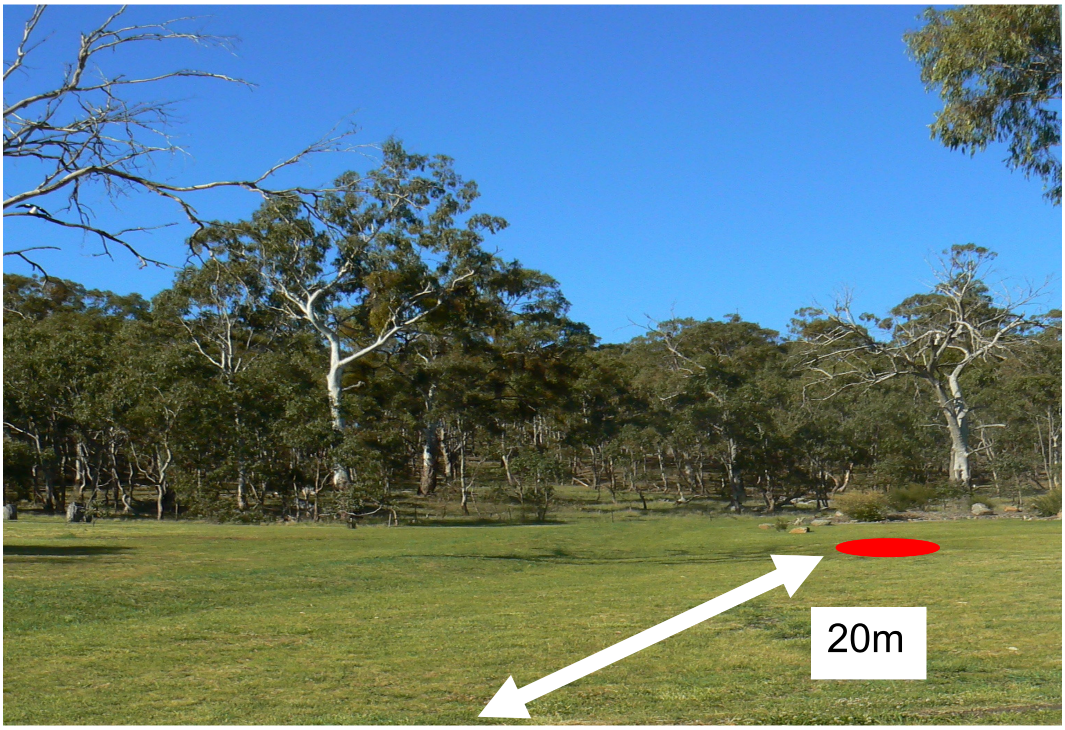


Figure 2.11. Stimulus presentation area taken from the experimenter's location. The red circle indicates the stimulus presentation area the arrow indicates the distance between the experimenter and the stimulus.

The presentation area also had to have no or few obstacles within a 20m radius to provide a clear view of the stimulus for the experimenter (Figure 2.11). Yet, during the testing period, the experimenter attempted to be as inconspicuous as possible. Apart from the inevitable need for placing or retrieving the stimulus, the experimenter remained behind structures and trees and also consistently wore dull-coloured clothes to blend in with the surroundings.

2.3.3 Experimental procedure

Testing took place between 0700h and 1100h, and at least 48 hours separated predator presentations to any one group. Each trial was allocated 45 minutes. This included a five- minute pre-test (to determine the behaviour of the magpies prior to the exposure of the stimulus) followed by the presentation of the stimulus.

Following the pre-test, the experimenter walked slowly towards to the pre-determined presentation area in a straight line and placed the stimulus on the ground. The wedge-tailed eagle, monitor lizard and snake were simply placed on the ground but the little eagle and the goshawk had their feet mounted on small metal stakes and these were pushed firmly into the ground.

A 30 minutes period was allocated for the magpies to detect the stimulus. This began once the stimulus was placed on the ground. Three criteria were assigned to determine if the stimulus had been detected:

1. At least one magpie approached within 5m of the stimulus.
2. The magpies emitted vocalisations and flew away from the presentation area.
3. A non-response to the stimulus was recorded when the magpies failed to do any of the above (failed to approach or flee).

Once any of the condition identified in the three points above occurred, the five-minute test began immediately.

The five-minute exposure time was selected based on previous experiments conducted by students of our laboratory. It was shown that a five-minute period of exposure produced the greatest number of responses (lower responses recorded in shorter time frames and decreases in response on exposure of 10 and 30 minutes respectively). Moreover, after periods longer than five minute exposure to a model predator, magpies began to show signs of stress (beaks open and feathers sleek). Hence, there were good ethical reasons to keep these presentations from to a five minute limit. Further, in my pre-experimental observations of actual magpie/predator interactions (mostly raptors), the experimenter was able to establish that these interactions generally did not exceed 5 minutes, predominantly because the raptor had moved away and beyond the territorial boundary. Hence, the selected time frame for exposure was also in line with observed natural interactions.

On conclusion of the five-minute scoring, the experimenter retrieved the stimulus, concealed it within a bag or covered it under a dark green and completely opaque blanket, walked away and only then the five-minute post-test began.

2.3.4 Methods of scoring behaviour

Two sampling methods were used throughout the field experiments: focal and group sampling (Martin and Bateson, 1993). The focal sampling method was selected to gather data on the response of an individual magpie throughout the pre-test, test and post-test, providing an opportunity to score changes of behaviour (presumed to be the effect of the presentation of a stimulus). Group sampling involved the experimenter scoring a number of behaviours for the entire group. It was imperative that the total number of events was scored for certain behaviours (i.e. such as swooping), in order to compare how often each behaviour was performed in toto in the presence of each stimulus over the total of the 5-minute test. The types of behaviour scored for both focal and group sampling will be described in Chapter 3.

2.3.4.1 Focal sampling

The focal bird was randomly selected prior to the commencement of a trial. One problem with the focal sampling technique is that the individual being sampled may move out of sight of the experimenter (Martin and Bateson, 1993). If the focal magpie moved out of sight of the experimenter, a time limit was given for the magpies to reappear (20 seconds or four intervals, see below). If the magpie remained out of sight, a new focal magpie from the same group was selected in order to maintain a standard 5 minute duration scoring for each testing phase.

The focal magpie was scored using the instantaneous recording method (Martin and Bateson, 1993) with an interval size of 5 seconds. The relatively short duration between intervals was selected in order to score as many events as possible. It was possible, of course, that an event could last longer than 5 seconds and this would have been scored in multiple samples. During focal observations the experimenter used a stopwatch and scored the behaviour of the magpie every 5 seconds.

2.3.4.2 Group Sampling

Continuous sampling of each behaviour was used when scoring the entire group. Group sampling was scored retrospectively using video footage. The video camera (see 2.4 below) had been set up to capture all events within a 5m radius around the stimulus. Group sampling was used for scoring group behaviour during the test phase of the presentation of the stimulus. As the number of magpies differed per group and across season (see Table 2.1), each measure was divided by the number of birds present during a trial. For example, if there were 5 magpies during a presentation of the little eagle and these magpies swooped 10 times, the number of swoops was standardised to 2 per birds.

2.3.4.3 Inter-observer reliability tests

An inter-observer reliability test was conducted using an observer naïve to magpie behaviour but trained in established methods of scoring behaviour. Seven trials were randomly selected and these were played to the observer. There was a strong and significant congruence of data collected between the naive observer and the experimenter (*r* = 0.98, p = 0.000).

2.3.4.4 Checks on scoring method

To check whether the method of standardising the scoring of the entire group (i.e. dividing the total number of scores by the number of magpies; see 2.3.4.2 above) was accurate, I analysed whether there was a relationship between the number of swoops scored during the focal magpie data and the number of swoops scored per bird (Figure 2.12).

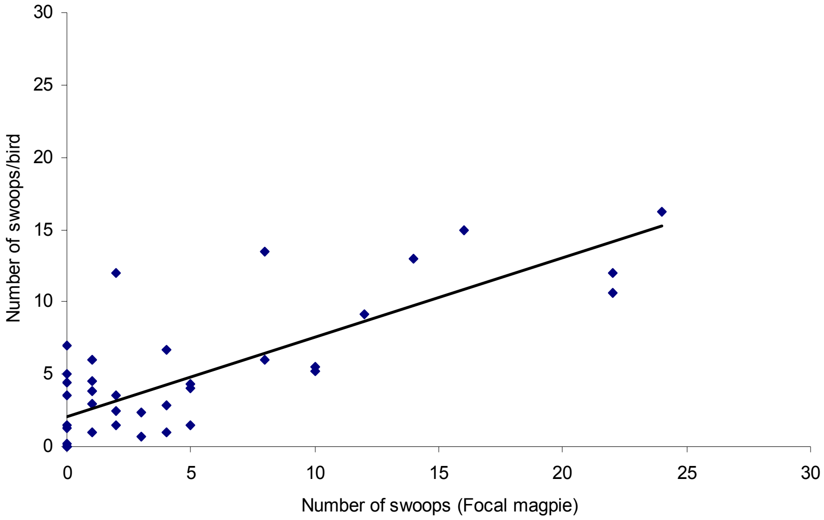


Figure 2.12. Correlation of the number of swoops scored for the focal animal and the number of swoops scored for the group adjusted for the number of birds. The relationship between the focal and group/bird data was strong and significant (Spearmans Rho = 0.786, p = 0.000).

There was a strong and significant relationship between the focal animal and the group scores (per bird). This suggests that the method of standardisation is accurate.

2.4 Materials

Each presentation of the model predators was filmed using a Panasonic digital video recorder (NVGS35). Alarm calls were recorded using a Tascam DAT recorder (DA-P1) and a Sennheiser microphone (ME66+K6P). Observation in the field were noted using pen and paper.

2.5 Statistical Analyses

Prior to any analyses, the data were tested for normal distribution (Shapiro-Wilk) and homogeneity of variances (Levene's test). If the data were not normal and/or had unequal variances, square-root or log transformations of the data were attempted. If these transformation were unsuccessful, non-parametric test were conducted. The experimental design used was a repeated measure with stimulus being the measure that was repeated. If the data were normal, an analysis of variance using a general linear model was performed. *Post hoc* analysis used the Tukey's test. Non-parametric data used a Friedman's test and *post hoc* analyses were a two-sample Wilcoxon signed ranks test.

CHAPTER 3. ETHOGRAM OF ANTI-PREDATOR BEHAVIOUR

3.1 Introduction

In this chapter, I present results of detailed observations of anti-predator behaviour by magpies made in the context of an extended preliminary experiment, and I describe specific sequences of their behaviour during experimentally manipulated ‘predator’ encounters (taxidermic models). Before a protocol of scoring methods could be established, it was important to undertake these preliminary observations. It was hoped that an ethogram could be established of the suite of behaviours that might be associated with encounters of potential predators. My observations had to remain open-ended, in a sense, so that I would not prejudge what I observed (Lorenz, 1965). Out of the many behaviours I observed, I was particularly interested in consistent sequences of events in such encounters. Usually, these are referred to as ‘stereotyped’ behaviour, not in the sense in which animal welfare uses it as an aberration and as of signs of stress (Mason, 1991), but as a fixed strategy in response to a specific stimulus (Tinbergen, 1951).

Some general information on mobbing in magpies is known. Genelly (1978), for instance, observed magpies approaching Australian kestrels (*Falco cenchroides*) on numerous occasions and flying directly at the predator. Koboroff and Kaplan (2006) reported that magpies may inspect moving snakes and Kaplan (2004) described mobbing behaviour of magpies as continuous vocalising and swooping of the predator. Largely, however, the literature uses general terms such as “attack”, “chase”, “harass” or “mob” (Carter, 1924; Lord, 1952; Austin, 1953; McGill, 1955; Watson, 1955; Robinson, 1956; Favaloro, 1981; Metcalf, 1989;

Debus, 1993; Brown *et al.*, 2000) to describe anti-predator behaviour of magpies. Details of how magpies approach predators, what specific types of behaviour they actually perform and whether they inspect predators are not revealed by these summary descriptions. Hence, it was imperative to describe how magpies respond to certain predators and ascertain what kind of stereotyped behaviours, if any, may be performed by the magpies during a mobbing event.

In magpies, as in many other avian species, mobbing is often accompanied by incessant vocalisations. However, few birds possess as many alarm calls as the magpie and some of these vocalisations play an important role in mobbing behaviour (Kaplan, 2006a). In a recently submitted paper, Kaplan *et al.* (submitted) categorised about 27 different alarm calls into five alarm call categories. These were elicited during presentations of taxidermic model predators (little eagle, wedge-tailed eagle and monitor lizard). Three call types were elicited at the same rate for all three stimuli but two call types were elicited by the two model eagles and in contexts where these predators are known threats (Kaplan *et al.*, submitted). The findings suggested that these two alarm calls might be "eagle" alarm calls and thus specifically related to predatory events. I will come back to the importance of vocalisations particularly in the discussion of predator inspection (Chapter 5).

For anti-predator strategies in magpies, I was able to draw on Brown and Veltman (1987), to some extent, who established an ethogram of a number of important behaviour types in magpies. This included a detailed description of foraging, of patterns of territorial advertisement and of some specific social behaviour. The most pertinent section of their paper that I thought might be relevant to anti-predator behaviour concerned “aggressive” behaviour, since this type of behaviour may be used in response to predators. Brown and Veltman (1987) described 12 types of “aggressive” behaviour. Four threat postures were named but, most importantly, six types of contact behaviour were identified namely, pecks, jump on, wrestle, bite, take down, and dive bomb. Some of these behaviours are very much part of juvenile play behaviour too (Pellis, 1981a; 1981b) and, as said before, may be retained into adulthood for specific reasons.

Table 3.1. Description of some of the types of behaviour described by Brown and Veltman (1987).

Behaviour	Description
Bipedal locomotion	Walking and running
Preening	The head is scratched with the foot. Manipulates primary and secondary feathers with bill
Fly	Magpie flaps its wings 3-4 per second and retracts its feet up to its body
Sit, alert	Feathers are flattened and the legs are straightened and the bill extended
Peck	Jab at conspecific with closed beak
Jump on	Leap on the back of a conspecific
Wrestle	Opponents lock feet together and attempt to peck and pin down each other
Bite	Pinches a conspecific’s body part between the mandible
Take down	Attempt to bring a conspecific down while in flight
Dive bomb	A magpie flies directly at a perching conspecific and knocks it off its perch

.

These types of behaviour (Table 3.1) were partly used as a guide to establishing a scoring sheet for my observations (see Section 3.2).

Here, I will discuss whether there are: (a) similarities between anti-predator behaviour and agonistic displays to conspecifics (b) valid comparison to be made between anti-predator behaviour of magpies and other avian species and (c) whether stereotyped sequences of behaviour are performed to all model predators or whether there are types of behaviour only associated with certain model predators.

3.2 Methods

This preliminary experiment was conducted observing five residential and permanent magpie groups between January and June 2005. All five groups that were tested contained juveniles. Each group was presented with a taxidermic model of a wedge-tailed eagle, little eagle and a monitor lizard. The models were presented once for 5 minutes per group in a random order in the centre of each group's territory. The entire group was observed and all behaviour was recorded. The materials and methods are otherwise as described in Chapter 2. Alarm calls were also recorded.

The behaviours that were scored in these observations are described in Table 3.2 and were derived both from Brown and Veltman (1987) and from my own previous experiments in a separate project (see Koboroff and Kaplan, 2006). It was important to be precise in scoring these behaviours as it was to be investigated whether the magpies may adapt their anti-predator behaviour to various predators.

Table 3.2. Description of the types of behaviour scored with comparison to Brown and Veltman's (1987) description.

Behaviour	Description	Brown and Veltman's (1987) terminology
Stationary on the ground	No locomotion. Substrate ground	N/A
Stationary on the perch	No locomotion. Substrate a perch. A perch was defined as a branch of a tree or a man-made object (i.e. power line) that was at least 2m off the ground	N/A
Walking	Walking while perching or on the ground	'Bipedal locomotion'
Running	Running while perching or on the ground	'Bipedal locomotion'
Flying	Same as Brown and Veltman (1987) Note this was scored separately from swooping.	'Fly'
Foraging	Same as Brown and Veltman (1987)	'Foraging behaviour' and 'food item manipulation'
Preening	Same as Brown and Veltman (1987)l	'Preening'
Alert posture	Tall posture with feathers sleeked. Head moves periodically from side to side along the horizontal axis	'Sit, alarm'
Wing extensions	While on the ground or perching, the magpie extends its wings. Note that this behaviour does not precede flight.	Similar to 'lands wings up' but it does not necessarily occur after flight
Physical contact	Coming into contact with the model predators	'Contact fighting'
Swooping	A dive towards the model and coming within 1m of it.	'Dive bomb'
Pecking	Attempting to or achieving contact with the model predator with the bill	Combination of 'Peck' and 'Bite'
Jumping	A vertical movement with some wing flaps but the magpie does not take flight and does not make contact with the model	A variation of 'jump on'
Circling	The magpie walks (occasionally runs) in an arc around the model predator.	N/A
Stationary viewing	Tall posture with feathers sleeked. Magpie is stationary. Head moves periodically from side to side along the horizontal axis to monocularly fixate the model	Variation of 'Sit, alarm'

3.3 Results

Of the fifteen types of behaviour that were observed (Table 3.3), eight were observed only during the presentations of the model predators. The behaviours that were excluded (walking, running, flying, foraging, preening and wing extensions) were either not a direct response to the predator or the behaviour was rarely observed.

Table 3.3. Types of behaviour observed.

Behaviour	Occurrence	Selected for further investigation
Stationary on the ground	Often	No
Stationary on the perch	Often	No
Walking	Often	No
Running	Often	No
Flying	Often	No
Foraging	Rarely	No
Preening	Often	No
Alert posture	Often	No (but further description given)
Wing extensions	Rarely	No
Physical contact	Rarely	Yes
Swooping	Often	Yes
Pecking	Often	Yes
Jumping	Often	Yes
Circling	Often	Yes
Stationary viewing	Often	Yes

3.3.1 Behaviour observed

Seven main types of behaviour were observed during the presentation of model predators. The various types of agonistic behaviour were performed either on the ground or in flight. Swooping was obviously an aerial behaviour while pecking and jumping were behaviours typically carried out whilst on the ground. Circling and stationary viewing were also typically ground based behaviours. Although stationary viewing may have occurred while the magpies were perching, it was difficult to determine from a distance whether the magpies were fixating the stimulus.

3.3.2. Aerial behaviour

3.3.2.1 Swooping

Swooping was recorded frequently throughout this experiment. It was identified as a flight towards and coming within 1m of the stimulus (Figure 3.1).

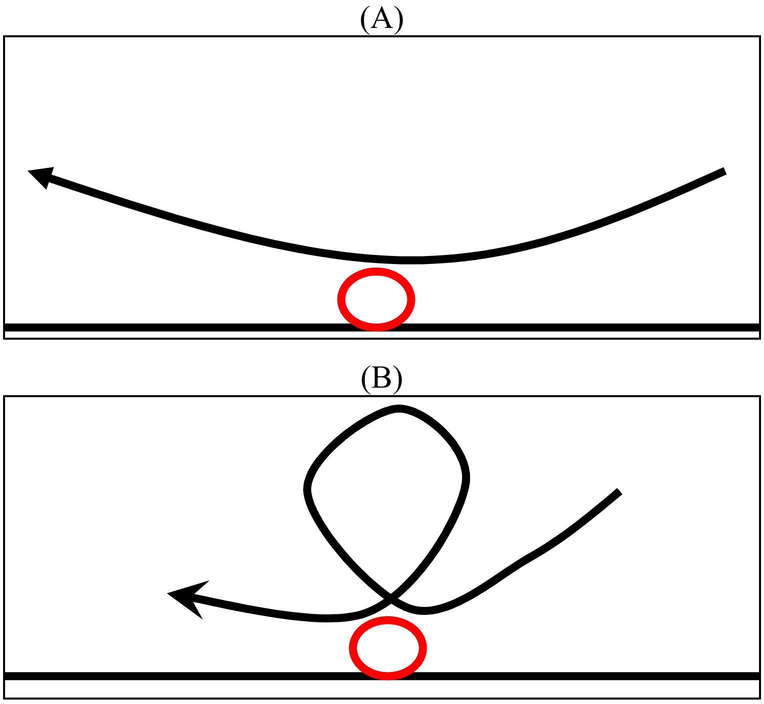


Figure 3.1. Diagrammatic description of swooping flight patterns. The red circle indicates the model predator from the side and the black line indicates the swooping path. (A) shows a direct swoop flight pattern. (B) shows a looping swoop flight pattern.

Swooping and dive bombing, as described by Brown and Veltman (1987), are similar except that swooping does not always result in contact with the stimulus but, from Brown and Veltman's (1987) description, it seems as though dive bombing does result in contact. Two forms of swooping flight patterns were observed consistently within and between groups. One was a direct flight in which the magpie flew towards the model predator and continued in same direction

(Figure 3.1A). The other was a direct flight towards the model predator but, instead of continuing in the same direction, the magpie flew up, turned mid air and returned to swoop the model again in a steep downward flight. This was termed a looping flight pattern (Figure 3.1B).

3.3.3 Ground based behaviour

3.3.3.1 *Pecking*

Pecking behaviour showed little variation between or within groups. During a "pecking event", an individual magpie was observed on the ground within a 5m radius of the model predator and it began to move towards the model with its wings extended and then attempted to peck the model. It was a fast manoeuvre involving a magpie moving quickly towards the stimulus and protruding its neck so that the beak, with the mandibles open, either touched or came close to touching the stimulus.

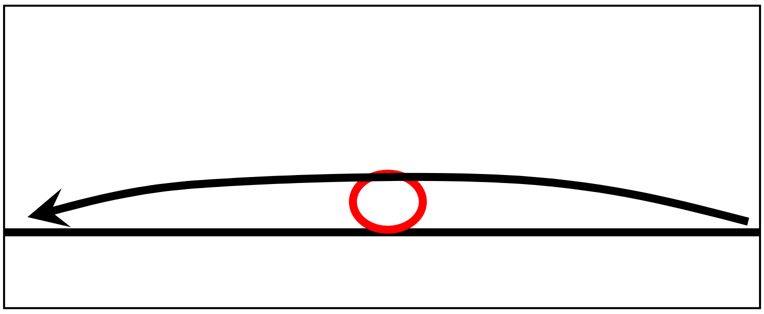


Figure 3.2. Diagrammatic description of a pecking event. The red circle indicates the model predator from the side and the arrow indicates the movement of the magpie.

The approach to the predator also usually involved running or, sometimes, a low flight no more than 1m above ground level (Figure 3.2). Pecking behaviour was similar to "bite" behaviour (Brown and Veltman, 1987) although "bites" apparently do not inflict pain on conspecifics (Brown and Veltman, 1987).

However, during some pecking events on the little eagle, feathers were plucked from the model and the magpies targeted the eyes of the model predator.

Note that 'pecking behaviour' elicited by the model predators as defined here was different to "pecks" described by Brown and Veltman (1987). In the former case, the beak was opened while in the later case the beak was described as closed.

3.3.3.2 Jumping

Jumping behaviour was recorded when a magpie was on the ground within 5m of the model.

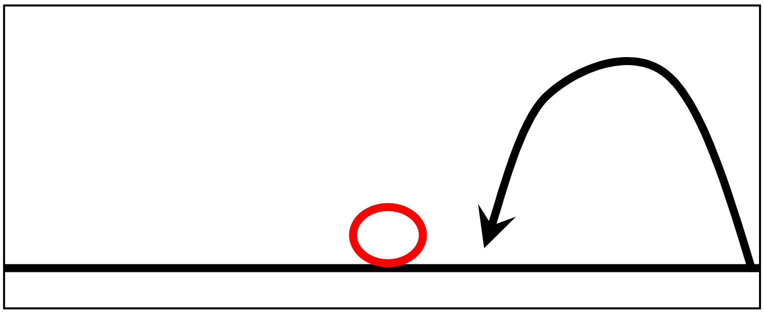


Figure 3.3. Diagrammatic description of a jumping event. The red circle indicates the model predator from the side and the arrow indicates the movement of the magpie.

The magpie jumped up (approximately 1-1.5m above the ground) with one or two flaps of the wings and landed on the ground again (Figure 3.3). It did not take flight during a jumping event. On occasion, the magpie jumped over the model but most jumps were performed next to the model. Note that the magpies did not attempt the make contact with the model predators at all during this behaviour.

3.3.3.3 Walking around the stimulus (Circling)

The magpies were observed to approach the stimulus while on the ground and walk/run around it in an arc at close proximity (termed circling hereafter; Figure 3.4).

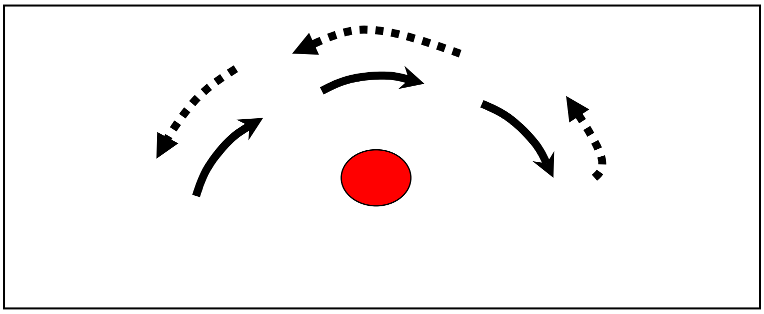


Figure 3.4. Diagrammatical description of a circling event (overhead view). The red circle indicates the model predator and the arrow indicates the movement of the magpie.

Typically, this behaviour of circling was performed as an arc, not as a full circle, and the magpie walked around the stimulus in both directions (i.e. clockwise and anti-clockwise).

The magpies walked in a semi-arc around the model then stopped, visually fixated it, and then began to walk the same way back in a semi-arc around the model once again.

3.3.3.4 Stationary viewing

The magpie was stationary on the ground within 5m of the model predator and fixating the model using its lateral fields of vision. The head turned back and forth for several such visual fixations. The magpie may adjust its posture slightly to enable it to view the model with the other eye. For example, in Figure 3.5, the magpie has moved slightly to its left in order to fixate the lizard with the right eye.

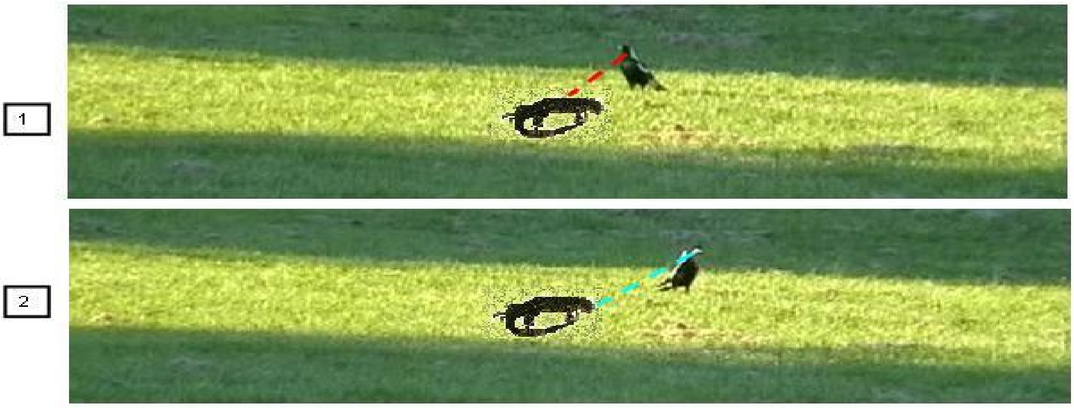


Figure 3.5. Sequence of video footage showing a stationary viewing bout. The red line indicates a left eye monocular fixation and the green line indicates a right eye monocular fixation.

In a later chapter (Chapter 6), this behaviour is analysed separately to determine whether viewing during an encounter with a predator is lateralised.

3.3.4 Physical contact

During some swooping and pecking events, the magpies made contact with the model. Contact was rarely scored but, when they did make contact, the force with which the magpies hit the model was considerable. They made contact using their legs or beak and this was directed mostly at the back of the head. Over the time of these experiments, the taxidermic raptor models lost feathers specifically on the nape of the neck. Also, the model was forced off balance and hit the ground face-down despite their weight and being anchored to the ground. This was rare, however.

3.3.5 Postural changes

In addition to the types of behaviour described above, it was noted that the magpies also adopted an erect, alert posture once a stimulus was presented (Figure 3.6). Brown and Veltman (1987), described this behaviour as “sit, alarm”. The difference between the two postures is clearly visible, even from a distance.

(A)

(B)

Figure 3.6. Relaxed and vigilance postures adopted by the magpies. (A) Relaxed posture of a magpie prior to the presentation of the model predator. (B) Vigilance posture during presentation of the model predator. Note how the feathers are sleeked and that the magpie is standing fully erect.

In the relaxed posture, the magpie's legs are not extended and the feathers may be ruffled, while the magpie in an alert posture extends its legs, stretches its neck and the feathers are sleek. The magpies adopted this posture immediately once the models were presented. All model predators elicited this posture. Unlike Brown and Veltman's (1987) description of this posture, the magpies did not take flight after they adopted this stance. Moreover, it was not always accompanied by alarm calls.

3.3.6 Alarm calls

The magpies performed numerous alarm calls during most of the presentations of the model predator and these are presented in Figure 3.7.

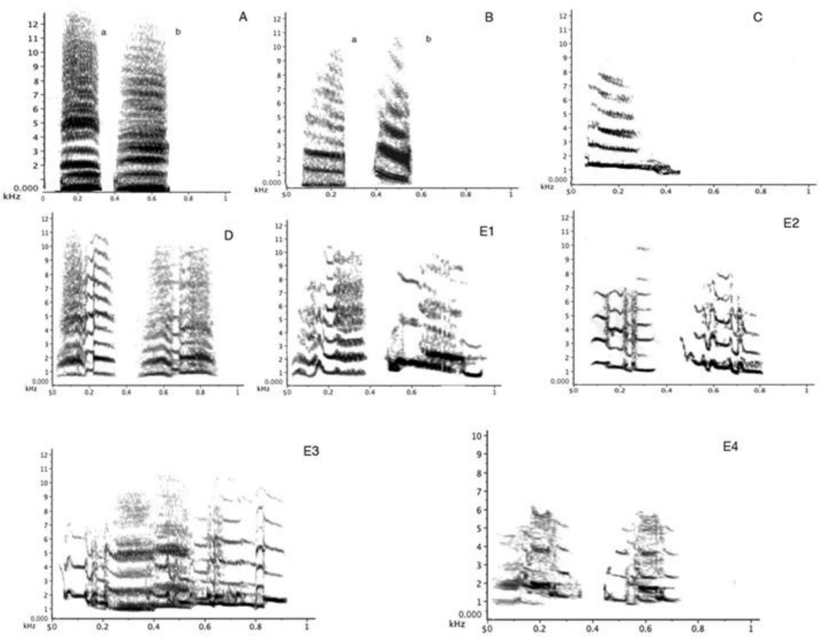


Figure 3.7. Sonogram of magpie alarm calls elicited by model predators. Call A, known as the 'noisy' call is performed during territorial conflict as well as during encounters with predators. Call B, is the most common alarm call (Kaplan, 2006b). Call C is a high alert alarm call. Calls D and E are only produced during an encounter with a predator. These two calls were elicited by the eagle models and only in areas where the eagles are known to be threats.

Calls A-C were elicited by all predators while calls D and E were specific to the eagle stimuli only. Irrespective of stimulus, calls A and B were the most common call type produced because these were generic and not stimulus dependent. A separate paper has just been submitted on this question (Kaplan *et al*., 2008).

The magpies immediately vocalised once a model was presented to them. However, one of the very crucial findings of this research presented in this thesis is that magpies do not always vocalise when approaching a predator. As will be shown later (Chapter 5), there are significant differences between non-vocal and vocal approaches towards predators which help to differentiate between mobbing and predator inspection.

3.3.7 Types of behaviour elicited by the various model predators

The magpies performed different types of behaviour depending on the predator that was presented (Table 3.4).

Table 3.4. Observation of behaviour during presentation of the model predators.

Behaviour	Little eagle	Wedge-tailed eagle	Monitor lizard
Alert posture	Yes	Yes	Yes
Physical contact	Yes	Yes	No
Swooping	Yes	Yes	No
Pecking	Yes	Yes	No
Jumping	No	No	Yes
Circling	No	No	Yes
Stationary viewing	No	No	Yes

The magpies spent time on the ground during the monitor lizard presentations and were swooping during the aerial predator presentation. Moreover, during the presentations of the lizard, jumping, circling and stationary viewing were observed but these types of behaviour were not observed during the aerial predator presentations.

3.4 Discussion

In a single event that is generally summarised as "mobbing", magpies actually performed a whole suite of behaviours but not all together in one presentation and not all for the same stimulus. Most studies on mobbing behaviour broadly define only two main types of behaviour namely mobbing calls and the posture of the animal (for example: Lombardi and Curio, 1985a; Flasskamp, 1994; Ostreiher, 2003; Krams *et al.*, 2006; Graw and Manser, 2007). Magpies clearly adopt a vigilance stance (posture with feathers sleeked) as shown in Figure 3.7 but they also performed swooping, pecking, jumping and viewing of the model predators.

Swooping and pecking (perhaps also jumping) are not unique to magpies. Such behaviours have been described in other species. These behaviours appear to be extremely confrontational to a potential predator. If a predator does not move from the area, it could suffer injury or even death. Therefore, this is indirect evidence to support the 'move-on' hypothesis (Curio, 1978). Indeed, there are some examples of other species performing pecks, such as the redwinged blackbird *Agelaius phoeniceus,* (Siglin and Weller, 1963) yellow-headed blackbird *Xanthocephalus xanthocephalus* (Siglin and Weller, 1963), toucan barbet *Semnornis ramphastnus* (Restrepo and Mondragón, 1998); swoops/dives: Black tern *Chlidonias niger* (Siglin and Weller, 1963), forster tern, *Sterna forsteri* (Siglin and Weller, 1963).

Some of the behaviours described in this chapter resemble those described by Brown and Veltman (1987). For instance, in territorial advertisement, magpies may perform a “swoop up” flight. Here, magpies fly in a straight line just above the ground then fly straight up and either return to the ground or turn around in flight and return to the perch. This behaviour closely resembles swooping behaviour elicited by the model predators. One possible explanation for the similarities is that swooping, especially looping swoops, may also display a magpies territory to neighbouring groups.

It is also noteworthy that some behaviours may first arise developmentally in a different context. For instance, Pellis (1981a; 1981b) described play fighting in juvenile magpies. Many of the behaviours described mimic the agonistic displays performed during hostile conspecific interactions in adults. However, some of the behaviours (such as swooping) also form part of the mobbing response to predators. Hence, play fighting may not only develop social skills but also hone anti-predator behaviour.

All behaviours were approach-type behaviour drawing the magpies within 5m of the stimulus. The magpies performed ground based behaviour when faced with the lizard and aerial behaviour when presented with the aerial predators. This suggests that magpies adapt their anti-predator behaviour to different predators and seem to have a sophisticated anti-predator repertoire since they do not increase or decrease mobbing intensity but perform completely different behaviours. Moreover, the alarm calls that the magpies produced varied between stimuli. Two calls were found to be specific to the eagles (Kaplan *et al.*, submitted.). Calls A-C are known to be produced in other contexts not involving predators such as conspecific intrusions (Kaplan, 2006c; Kaplan, 2006a) but calls D and E were produced only during the model eagle presentations. Indeed, one of them, Call D was identified by Brown and Veltman (1987) as a call used when a magpie is in the air mobbing an aerial predator. Overall, the alarm calls of the magpies comprises a complex repertoire of vocalisations (Kaplan *et al.*, submitted). The function of these calls may be to communicate to conspecifics predator type (Call E) and the degree of threat (Call D). While other call types, such as Call A, may form part of the mobbing repertoire aimed at harassing the predator to make it leave the area.

It was important to identify specific behaviour during the mobbing response. Descriptions such as “attack” and “mob” were not able to entirely describe the interaction between predator and prey. Indeed, the identification of the behavioural elements of mobbing behaviour by magpies has lead to the discovery of various mobbing strategies performed to a variety of predators and having established the specific behavioural strategies it was then possible to conduct the experiments using these categories as descriptors in order to delineate the complexities of approach behaviour in predator encounters.

CHAPTER 4. MOBBING BEHAVIOUR OF AUSTRALIAN MAGPIES

4.1 **Introduction**

The anti-predator strategy that an animal employs in response to a predator is influenced by a variety of factors. The species of predator is one such factor. That is, animals may not have a generic response to all threats but have specific responses to a specific species of predator. Indeed, many animals vary their anti-predator behaviour according to the predator with which they are confronted (Kruuk, 1964; Burger, 1974; FitzGibbon and Lazarus, 1995; Graw and Manser, 2007). Another factor influencing anti-predator behaviour may be the presence or absence of young. For instance, females with offspring may be more vigilant (Halofsky and Ripple, 2008) and increase predator directed behaviour, such as mobbing, than non-parenting adults (Swaisgood *et al.*, 2003). Indeed, there are seasonal variations in behaviour that coincide with the presence or absence of young (Shedd, 1982; Shedd, 1983). Here, I investigate whether stages of juvenile development and the predator type or species would influence approach behaviour in the Australian magpie.

In the ethogram, I presented observations that demonstrated variation in the behaviour of magpies towards the aerial predators and the ground predator, lizard. However, so far I have not established the intensity of the magpies’ response. It also remains to be shown that different anti-predator strategies are based on assessment and are consistent, in each case. The latter remains to be explored in Chapter 7. Indeed, mobbing intensity can provide vital information about the threat that animals perceive. For instance, meerkats mob certain species of snakes more than others which suggests that they perceive some snakes as a greater threat (Graw and Manser, 2007). Californian ground squirrels, by detecting the auditory differences in the intensity and spectral composition of rattling sound, perceive larger snakes as a greater threat than smaller snakes (Swaisgood *et al.*, 2003). They also perceive snakes with a higher body temperature as more of a threat than those with a lower temperature (Swaisgood *et al.*, 2003). Indeed, there is direct evidence that warmer snakes are a greater threat than cooler ones because, at raised body temperatures, they can strike faster than at lower temperatures (Rowe and Owings, 1990). Mobbing intensity may thus not only reflect a perceived threat but the actual threat. In this experiment, I investigated whether the intensity of mobbing and inspection behaviour would vary depending on which model predator was presented to the magpies. Intensity of response was determined by scoring the total number of times the magpies performed mobbing behaviour. Here I will now take the preliminary experiment and expand it to add another two model predators and to a full sample size.

There is some evidence to suggest that the intensity of approach behaviour, particularly mobbing, varies according to the season. Shedd (1982) found that American robins (*Turdus migratorius*) mobbed more intensely during the breeding season. Shedd (1983) also found an increase in mobbing intensity during the breeding season for black-capped chickadee (*Parus atricapillus*) but intensity decreased following the dispersal of the juveniles. Mobbing behaviour may thus serve to protect young. However, it may not be simply the presence of juveniles but their age or developmental stage that may have a stronger influence on anti-predator behaviour. In Californian ground squirrels, adults take fewer risks in predator encounters when juveniles are older (Swaisgood *et al.*, 1999). This may be so because older juveniles may be less vulnerable to predators and thus require less protection (Swaisgood *et al.*, 1999).

Mobbing is not the only behaviour that varies across time. Exploration may also be influenced by seasons. Mettke-Hofmann (2007) found that exploration behaviour peaks during the breeding season. Therefore, if exploration can be influenced by seasonal variation, it would be expected that inspecting predators may also vary across time.

Following the evidence so far available only in mammals, as in Californian ground squirrels, the presence and age of juveniles influences anti-predator behaviour of the adults (Swaisgood *et al.*, 1999; Swaisgood *et al.*, 2003). I therefore selected three time periods, called stages from here on, which coincide with juvenile age/development of magpies. The first stage (September 2005 to January 2006) coincided with the presence of raising juveniles that had recently fledged (fledging occurred in early to mid September 2005). In this stage, offspring were at their most vulnerable and for up to 3 months post fledgling magpie juveniles are still being fed by the adults (Kaplan, 2004). Hence, the response of the adults to the model predators was predicted to be the most intense during this stage compared to other times of the year.

During the second stage (February to April 2006) juveniles began to be more independent (involved in independent feeding and often moving about by themselves or in sibling groups), aged approximately 5-7 months. Juvenile magpies in the region studied generally disperse from the natal territory at around 8 to 10 months of age (Kaplan, 2004). However, during this stage the juvenile remained in their natal territories. It was hypothesised, following the findings of Swaisgood *et al.*(2003), that the response of the magpies to the model predators should decrease in intensity as the juveniles would no longer require as much protection as they did immediately post-fledging.

The third stage selected (June to August 2006) is generally the time of year in which juvenile birds either have dispersed or are about to do so. In 2006, some juveniles were still in their natal territory. Hence, juveniles were present during all three stages of testing. This is the time of year when magpies in the region begin to close their territories, in preparation for the next breeding season, and boundaries are defended. It is also possible that they defend their territories from predators with particular intensity in preparation for the next breeding season.

4.2 **Methods**

Fourteen magpie groups were presented with each of five model predators (wedge-tailed eagle, little eagle, brown goshawk, monitor lizard and snake). Each model was presented once per group per stage (i.e. Stage 1: September 2005 to January 2006; Stage 2: February to April 2006; Stage 3: June to August 2006). The order of presentation of the models was random within a stage and an inter-test interval of at least 48 hours was given to any one group. The reasons for selecting these predators were outlined in detail in Chapter Two. Suffice it to say here that, as described, there is evidence that these species are, in fact, natural enemies of magpies.

Each trial was conducted over a 15-minute period consisting of a 5-minute pre-test, 5-minute test (presenting the stimulus) and a 5-minute post-test. During the entire trial, the experimenter scored a focal magpie for the number of swoops, pecks, jumps, circling and stationary viewing.

Table 4.1. Sample size for each stage of testing.

Stage	Months	Number of presentations	Total number of groups
Stage 1	September 2005 to January 2006	70	14
Stage 2	February to April 2006	105	14 (plus 7 groups that had not been tested previously)
Stage 3	June to August 2006	70	14

In order to see whether agonistic behaviour and/or inspection behaviour varied across stages, swooping, jumping, pecking, circling and stationary viewing were analysed from video-footage (see Chapter 3 for detailed descriptions of these behaviours). During Stage 1 (September 2005 to January 2006) the type of swooping pattern was scored in order to determine whether there were subtle differences in response of the magpies to the various aerial predators.

The data were tested for normality (Shapiro-Wilk) and homogeneity of variances (Levene's test). Most of the data were found to be skewed and they did not have equal variance. Therefore, non-parametric repeated measures analyses were conducted using the Friedman's test with stimulus as the repeated measure (little eagle, wedge-tailed eagle, brown goshawk, lace monitor and snake). The Wilcoxon Signed Ranks test was used for *post hoc* analyses. For data that were normal/equal variances, parametric analysis was conducted using a general linear model with stimulus as a repeated measure.

4.3 **Results**

Four of the model predators (little eagle, wedge-tailed eagle, brown goshawk and monitor lizard) elicited approach behaviour during the majority of presentations across all stages (71%-86% out of 42 trials per stimulus). However, the snake was presented to the magpies across all stages for a total of 42 presentations and, out of these, the magpies approached it in only four trials. When they approached the snake, it was only briefly (<1 minute) and they approached it while on the ground. They performed circling and, occasionally, stationary viewing but did not vocalise. During the majority of presentations when the magpie neither approached nor avoided the snake**,** it was noted that the magpies appeared to have viewed the stimulus from a distance of greater than 5m. Generally, they were found perching nearby and were observed tilting their heads to the side to look down and visually fixate the model monocularly. Since the snake elicited very few approaches or any other distinct behaviour, trials involving the snake were not included in the analyses.

For the other model predators, there were also trials that elicited no recording of a given behaviour. In these few cases, the magpies neither approached nor avoided the little eagle (N=5), wedge-tailed eagle (N=8), brown goshawk (N=7) or the monitor lizard (N=13).

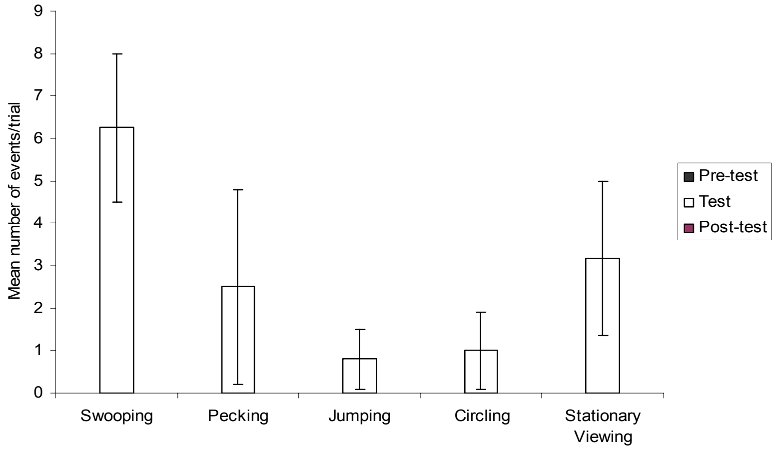
The magpies rarely avoided any of the predators. In fact, no avoidance behaviour was observed during presentations of the little eagle, wedge-tailed eagle and monitor lizard. However, two (out of 42) brown goshawk presentations elicited avoidance behaviour (magpies flying away to the other end of the territory) accompanied by alarm calling.

In the following sections, the results are, first, presented for each behaviour observed in the pre-test, test and post-test periods across all stages (1, 2 and 3) and for all model predators (except the snake). This is followed by presentation of results of Stage 1 in detail for each behaviour observed for the test period only (i.e. presentation of the model predators). The data are then presented across all stages (of juvenile development) but only during the test period for each stimulus and separately across all three stages in order to take into account possible changes in behaviour according to the stage of juvenile development.

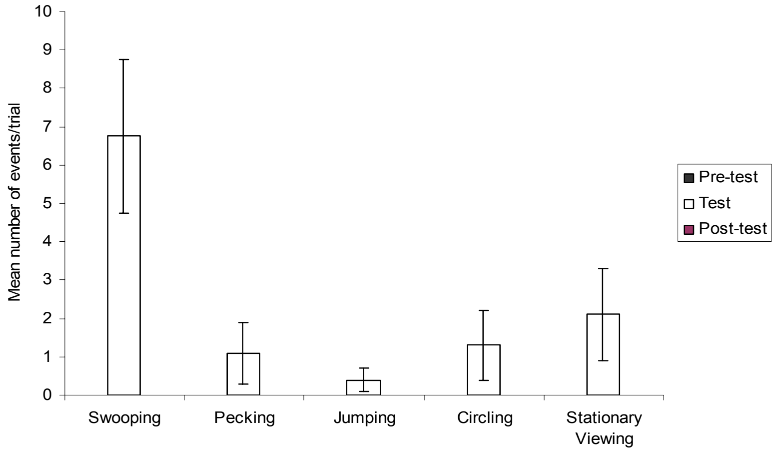
4.3.1 Results for each testing period across each stage

During the pre-test and post-test behaviours such as swooping, pecking, jumping, circling and stationary viewing were absent. They were specific to the testing period and hence no statistical comparisons of pre- and post-tests with the test phase were made because the differences were obvious (Figure 4.1 to 4.5).

(A) Stage 1: little eagle presentations



(B) Stage 2: little eagle presentations



(C) Stage 3: little eagle presentations

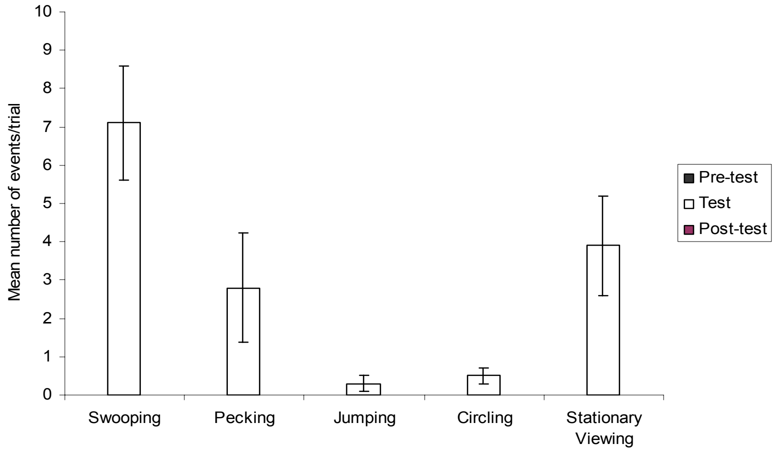
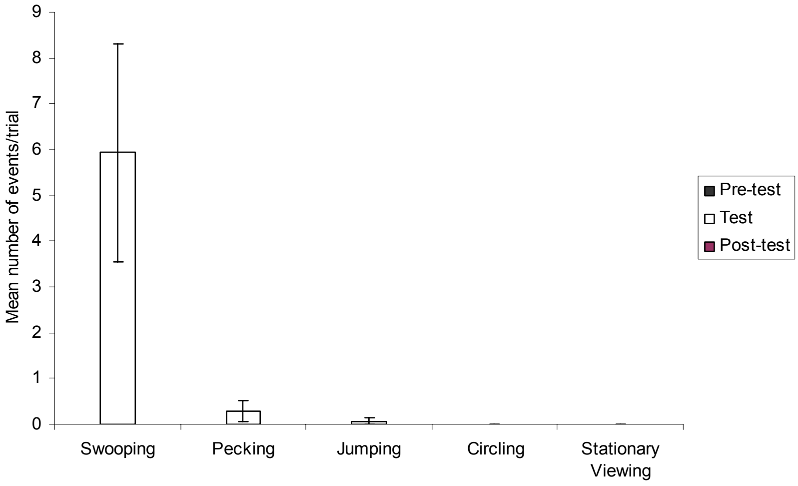
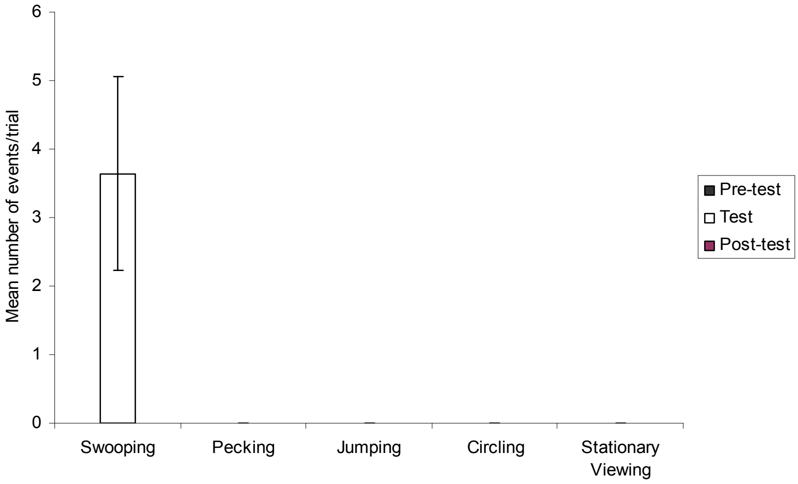


Figure 4.1. The results for the pre-test, test and post-test periods for the little eagle across each stage of juvenile development. The mean number of events ± SEM are plotted for each behaviour (X axis). These data were obtained from the focal magpie scoring method (see Ch. 2, 2.3.4.1). None of the predator derived behaviours were scored during the pre-or post-tests because these behaviours seemed to be specifically related to the stimulus. There was nothing to swoop, peck, jump, circle or view either before the model was placed or after it was removed. Hence, no values are plotted for the mean and SEM for both pre-and post-test periods.

(A) Stage 1: wedge-tailed eagle presentations



(B) Stage 2: wedge-tailed eagle presentations



(C) Stage 3: wedge-tailed eagle presentations

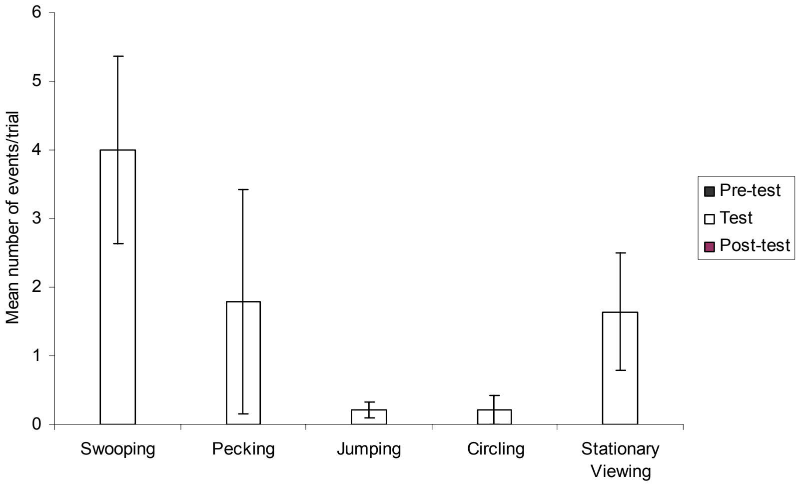
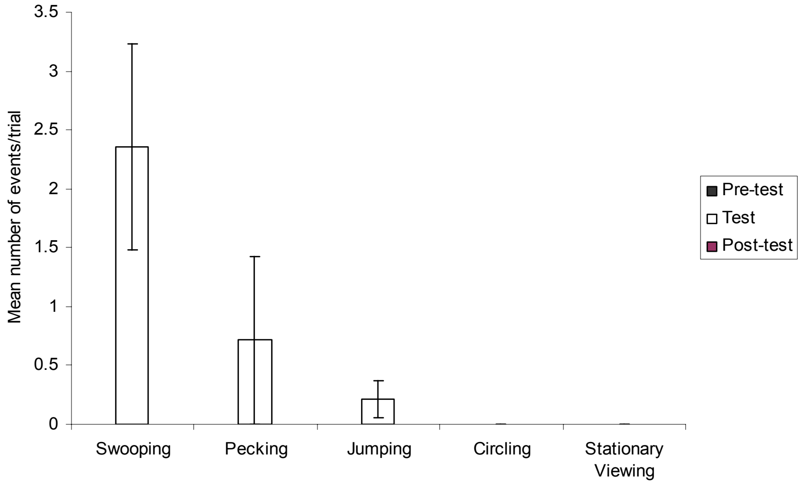
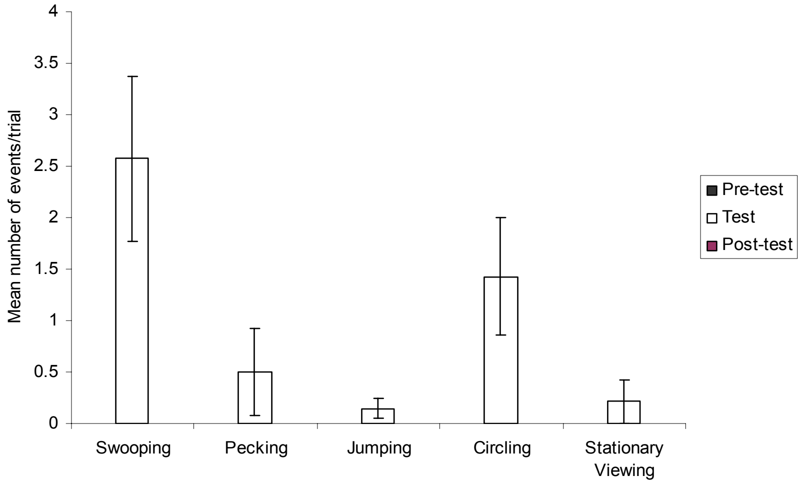


Figure 4.2. The results for the test period for the wedge-tailed eagle across each stage of juvenile development (pre- and post-tests scored zero) as presented in Figure 4.1.

(A) Stage 1: brown goshawk presentations



(B) Stage 2: brown goshawk presentations



(C) Stage 3: brown goshawk presentations

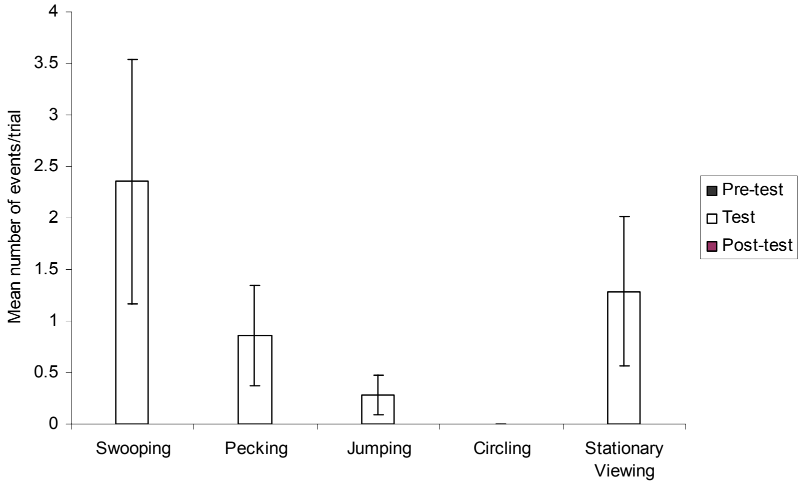
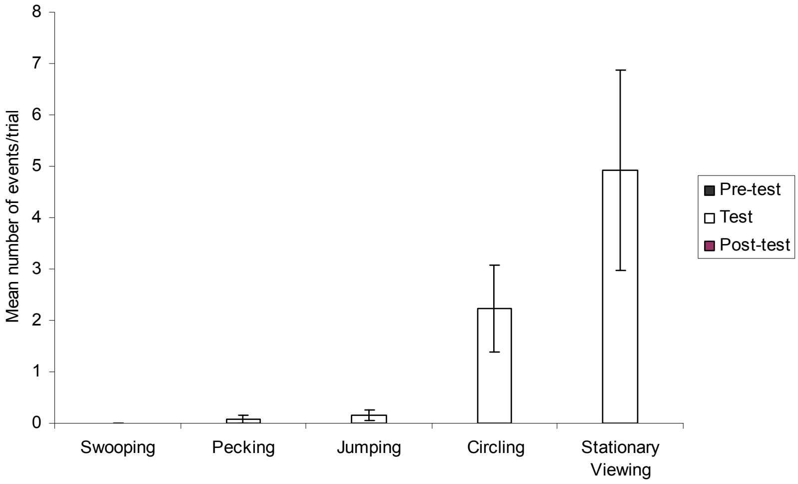
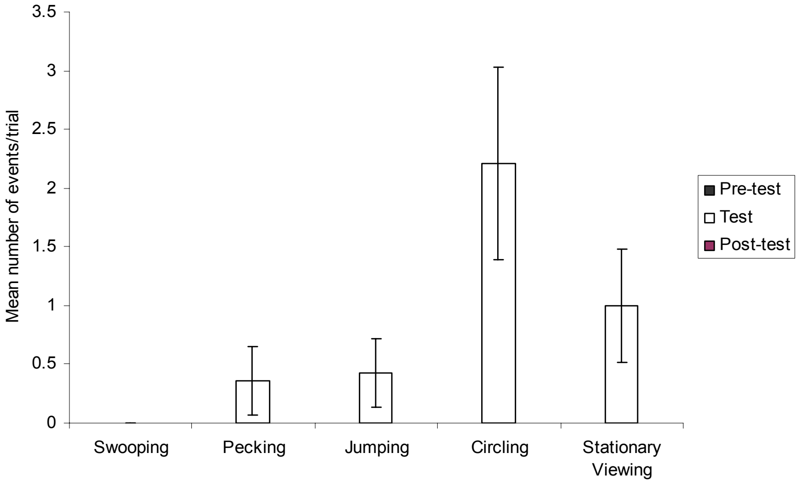


Figure 4.3. The results for the test period for the brown goshawk across each stage of juvenile development (pre- and post-tests scored zero) as presented in Figure 4.1.

(A) Stage 1: monitor lizard presentations



(B) Stage 2: monitor lizard presentations



(C) Stage 3: monitor lizard presentations

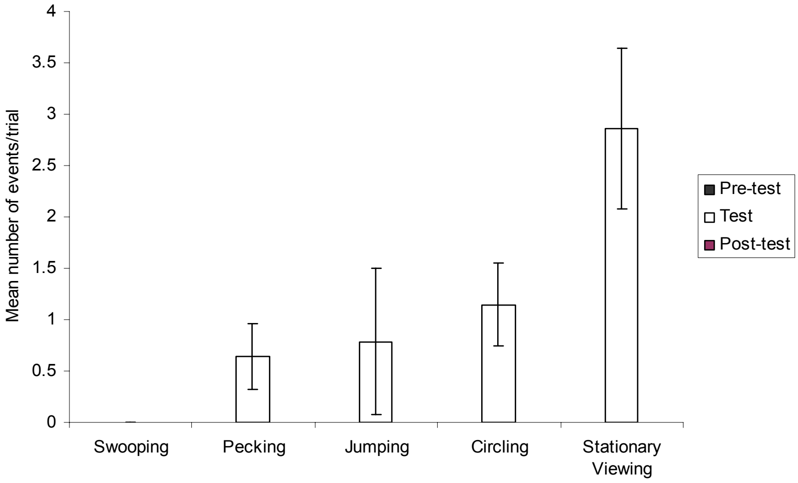


Figure 4.4. The results for the test period for the monitor lizard across each stage of juvenile development (pre- and post-tests scored zero) as presented in Figure 4.1.

4.3.2 Detailed analysis of the test period during Stage 1 (September 2005 to January 2006: high juvenile dependency)

The results presented here are for stage 1 only. Data for the other stages are presented in Appendix I. The stimuli had no significant effect on the number of magpies recruited (GLM, with stimulus as the repeated measure, $F_{(3,39)} = 1.532$, $p = 0.221$). The number of events of physical contact with the stimuli also did not vary between stimuli (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 7.138, p = 0.068). However, the magpies did make contact with the aerial predators on 13 trials (out of 42), whereas no contact was made with the monitor lizard.

4.3.2.1 Aerial behaviour (swooping)

The stimuli had a significant effect on the number of swoops (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 20.326, p = 0.000; Figure 4.5).

More swoops were given in response to presentations of the aerial predators compared to the lizard (little eagle: Wilcoxon, Z = -3.059, p = 0.002; wedge-tailed eagle: Wilcoxon, Z = -3.064, p = 0.002; brown goshawk: Wilcoxon, Z = -2.936, p = 0.003; Figure 4.5). The monitor lizard elicited only three swoops in one trial and no swoops in any other. The mean number of swoops for all of the aerial predator presentations combined was 5.34 ±0.99 SEM per 5-minute trial.

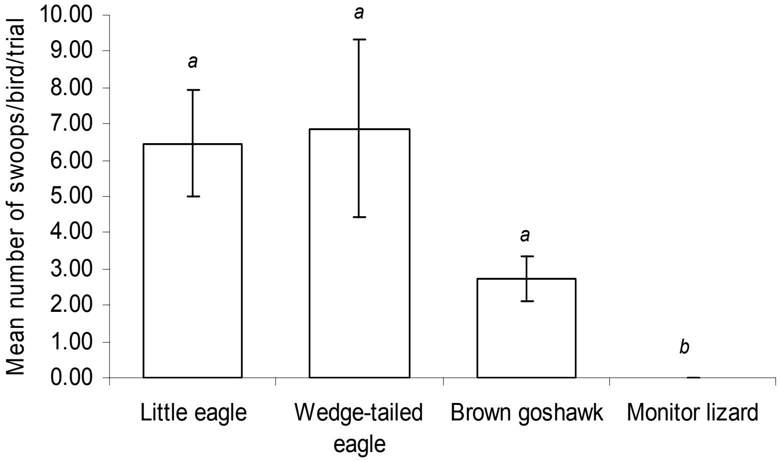


Figure 4.5. The number of swoops elicited by the model predators during Stage 1. The mean number of events per bird ± SEM are plotted for each stimulus. *a* indicates a significant difference from *b* ($p<0.050$). These data demonstrate that the magpies performed more swoops at the aerial predators compared to the monitor lizard.

The magpies also performed different flight patterns during swooping. For these data, the monitor lizard was excluded because it rarely elicited swooping behaviour.

Although direct swooping flights showed no difference between the aerial predators (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 0.452, p = 0.798; Figure 4.6), the number of looping swoops scored was different according to the stimulus (Friedman's test, with stimulus as the repeated measure, N=14, Chi-square = 6.720, p = 0.035). The brown goshawk elicited significantly fewer looping swoops than did the little eagle (Wilcoxon, Z = -1.951, p = 0.051; Figure 4.6) and the wedge-tailed eagle (Wilcoxon, Z = -2.201, p = 0.028; Figure 4.6)

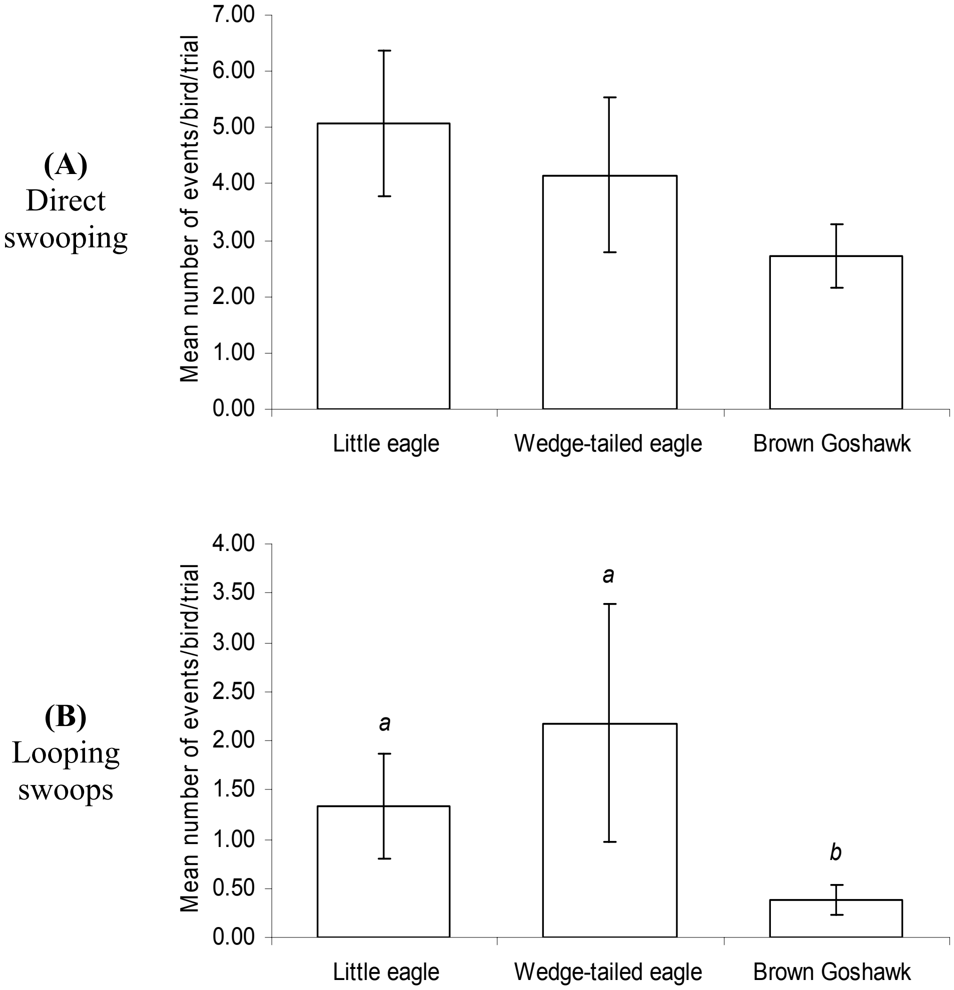


Figure 4.6. Swooping flight patterns elicited by the aerial predators during Stage 1. (A) direct flight pattern and (B) looping flight pattern. For both (A) and (B), the mean number of events per bird (number of events divided by the number of magpies) ± SEM are plotted for each stimulus (X axis). *a* indicates a significant difference from *b* ($p<0.050$). Figure 4.6A shows that the magpies performed a similar number of direct swoops at all of the aerial predators and Figure 4.6B shows they performed significantly fewer looping swoops to the goshawk than to the two eagles.

Indeed, the brown goshawk elicited only 9% of the total number of looping swoops scored for all presentations.

4.3.2.2 Ground-based behaviour

The presentation of the model predators did not significantly effect the number of pecks (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 1.929, p = 0.587; Figure 4.7), and the number of jumps (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 7.958, p = 0.093; Figure 4.7).

However, the various stimuli elicited different numbers of circling events (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 11.821, p = 0.008; Figure 4.7). Subsequent analyses showed that the monitor lizard elicited significantly more circling events than the wedge-tailed eagle (Wilcoxon, Z = -2.395, p = 0.017; Figure 4.7) and the brown goshawk (Wilcoxon, Z = -2.703, p = 0.007; Figure 4.7).

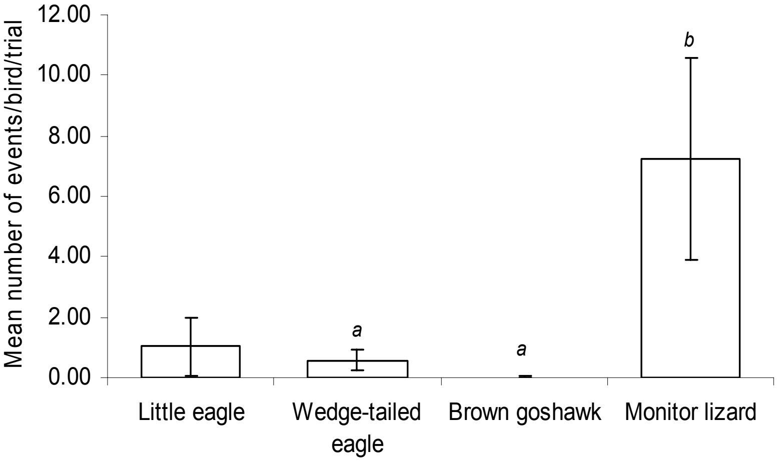


Figure 4.7. The number of circling events elicited by the model predators during Stage 1, presented as in Figure 4.5.

There was a significant effect of the stimulus on the number of stationary viewing events (Friedman's test, with stimulus as the repeated measure, N =14, Chi-square = 8.486, p = 0.037; Figure 4.8).

There were significantly more stationary viewing events scored during the monitor lizard presentations compared to the presentations of the wedge-tailed eagle (Wilcoxon, Z = -2.118, p = 0.034) and the brown goshawk (Wilcoxon, Z = -2.701, p = 0.007; Figure 4.8).

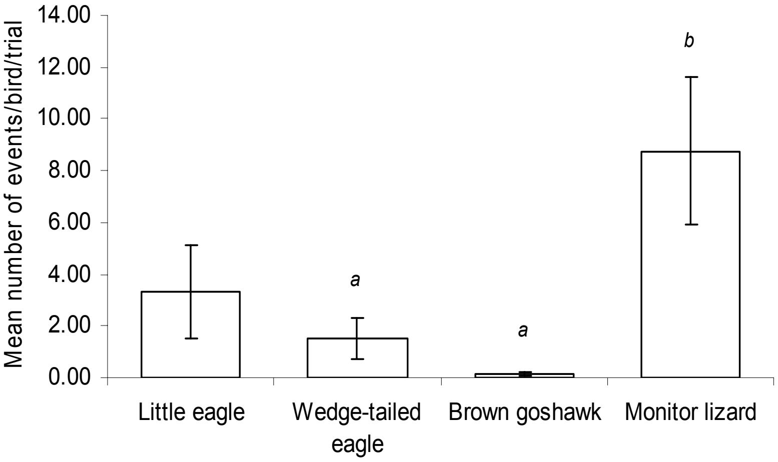


Figure 4.8. The number of stationary viewing events elicited by the model predators during Stage 1 presented as in Figure 4.5.

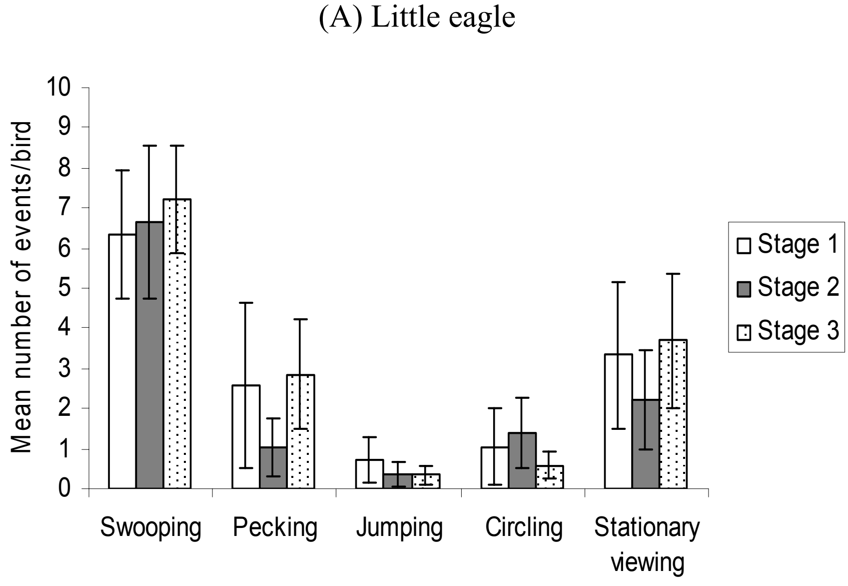
4.3.3 Response by magpies to each predator across all three stages (Stage 1: Sept 2005 to Jan 2006; Stage 2: Feb to April 2006; Stage 3: June to Aug 2006)

Since there were repeated presentations of the stimuli to each magpie group, there was, potentially, a cumulative effect of repeat presentations (i.e. habituation to the model predators). To control for this, seven groups, which had previously not been used in experimentation, were presented with the model predators in Stage 2.

Swooping behaviour was used as the measure to determine if there was an effect of repeated presentations since this was the most common response, particularly to the aerial predators. Hence, this behaviour should be most affected by habituation. The data were analysed by combining all swooping scores and comparing the seven new groups with the 14 groups that had been tested previously. The result of these trials showed no significant difference in swooping behaviour (Mann-Whitney, U = 1384.0, p = 0.559) between the groups that had been tested previously (5.56 swoops per bird ± 0.91 SEM) and those that had not (5.48 swoops per bird ± 1.74 SEM). Hence, there was no apparent habituation to the predators. [Note that those seven groups were not part of subsequent analyses in this Chapter]. In this section, the data were analysed for each model predator across each season to determine whether the response of the magpies towards each of the predators alters across the developmental stages of the juveniles (high juvenile dependency, low juvenile dependency and pre-dispersal of juveniles). The data for each model predator (little eagle, wedge-tailed eagle, brown goshawk and monitor lizard) across each stage are displayed in Figures 4.9 and 4.10.

In all six types of behaviour measured (swooping, pecking, jumping, circling, stationary viewing and physical contact), there were no significant main effects of time period for the little eagle, wedge-tailed eagle and the brown goshawk.

There was, however, a significant effect of time period on the number of pecks scored during the monitor lizard presentations. There were significantly more pecks scored during the final stage prior to juvenile dispersal than during the other two earlier stages (Wilcoxon, Stage 1 vs Stage 3 Z = -2.035 p = 0.042; Stage 2 vs Stage 3, Z = -2.375, p = 0.018; Figure 4.10).



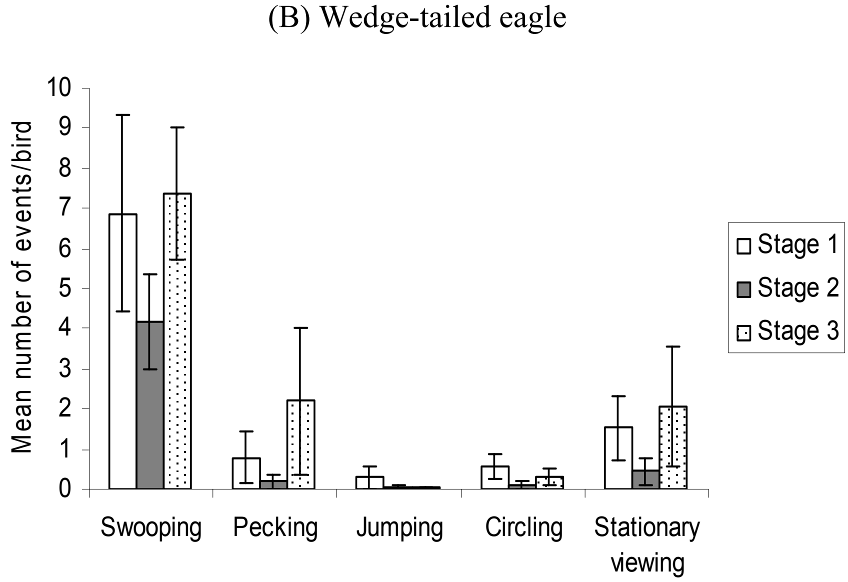
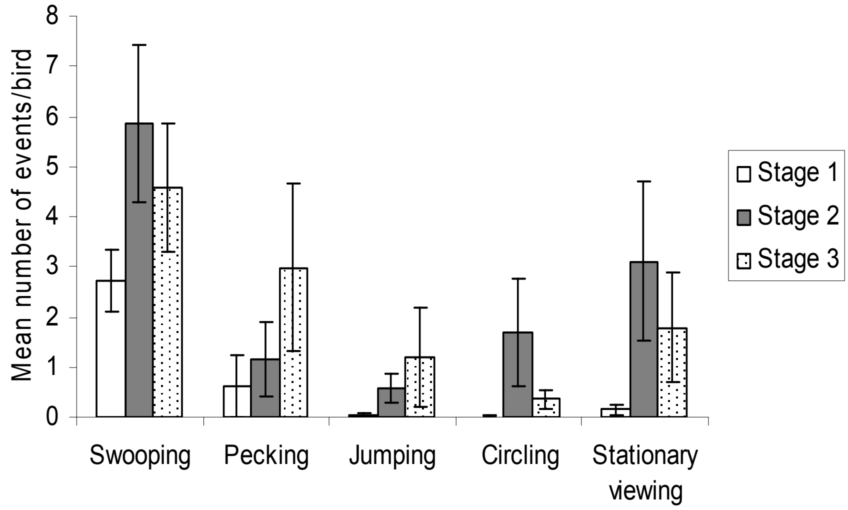


Figure 4.9. Mean response to the little eagle (A) and wedge-tailed eagle (B) across the three Stages. For each graph, the mean number of events per bird ± SEM is plotted for each behaviour (X axis). The white bars represent data for Stage 1 (high juvenile dependency). The grey bars indicate data for Stage 2 (low juvenile dependency). The bar with the dots indicates data for Stage 3 (prior to juvenile dispersal). This figure demonstrates that juvenile dependency does not affect the response towards the little eagle and the wedge-tailed eagle.

(A) Brown goshawk



(B) Monitor lizard

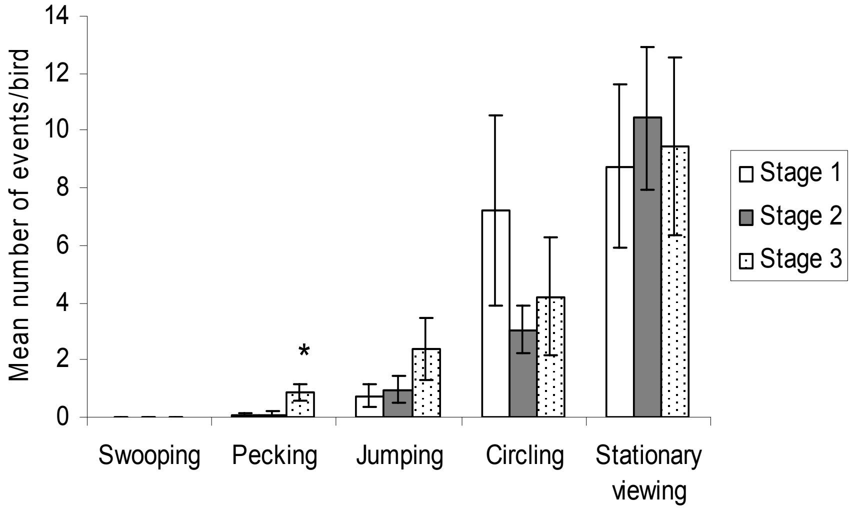


Figure 4.10. Response to the brown goshawk (A) and monitor lizard (B) across the three stages, presented as in Figure 4.9. * indicates a significant difference ($p<0.05$). Similar to the little eagle and wedge-tailed eagle, there was no change in the response to the brown goshawk. However, there were significantly more pecks to the monitor lizard during Stage 3 compared to the other earlier Stages.

4.4 Discussion

First, the absence of responses to the model snake needs to be considered. The snake was the only model that was not a taxidermic specimen. Thus, perhaps, the model snake may not have been realistic enough to have elicited a response from the magpies. However, this is unlikely because, in an earlier study, the same model snake was presented to groups of magpies and the adult magpies avoided it while the juveniles approached it (Koboroff and Kaplan, 2006). The difference in response might be explicable by the differences in presentation. In the earlier study the snake was moved along the ground while in this set of trials it was stationary.

The anti-predator behaviour expressed by the magpies varied according to the stimulus presented. There were significant differences in response to the aerial and ground predators (agonistic behaviour encompassing swooping, pecking and jumping). Magpies were more overtly agonistic to the aerial than to the ground predators. Moreover, they circled and viewed the lizard almost exclusively and thus spent more time on the ground than during presentations of the aerial predators.

Particularly noteworthy, as was stated in Chapter 3, is the fact that the responses of the magpies did not only vary in intensity according to stimulus but they actually performed different behaviours when faced with different predators. Although the magpies responded similarly to the little eagle and wedge-tailed eagle, there were some differences between their responses to the goshawk in comparison to responses to the two eagles. The little eagle elicited significantly more agonistic behaviour than the goshawk and there was a difference in swooping flight patterns given to the eagles and the goshawk. The number of direct flights at the model was similar for all aerial predators but the number of looping flight patterns was significantly lower for the goshawk than for the eagles.

The differences in swooping flight patterns performed by the magpies in response to the eagles and the goshawk may be associated with their respective hunting and flight abilities. The little eagle and wedge-tailed eagle have similar hunting techniques as they both tend to fly down from a soaring flight to capture their prey (Debus, 1984; Marchant and Higgins, 1993) but the goshawk is an ambush predator (Marchant and Higgins, 1993), a fast and particularly agile flier. The goshawk is likely to be faster and more agile than the little eagle and most certainly is faster and more agile than the much larger wedge-tailed eagle. Indeed, goshawks may be a match for magpies or even faster. Since there is evidence to show that the aerial predators do have different hunting techniques and/or abilities, it is possible that the magpies may have adapted their anti-predator behaviour according to the hunting characteristics of the predators.

Certainly, the goshawk elicited avoidance behaviour from the magpies as well as fewer agonistic and looping swoops (which are slow and involve two approaches towards the stimulus unlike direct swoops which involve only one approach). A looping flight pattern may present a greater risk of capture by the predator and was therefore avoided in the case of the goshawk, suggesting an assessment of threat. Thus, the magpies do not have only one anti-predator strategy that they employ for all predators. My results show that magpies responded differently to ground and aerial predators.

Overall, there was little evidence to support the original hypothesis that mobbing or inspection behaviour varies according to the age of the juveniles. There was only one measure that showed a significant difference between the three stages. Pecking behaviour during presentations of the lizard was significantly higher in Stage 3 (June to August 2006 the juveniles are least dependent on the adults), compared to the other two stages (Stage 1-September 2005 to January 2006 when juveniles are most dependent on the adults and are still being fed; Stage 2 February to April 2006 when juveniles are no longer as dependent on the adults and are independent feeders). As mentioned, monitor lizards are known nest predators (Weaver, 1989) and during Stage 3 the magpies were observed collecting material for nest building. Therefore, pecking behaviour may have increased in an attempt to move the predator away from the nest area. Apart from increased pecking, however, there was no other evidence that overall mobbing intensity towards the monitor lizard increased. With the exception of pecking behaviour during the monitor lizard presentations, there were no other measures that showed a significant difference from one stage of juvenile dependency to the next. Hence, these results suggest that juvenile dependency has little effect on the anti-predator behaviour of magpies. This contrasts with established findings that have shown that parents respond differently during different stages of juvenile development (Owings *et al.*, 1986).

The fact that the anti-predator behaviour of magpies does not alter according to the time of year is interesting because a number of studies have shown that mobbing can be influenced by the seasons. For instance, hooded crows (*Corvus corone cornix*) mob predators with a greater intensity in spring and autumn than in winter or summer (Slagsvold, 1985). The breeding season seems to be the time of year that is most likely to affect the intensity of mobbing, but not so in magpies.

Even though there is little evidence to support seasonality in magpie anti-predator behaviour, there was evidence to support the results discussed in the previous section: magpies change their anti-predator behaviour according to the type of predator. This was demonstrated in the distinct difference in response to the aerial and ground predators and even between the different aerial predators. The difference in responses of the magpies to the aerial and ground predators was maintained throughout the stages of juvenile development.

To conclude, it seems that anti-predator behaviour in magpies is not affected by the age of juveniles. Instead, the factor that is far more influential on their behaviour is the species of predator.

CHAPTER 5. PREDATOR INSPECTION OF THE MONITOR LIZARD

5.1 Introduction

So far, I have focused on ways in which the magpies approached the predators and mobbed them. In this chapter as in the previous one, I will discuss results gathered in the same Experiment 1 but will present those which seemed to be inconsistent with mobbing behaviour. In some of the trials to be discussed here only one magpie approached the predator model. As mobbing behaviour is generally considered to be a group response (Curio, 1978; Caro, 2005b), in this chapter, I will investigate whether there are sustained differences in behaviour between instances involving one magpie approaching a predator and those involving more than one magpie.

Mobbing varies considerably between species and, as shown in this study, also within a single species. Hence, approach of a predator by a single magpie may just be dismissed as another variation of mobbing. However, from previous research, there is now ample evidence to suggest that two main behaviours are essential characteristics of mobbing: alarm vocalisations and agonistic behaviour and when one or both of these key characteristics are absent, it is not self-evident that single silent approaches are “mobbing” behaviour.

Alarm vocalisations are essential to four hypotheses about the function of mobbing. (1) Alarm vocalisations may recruit group members (Hurd, 1996) and alert others to the presence of a predator (Krama and Krams, 2005), (2) may provoke the predator to leave the area (Flasskamp, 1994), (3) may attract another predator to the area that will chase away the existing threat (Curio, 1978), (4) and silence offspring (Windsor and Emlen, 1975). Moreover, since alarm vocalisations are involved in recruiting group members, they are also indirectly related to the hypotheses called the ‘confusion effect’ and ‘selfish herd effect’ (as outlined in Chapter 1) since both of these hypotheses rely on numerous individuals mobbing. Mobbers that perform agonistic behaviour, along with alarm vocalisations, may harass the predator and this may result in it leaving the area. Hence, alarm vocalisations and agonistic behaviour are fundamental elements of mobbing.

Presumably, however, both alarm vocalisations and agonistic behaviour can be performed by one individual. However, a further two hypotheses, the ‘cultural transmission hypothesis’ and ‘coming to the aid of a distressed relative’ (Curio, 1978) can clearly only occur if there is more than one individual present. Moreover, the more individuals mob a predator the greater the chance that a predator leaves the area and the risks that the individual mobbers take is reduced (Brown and Hogland, 1986). Hence, one can deduce that there are probably three main elements of mobbing behaviour: alarm vocalisations, agonistic behaviour and recruitment of group members and in the instances that I will present here, most if not all the defining elements of mobbing behaviour are missing in the approaches of single magpies. Thus, I will compare the responses of magpies when they approach the predator alone or within a group.

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5.2 Methods

The results in this chapter were analysed using the data (42 trials) of Experiment 1 specifically on presenting the monitor lizard. For my analyses here, I selected the trials that involved a single magpie approaching the model predator (i.e. within 5m and did so for at least one minute or more) and compared these to trials involving more than one magpie approaching the model predator. Trials with approaches of less than one minute were excluded because too few scores can be recorded in such a relatively short period of time. However, there were trials that began with only one magpie and ended with the entire group mobbing the model predator (i.e. there was a latency to recruit group members). Hence, the time in which only one magpie was present was analysed separately from the time following group recruitment. Trials involving a single juvenile magpie approaching the model predators were excluded since there is some evidence to suggest that responses of juveniles to predators may differ from those of adults (Koboroff and Kaplan, 2006). Therefore, all focal birds scored were adults.

Eight trials in which a single magpie approached the lizard fulfilled the criteria for further analysis (i.e. approach alone and remain near the lizard for at least one minute and excluding juveniles) while 20 trials involved more than one magpie approaching the lizard. The method for presenting the stimuli and other details of the experiment as detailed in Chapter 2.

The monitor lizard was the most suitable stimulus to compare the behaviour of individuals approaching the model either alone or within a group since the behaviour rarely occurred, if at all, when presenting any other stimuli (involving a single magpie or a group of magpies approaching). Comparisons between single and group approaches could be compared on the basis of these ground predator presentations.

5.2.1 Behaviours scored

It was predicted that trials involving a group of magpies approaching the lizard would perform more agonistic behaviours per bird than trials involving a single magpie, based on findings that mobbing required recruitment of individuals (Curio, 1978; Caro, 2005b). To see whether there were differences between single and group approaches, I analysed the number of alarm vocalisations, agonistic behaviour, circling, stationary viewing and the duration of time spent on the ground. Video footage of each trial made it possible. A detailed description of each behaviour was provided in Chapter 3.

Alarm calling was scored by counting the total number of alarm calls (regardless of call type) heard from the video. The number of swoops, pecks and jumps were added together as a collective score of agonistic behaviour. In addition to these measures, the location of the magpie in relation to the model was also scored. The 5m radius around the lizard was subdivided into four Sections: A, B, C and D (Figure 5.1). The back and left front leg of the lizard was located in Section A, the head, front right leg and tail of the lizard were located in Section B, the back including the tail and the left back leg were located in Section C and the right back leg and the tail were located in Section D (Figure 5.1). The total amount of time the group spent in each Section was scored and then adjusted by the number of magpies present.

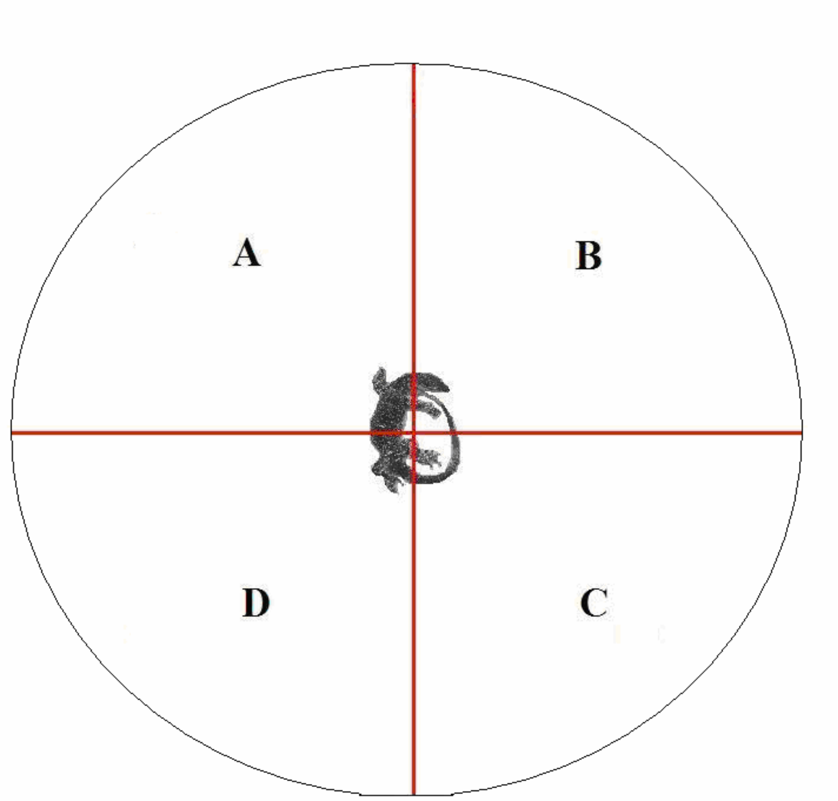


Figure 5.1. Sections around the lizard used for scoring the orientation of the magpies towards the lizard.

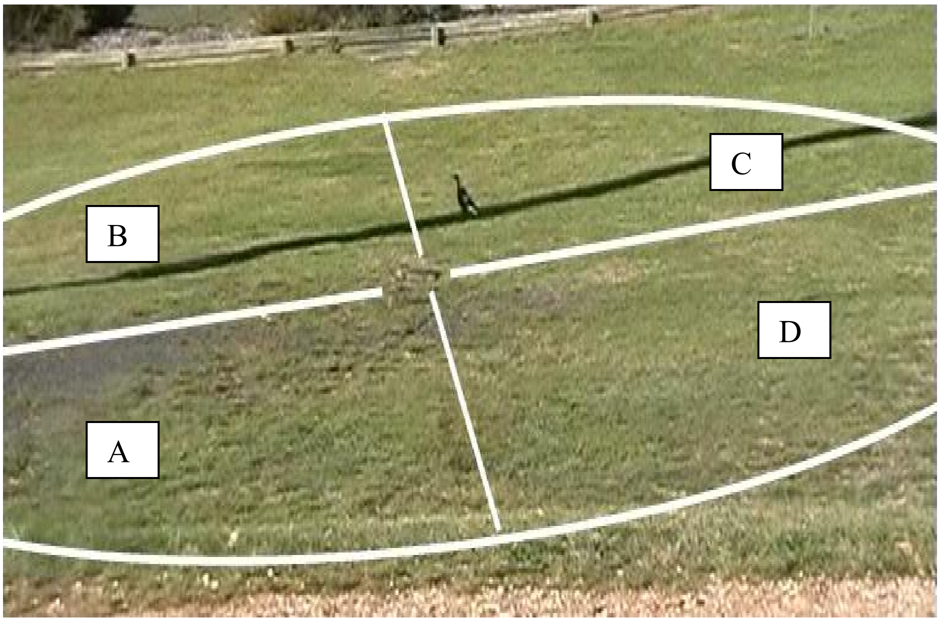


Figure 5.2. Video footage of a presentation of the monitor lizard. The white lines indicate the grid and the circle is the 5m radius around the monitor lizard. Note that the magpie is in Section C.

5.2.2 Statistical analyses

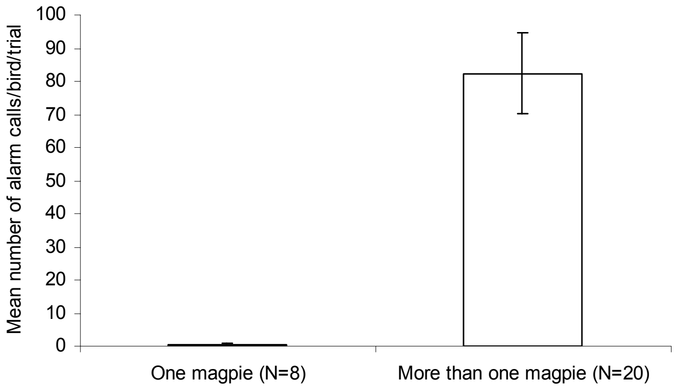
To compare results between a single magpie approaching the lizard to a group, the data for the group were standardised by dividing the total number of a particular measure by the number of magpies present. In other words, the data for the group are presented as the total number of a measure per bird (i.e. number of alarm vocalisations per bird). All measures were standardised using this method.

The data were analysed using non-parametric statistics because the data were not balanced (i.e. N = 8 for the number of trials in which one magpie approached the lizard and N = 20 for trials in which a group approached it). Mann-Whitney U test was used to analyse vocalisations, duration of time spent on the ground, agonistic behaviour, circling and stationary viewing. To analyse the data on the position of the magpies, Kruskal-Wallace was used with the section (i.e. Sections A, B, C and D) as the factor. Wilcoxon signed ranks was used for *post hoc* analyses of the position data.

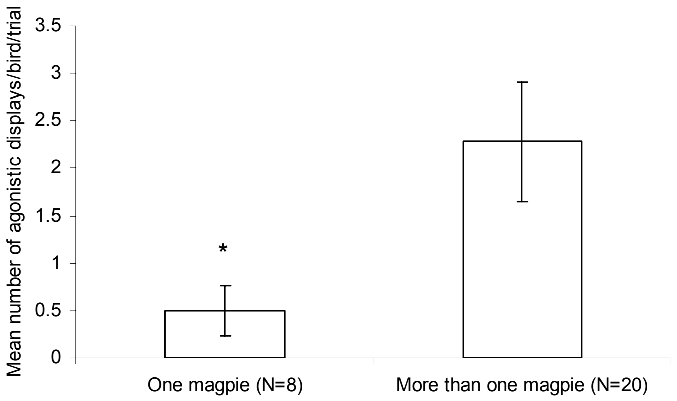
5.3 Results

The magpies that approached the lizard alone emitted no alarm calls and were silent (only three vocalisations were recorded during one trial and no vocalisations were scored during the other seven trials). By contrast, the groups of magpies were constantly vocalising (82.4 ± 12.1 SEM vocalisations per birds per five-minute trial). Since the contrast in alarm calls between single and group approaches were obvious, no statistics were conducted Figure 5.3A.

(A) Alarm Calls



(B) Agonistic Displays



(C) Circling

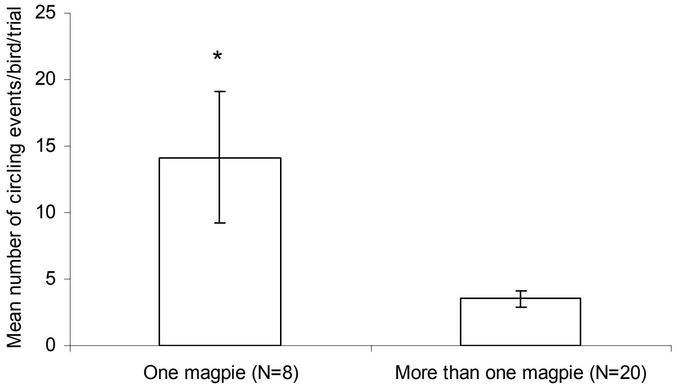


Figure 5.3. Comparisons of alarm vocalisations, agonistic behaviour and circling between the response of one magpie approaching the lizard alone and more than one magpie approaching the lizard. (A) alarm calls, (B) agonistic displays and (C) circling. * indicates a significant difference ($p<0.05$). Note that no statistics were performed on the alarm call data since the difference between single and group approaches was obvious. Figure 6.2 demonstrates that the magpies are much more agonistic when they approach the lizard in groups and they circle around the lizard (i.e. inspecting it) more when they approach it alone.

Furthermore, the magpies that approached alone rarely performed agonistic behaviour and this was lower than the number of agonistic displays scored for group approaches but this was not quite significant (Mann-Whitney, U = 43.5, p = 0.057; Figure 5.3B). In fact, only three agonistic displays were scored in all eight trials. In comparison, agonistic behaviour was scored during 15 trials involving groups of magpies approaching the lizard (2.28 ± 0.63 SEM agonistic displays per birds). Significantly more circling events were scored in single magpie approaches than in group approaches (Mann-Whitney, U = 24.5, p = 0.005; Figure 5.3C).

No statistical differences were found between single and group approaches for either stationary viewing (Mann-Whitney, U = 72.0, p = 0.684) or time spent on the ground (adjusted for the number of magpies; Mann-Whitney, U = 48.0, p = 0.104).

5.3.1 Position of magpies near the lizard

As described before, within a 5m radius a grid was established, subdivided into four sections (A,B,C,D), in order to distinguish (as had occurred in research on predator inspection in fish) between approaches to the head regions (A, B) or the tail regions (C, D). These data, presented in Figures 5.4 and 5.5, were analysed by determining the sections that single magpies and groups of magpies (adjusted for the number of magpies: duration of time in each section per bird) spent most of the time. The duration of time spent in each section was then compared between the trials in which a single magpie approached and those in which the group approached the lizard.

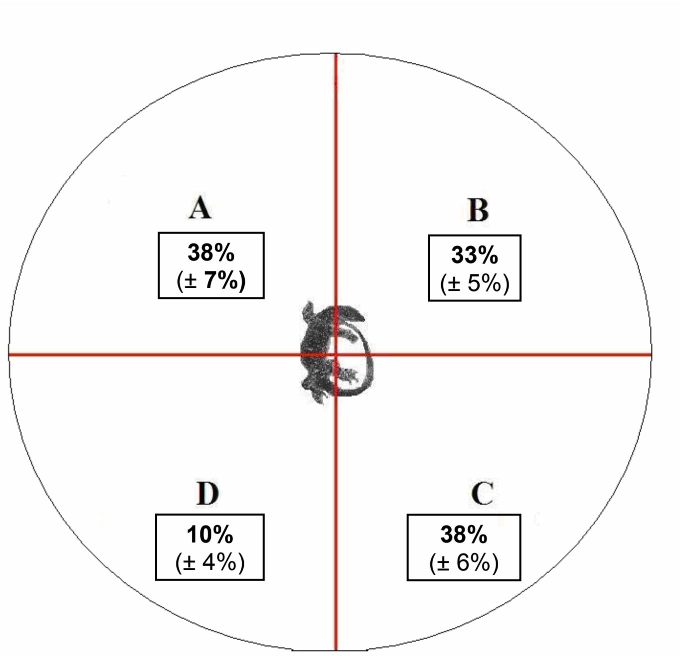


Figure 5.4. Percent duration of time (s) spent in each section around the lizard when only one magpie approached it. Data are shown as a mean percentage of time (± SEM). Note, the magpies spent almost equal time within Sections A (at the back of the lizards head) and C (the side of the lizard but still in view of its head) and slightly less time in Section B (facing the lizard's head) and hardly any time in Section D (the back of the lizard).

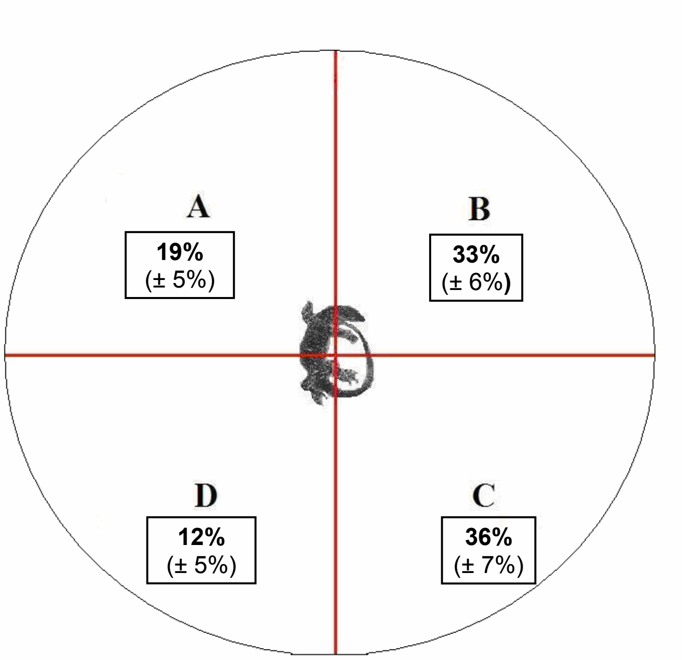


Figure 5.5. Duration of time (s) spent in each Section around the lizard when more than one magpie approached it. Data are shown as a mean percentage of time (± SEM). This figure illustrates that, when groups of magpies approached the lizard, they spent most of the time (69% ± 6% SEM) in Sections B and C and less time in Sections A and D (31% ± 5% SEM). That is, they spent most of their time to the side of the lizard on which its head was facing and avoided the area that was largely out of the lizard's gaze.

For single magpie approaches, there was a significant effect of the section in which a magpie spent time (Kruskal Wallace, Chi-Square = 10.848, p = 0.013). They spent significant less time in Section D compared to Sections A and B (Wilcoxon, Section D vs Section A, Z = -2.103 p = 0.035; Section D vs Section B, Z = -2.383, p = 0.017; Figure 5.4). Clearly, the single magpies moved around the front of the lizard and around its head but spent little time towards the back of it (Section D).

When the magpies approached the lizard as a group, there was a significant effect of the time spent within each section around the model (Kruskal Wallace, Chi-square = 15.182, p = 0.002; Figure 5.5). The magpies spent significant less time within Section D in comparison to Sections B (Wilcoxon, Z = -2.461, p = 0.015) and Section C (Wilcoxon, Z = -2.838, p = 0.005) but this was not different from the time they spent in Section A (Wilcoxon, Z = -1.732, p = 0.093).

In total, the magpies spent 69% ± 6% SEM of the time to the right of the lizard. This was significantly higher than the time they spent to the left of the lizard (Wilcoxon, Z = -2.502, p = 0.012). This shows that they were facing the lizard since the head of it faces towards Sections B and C. Note the tail position too. The tail curved to the right in this model would mean that in any tail attack (swipe) the greatest velocity and force would occur to the left (Section D) but the tail would also move through Section C. Within close proximity, this is the most dangerous part of the lizard and it was avoided.

5.4 Discussion

There were significant differences in response to the monitor lizard depending on whether a magpie approached it alone or as a group. Both agonistic and alarm vocalisations were nearly absent when a single magpie approached compared to a group. These results raise the question of how to define the differences.

Mobbing is considered to be a group behaviour (Caro, 2005b). However, there is some evidence to suggest that some individuals mob in the absence of group members. Ostreiher (2003) investigated whether Arabian babblers would mob a model snake when alone or whether they required a group member to facilitate mobbing. The results showed that both individual and pairs of babblers performed mobbing behaviour. Brown and Hogland (1986) compared mobbing behaviour of solitary nesting and colonially nesting swallows (*Hirundo spp.*) and found that the solitary nesters performed more swoops compared to the colonial nesters mobbing within groups. The studies by Ostreiher (2003) and Brown and Hogland (1986) contrast with my findings in that their findings showed that not only do individuals that are alone perform mobbing behaviour, but the intensity of mobbing increases when they are alone. Lone magpies not only did not mob the lizard at all but they behaved altogether differently. They did not produce alarm vocalisations or perform agonistic behaviour. Indeed, they approached silently, while looking and walking around the lizard. They also spent more time in the head region (head turned away). The magpies approaching the same lizard within a group alarm called constantly and used agonistic displays. Thereby, groups of magpies focus their attention directly to the lizard while lone magpies tended to be more curious by spending more time around the entire lizard. Overall, these are obvious differences in strategy. The silent approach is much more akin to inspection behaviour, while the noisy approach of the groups is akin to mobbing behaviour.

As I outlined in the introduction to this chapter, the hypotheses on the function of mobbing fundamentally involve recruitment of group members, alarm calling and agonistic behaviour. Since the magpie that approached the lizard alone, did not recruit, alarm call or perform agonistic behaviour, then this demonstrates that these magpies were not mobbing the lizard. Hence, the approach behaviour of the lone magpies facing the lizard, is a rather typical example of predator inspection (i.e. no mobbing whatsoever but simply inspecting the predator). Other scores also reinforce the conclusion that approaching alone is predator inspection and not mobbing. The magpies that approached the lizard alone circled it significantly more often than magpies approaching the lizard in a group. Since circling was often followed by the magpies pausing to view the lizard, they may have been moving around the lizard to gather information.

This is not to say that predator inspection does not occur in the context of mobbing. For instance, there was no difference in stationary viewing (magpies remain still and turn their heads from side to side to view the stimulus with the lateral fields) between lone and group approaches. However, in the next chapter, I will present data that demonstrates that the visual information obtained during mobbing or inspection is processed in different hemispheres of the brain which suggests that the strategy that magpies used when approaching the predator alone may be functionally different to the strategy used when they approach in a group.

CHAPTER 6. HEMISPHERIC SPECIALISATION (EYE PREFERENCE) DURING RESPONSES TO A PREDATOR

6.1 Introduction

In this chapter, the data from Experiment 1 (i.e. data from all stages 1-3) were considered further, this time analysing eye use in viewing the model predator. By doing so it may be possible to establish whether any anti-predator assessments are lateralised. Lateralisation of the brain, which refers to the ability of the two hemispheres of the brain to conduct different functions, is common in vertebrates and particularly strong in birds at both the structural and functional levels of organisation (summarised by Rogers and Andrew, 2002). In birds that have their eyes positioned on the sides of the head, laterality can be determined by scoring left and right eye use to view a particular object/stimulus (Rogers, 1997; McKenzie *et al.*, 1998). While vigilance for predators has been found to be lateralised (see below), no study has investigated whether other anti-predator behaviours, such as mobbing or inspection, are lateralised. The response of magpies towards the monitor lizard provided an opportunity to explore eye preference during a simulated predator-prey encounter since the magpies responded to the lizard by approaching it on the ground to within 5m and remaining there for the majority of the trial (Chapter 4). Hence, the eye use of the magpies prior to performing various types of behaviour could be determined by examining the video footage. Moreover, since the types of behaviour that the magpies performed during the presentations of the model lizard were both agonistic and investigatory, eye preference before performing a range of anti-predator behaviour could be scored. A shortened version of this Chapter has been published in Brain Research Bulletin (Koboroff *et al.*, 2008) see Appendix II.

Lateralisation in birds has been studied primarily using tests conducted in the laboratory, mainly on domestic chicks (Rogers, 2002) and pigeons (Güntürkün, 1997). In fact, very few studies have investigated lateralised visual processing in wild birds. Franklin and Lima (2001) tested wild juncos as they fed alongside a wall and the juncos preferred to stand so that they could monitor the surrounds with the right eye. Research into laterality of blacked-winged stilts (*Himantopus himantopus*) found a population bias for capture of prey on the right side and courtship behaviour on the left side (Ventolini *et al.*, 2005). Rogers and Kaplan (2006) reported a left eye (LE) preference in kookaburras (*Dacelo novaeguineae*) to view the ground in search of moving prey. Lastly, the Australian magpie (*Gymnorhina tibicen*) has been shown to exhibit preferred use of the LE prior to flying away from a human approaching the bird from behind (Hoffman *et al.*, 2006). Moreover, Rogers and Kaplan (2006) presented playbacks of magpie alarm calls and they found that magpie scanned the sky with the left eye.

Two studies on wild birds investigated vigilance (Franklin and Lima, 2001; Hoffman *et al.*, 2006), whereas vigilance or reaction to a predator has received some attention in laboratory studies on laterality (Rogers, 2000; Rogers *et al.*, 2000; Lippolis *et al.*, 2002). Rogers (2000), for example, found that the domestic chick detects an advancing predator more often with the left eye than the right and Dharmaretnam and Rogers (2005) found that chicks preferred to examine overhead predators using the left eye. However, no previous study has investigated whether responses following detection of a predator (i.e. mobbing and other anti-predator behaviour) are lateralised.

It was hypothesised that magpies would show eye preferences as they approached a predator, either to inspect it or to mob it, since approach to a predator requires continual assessment and decisions about whether to continue to approach or to withdraw, as has been studied in some detail in fish (Dugatkin and Godin, 1992). Avoidance and approach behaviour are likely to be controlled by different hemispheres of the brain and, based on previous research, it is likely that the left hemisphere (LH) controls approach and the right hemisphere (RH) withdrawal (Davidson *et al.*, 1990; Cameron and Rogers, 1999). Furthermore, since mobbing may involve physical contact with a predator (Shields, 1984), it is a strong agonistic response and is thus likely to be controlled by the RH, as shown in other vertebrates (e.g. Anolis lizards, Deckel and Jevitts, 1997; and toads, Robins *et al.*, 1998; Vallortigara *et al.*, 1998), including domestic chicks (Vallortigara *et al.*, 2001).

6.2 Method

Data were derived from Experiment 1 and were obtained by analysing video footage of trials presenting the monitor lizard in all three stages. The trials testing responses to the ground predator were selected because the magpies spent the most time on the ground within 5m from the lizard and thus were continually within the frame of the video footage. In Experiments 1, the monitor lizard was presented to 14 groups on three separate occasions. Pseudoreplication was avoided by identifying individual magpies and scoring a particular individual in only one of the trials. Individual magpies were identified by noting the wing markings, which, as shown in details in Chapter 2 (2.2.3.1) can be used as a reliable identification marker in *Gymnorhina tibicen* (Kaplan, 2004).

A total of 15 trials were selected out of 42 trials for analysis as, in these cases, eye preference could be accurately scored from the video footage. Each individual magpie that approached the lizard was scored. Data were collected for a total of 55 magpies. For details of presenting the monitor lizard see Chapter 2.

During the presentations of the monitor lizard, the magpies jumped near the lizard, they moved around the lizard (circling) and they stood and fixated the lizard while in an alert posture (stationary viewing). They were also occasionally seen attempting to peck at the lizard. These behaviours were described in detail in Chapter 3. Additionally, it was found that the magpies moved from/to the lizard while remaining within the 5m radius of the lizard. I have, therefore, added here new sub-categories of approach and withdrawal bearing in mind, however, that either distance change occurred within 5m of the stimulus which I had described and analysed overall as ‘approach’. Taking into account this noticeable stepping backwards and forwards allowed finer discrimination of the behaviour.

Hence, eye preference was scored prior to the magpie withdrawing, approaching, jumping, pecking at the stimulus, circling or viewing it. Withdrawing and approaching were scored as walking or running (flying or jumping was not included) directly towards or away from the lizard, respectively. Excerpts from video sequence showing scoring of eye use prior to an approach are shown in Figure 6.1

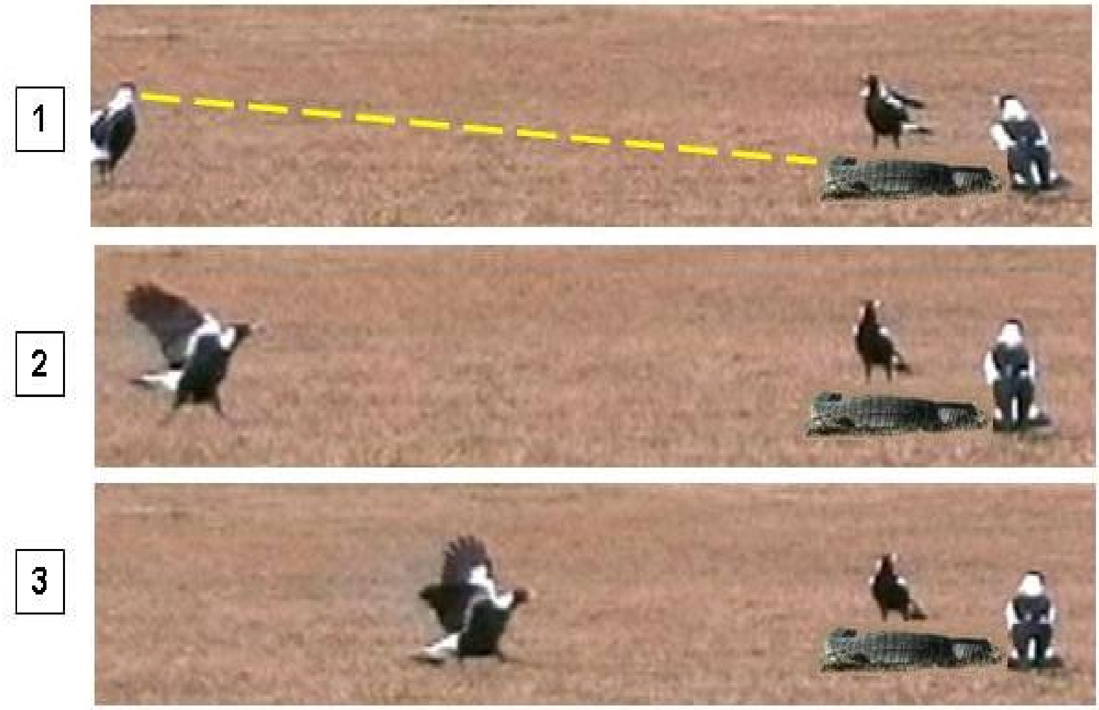


Figure 6.1. Video footage showing eye use prior to an approach towards the monitor lizard. Note the magpie on the right of the frames as it approaches the lizard. (1) Shows a magpie fixating the monitor lizard with its right eye. (2). The magpie then views the model binocularly. (2-3). The magpie approaches the lizard. The dashed lines indicate the line of sight, yellow = right eye.

Eye use to fixate the stimulus prior to performing a particular behaviour was scored by replaying the videotape in slow-motion. A monocular fixation was scored when a magpie fixated the stimulus for at least one second with the beak held approximately 90° relative to a line from the eye to the lizard. Since the monocular visual fields of a magpie (laterally placed eyes) are 143-149° on each side of the head and binocular field is 28-34° frontal (Rogers and Kaplan, 2006), the 90° angle was chosen to ensure that the fixation scored was indeed monocular (Figure 6.2).

Stationary viewing was scored as the first fixation in a bout in which the magpie may have turned its head from side to side while standing stationary and alert (Figure 6.3). By recording only the first eye fixation on the stimulus during a viewing bout, runs were avoided.

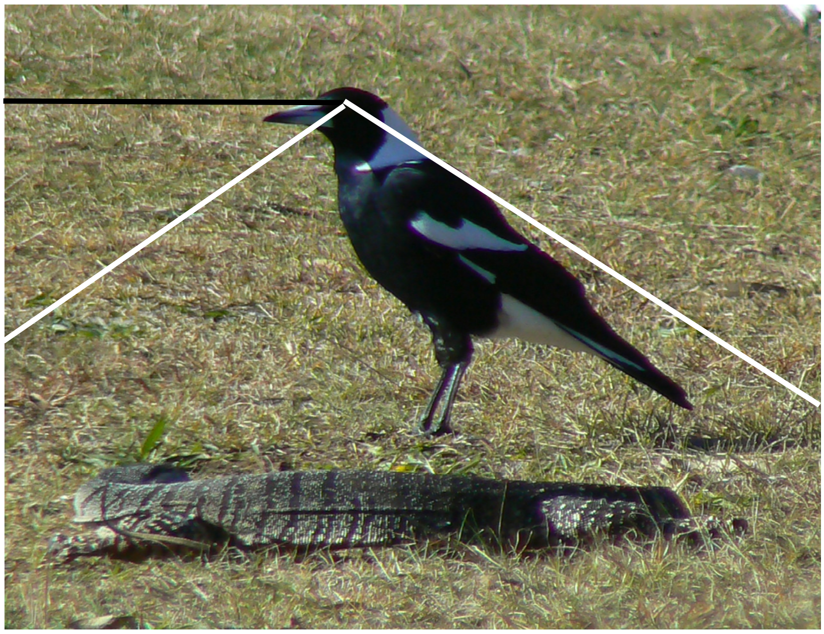


Figure 6.2. Scoring monocular fixations. Black line indicates the angle of the beak. White lines indicate the estimated monocular field of the left eye.

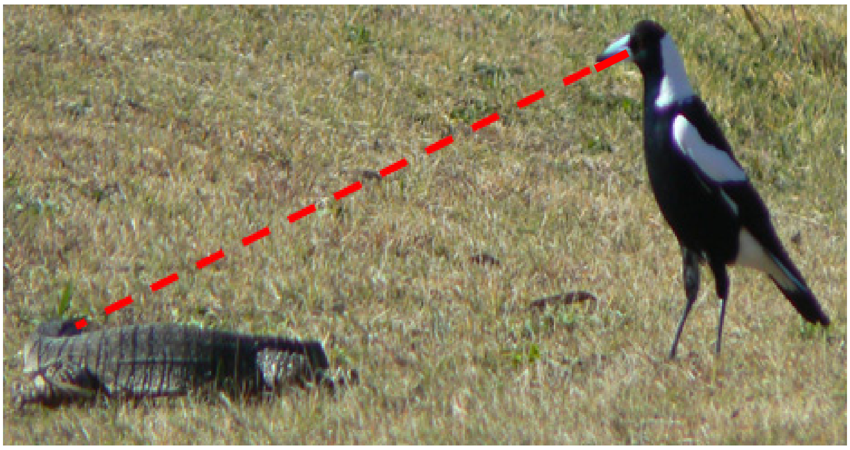


Figure 6.3. Monocular fixation, on this occasion with the left eye, during stationary viewing. Note the extension of the neck typical of a vigilance posture. The dashed line indicates the estimated line of sight.

The data were analysed using a G-test (log-likelihood chi-squared test), which analyses each individual's score whilst taking into account the number of scores per individual (Sokal and Rohlf, 1995).

6.3 Results

The eye preferences are presented in Figure 6.4. The percentages of LE preference were calculated as LE/LE+RE x 100. There was a significant LE bias (85.0% ± 4.2 SEM) to view the lizard prior to withdrawing from it ($G_{(14)} = 117.61$, $p < 0.001$). By contrast, there was a significant RE bias (27.6% ± 6.6 SEM) to view the lizard prior to approaching it ($G_{(12)} = 107.79$, $p < 0.001$).

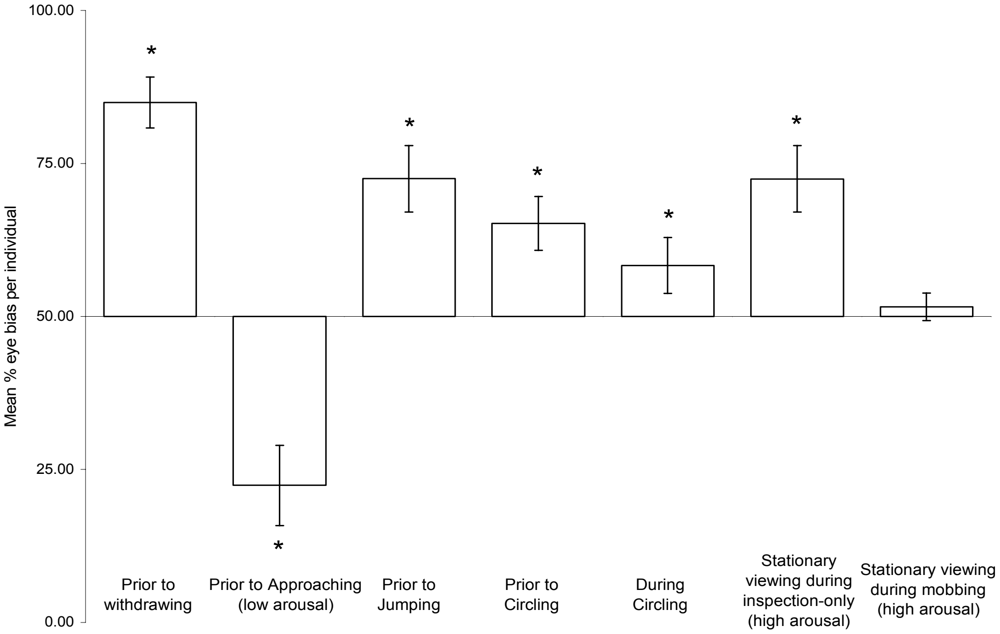


Figure 6.4. Percentage eye bias. The data are plotted as mean percent left eye preference for each of the behaviours scored, with standard errors. Values above 50% indicate a left eye and those below 50% a right eye bias. 50% indicates no bias. * indicates $p < 0.001$

Prior to jumping, the magpies viewed the lizard significantly more often with the LE (72.5% ± 5.4 SEM) than with the RE ($G_{(16)} = 107.89$, $p < 0.001$). Pecking was scored but there were insufficient data to analyse using a G-test. However, there was a suggestion that eye use prior to pecking was primarily with the LE (82.0% ± 7.2 SEM, N = 6).

Prior to circling the lizard, the magpies viewed the stimulus with a significant LE preference (65.2% ± 4.4 SEM, $G_{(34)} = 215.43$, $p < 0.001$). During circling events, the significant LE bias continued as the direction of circling was predominately anti-clockwise (58.3% ± 4.6 SEM, $G_{(23)} = 111.47$, $p < 0.001$).

There was a significant LE bias when the magpie adopted the alert posture to view the lizard during inspection-only tests (72.5% ± 5.5 SEM, $G_{(4)} = 60.40$, $p < 0.001$), but no significant eye bias to view the lizard in the alert posture during mobbing tests (51.6% ± 2.2 SEM, $G_{(9)} = 7.82$, $p > 0.050$). Inspection-only tests were those in which the magpies approached the lizard alone and produced no vocalisations or agonistic behaviour (N=6). Mobbing tests referred to trials in which the magpies vocalised continuously and approached as a group N=11). Note that there were eight inspection-only and 20 mobbing tests recorded in total. However, eye use could not be measured in all tests because it was too difficult to determine whether the magpies were fixating the stimulus. Hence, the reduced sample size of inspection-only and mobbing tests.

6.4 Discussion

Magpies show significant and strong eye preferences prior to performing some types of anti-predator behaviour. They used the left eye/right hemisphere (LE/RH) prior to withdrawal and the right eye/left hemisphere (RE/LH) prior to an approach. The former result is consistent with that of Hoffman *et al.* (2006), who found that magpies use the LE to view a human approaching them from behind if their next behaviour was fleeing. Viewing prior to approach was low arousal (alert posture not adopted) and the RE was used. Withdrawal is therefore a behaviour that results from processing visual information in the RH, whereas approach follows processing by the LH. This specialisation of the hemispheres for approach and withdrawal has been noted in other species, even in humans. For example, in humans the RH expresses negative emotions such as fear and aggression, as well as withdrawal, whereas the LH expresses positive emotions and approach (Davidson *et al.*, 1990). The results obtained on withdrawal and approach behaviour of magpies are, therefore, consistent with established findings.

As summarised by Vallortigara *et al.* (2008), the RE/LH interprets visual inputs and uses learned templates. It also uses focused attention. It is conceivable that the RE preference displayed by magpies prior to approaching may be focussed attention of the predator using learnt information about the stimulus. Given that approach to a predator is a risky behaviour, this explanation is plausible. The RE preference suggests that the magpie relies on learnt information about the predator before it approaches.

Jumping and pecking are agonistic behaviours, identified as part of the mobbing response towards predators and often involve physical contact with the predator (Shields, 1984). Research on other species has established that the RH is dominant for agonistic responses (summarised by Rogers, 2002):e.g. chicks (Vallortigara *et al.*, 2001), toads (Robins *et al.*, 1998; Vallortigara *et al.*, 1998) and the *Anolis* lizard (Deckel and Jevitts, 1997) all strike preferentially at conspecifics on their left side. Hence, the strong LE/RH bias that the magpies demonstrated in my study provides more evidence that the RH controls agonistic behaviour. Furthermore, the results demonstrate that the agonistic behaviours controlled by the RH are directed not only at conspecifics but also at a potential predator.

The LE/RH bias prior to and during circling is somewhat more difficult to explain since circling does not involve approach or withdrawal, and it is not obviously an agonistic response although it could involve aspects of the latter. Circling must involve inspection of the predator using the LE. Hence, inspection during circling and alert viewing during inspection-only trials involves a significant preference to use the LE.

The LE was used when viewing the lizard in a high alert posture during inspection-only tests, when high arousal levels are indicated by the extended neck posture. This finding is consistent with the earlier research on chicks showing that viewing an overhead predator with the LE elicits more distress calls than viewing it with the RE (Dharmaretnam and Rogers, 2005). Chicks also use the LE to examine novel objects (Rogers, 2000) and the details of a stimulus: the LE detects small changes in familiar stimuli, whereas the RE detects large changes that represent categories rather than details (Vallortigara and Andrew, 1994; Vallortigara *et al.*, 2008). Hence, it is possible that the magpies viewed the lizard merely as a novel stimulus, rather than a predator *per se*. However, this is unlikely since their responses to the taxidermic lizard involved mobbing behaviour (16 of the 22 tests), which is a typical response to predators and not novel stimuli (see Chapter 8). This suggests that, when the magpies adopted the alert posture and viewed the lizard using the LE, they were doing so to examine the potential predator in more detail. I think that it is most likely that the magpies were viewing the lizard with the LE to process the details of the stimulus and assess whether this potential predator was a threat. This contrasts to a RE preference before approaching the predator, as mentioned above, and this RE use differed from LE viewing in that the birds did not adopt the high arousal posture. In other words, there are two types of viewing the predator: LE-high-alert viewing and RE-low-arousal viewing followed by approach.

The lack of eye bias in stationary viewing during mobbing is intriguing since mobbing is primarily an agonistic response and yet no LE/RH bias was observed. The lack of bias may indicate a balance between approach and withdrawal and, hence, continuous assessment with the LE (withdrawal) and RE (approach). Use of the monocular fields of both the LE and RE would also ensure that both small and large (category) changes are detected.

The possible function of stationary viewing during mobbing must now be distinguished from stationary viewing during inspection. Viewing during inspection allows magpies to gather information about the predator (Dharmaretnam and Rogers, 2005), which requires attention to the details of the stimulus and thus would explain the LE/RH bias. Viewing during mobbing requires an assessment of the situation rather than being solely to gather detailed information about the predator. As a consequence, both the LE and RE may be used prior to mobbing.

In summary, brain lateralisation in birds is frequently expressed as a preference to view stimuli with one eye using the lateral monocular visual field. My results confirm existing data on lateralisation in birds obtained from laboratory studies and extend these to behaviour of birds in the natural environment (Table 5.1). The RH hemisphere appears to control most aspects of predator-prey interactions, from detection (Vallortigara *et al.*, 2001) through to mobbing and high alert inspection behaviour. Even withdrawal/escape from the predator is controlled by the RH in magpies, as in other species (Lippolis *et al.*, 2002; Lippolis *et al.*, 2005).

Table 6.1. Summary of previous findings and new findings from this thesis.

Research	Left Hemisphere	Right Hemisphere
Previous research (see Vallortigara *et al.* 2008)	Detects invariance Uses learned templates Focus attention Approach	Detects variance (novelty) Diffuse attention Withdrawal Expresses intense emotions
New findings (this thesis	Approach predator (low arousal)	Withdraw from predator Viewing during Inspection behaviour (high arousal)

The evolutionary implications of the relationship between RH and predator-prey interactions suggest that a suite of anti-predator strategies may have been organised within the RH. Approach to the predator is the exception: approach follows use of the RE/LH and does not involve high alert. As shown in chicks, the RE/LH is used to focus attention on the cues that indicate large (category) differences between stimuli (Vallortigara and Andrew, 1994; Rogers, 2008), which suggests that magpies may be approaching in order to examine the stimulus more closely. This interpretation is supported by the fact that such approaches were not followed by mobbing or agonistic interactions with the predator. The counterbalanced specialisation of the LH for approach and the RH for withdrawal is notable given that the same specialisation occurs in humans (Davidson *et al.*, 1990).

Chapters 4, 5 and 6 analysed the data set in three different ways, in terms of mobbing behaviour, inspection behaviour and also showing lateralised behaviour. The latter perhaps made it clearer than ever other behavioural differences in the data on inspection and mobbing that the two activities were functionally different. Mobbing events had no eye bias for viewing but inspection did. During a mobbing event, viewing was 51.6% LE (± 2.2 SEM) and during inspection-only tests it was 72.5% LE (± 5.5 SEM). Such profound differences support my view that inspection behaviour and mobbing behaviour are not a continuum and should not be confused. They arise from different origins and appear to have different purposes.

STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Text	106-118
Figure 6.1	110
Figure 6.2	111
Figure 6.3	111
Figure 6.4	112
Table 6.1	117

Name of Candidate: Adam Koboroff

Name/title of Principal Supervisor: Prof. Gisela Kaplan

[redacted]
Candidate

29 July 2008
Date

[redacted]
Principal Supervisor

22 July 2008
Date

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name (please print clearly)	**% of contribution**
Candidate	Adam Stephen Koboroff	70%
Other Authors	Prof. Gisela Kaplan	15%
	Prof. Lesley Rogers	15%

Name of Candidate: Adam Koboroff

Name/title of Principal Supervisor: Prof. Gisela Kaplan

[redacted]
Candidate

29 July 2008
Date

[redacted]
Principal Supervisor

22 July 2008
Date

CHAPTER 7. PRESENTING A PREDATOR MODEL IN DIFFERENT POSTURES AND CONTEXTS

7.1 Introduction

This chapter presents data from two experiments, Experiments 2 and 3, also using magpie groups. Since the magpies had shown variation in mobbing strategy to different aerial predators and performed inspection-only when confronting a ground predator, it was therefore possible to ask whether they make further and even finer discriminations when presented with variations in the same predator. The aim of these two experiments was to examine whether magpies maintain the same anti-predator strategy to a predator regardless of the predator's behaviour or posture or whether they alter it depending on circumstances.

Experiment 2 made some specific postural changes to the presented predators but used the same taxidermic models and the same experimental design as in earlier experiments (more below). Coss and Ramakrishnan (2000) presented wild bonnet macaques (*Macaca radiata*) with taxidermic models of a spotted and dark-brown leopard (*Panthera pardus*) in two postures, upright and upside down. The macaques were familiar with the spotted leopard but not the dark-brown morph and, indeed, they were more fearful of the familiar spotted morph. The results from the study showed that macaques were more fearful of the spotted model presented upright compared to the same model presented upside-down (Coss and Ramakrishnan, 2000). Hence, the macaques distinguished between different postures of the same predator and perceived them as varying degrees of threat.

Indeed, other studies have found that animals perform different anti-predator behaviour depending on the predators' behaviour and/or posture (Hamerstrom, 1957; Fitzgibbon, 1994; Brown *et al.*, 2001a; Brown and Schwarzbauer, 2001; Brown and Dreier, 2002). For instance, Hamerstrom (1957) showed that the posture of a falcon influenced the intensity of a mobbing response by bird assemblages. A captive falcon was exposed to bird assemblages when it was hungry and when it had just been fed: a falcon has specific body postures depending on whether it is satiated or not (Hamerstrom, 1957). Hamerstrom (1957) found that an unfed falcon was mobbed on more occasions than a fed falcon. This study suggests that birds can assess different levels of threat imposed by the same predator on the basis of body posture alone.

Similar results have been found in fish. In three studies (Brown *et al.,* 2001a; Brown & Schwarzbauer, 2001b; Brown & Dreier, 2002), fish were exposed to predators that had been fed either on conspecifics of the tested species or on another fish diet. Inspection of the predators fed on conspecifics involved smaller group sizes, lower frequency of inspection events and more inspection visits per fish compared to inspection behaviour performed to the predators fed on other diets. There was also an increase in the proportion of visits to the tail end of a predator with avoidance of the area around the mouth in cases where the predator was fed on the species tested. This form of risk assessment known as 'attack cone avoidance' has already been mentioned (see Ch. 1, 1.4.3.1), and, as I have shown, there was evidence, in single magpies inspecting the monitor lizard, of such avoidance of specifically dangerous areas of the predator (the potential tail flick by the monitor lizard in this case).

In the third experiment, an aerial predator was presented with or without a dead magpie. It is known that past experiences may also play a role in changing and adapting anti-predator strategies. Kruuk's (1976) study showed some evidence that mobbing behaviour by gulls changed according to past experiences with particular predators. In this study, Kruuk (1976) presented predators alone, then with a dead gull, and then again alone. The mobbing behaviour of the gulls increased in intensity when the dead gull was presented and this intensity was maintained on the next presentation when the predator was once again presented alone. Thus, this was interpreted as the gulls performing predator inspection. Hence, Experiment 3 attempted to replicate Kruuk's (1976) study to see whether it would elicit mobbing or inspection behaviour since this is often cited as evidence of predator inspection (rather than mobbing alone) in birds (Pitcher, 1992; Fitzgibbon, 1994; Leal and Rodriguez-Robles, 1997).

7.2 Methods

7.2.1 Testing response to unnatural posture

If one of the functions of predator inspection is to recognise and assess potential threats, then inspection should increase in unfamiliar situations involving predators. Hence, by presenting the stimulus in an unnatural posture, similar to the experiment by Coss & Ramakrishnan (2000), it was hypothesised that inspection behaviour should increase.

For Experiment 2, only two stimuli were selected because the aim of the experiment was to polarise possible responses into mobbing or inspection and to ascertain whether altered postures would intensify a specific strategy. The little eagle was selected as this was a stimulus that was mobbed consistently and was approached most often in previous trials. Moreover, in Experiment 1 (Chapter 4), there was little evidence that magpies performed predator inspection when faced with a little eagle. Hence, any evidence of inspection of the little eagle now presented in a novel posture would constitute a clear change in strategy. The monitor lizard was selected because this stimulus, in contrast to the little eagle, had consistently elicited inspection behaviour, as shown in the previous experiment (Chapter 6). As this stimulus already elicited inspection behaviour, the novel posture was hypothesised not to change this strategy significantly but perhaps increase its occurrence.

The unnatural posture chosen was a posture that would not occur in a live specimen of the species. The model of the little eagle was placed face down. Because the legs were rigid, the body created an angle of approximately 35° towards the ground (Figure 7.1).

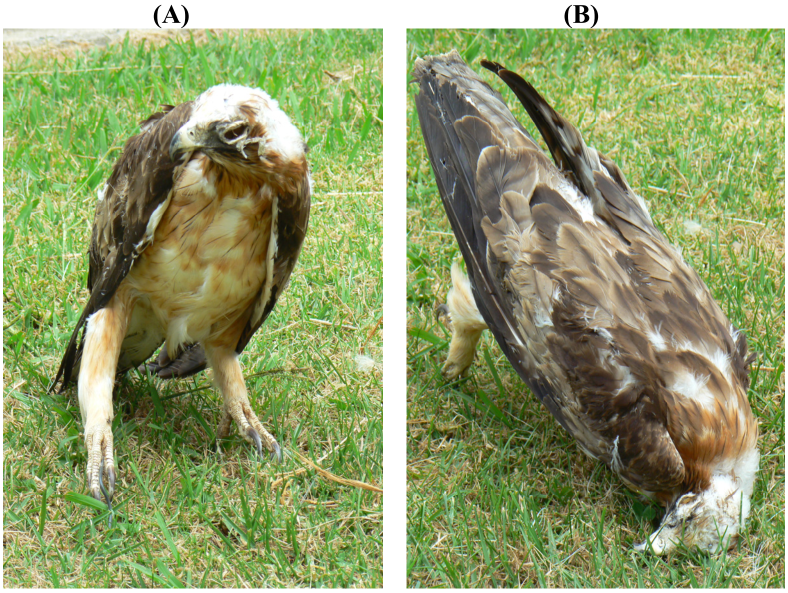


Figure 7.1. Presentation of the little eagle. (A) The little eagle in an upright posture. (B) The little eagle face-down.

To achieve an unnatural posture for the monitor lizard, the model was turned upside-down. This too was a posture which would not be seen in a live specimen (Figure 7.2).

Figure 7.2. Presentation of the monitor lizard. (A) The monitor lizard in an upright posture. (B) The monitor lizard upside-down.

Experiment 2 was conducted using eight groups of magpies between May and June 2007. This set of presentations consisted of 36 trials (two presentations in different posture of the two stimuli i.e. four presentations per group) in which the little eagle and monitor lizard were presented randomly either upright or in an unnatural posture. Each presentation was separated from the next by a minimum interval of 48 hours. Each trial was again conducted over a 15-minute period (5-minute pre-test, 5-minute test and a 5-minute post-test). A focal animal was randomly selected prior to each trial and scored, using 5-second interval sampling throughout the 15-minute trial.

Using video footage, the entire group was scored using continuous sampling of four types of behaviour. These were swooping, jumping, circling and stationary viewing (for a full description of these behaviours see Chapter 3). These scores were standardised by the number of magpies present (i.e. total score divided by number of magpies). The data were analysed using a Wilcoxon signed-ranks test to compare between the two postures.

7.2.2 Presentation of a model predator in a different context

In Experiment 3, only one predator model (little eagle) was used. The little eagle was selected for these tests because it had been mobbed consistently on previous presentations and because it is the most common aerial predator throughout the Armidale area (Debus, 1984). The same taxidermic model of the little eagle was presented in a natural posture either on its own or with a dead magpie lying in front of it. This was done to replicate Kruuk's (1976) study of black-headed gulls. To reiterate, Kruuk's (1976) sequence of trials involved presentations of a model predator alone, then the model predator with a dead gull and, thereafter, the model predator alone again. I followed this design but added one extra treatment by also presenting the dead magpie alone. If magpies did the same as gulls, their response to the little eagle during or following the presentation of the little eagle together with the dead magpie should intensify.

This third experiment was conducted in August 2007, using eight groups again. Four groups had been tested in the Experiment 2 and another four groups were selected which had been used in Experiment 1 a year earlier but not in Experiment 2.

The dead magpie, a road kill but completely intact, did not belong to any of the groups used in this experiment. The body was stored in a freezer and was only taken out during testing. The dead magpie was placed belly up in front of the little eagle's talons.

Each group was tested four times, with at least a 48 hours interval between tests. The stimuli were presented in this order: (1) dead magpie presented alone, (2) little eagle presented alone, (3) dead magpie and little eagle presented together and (4) little eagle presented alone once more. The order of presenting the stimuli was not random because this order was required to test the effects of a simulated predatory event.

The behaviour scored in Experiment 3 had to determine the intensity of response and inspection behaviour by magpies. Hence, swooping, pecking, jumping, alarm calling and physical contact were scored to measure the intensity of harassment. In addition, the number of magpies recruited was also scored in case more group members were recruited in subsequent exposure to the little eagle after it was presented together with a dead magpie. Circling and stationary viewing were scored to measure inspection behaviour. These scores were weighted by the number of bird present.

Each trial was conducted in the same time-frame as previous experiments (15-minute period consisting of a 5-minute pre-test, 5-minute test and a 5-minute post-test).

7.3 Results

7.3.1 The presentation of little eagle and monitor lizard presented in two postures

Predator-dependent behaviour such as, swooping, pecking, jumping, circling or stationary viewing had, of course, no scores during the pre-test or post-test.

The effect of postural change of the little eagle was significant for swooping, jumping, circling and stationary viewing. In the upright posture the little eagle elicited more swoops compared to the little eagle presented face down (Wilcoxon, Z = -2.581, p = 0.012; Figure 7.3A). By contrast, the number of jumps, circling and stationary viewing events was significantly higher during presentations of the little eagle in the face down posture compared to presentation of it in an upright posture (Wilcoxon, Z values ranged from = -2.240 to -2.251, p values ranged from = 0.012 to 0.025; Figure 7.3B-D).

The posture of the monitor lizard had no significant effect on the behaviour of the magpies. There was no significant effect of posture on swoop, jumping, circling, or stationary viewing (Wilcoxon, Z values ranged from = -1.014 to -1.859, p values ranged from = 0.063 to 0.208).

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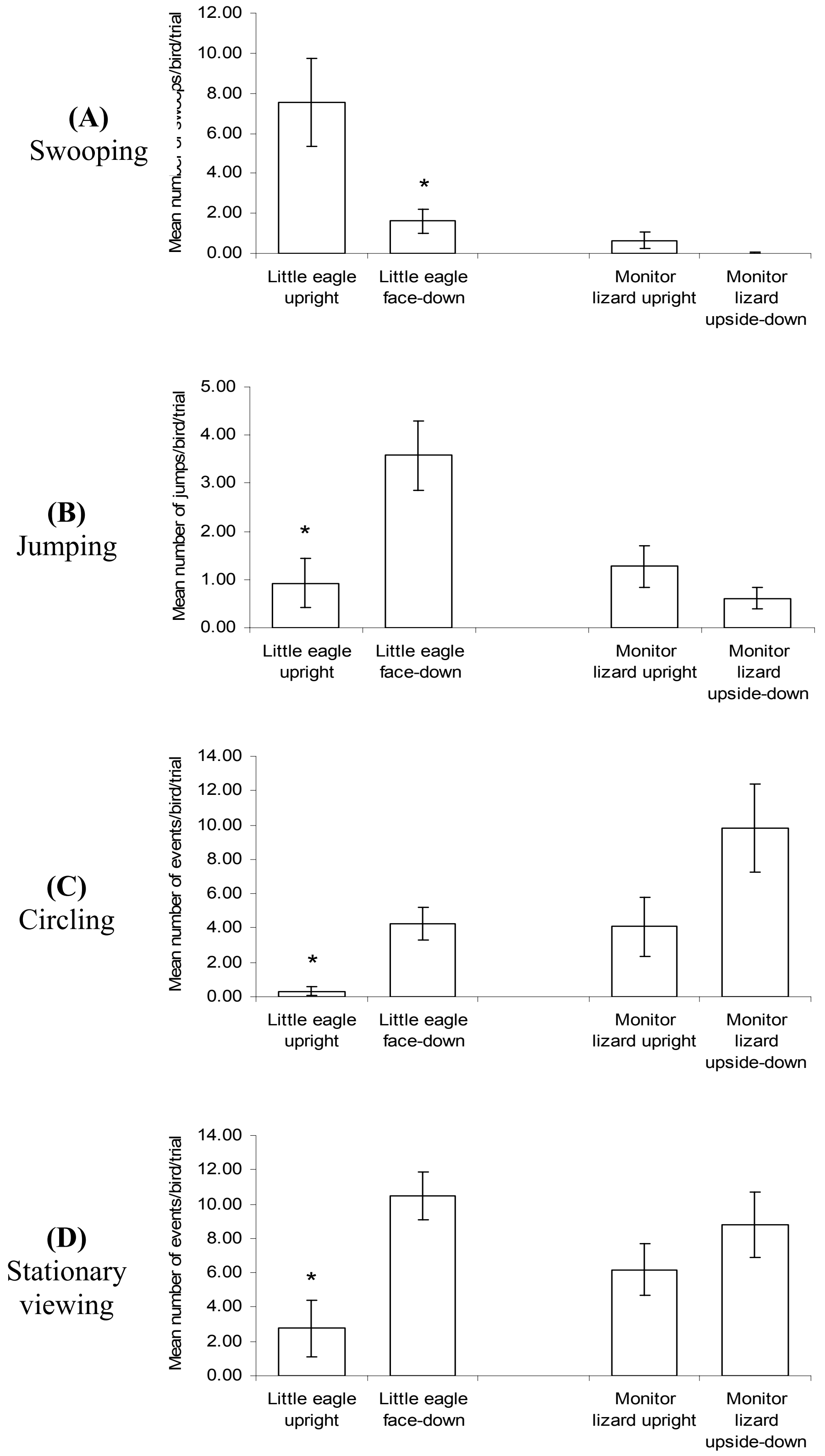


Figure 7.3. The response of the magpies to the model predators in different postures. (A) swooping, (B) jumping, (C) circling and (D) stationary viewing. For each graph, the mean number of events per bird (number of events divided by the number of magpies) ± SEM are plotted for each stimulus (X axis). * indicates a significant difference ($p<0.050$). The magpies altered their behaviour towards the little eagle when it was presented in different postures. There was not, however, any significant effect of the presentations of the lizard in different postures.

In none of the trials presenting the little eagle, did one magpie approach the eagle alone. The monitor lizard presented upside down was approached by one magpie during one trial. This magpie did not alarm call or perform any agonistic behaviour but it did circle (23 events) and view (17 events) the lizard. In a further two trials there was a considerable latency to recruit group members (66 and 135s respectively).

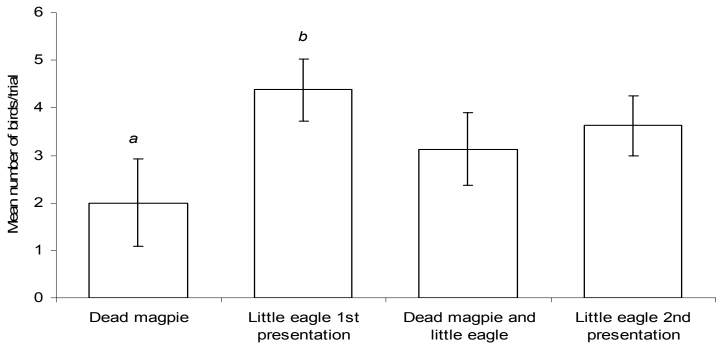
7.3.2 Responses to a predator seen with a dead conspecific (replicating Kruuk's experiment)

There were no scores of swooping, pecking, jumping, circling or stationary viewing before (pre-test) or after (post-test) the stimuli were presented.

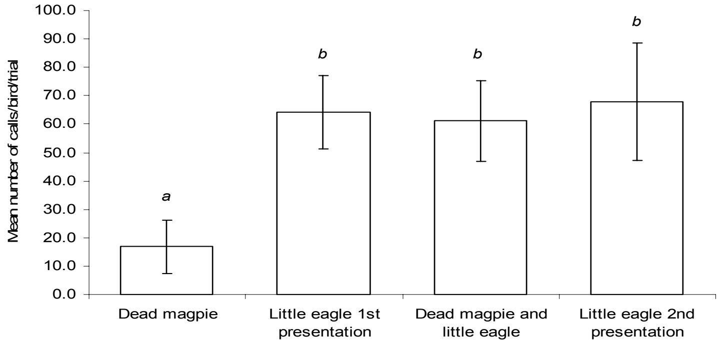
The number of magpies that were recruited was significantly affected by the stimuli (GLM, with stimulus as the repeated measure, DF = 3, F = 6.569, p = 0.003; Figure 7.4A). The dead magpie had significantly fewer magpies approaching it than the first little eagle presentation (p = 0.024) but no difference was found between all presentations of the eagle and the dead magpie presented alone (p>0.05).

There was a significant effect of stimulus on the number of alarm calls (Friedman's test, with stimulus as the repeated measure, N = 8 Chi-square = 10.050, p = 0.018; Figure 7.4B). The dead magpie elicited significantly fewer alarm vocalisations compared to all other treatments (Wilcoxon, Z ranged from -2.100 to -2.521, p ranged from 0.012 to 0.036; Figure 7.4B).

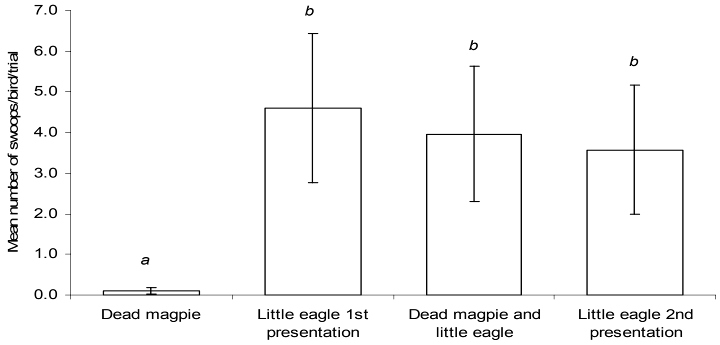
(A)
Number of magpies



(B)
Alarm Calls



(C)
Swooping



(D)
Jumping

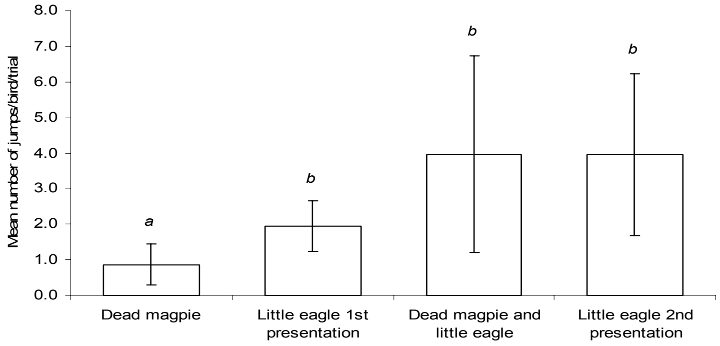


Figure 7.4. The response of magpies to the dead magpie and little eagle in all four treatments. (A) number of magpies recruited, (B) alarm vocalisations, (C) swooping and (D) jumping. For each graph, the mean number of events per bird (number of events divided by the number of magpies) ± SEM are plotted for each stimulus (X axis). *a* indicates that it is significantly different from *b* ($p<0.050$). This graph illustrates that the effect of presenting the dead magpie with the little eagle had no influence on the behaviour of the magpies.

The number of swoops was significantly different between the stimuli presented (Friedman's test, with stimulus as the repeated measure, N = 8 Chi-square = 6.569, p = 0.003; Figure 7.4C). This was again due to a lower response towards the dead magpie compared to the three presentations involving the little eagle (Wilcoxon, Z ranged from -2.043 to -2.521, p ranged from 0.012 to 0.041; Figure 7.4C).

Jumping behaviour was significantly affected by the stimuli that were presented (Friedman's test, with stimulus as the repeated measure, N = 8 Chi-square = 8.410, p = 0.038 Figure 7.4D). The presentations of the little eagle alone and together with the dead magpie elicited significantly more jumping events than the presentation of the dead magpie alone (Wilcoxon, Z-values ranged from: -2.023 to -2.207, p-values ranged from: 0.0027 to 0.043 Figure 7.4D)

The stimuli had no effect on pecking, physical contact, circling or stationary viewing (Friedman's test, with stimulus as the repeated measure, N = 8 Chi-square ranged from 1.929 to 8.000, p-values ranged from: 0.128 to 0.587).

7.4 Discussion

7.4.1 Effects of changed postures on magpies response

Overall, incidents of agonistic behaviour were higher towards the little eagle than towards the monitor lizard, regardless of posture. This further confirms the results presented in Chapter 4 as magpies displayed considerably more agonistic behaviour towards the three aerial predators than towards the monitor lizard.

The statistically significant changes in displays of agonistic behaviour (swooping and jumping) between the little eagle upright and face down can be interpreted in several ways. Their behaviour showed that they responded to postural changes of the same predator. This is similar to findings by Coss & Ramakrishnan (2000) and Hamerstrom (1957). A question of interest is why magpies adopt such very different anti-predator behaviour in any of these specific circumstances. It is possible that the magpies perceived the two postures of the little eagle as varying degrees of threat. Although there was no clear decrease in overall mobbing intensity, one type of agonistic behaviour decreased (swooping as an aerial strategy) while another increased (jumping as a ground strategy). The different response to the two postures of the little eagle suggests a more complex behaviour and signals a change of strategy. If, in fact, the variation in mobbing intensities can be used to determine perceived risk by animals then it can be deduced that the magpies perceived the upright posture of the little eagle as a greater threat than the face-down posture.

My prediction that the presentation of the model predators in an unnatural posture will elicit more inspection behaviour compared to the same model predators in a natural posture, proved to be correct especially with respect to the little eagle for circling and stationary viewing. For the lizard, circling and stationary viewing remained the same for both postures. It is interesting that only the postural changes of the little eagle, and not of the lizard, elicited more viewing behaviour from the magpies. However, as was shown in Chapters 4 and 5, the lizard was obviously viewed constantly when it was presented in a natural, upright, posture. As predicted, in the case of the lizard, the strategy did not change and was not expected to change appreciably because the aspects of predator inspection were already fully expressed in the magpie’s dealings with the ground predator when it had been presented in an upright position.

The difference in viewing behaviour, i.e. circling and stationary viewing in the little eagle presentations (upright and face down), suggests that the model presentations of this potentially dangerous predator required more assessment when in an unnatural posture than the same model in a natural posture. Dugatkin and Godin (1992) pointed out that when potential prey cannot identify a predator because it is partially occluded, predator inspection events will increase. However, the increase in inspection behaviour during the presentation of the little eagle face down does not actually suggest a period of uncertainty because there was no latency to recruit group members and the magpies continually performed agonistic behaviour. However, the magpies may have been monitoring the predator. Indeed, some studies have suggested that predator inspection increases when a predator is actively hunting compared to a predator that is resting (Magurran and Girling, 1986; Pitcher, 1986; Fitzgibbon, 1994). Hence, when the model was placed in an unusual position, it appears that the magpies recognised both the predator (vocalising and recruiting) but also the unusual posture (viewing and circling).

7.4.2 Effects of presentation of dead magpie together with a predator

The only significant differences found were between the presentations of the dead magpie and all presentations involving the little eagle. The presence of the dead magpie on its own made fewer magpies approach and elicited lower numbers of alarm calls, swooping and jumping instances compared to trials in which the little eagle was presented. No differences were found between the presentations of the little eagle, regardless of the presence or absence of the dead magpie. Consequently, there is no evidence to suggest that the presentation of the little eagle with a dead magpie affected the magpies' response. Hence, these data do not confirm Kruuk's (1976) results.

The difference between the results presented here and Kruuk's (1976) study may possibly be explained as a consequence of the different social organisation of the two species. Gulls are not territorial and are flock birds, whereas magpies are territorial and form family groups. The increased mobbing behaviour of the gulls during the predator/dead conspecific presentation (Kruuk, 1976) could, perhaps, have been directed at aiding the conspecific. By contrast, it may be unlikely that magpies would come to the aid of a conspecific from another territory, as all other magpies are usually considered intruders. Note that they attacked the dead magpie as they would an unfamiliar magpie within their own territorial boundaries (Farabaugh *et al.*, 1992; Kaplan, 2004). In assessing responses to a predator, it is obviously important to take into account the social organisation of the species.

CHAPTER 8. INSPECTION BEHAVIOUR BY ZEBRA FINCHES

8.1 Introduction

In Chapter 1, it was hypothesised that territorial species tend to mob whereas non-territorial species tend to perform predator inspection. Magpies were used as a model species for territorial birds and zebra finches selected as a model of a nomadic species with home ranges. Magpies were shown to often engage actively and consistently in mobbing behaviour thought to be characteristic of territorial species but, as was shown, there was also clear evidence of inspection behaviour (Chapter 5). By contrast, zebra finches were predicted to exhibit more inspection than mobbing behaviour and, in this chapter, some specific anti-predator strategies of zebra finches are examined in detail.

The differences in anti-predator behaviour between these two species may be related to body size, life patterns and ecological niches. For instance, the size difference between magpies (255-385g: Schodde and Mason, 1999) and zebra finches (9.4-16.2g: Zann, 1996) is substantial. Mobbing behaviour in small birds, such as the zebra finch, may not be as effective as mobbing in magpies since magpies have more effective weapons than zebra finches (large claws and strong beaks). Zebra finches are found mainly in grasslands of the drier inlands and the rhythm of their lives is determined by the availability of seeds and water. Their searches for these resources can take them over hundreds of kilometres in a single season. They travel and live in small to large flocks and nest colonially (Zann, 1996) but, like magpies, they may form life-long pair bonds with their mates (Butterfield, 1990). Inspection behaviour may need to be part of the standard repertoire of zebra finches since they so often have to change their physical environment and would possibly contact different predators accordingly.

Zebra finches have a number of predators including snakes, lizards and numerous raptors (Zann, 1996). Fledgling zebra finches suffer high mortality rates mostly due to predation (Zann and Runciman, 1994). As mentioned in Chapter 1, between fledging and independence, 67% of young are lost. Overall, 80% of fledglings do not survive past the age of 80 days (Zann and Runciman, 1994).

What we know so far of anti-predator behaviour of zebra finches is that they tend to flock together in flight when an aerial predator is actively hunting (Zann, 1996). If suddenly confronted by a predator midair, they all descend rapidly together, using criss-cross movements, and then try to seek cover in shrubs (Zann, 1996). Although there is no evidence of wild zebra finches mobbing predators (Zann, 1996), Lombardi and Curio (1985a; 1985b) have suggested that they do mob. In two laboratory experiments, they presented pairs of zebra finches with either a live Pygmy owl or a starling. They found that zebra finches vocalised, flicked their tails and wings and moved their heads from side to side to fixate the stimuli monocularly. However, the experimental setup may have somewhat constrained the response of the zebra finches. In fact, their response may have been more of an indication of the experimental design rather than a response to the predator since the zebra finches had no place to which they could escape.

It is now important to determine in more detail than has occurred previously the function of inspection behaviour in a species that is thought to inspect rather than mob. I would like to emphasise that a distinction has to be made between inspection of a predator and other forms of inspection: there are other functions of inspection behaviour not related to predators. Many animals approach and inspect novel objects (Heinrich, 1995b; Gomez-Laplaza and Morgan, 2000; Mettke-Hofmann *et al.*, 2002; Groothuis and Carere, 2004; Mettke-Hofmann *et al.*, 2005b). This makes evolutionary sense since animals must explore their environment to locate new food sources (Mettke-Hofmann *et al.*, 2002; Mettke-Hofmann *et al.*, 2005b). Indeed, a study of 61 parrot species by Mettke-Hofmann *et al.* (2002) found that there was a relationship between the propensity to inspect or avoid a novel object and the diet and/or habitat. Hence, the evolution of inspection behaviour within a species may be a result of ecological pressures.

Apart from exploration as a method for finding new food sources or new territories, as had been elaborated on in Chapter 1, juveniles of many species need to learn about their environment. For example, juvenile common ravens (*Corvus corax*) preferentially collect items within their environment that they have never seen before (Heinrich, 1995b). In subsequent observations, the novel items that were inedible were soon ignored and only the edible items were collected. This suggests that the juvenile ravens needed to explore and learn about their environment before they were able to identify food reliably.

There is also evidence that juveniles engage in inspection to learn about predators, and that juveniles and adults may respond similarly to predators. Apparently, Californian ground squirrel pups already perform anti-predator behaviour in the same manner as adults do (Goldwaite *et al.*, 1990). Moreover, while predator inspection is generally recognised as an aspect of behaviour in relation to predators, the intensity and frequency of such behaviour appears to vary with experience. For instance, experience with predators has been shown to be an important factor in some fish species. Fish from areas with predators inspect them differently than fish that live in areas that are not occupied by predators (Walling et al., 2004). For instance, experienced fish avoid the head of the predator more than fish that have had no experience with predators (Walling *et al.*, 2004); that is, they inspect more cautiously and perhaps gather enough information about the predator during fewer visits.

The aim of this chapter is to examine whether inspection in zebra finches is merely part of exploration of their environment or whether a particular aspect of inspection is specifically concerned with predator-prey encounters. To investigate this, two experiments were conducted. Experiment 4 examined whether finches that were originally housed in outdoor aviaries and had, presumably, been exposed to some threatening species (i.e. cats, raptors or lizards) discriminate between a novel object, that does not resemble a predator in any way, and a model predator. It was hypothesised that inspection of a novel object should decrease rapidly but inspection of a model predator would remain constant (Magurran and Girling, 1986; Walling *et al.*, 2004).

Experiment 5 investigated whether both naïve and experienced finches (experience meaning here that they have had prior exposure to predators) discriminate between model predators and a novel object. One of the functions of predator inspection postulated in the literature is that animals, especially juveniles, may approach predators in order to gather information about them (Dugatkin and Godin, 1992). Alternatively, animals may approach a predator to monitor its behaviour (Dugatkin and Godin, 1992). If learning about how to deal with predators is important, I would expect to find a difference between naïve and experienced finches in terms of their responses to predators and novel objects not resembling predators.

8.2 General Method

8.2.1 Subjects

Twenty adult zebra finches were purchased from local breeders which housed the birds in outdoor aviaries, 10 (5 males, 5 females) on the 26/4/05 and 10 (6 males, 4 females) on the 12/9/05. Four birds (3 males, 1 female) were bred between April and September 2005. A further 19 birds were bred between February and August 2007. Hence, 20 adult finches were purchased and 23 finches hatched in the university aviaries.

Housing and breeding of the zebra finches as well as the trials were conducted with the authority of the Animal Ethics Committee of the University of New England.

8.2.1.1 *Identifying individual finches*

The zebra finches were identified by plumage and beak colourations. Ring bands were not used since this might have affected their behaviour (Hunt *et al.*, 2001). Identification criteria differed depending on sex. Female zebra finches were first identified by noting their colour morph, such as wild type (the common plumage type found in the wild), fawn or white morphs. A further two characteristics were used to discriminate birds of the same morph: (1) beak colour, (2) size and shape of the markings on their heads.

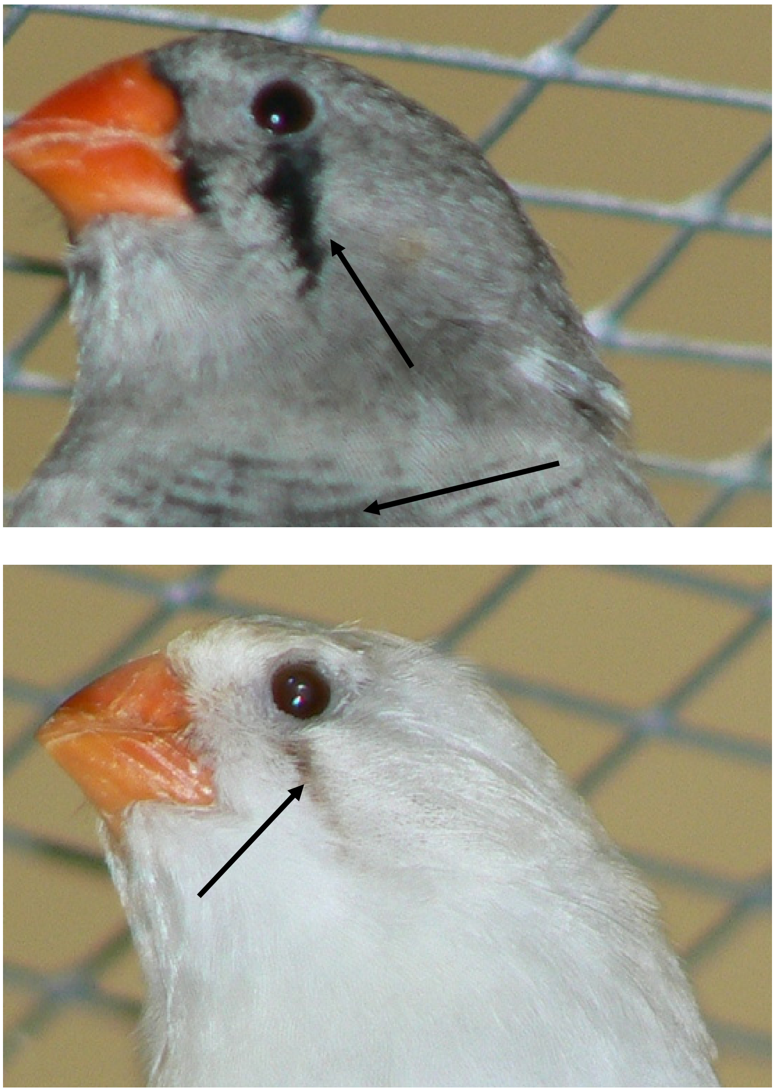


Figure 8.1. Identifying individual female finches. The plumage of the female finches provided the most distinguishing marks but the size and shape of some of the markings on the head of the birds were also used to identify individuals (see black arrows).

The males, like the females, were first categorised by their colour morph. The males have more markings to discriminate between individuals of the same morph than do female finches. Hence, the characteristics that were used to identify individual males of the same morph were: (1) beak colour, (2) size and shape of chest band, (3) white patch underneath beak and (4) the colour of the pattern underneath the wings.

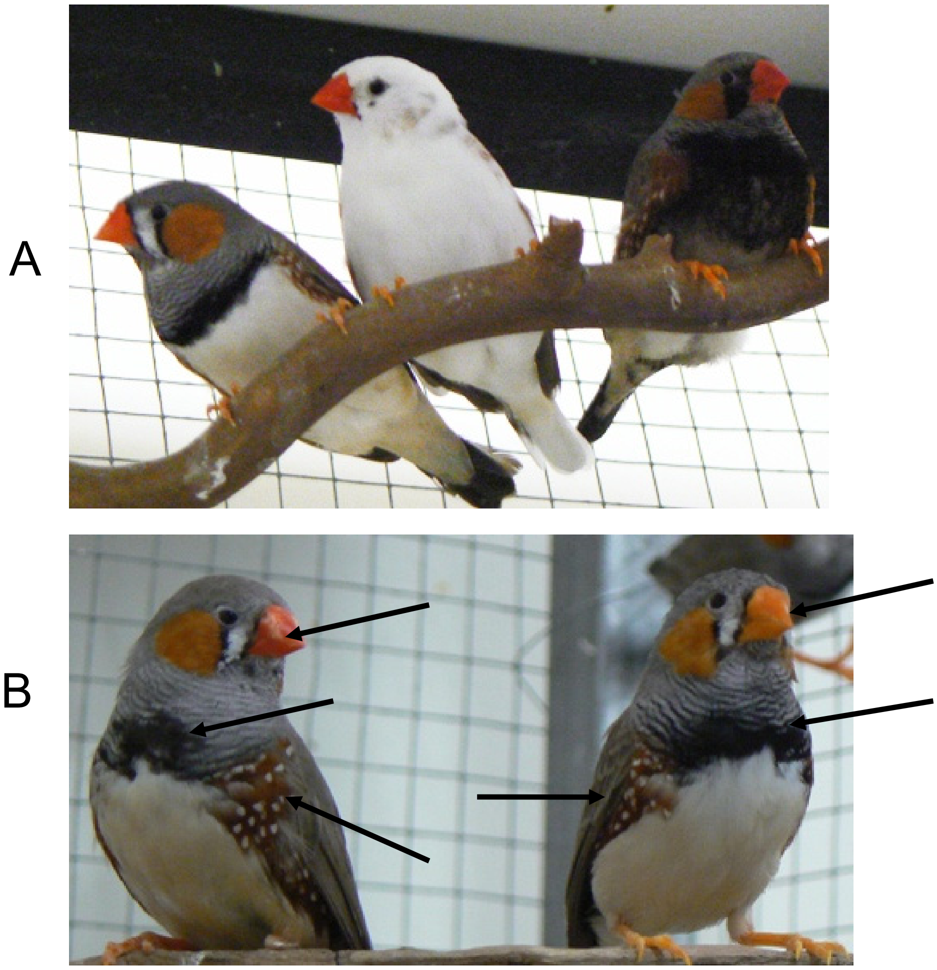


Figure 8.2. Identifying individual male finches. Photograph (A) shows two morphs (white and wild-type plumage) and two distinct variations of the wild-type plumage. These distinctly different plumage types made identifying individuals relatively simple. Photograph (B) shows two wild-type individuals and the three distinctive markings (shown by the black arrows) that were used to identify these individuals. The individual on the left has a red beak and on the right this individual has an orange beak, the chest band on the individual on the left does not completely extend across its chest while the individual on the right does, the wing markings on the individual on the left extends higher up the chest than the individual on the right.

All of these markings were entirely distinctive between individuals and the birds were housed in relatively small home groups which made identifying individuals more accurate and errors very unlikely to occur.

8.2.2 Housing

Each aviary was furnished with natural perches of local *Eucalyptus* trees. Two nest baskets were provided for each pair. A thermostat was located in the home room to keep ambient temperature in a range of 18-27˚C. Light cycle was 13L:11D, on at 06.00h and off at 19.00h. A small lamp with a 40 watt globe was placed in the centre of the room and was activated at 1830h and switched off again at 1930h. This was to provide a cue to the birds to begin to roost and to provide some light once the main light source was switched off. A Hitachi 40 Watt fluorescent light with an UV output of 7.5 was activated for 30 minutes from 07.30h to 08.00h daily to provide a source of UV light.

8.2.2.1 Home room

The birds were housed in five aviaries and one cage (Table 8.1) located in a single room (home room 4.9mL × 3.0mW × 2.7mH). All experiments were conducted in a testing aviary in a separate room away from all housing.

Table 8.1. Dimensions (in cm) of aviaries in the home room and the testing aviary. Note that groups were housed in different aviaries after breeding.

Aviary	**Length**	**Width**	**Height**	**Aviary housing before breeding**	**Aviary housing during breeding**	**Aviary housing after separation of sexes**
1	71.8	163.8	168.0	4♂	1♂ &1♀	7♀
2	71.8	163.8	168.0	4♀	2♂ &2♀	8♂
3	90.0	90.0	180.0	6♀	1♂ &1♀	7♀
4	65.0	145.0	170.0	6♂	1♂ &1♀	8♂
5	140.0	60.0	170.0	-	4♂ &4♀	11♂
6	45.0	34.0	100.0	-	1♂ & 1♀	2♀
TOTAL	-	-	-	20 (10♂ & 10♀)	20 (10♂ & 10♀)	43 (27♂ & 16♀)

From September 2005 until February 2007, all birds were housed in same-sex groups to prevent breeding, with the exception of a period between February and August 2007 when male-female pairs were housed together.

Figure 8.3. Furnishing of the home room. Note, there are three home aviaries on the right and two on the left. The white cage in the centre of the room is the cage used to transport a pair to the testing aviary. The light reduction (via a lamp) used for a cue to begin roosting is in the centre of the room, next to the transport cage.

Breeding ceased in August 2007 and the breeding pairs were separated into the former same-sex aviary groups and the juvenile finches also placed into same-sex groups.

8.2.2.2 Testing room

All experiments were conducted in a separate aviary located in a separate room from that housing the home aviaries. The testing aviary (3.0m × 1.4m × 1.7m) was refurnished according to the needs of each experiment (details in specific method sections) (Figure 8.3). During trials, the experimenter remained behind a barrier out of visual range of the finches.

The testing room contained a camcorder, a Panasonic digital video recorder (NVGS35) located directly behind the stimulus presentation area. The video camera was set up in such a way that approximately 95% of the testing aviary could be captured on film. However, the set-up of the camera was different for Experiments 4 and 5 (see Sections 8.3.3 and 8.6.3) but, suffice it to say here that, the entire stimulus presentation area (i.e. the area that the finches could view the stimulus) was captured on film for both experiments.

8.2.3 Husbandry

A minimum of three food dishes and two water dishes per aviary were provided. Food, water and cuttlefish bone were supplied *ad libitum*. The seed used was a mixture of two commercial brands Lovitts Canary and Finch Mix and Trill Finch Food. Vitamin and calcium supplements were provided once a fortnight and lettuce was provided once a week. The cage floor was lined with newspaper and replaced one a week.

8.2.4 Experiments

Prior to conducting any experiment, a pilot study was conducted to determine which model predators elicited inspection behaviour and to establish a scoring methodology.

8.2.4.1 Stimuli

During the pilot study, the finches were presented with three stimuli: a realistic model snake and taxidermic specimens of a brown goshawk and a monitor lizard (the same models as were used for the magpies). These three models represent natural predators of the zebra finch. Brown goshawks have been reported to hunt zebra finches at waterholes (Evans *et al.*, 1985; Zann, 1996) as have snakes (Zann, 1996). Snakes and monitor lizards are known nest predators of zebra finches (Immelmann, 1962; Zann, 1996) and since brown goshawks have been observed near zebra finch nest sites, they are presumed to be nest predators (Zann, 1996).

8.2.4.2 Method of pilot study

For the pilot study, the zebra finches were tested together (as aviary home groups) in the testing aviary. There were four aviary groups (N=4) of zebra finches (see Table 8.1 for group sizes and sex). One home group was tested at a time. Collecting the finches for transport to the testing room was achieved by turning off the lights. Zebra finches have poor eyesight in dim light and can be collected from their perches. The experimenter was able to take each finch and place it in a small transport box and then release the entire group into the testing aviary. They then remained in the testing room for five days to allow them to adjust to the new surroundings and, additionally, for three testing days, during which time each of the three model predators was presented once daily at 09.30h, leaving a 24 hour interval between model predator presentations. Each stimulus was presented for five minutes.

To present the stimuli, the experimenter placed the stimulus in the aviary through a door cut into the aviary wire. The experimenter stood behind the visual barrier and reached around to place the stimulus. The stimulus was retrieved using the same procedure. Note, only the arm of the experimenter was visible to the birds. The experimenter was otherwise visually isolated from the birds throughout the trial so that their behaviour was not influenced by the experimenter's presence. During trials, the experimenter observed the behaviour on a monitor and scoring was largely taken from the video-footage.

8.2.4.3 Outcome of pilot study

Each of the zebra finch groups approached the stimuli on all occasions (i.e. came within 80cm of the stimulus). However, they did not spend the entire duration of the presentation close to the stimulus. They moved back and forth in the aviary. During the approaches towards the stimuli, the zebra finches performed monocular fixation movements that have been described by Lombardi and Curio (1985a; 1985b). I classified this behaviour as inspection. To ensure that the bird was fixating the stimulus monocularly during an inspection event, the angle of the birds beak to the stimulus had to be 90° or more. Zebra finches have laterally placed eyes with a 170° monocular field of vision (Bischof, 1988). Therefore, for a zebra finch to monocularly fixate a stimulus, it needs to make an exaggerated head movement. This provides an opportunity to score whether there is a preference to view stimuli with one eye over the other. Indeed, Alonso (1998) tested zebra finches' ability to distinguish between pebbles or seed on the floor and which eye is used to fixate on the floor. It was found that the zebra finches were more successful at selecting seed over the pebbles if they used the right eye.

The duration of an inspection event was scored by viewing playback of video recordings and using computer software (ODLog) to accurately records timing of manual scoring.

The results of the pilot study showed that the monitor lizard elicited most inspection behaviour (21.4 (s) ± 11.6 SEM) compared to the snake (4.7 (s) ± 2.0 SEM) and the goshawk (1.6 (s) ± 1.6 SEM).

8.2.5 Statistical analyses

Data were analysed for normality and equal variances and if the analyses demonstrated that the assumptions for parametric test were not met, non-parametric statistics were conducted. The type of test used is described fully in each methods section. Data were analysed using repeated-measures (either stimulus or testing day was the repeated measure).

8.2.6 Testing exploration versus predator inspection

Experiment 4 was conducted between August 2005 and June 2006. The aim of this experiment was to investigate the response of the original batch of adult zebra finches (bred outdoors and so exposed to some predators) to a novel object and a model predator. It was hypothesised that the zebra finches should habituate to the novel object but not to the model predator. Even though this batch had been purchased from a commercial breeder and little was known about their history or age, I was able to establish that they had been housed in outdoor aviaries prior to purchase. It is highly likely, given that these aviaries were located in rural Australia, that the birds had encountered lizards, rodents and other free-ranging animals (i.e. dogs, cats and native birds, including their natural predator such as brown goshawks) in such an environment. In other words, they may not have had any encounters with a monitor lizard but they may have had exposure to other lizards and other threatening animals.

Similar experiments using novel objects and realistic model predators have been conducted using fish and the results showed that fish habituated rapidly to novel objects but continually inspected model predators (Magurran and Girling, 1986). This is not to say that habituation to predators does not occur - there is evidence that fish habituate to predators over numerous encounters (Huntingford and Coulter, 1989) but that the rate of habituation is much slower and less stable to a predator than to a novel object. Indeed, previous studies on domestic chicks have found that only four to five presentations is required for the chicks to habituate to a novel visual stimulus (Rogers and Anson, 1979; Andrew, 1991).

8.2.6.1 Sample Size

The zebra finches were tested in same-sex pairs from the same group in which they were housed. Testing of individuals was tried but was found to be unsuccessful, because the birds tended to freeze and not move or feed in the testing aviary and this was considered undesirable for the bird as well as for the testing procedure. In all cases, the pairs were cage mates. Zebra finches in captivity may form same-sex pair bonds (Adkins-Regan and Krakauer, 2000). To determine whether individuals had formed a bond, each cage group (N = 4 groups) was observed for 30 minutes across four consecutive days and the interactions between the individuals were noted. Seven pairs (five same-sex male pairs and two same-sex female pairs) were considered to have formed same-sex pairs. Individuals that had formed a bond were seen allopreening and no agonistic displays were observed. By contrast, there were constant agonistic events observed between other pairs or towards an individual not part of a pair. The individuals that had formed pair-bonds were selected for testing.

8.2.6.2 Stimuli

Following the results of the pilot study, the monitor lizard was selected as the model predator since, as reported above (8.2.4.3), it elicited consistently the most inspection behaviour. The novel object was a large white opaque plastic container with a red lid (height 16cm, base diameter 9cm, lid diameter 5cm).

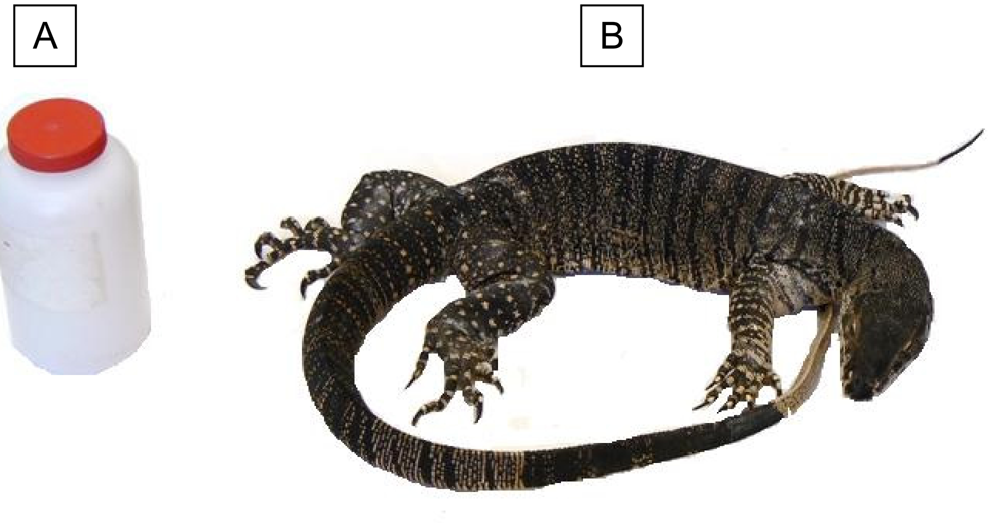


Figure 8.4. Novel object (a) and monitor lizard (b).

The size of the novel object was meant to attract the zebra finches' attention. If the novel object was too small and inconspicuous, the zebra finches might not have noticed it. Moreover, the novel object and the predator model had to be of comparable size so that any differences in response could not be attributed to size as the determining factor. The zebra finches had not been exposed to any such objects during the time for which they were housed at the Animal House of the University of New England.

8.2.6.3 Testing aviary

The testing aviary was designed to have two distinct areas. Section A was the half of the aviary where the stimuli were presented and Section B was the other half of the aviary furthest from the stimulus presentation area (Figure 8.5).

Two perches were placed in Section B. Perch 1 was located behind a visual barrier to provide a place of refuge at the furthest distance possible from the stimulus presentation area (170cm from the area). Perch 2 was 90cm long and it was placed in the back left hand corner of the aviary. Hence, the finches could view the stimulus while keeping a distance from it.

Section A had 5 perches that were less than 80cm from the stimulus presentation area. Perches 3 and 4 consisted of multiple branches that extended from the aviary floor to the roof. Each perch had branches extending towards the stimulus presentation area (50cm to 80cm from the presentation area).

Two perches (6 and 7) extended to either side of the stimulus presentation area and provided a vantage point for the finches to inspect both sides of the stimulus. These perches were 20cm from the stimulus presentation area. Perch 5 was 40cm directly in front of the stimulus presentation area. It was 80cm long and provided a frontal view of the stimulus presentation area. This perch was suspended by string from the roof of the aviary (30cm from the roof) and was 30cm higher than the stimulus presentation area.

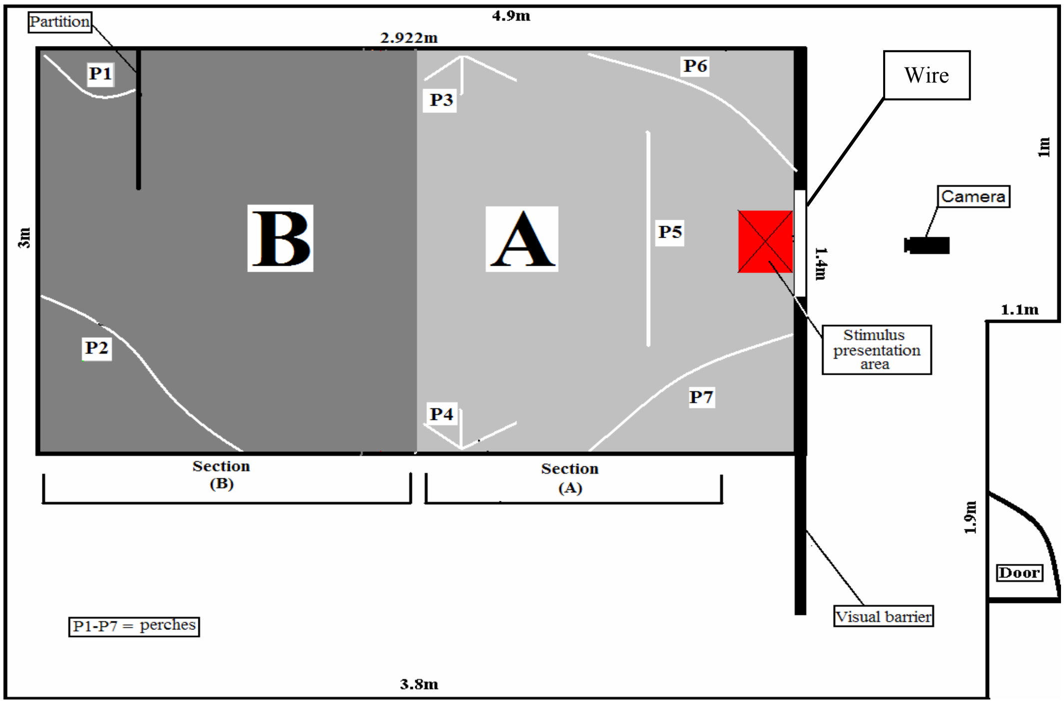


Figure 8.5. Testing aviary during Experiment 4. The stimulus presentation area was located in Section A. The furthest perches from the stimulus (P1 and P2), at least 1.7m from the stimulus presentation area, were located in Section B. This section was classified as an avoidance area. Perches 3-7 were less than 80cm from the stimulus presentation area and these were classified as an approach area. Perches 3-4 were 80cm from the stimulus presentation area while Perches 5-7 were less than 40cm from the stimulus presentation area. The camera was located behind the stimulus presentation area outside of the aviary. The view from the camera incorporated the entire aviary. The experimenter was located behind the visual barrier.

The stimulus presentation area was 40cm × 60cm and it was 140cm from the floor of the aviary. The camera was placed 30cm above the stimulus presentation area and 1.2m from the aviary. The frame incorporated most of the aviary with the exceptions of the refuge area.

The experimenter was located behind a visual barrier and observed the finches through a monitor. Detailed scoring used playback which allowed frame by frame analysis, particularly for scoring eye use.

8.2.6.4 Trial Period

Each stimulus was presented once per day at 9.30h and 10.30h over 4 days (56 trials in total, 8 trials per pair). The order of presentation per day was random. An interval of 30 minutes was allowed between each trial with each stimulus on one day. The number of days of repeated presentations was determined by the response of the finches to the stimulus. Once no decrease in inspection behaviour had occurred from one day to the next, the stimuli were then presented for an extra day to determine whether habituation was stable.

8.2.6.5 Presentation of Stimuli

At the end of the 5-minute pre-test, the experimenter opened a small door that was cut into the aviary wire and placed the stimulus on a platform. Following the conclusion of the test, the experimenter retrieved the stimulus and closed the door.

8.2.6.6 Scoring Method

8.2.6.6.1 Location

The duration of time spent in Section A or B and the number of times each section was visited were scored. The score was the total duration that the pair spent within each section. Each individual was scored and the final number was the total for the pair. The duration of time spent inspecting the stimuli (i.e. duration of time spent performing monocular fixation movements) was also scored. Hence, continuous sampling of both birds was scored.

8.2.6.6.2 Inspection Behaviour

Monocular fixation movements were scored when a zebra finch approached the stimulus (i.e. in Section A) and moved its head from side to side (Figure 8.6).

8.2.6.6.3 Eye use

To score monocular fixations during an inspection event, the video footage was replayed in slow-motion. A monocular fixation was scored when there was a 90° angle measured from the direction of the beak of the zebra finch in relation to the stimulus. As mentioned above, the monocular visual field of the zebra finch is quite large (170° in the horizontal plan laterally placed eyes), thus scoring a fixation at a 90° angle from the beak to the stimulus ensured that the fixations were indeed monocular especially since their binocular field is 30-40°. During an inspection event, a zebra finch turns its head from side to side (Figure 8.6).

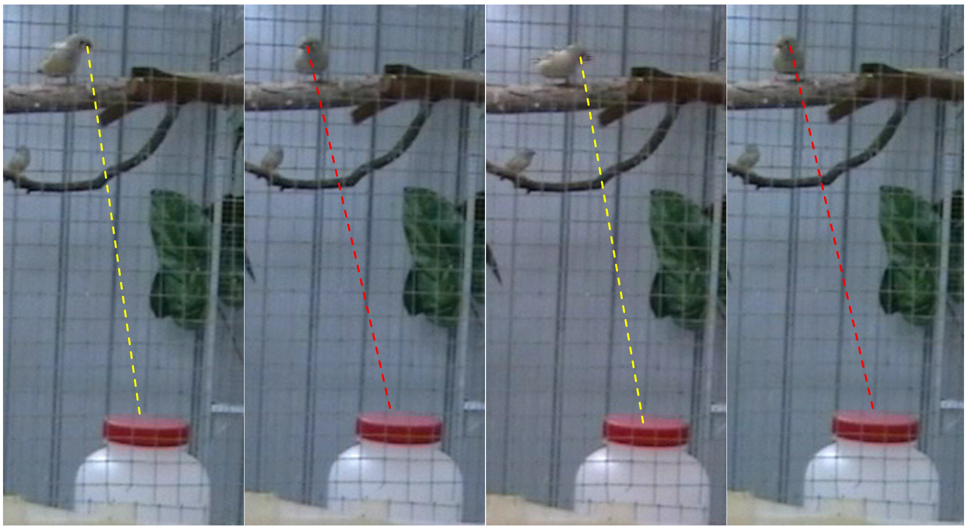


Figure 8.6. Sequence of video footage showing inspection of the novel object. The yellow line indicates a right eye fixation while the red line indicates a left eye fixation. Hence, this finch views the novel object first with the right then left and again right then left.

Only the first monocular fixation of the stimulus in an inspection bout was scored since this should reflect the initially preferred hemisphere for processing input from the stimulus.

8.2.6.7 Statistical Analyses

All of the data were analysed using non-parametric tests apart from the data for time spent avoiding the stimuli. The non-parametric data were analysed using Friedman’s test with testing day as the repeated measure. *Post hoc* analyses used a two-sample Wilcoxon signed ranks tests. The parametric data were analysed using paired T-tests. Note that the sample size is the number of pairs, not the number of individuals.

8.2.7 The role of experience in predator inspection

In Experiment 5, I investigated whether the response of the outdoor-bred birds to model predators differed from the response of predator-naïve zebra finches. For this purpose, 23 zebra finches were bred indoors at the animal house facility and were not exposed to any threatening stimuli.

The zebra finches were presented with two model predators (snake and monitor lizard) and a novel object (same jar but with golden coloured lid, Figure 8.4). I predicted that inspection behaviour by naïve zebra finches should decrease rapidly to all stimuli performed but inspection behaviour performed by the experienced finches would decrease only to the novel object. Previous research has found that predator-naïve fish (i.e. that live in areas without predators) inspect both unrealistic and realistic models of a predator, whereas experienced fish only continue to inspect the realistic models of the predator (Walling et al., 2004). Experiment 5 was conducted between September 2007 and May 2008.

8.2.7.1 Sample Size

In Experiment 4, it was established that allopreening events between finches was a reliable way of determining whether individuals had formed same-sex pairs. This method was used again to select the same-sex pairs for this experiment. Interestingly, new pairs had been established between the experienced finches that had been tested in Experiment 4. This was probably due to several factors, (1) the death of two individuals that had formed bonds with other finches (2) the separation of the groups for breeding purposes also seemed to influence the social organisation and (3) the reorganisation into same-sex groups per aviary after breeding. Seven individuals that were tested in Experiment 1 and five experienced finches that had not been previously tested were selected on the basis that they had formed new pair bonds. The same method was used to determine which naïve finches had paired. Observations were made over two 15 minute periods. During this time, the individuals that were allopreening each other were noted and these pairs were selected for testing.

Six same-sex pairs of naïve finches (four female pairs and two male pairs) and six same-sex pairs of experienced finches (four female pairs and two male pairs) were tested.

All naïve individuals were independent feeders by the time of testing and, even though the age of birds at the time they were tested varied (60-106 day post-fledging); they had their complete adult plumage, which is an indicator of sexual maturity (Zann, 1996). In other words, all naïve finches were considered to be adult subjects although none of the naïve birds were older than 4½ months at the time of testing.

8.2.7.2 Stimuli

A new novel stimulus was used in Experiment 5. It was a jar, as in Experiment 4, but with a differently coloured metallic (golden in colour) lid.

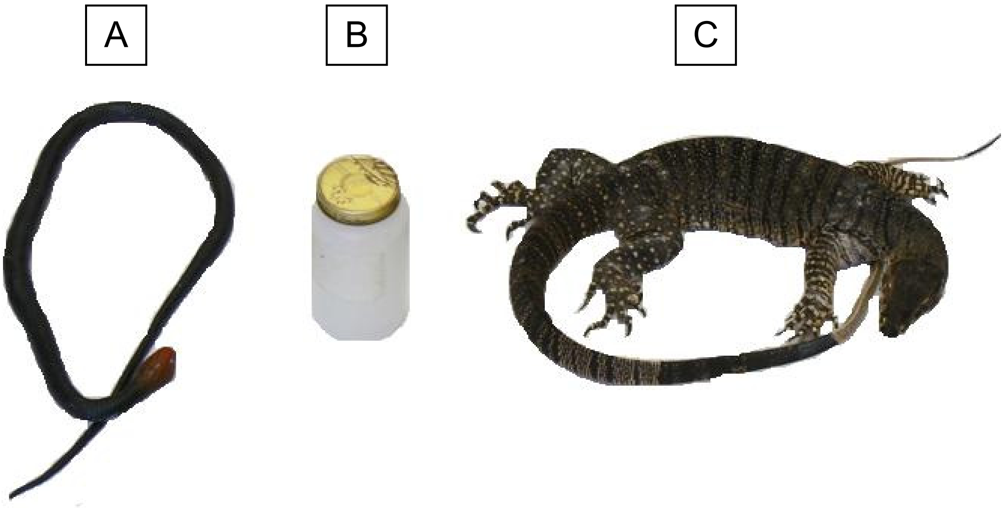


Figure 8.7. Stimuli presented in Experiment 5.

In this experiment, two model predators were used the monitor lizard and a snake. The snake was added for several reasons. The adult finches had only been exposed to the snake once (during the pilot study) while they had been exposed to the lizard seven times. Habituation to predators does occur (Huntingford and Coulter, 1989) and multiple presentations of the model lizard could have resulted in the zebra finches habituating to it during this experiment. The presentation of the lizard and the snake model also allowed comparison between a predator model familiar to the finches with one that was relatively unfamiliar to them.

The number of trials for each pair was 16 spread across four consecutive days. Each day, the four treatments were conducted (i.e. the control, novel object, snake and monitor lizard were presented each day). The stimuli and control were tested in a random order between 0930h-1230h with a 30-minute interval between trials.

8.2.7.3 Testing Aviary

In Experiment 4, the zebra finches were able to see the stimulus throughout the test even if they were located in Section B. In other words, although the zebra finches may have been avoiding the stimulus while in Section B, they might have been observing it from the back of the aviary. For this experiment, a slight alteration was therefore put in place. In order to permit scoring when the zebra finches were avoiding and when they were monitoring the stimulus, a visual barrier was placed in the centre of the aviary. This enabled the finches to fly to either side of the barrier. They could observe the stimuli from two locations: perches in the middle of the aviary or the perches in the section where the stimulus was presented. This barrier effectively created a choice for the finches to either completely avoid the stimulus or enter an area where they could view the stimulus.

There were two potential presentation areas, one in each section (Figure 8.8). The side on which the stimuli were presented was determined by the area that the finches most frequented. This meant that any avoidance behaviour would be clear if they moved away from the area where they spend most of their time when no stimulus was presented.

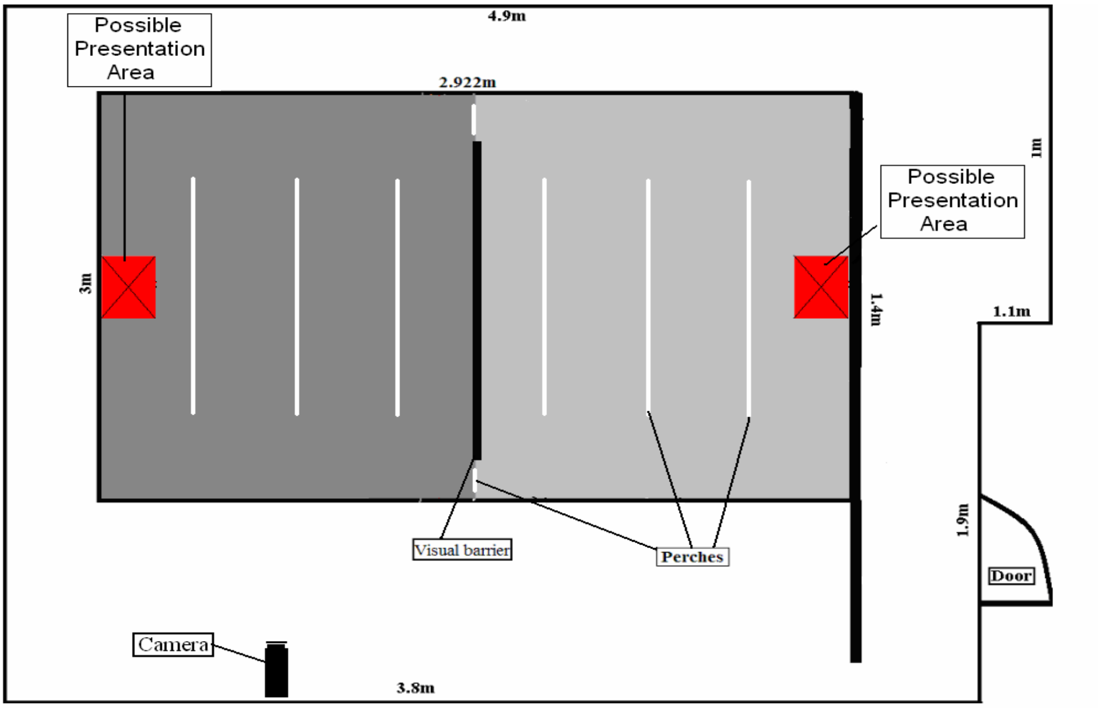


Figure 8.8. Testing aviary during Experiment 5. Three perches (51cm length) were placed within each section and they were equal spaced apart (38cm). Two perches were placed either on side of the visual barrier (25cm long). Note one food and one water dish were located in each section. The camera focused only on the section where the stimulus was placed and the middle perches. The stimulus was placed in one section only.

To determine on which side they spent their time, observations were made during the two days of habituation. There were eight observations in total (four per day). The experimenter noted the location of the birds before entering the testing room. In addition, notes were taken on which feeding dish was used by the finches since they tended to use only one of two dishes available.

8.2.7.4 Trial Period

For Experiment 5, there were four consecutive days of testing which allowed three days to habituate and one additional day to test whether habituation was maintained.

A control treatment was added to this experiment in order to test whether there was any influence on the behaviour of the zebra finches from the procedure in which the stimulus was placed. During these trials, the same procedure was followed (i.e. pre-test, test and post-test) but no stimulus was presented. Following the pre-test, the experimenter opened the wire door where the stimuli were usually presented and put his arm in the aviary for 5sec to replicate the placement of a stimulus. This was repeated at the end of the test to replicate the retrieval of the stimulus.

8.2.7.5 Scoring

The preference of the zebra finches to be in or out of visual contact with the stimuli was scored by recording the duration of time spent within each section. This is presented as the percentage of time spent within visual contact.

The time spent inspecting the stimuli was again scored as the duration of monocular fixation movements (Figure 8.6). An additional behaviour was scored in this experiment, one not scored in Experiment 4. The activity of the finches was scored as the number of flights they performed. A flight was defined as an individual alighting a perch or substrate and remain in flight for at least one second.

8.2.7.6 Statistical Analyses

The data presented in this section were analysed using non-parametric statistics. To analyse data that compared between stimuli for both experienced finches and naïve finches, a Friedman's test was conducted (testing day was the repeated measure) and two-sample Wilcoxon signed rank test was used for *post hoc* analyses. To test between experienced finches and naïve finches, Mann-Whitney tests were performed.

8.3 Results

8.3.1 Testing exploration versus predator inspection

The following sections (8.4.1 to 8.4.2) present data from Experiment 4 in which a novel object and a model monitor lizard were presented to outdoor-bred birds.

8.3.1.1 Testing Period

There was a main effect of testing period (pre-test, test and post-test) on the time spent in Section A (i.e. near the stimulus presentation area) in the monitor lizard presentations (Friedman's test, with testing day as the repeated measure, N = 28, Chi-square = 17.532, p = 0.001; Figure 8.9). The birds spent significantly less time in Section A when was presented of the monitor lizard there than they did either before (Wilcoxon, Z = -3.194, p = 0.001) or after it was presented (Wilcoxon, Z = -3.210, p = 0.001; Figure 8.9). Indeed, the finches spent significantly less time in Section A in the monitor lizard presentations than in presentations of the novel object (Mann-Whitney, U = 367.000, p = 0.002; Figure 8.9). While the time spent in Section A varied across the testing periods in the monitor lizard trials, there was no significant effect of the number of visits in Section A (Friedman's test, with testing day as the repeated measure, N = 28, Chi-square = 0.240, p = 0.887; Figure 8.10).

There was no significant effect of time spent in Section A in the presentations of the novel object (Friedman's test, with testing day as the repeated measure, N = 28, Chi-square = 1.504, p = 0.472; Figure 8.9). The birds did not avoid Section A when the novel object was presented there, nor did they increase the time spent in Section A. Furthermore, the presentation of the novel object did not significantly effect the number of visits in Section A across the pre-test, test and post-test periods (Friedman's test, with testing day as the repeated measure, N = 28, Chi-square = 3.920, p = 0.141; Figure 8.10).

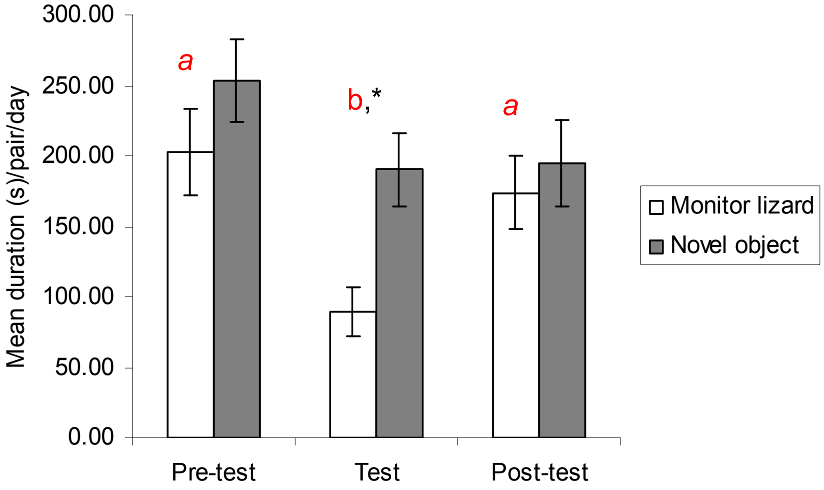


Figure 8.9. Time spent within Section A across the pre-test, test and post-test. The mean ± SEM duration of time (s) spent within Section A are plotted for the pre-test, test and post-test (X axis). *a* indicates that it is significantly different from *b* ($p<0.050$) and * indicates a significant difference between the time spent in Section A on presentation of the novel object and monitor lizard.

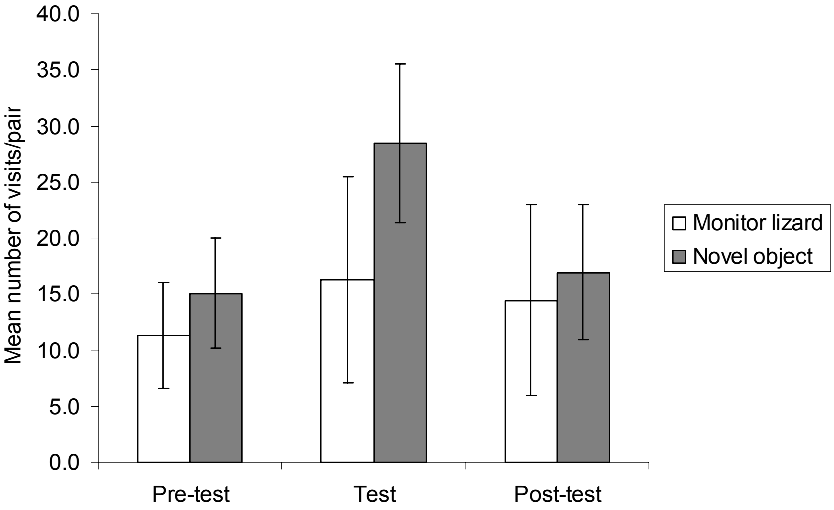


Figure 8.10. Number of visits to Section A across the pre-test, test and post-test irrespective of testing day. The mean ± SEM number of visits are plotted for the pre-test, test and post-test (X axis). No significant difference was found across the testing periods for both the monitor lizard and novel object presentations.

Therefore, these data show that the zebra finches tended to avoid the monitor lizard more than the novel object. Indeed, the latency to enter Section A (i.e. latency to approach the stimulus) was significantly longer to the lizard than to the novel object (paired T-test, t = -2.952, p = 0.026; Figure 8.11)

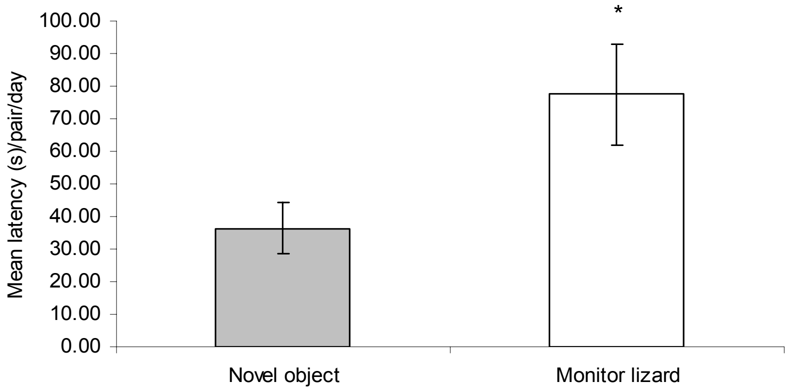


Figure 8.11. Latency (s) to approach either the novel object or monitor lizard. The mean ± SEM latency (s) to approach each stimulus (X axis). * indicates $p<0.05$. These data suggest that the zebra finches avoided the lizard more than the novel object as they took longer to approach the lizard.

Hence, the zebra finches clearly, avoided the monitor lizard while showed no avoidance of the novel object.

8.3.1.2 Inspection behaviour

Now the effect of repeated daily presentation was tested. Duration of inspection to the monitor lizard did not vary significantly over the days of testing (Friedman's test, with testing day as the repeated measure, N = 7, Chi-square = 8.233, p = 0.144; Figure 8.12). However, there was a significant difference across testing days for the novel object presentations (Friedman's test, with testing day as the repeated measure, N = 7, Chi-square = 12.143, p = 0.033). Most of the inspection of the novel object occurred on Day 1 (up to 49% ± 12% SEM of all inspections) during the first presentation but note the large variability of scores on Day 1 (Figure 8.12).

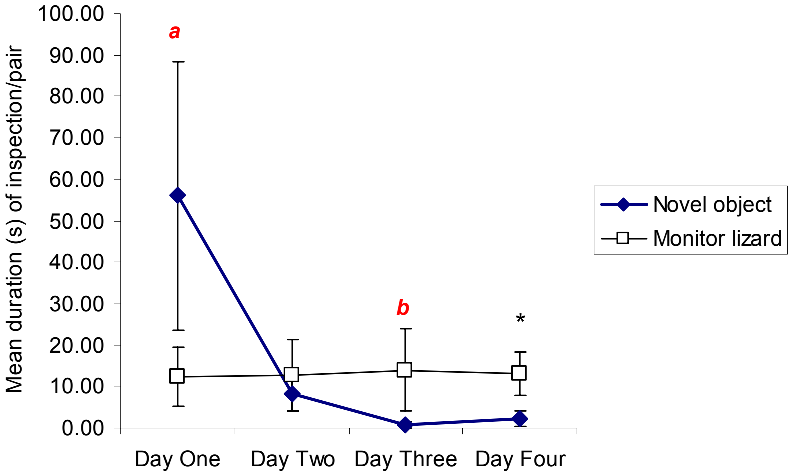


Figure 8.12. Inspection of the novel object and the monitor lizard across the four testing days. The mean ± SEM of duration of time (s) spent inspecting the stimulus are plotted for each testing day (X axis). *a* indicates that it is significantly different from *b* ($p<0.050$) and * indicates a significant difference of inspection between the novel object and monitor lizard. These data show most of the inspection towards the novel object occurred on Day 1 while the inspection of the monitor lizard was not significantly effected by testing day.

Indeed, *post hoc* analyses revealed that the zebra finches inspected the novel object significantly more often on Day 1 than on Day 3 (Wilcoxon, Z = -2.366, p = 0.018; Figure 8.12). The trend between Day 1 and Day 2 was not significant (Wilcoxon, Z = -1.733, p = 0.096), and the same was the case for the differences between Day 1 and Day 4 (Wilcoxon, Z = -1.863, p = 0.063; Figure 8.12). Nevertheless, it is clear that the birds habituated to the novel object. Indeed, inspection behaviour to the novel object had decreased to the point that the duration of inspection was significantly higher to the monitor lizard on Day 4 (Wilcoxon, Z = -2.207, p = 0.028; Figure 8.12).

The number of inspection events across the testing days will now be compared for each stimulus. The number of inspection events to the novel object did not change over the repeated presentations (Friedman's test, with testing day as the repeated measure, N = 7, Chi-square = 6.789, p = 0.079l; Figure 8.13). By contrast, there was a significant effect of testing day on the number of inspection events of the monitor lizard (Friedman's test, with testing day as the repeated measure, N = 28, Chi-square = 9.667, p = 0.022).

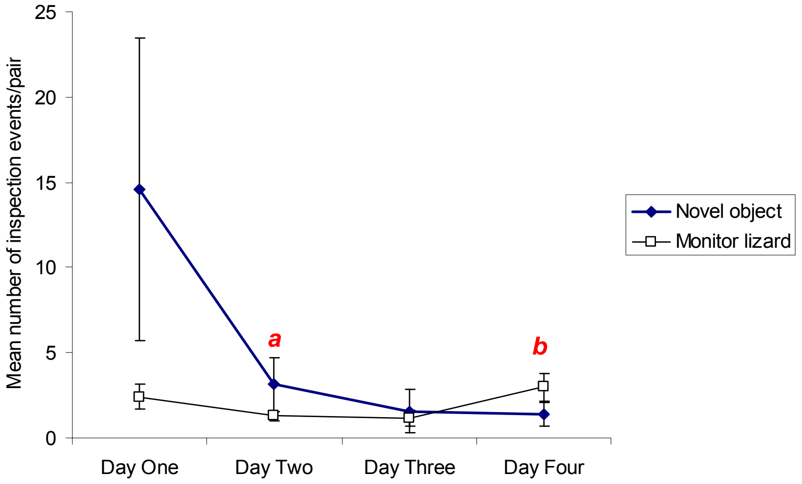


Figure 8.13. The number of inspection events across each testing day. The mean ± SEM of the number of inspection events for both stimuli are plotted for each testing day (X axis). *a* indicates that it is significantly different from *b* (p<0.050). There was no significant difference across testing days for the novel object presentations but there were significantly more inspection events of the lizard on Day 4 compared to Day 2.

The lizard elicited significantly more inspection events on Day 4 than it did on Day 2 (Wilcoxon, Z = -2.232, p = 0.028; Figure 8.13). There was no difference between the novel object and monitor lizard in the number of inspection events on any of the testing days (Wilcoxon, Z-values ranged from -0.137 to -1.439, p-values ranged from 0.150 to 0.891, Figure 8.13).

During an inspection event, the eye used to fixate the stimulus was scored. There were insufficient data to analyse eye use to view each stimulus per day because, on some days, there were very few fixations scored for each pair of birds or not all pairs inspected the stimulus. Therefore, these data were analysed using all scores together regardless of testing day but separating the scores for each stimulus. The data for eye use are presented in Table 8.2.

Table 8.2. Eye used to view the stimuli. The mean ± SEM % left eye (calculated as LE/LE+RE ×100) and the direction of head switches are presented. * indicates a significant bias ($p<0.05$)/

Stimulus	% Left eye fixations	Head switch to the left eye	Head switch to the right eye
Novel object	42 % * ± 6% SEM	9	9
Monitor lizard	65 % * ± 7% SEM	17	2

The zebra finches showed a weak but significant bias to view the novel object with the right eye first ($G_{(5)} = 57.43$, $p < 0.001$). By contrast, they preferentially used the left eye first to fixate the lizard ($G_{(5)} = 103.5$, $p < 0.001$).

These data were collected of monocular fixations of 1 second or more. However, there were occasions when the zebra finches fixated for less than 1 second (8% of 456 inspection events). During these shorter fixations, the zebra finch landed on a perch near the stimulus, turned its head to fixate the stimulus and then quickly turned its head to view the stimulus for longer with the opposite eye (hereafter referred to as “head switches”).

There was no clear bias for the direction of a head switch during the novel object presentations but 89% of head switches during the lizard presentations moved from the right eye to the left eye. Taken together (i.e. switches plus initial fixations) the birds show a clear preference to view the predator with the left eye.

8.3.2 The role of experience in predator inspection

The data presented here compared the response of finches that were raised in outdoor aviaries with finches that were bred indoors and therefore have had no experience with predators.

8.3.2.1. Testing period

To score the duration of time in visual contact with the stimuli, the percentage of time spent in the sections from which the finches could have viewed the stimulus (i.e. in the section where the stimulus was presented and in the middle sections) was scored. For the naïve finches, this measure varied significantly with the testing phase during the novel object presentations (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 11.165, p = 0.004; Figure 8.14). The naïve zebra finches spent significantly more time in the stimulus presentation area during the pre-test than during the test (Wilcoxon, Z = -2.613, p = 0.009; Figure 8.14), or the post-test (Wilcoxon, Z = -2.912, p = 0.004; Figure 8.14). There was also a significant effect of the testing phase on the duration of time spent in visual contact of the snake (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 8.079, p = 0.018; Figure 8.14). This significant result was due to the naïve finches spending more time in view of the stimulus presentation area during the pre-test compared to the test but this was not quite significant (Wilcoxon, Z = -1.851, p = 0.064; Figure 8.14). There was no significant difference across the testing periods (pre-test, test and post-test) for either the monitor lizard (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 3.722, p = 0.156; Figure 8.14) or the control trials (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 2.493, p = 0.287; Figure 8.14).

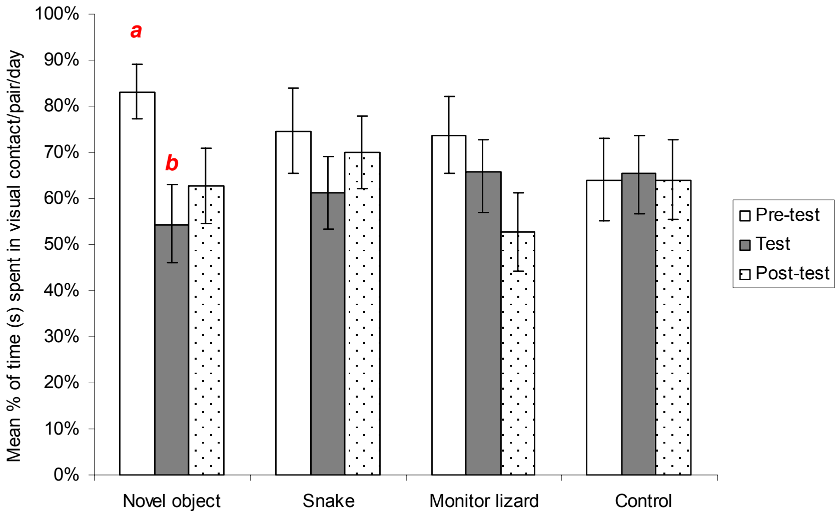


Figure 8.14. Time that the naïve finches spent in visual contact with the stimulus presentation area. The mean percent duration (s) ± SEM are plotted for each stimulus (X axis). *a* indicates that it is significantly different from *b* (p<0.050).

The results for the experienced finches were entirely different from those of the naïve finches. The time spent in visual contact with the snake did vary significantly with the testing phase for the experienced finches (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 5.846, p = 0.054; Figure 8.15). The experienced finches spent more time out of visual contact of the presentation area during the test than spent in this section of the aviary during the pre-test (Wilcoxon, Z = -2.243, p = 0.025; Figure 8.15). In other words, they avoided the snake.

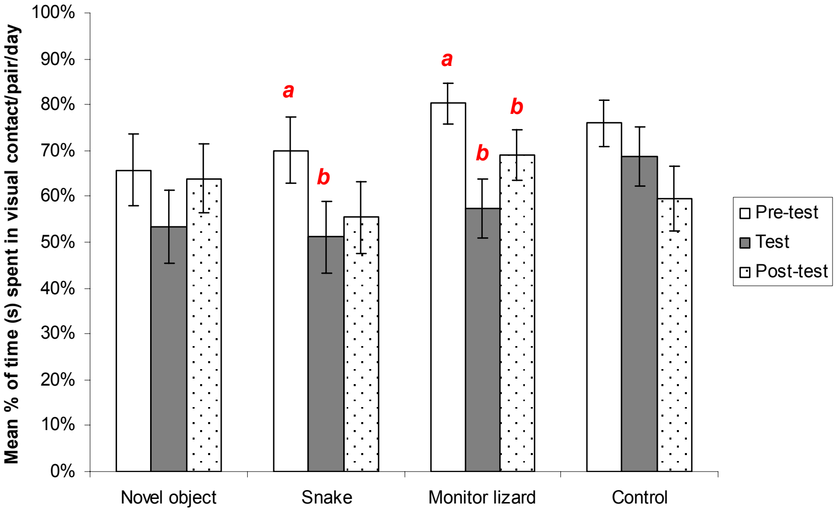


Figure 8.15. Time that the experienced finches spent in visual contact with the stimulus presentation area as presented in Figure 8.14.

There was a similar significant result for the test with the lizard (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 5.700, p = 0.058; Figure 8.15). More time was spent in the area of visual contact during the pre-test than the test (Wilcoxon, Z = -2.427, p = 0.015; Figure 8.15) and during the pre-test than the post-test (Wilcoxon, Z = -1.979, p = 0.048; Figure 8.15).

No significant differences were found in the time spent in visual contact of the presentation area for trials involving the experienced finches during presentations of the novel object (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 2.842, p = 0.241; Figure 8.15) and the control trials (Friedman's test, with testing day as the repeated measure, N = 20, Chi-square = 3.367, p = 0.18; Figure 8.15). Hence, the experienced finches avoided the model predators but showed no such avoidance of the stimulus presentation area during the novel and control trials.

8.3.2.2 Response of naïve finches to the novel object

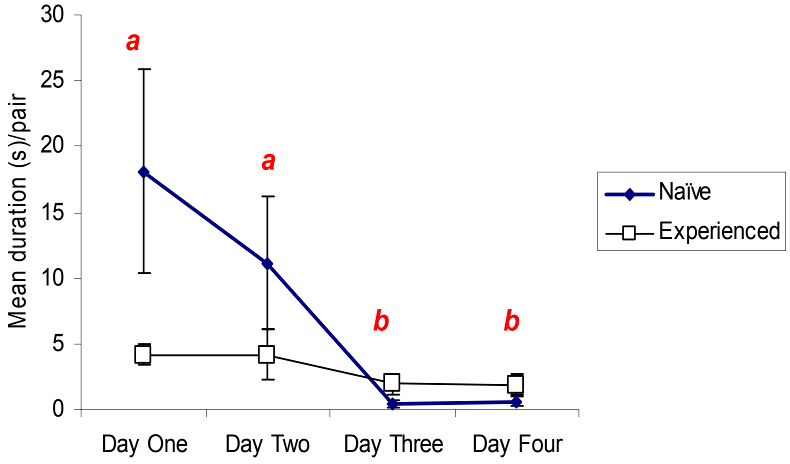
There was a significant effect of testing day on the duration of inspection behaviour during presentations of the novel object (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 13.909, p = 0.003, Figure 8.16A). The finches inspected the novel object for longer on Days 1 and 2 compared to Days 3 and 4 (Wilcoxon, Z-values ranged from: -2.023 to -2.201, p-values ranged from: 0.028 to 0.048; Figure 8.16A).

The number of inspection events also varied according to testing day (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 11.094, p = 0.011, Figure 8.17A) as more inspection occurred on Day 1 than on Days 3-4 (Wilcoxon, Z-values ranged from: -2.021 to -2.027, p-values ranged from: 0.027 to 0.028; Figure 8.17A).

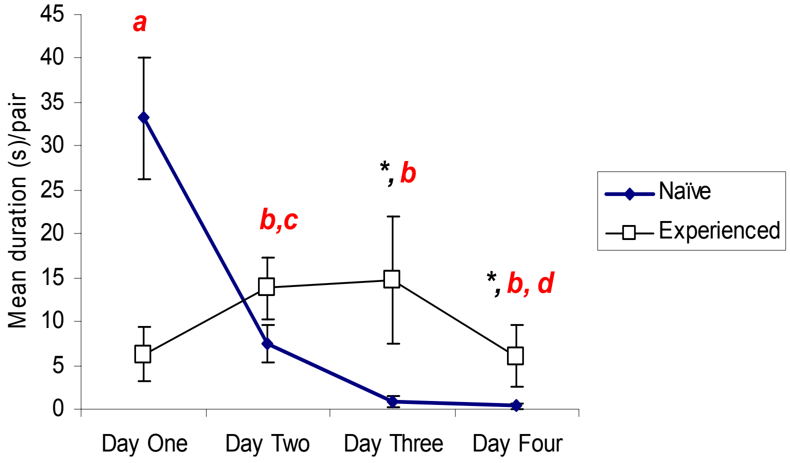
8.3.2.3 Response of naïve finches to the snake

The naïve finches habituated to the snake since there was a significant reduction in the duration of inspection across the testing days (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 13.000, p = 0.005; Figure 8.16B). Significantly more inspection of the snake occurred on Day 1 compared to Days 2-4 (Wilcoxon, Z-values ranged from: -1.992 to -2.201, p-values ranged from: 0.028 to 0.048; Figure 8.16B). The number of inspection events was also effected by testing day (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 10.579, p = 0.014; Figure 8.17B). More inspection events occurred on Day 1 than on Days 2-4 (Wilcoxon, Z-values ranged from: -1.992 to -2.191, p-values ranged from: 0.028 to 0.042; Figure 8.17B).

(A) Novel object



(B) Snake



(C) Monitor lizard

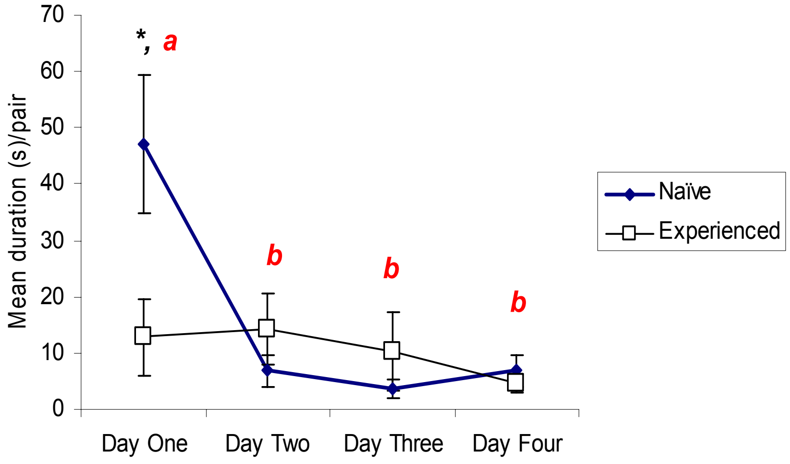
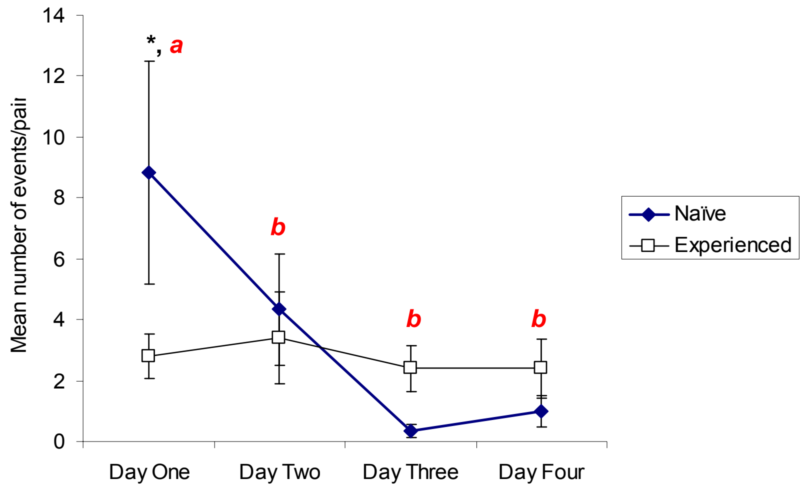
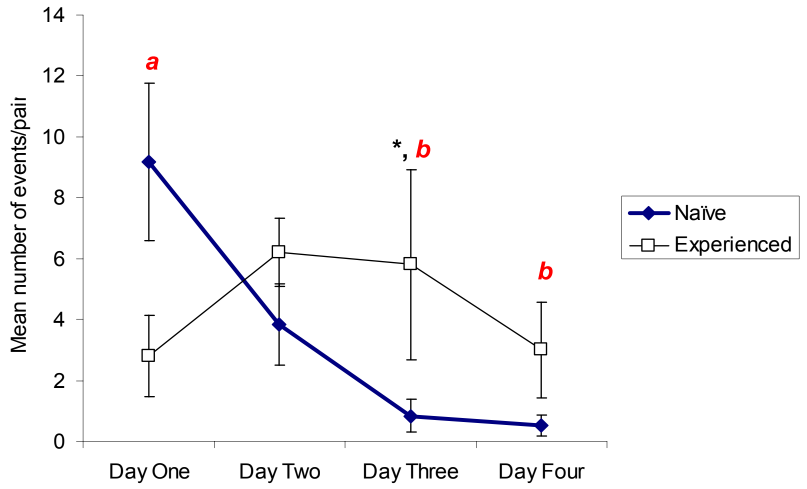


Figure 8.16. Duration of inspection behaviour by experienced and naïve zebra finches of the three stimuli across the four testing days. (A) Novel object, (B) snake and (C) monitor lizard. The mean ± SEM % duration of time (s) spent inspecting the stimulus are plotted for each testing day (X axis). *a* indicates that it is significantly different from *b* ($p<0.050$) and * indicates a significant difference of inspection between the naive and adult finches. Note that inspection behaviour decreases significantly over the testing days for the naïve subjects while the experienced finches inspect both model predators consistently but rarely inspected the novel object.

(A) Novel object



(B) Snake



(C) Monitor lizard

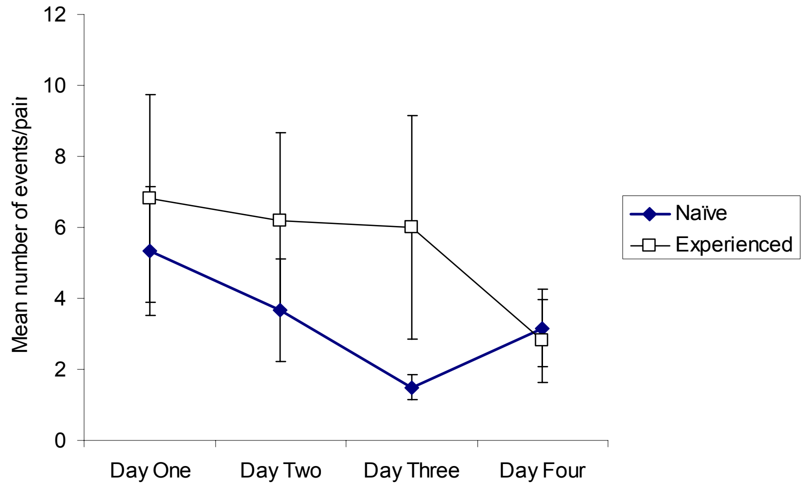


Figure 8.17. Number of inspection events by experienced and naïve finches of the three stimuli across the four testing days as for Figure 8.16.

8.3.2.4 Response of naïve finches to the monitor lizard

The time spent inspecting the lizard decreased significantly across the days of testing (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 9.000, p = 0.029; Figure 8.16C). The lizard was inspected by the naïve finches significantly more often on Day 1 compared to Days 2-4 (Wilcoxon, Z-values ranged from: -1.992 to -2.201, p-values ranged from: 0.028 to 0.048; Figure 8.16C). The number of inspection events, however, was not affected by testing day (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 3.105, p = 0.376; Figure 8.17C).

8.3.2.5 Comparison between the stimuli

The duration of inspection that occurred on each day was similar for each stimulus; that is, there was no effect of stimulus on inspection behaviour on Day 1 (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 0.333, p = 0.846), Day 2 (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 1.000, p = 0.607), Day 3 (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 5.429, p = 0.064) and Day 4 (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 4.111, p = 0.128). Inspection behaviour thus decreased for each stimulus across presentations, but the amount of inspection each day was similar for all stimuli.

8.3.2.6 Experienced finches

In contrast to the naïve finches, the experienced finches were less responsive to all stimuli and did not appear to habituate. Inspection behaviour was not significantly affected by testing day during the novel object presentations (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 3.482, p = 0.323; Figure 8.16A). The experienced finches inspected it consistently across testing days. However, the total duration of inspection was low (3.1 (s) ± 6 SEM) and this was significantly less in the experienced than in the naïve finches (7.6 (s) ± 6 SEM; Independent t-test, t = 2.403, p = 0.037). Inspection behaviour of the snake by the adult finches was not significantly affected by testing day for the snake (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 5.000, p = 1.72; Figure 8.16A). There was also no significant change of inspection behaviour over the testing days during the presentation of the lizard (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 5.560, p = 0.907; Figure 8.16A).

The number of inspection events by the experienced finches was not affected by testing day for the novel object (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 0.849, p = 0.838; Figure 8.17A), snake (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 4.875, p = 0.181; Figure 8.17B) or the lizard (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 0.536, p = 0.911; Figure 8.17B).

8.3.2.7 Comparison between naïve and experienced finches

There was no difference between naïve and experienced finches in the duration of inspection across days during the presentation of the novel object (Mann-Whitney: U-values ranged from 27.5 to 46.5, p-values ranged from 0.067 to 0.394 Figure 8.16A). However, there were more inspection events scored on Day 3 for the experienced finches than the naïve birds (Mann-Whitney: U = 2.000, p = 0.013; Figure 8.17A).

The snake elicited significantly more inspection from the naïve finches on Day 1 compared to the experienced finches (Mann-Whitney: U = 3.00, p = 0.015; Figure 8.16B) but the experienced finches inspected it more on Days 3 and 4 (Mann-Whitney: Day 3, U = 5.000, p = 0.041; Day 4, U = 4.000, p = 0.026; Figure 8.16B). The number of inspection events by the naïve finches was significantly higher on Day 1 than for the experienced finches (Mann-Whitney: U = 4.5000, p = 0.054; Figure 8.17B).

The naïve finches inspected the monitor lizard significantly more than the experienced finches on Day 1 (Mann-Whitney: U = 5.000, p = 0.041; Figure 8.16C). However, there was no difference between naïve and experienced finches on the subsequent exposures (Mann-Whitney: U-values ranged from 36.000-42.000, p-values ranged from 0.686 to 0.935 Figure 8.16C). Moreover, there was no difference between the naïve and adult finches for the number of inspection events scored across all days (Mann-Whitney: U-values ranged from 11.000 to 14.500, p-values ranged from 0.459 to 0.926; Figure 8.17C).

8.3.2.8 Activity during presentations of the stimuli

The activity of the finches was measured as the number of flights they performed. The stimuli significantly effected the activity of the adult finches (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 12.200, p = 0.007; Figure 8.18) but not that of the naïve finches (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 1.500, p = 0.682; Figure 8.18). The activity level of the adult finches was significantly lower during the snake presentation compared to all other treatments (Wilcoxon, Z = -2.201, p = 0.028 for all cases; Figure 8.18).

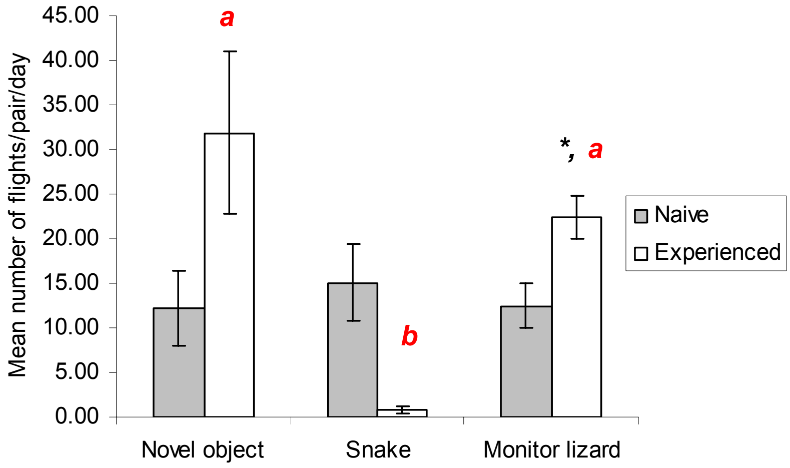


Figure 8.18. Activity level of the finches during the presentation of the various stimuli. The mean number of flights (s) ± SEM are plotted for each stimulus (X axis). *a* indicates that it is significantly different from *b* ($p<0.050$) and * indicates a significant difference in activity between the naive and experienced finches.

The experienced finches were significantly more active during the presentations of the lizard than were the naïve finches during the presentations of the same stimulus (Mann-Whitney, U = 3.000, p = 0.015; Figure 8.18).

8.3.2.9 Inspection once the stimulus had been removed

Interestingly, inspection of the stimulus presentation area occurred even after the stimuli had been removed. There was a significant effect of stimulus on inspection behaviour during the post-test for the experienced finches (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 6.870, p = 0.032, Figure 8.19) and naïve finches (Friedman's test, with testing day as the repeated measure, N = 6, Chi-square = 7.538, p = 0.023, Figure 8.19).

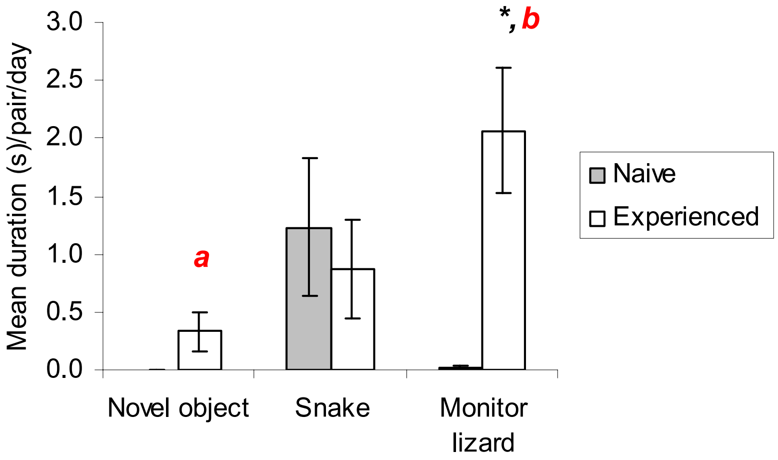


Figure 8.19. Duration of inspection behaviour of the stimulus presentation area after the stimuli had been removed (post-test). The mean duration (s) ± SEM are plotted for each stimulus (X axis). *a* indicates that it is significantly different from *b* ($p<0.050$) and * indicates a significant difference of inspection between the naive and experienced finches. Even after the stimuli had been removed, the finches inspected the area where the stimuli had been presented. The monitor lizard elicited more post-test inspection than the other stimuli for experienced finches. Note that the naïve finches carried on inspecting the snake after its removal but this was not quite significantly different to the novel object or monitor lizard ($p<0.070$).

For the experienced finches, there was significantly more inspection following the presentations of the lizard than the novel object (Wilcoxon, $Z = -2.207$, $p = 0.028$) and the snake (Wilcoxon, $Z = -1.892$, $p = 0.058$; Figure 8.19). In addition, the experienced finches performed more inspection following the lizard presentations than the naïve finches (Mann-Whitney, $U = 0.000$, $p = 0.002$; Figure 8.19). The significant main effect of stimulus on inspection behaviour for the naïve finches was due to the difference between the novel object and the snake, and the lizard and the snake. However, *post hoc* analyses revealed that these differences were not quite significant (Wilcoxon, $Z = -1.992$, $p = 0.068$ in both cases; Figure 8.19).

8.4 Discussion

8.4.1 Testing exploration versus predator inspection

The hypothesis that inspection of a novel object will decrease from the first presentation and not for the lizard proved to be correct for the finches that had been raised in outdoor aviaries with exposure to predators. Most of inspection behaviour of the novel object occurred on Day 1. The decrease in incidents of inspection of the novel object indicates that the finches habituated to the novel object. In fact, this result is congruent with the findings on domestic chicks: it has been found that chicks habituate to novel visual stimuli after four to five presentations (Rogers and Anson, 1979; Andrew, 1991). There was no evidence, however, that the finches habituated to the monitor lizard. In fact, the number of inspection events significantly increased on Day 4 compared to Day 2. Therefore, these results demonstrate that the monitor lizard elicited consistent inspection behaviour from the finches while the novel object elicited interest primarily on first exposure.

The finches also avoided the lizard more often than the novel object. These results are similar to the findings of Walling *et al.* (2004). The latter researchers discovered that fish that had had experience with predators made fewer trips to inspect such predators than naïve fish. Since the finches avoided the lizard more than the novel object, these results appear to reflect that they have had some experience with predators. However, since the finches are unlikely to have been exposed to monitor lizards *per se* during their early life, the predator experience must have been generalised. Certainly, the experienced zebra finches seemed far more cautious in the presence of the monitor lizard than they were in the presence of the novel stimulus.

The prediction that the finches would use the left eye (LE) to view both stimuli was incorrect. The LE was used to view the lizard and this confirms other findings that the right hemisphere (RH) is used to process visual information about predators (Dharmaretnam and Rogers, 2005). This bias was quite strong and it was significant.

The finches showed a weak but significant right eye/left hemisphere bias for inspecting the novel object. This is inconsistent with previous research which has found that visual information about novel objects is processed in the RH (Rogers, 2000). Nonetheless, the results have shown that visual information about the novel object and the lizard are processed in opposite hemispheres. Hence, inspection of a predator and inspection of a novel stimulus show different functional processes.

8.4.2 Influence of experience on predator inspection

The time that the naïve finches spent inspecting the stimuli decreased significantly. Not only did inspection decrease across testing days for each stimulus but also there was no difference in inspection behaviour between the stimuli. Naïve, inexperienced fish have been found to inspect non-predator and predator stimuli similarly (Walling *et al.*, 2004). Indeed, animals that have not had experience with predators may not be capable of distinguishing between a predator and non-predator stimulus (Kullberg and Lind, 2002). In addition, the fact that the naïve finches did not inspect the model predators may be a result of them not perceiving these stimuli as a threat. It has been shown that the threat an animal perceives a predator to be may vary across developmental stages (Patterson *et al*., 1980). However, any differences in anti-predator behaviour between naïve and experienced finches due to development is, perhaps, unlikely in my sample since both the experienced and naïve finches were adult birds, albeit the experienced finches were older.

The hypothesis that inspection behaviour by the experienced finches towards the novel object decreases across days was not supported because they rarely inspected the novel object from the first exposure. Since the novel object was presented to the experienced finches in Experiment 4, they may have already categorised it even with the alterations that were made (i.e. different coloured lid Figures 8.4 and 8.7). Hence, habituation occurred during the first presentation. Indeed, Mettke-Hofmann *et al* (2006) found that birds that have had experience with exploration rapidly categorise future exposures to stimuli. That is, inspection behaviour decreases the more experience an individual has had.

The finches inspected the stimulus presentation area even after the predator stimulus had been removed. The continuation of anti-predator behaviour following an encounter, or simulated encounter, with a predator has been found in other species. For instance a study by Swaisgood *et al.* (1999) presented playbacks of Pacific rattlesnakes (*Crotalus viridis oreganos*) to Californian ground squirrels. From the sounds alone, they responded more strongly to the rattle of larger, warmer snakes. What makes this study relevant to the results found in this experiment using zebra finches is that the squirrels continued to perform anti-predator behaviour 10 min after playback of the rattlesnake sound presentation. It seems, in both the finches and squirrels, arousal levels were high and the encounters with a dangerous predator continued to preoccupy the animals.

The aviary was designed so that the finches could either completely avoid the model predator or actively approach it. The control trials did not influence the finches' movements and activity patterns in the aviary but the stimuli did. The area of the aviary in which the naïve finches spent most time during the pre-test changed once the novel object was presented. Interestingly, the data show that they avoided this novel stimulus but none of the model predators were avoided. By contrast, the experienced finches did not alter their movements when the novel object was presented and showed very little interest in it but their behaviour was affected by the presentations of the predator stimuli. They clearly avoided both the snake and the lizard. Moreover, the activity levels of the experienced finches decreased significantly during the presentation of the snake. Similar to the results in Experiment 4, the experienced finches seemed to avoid the predators and perhaps approached them only for further monitoring.

CHAPTER 9. GENERAL DISCUSSION

9.1 Introduction

The aim of this study was to establish whether birds perform both strategies of approach to predators: mobbing and predator inspection. The Australian magpie and the zebra finch were selected to investigate this aim in a series of five experiments conducted in the field and in laboratory trials. It was found that magpies discriminate between a range of predators and that they make variations to their anti-predator behaviour depending on the species of predator that they encounter (Chapter 3 and Chapter 4). The magpies anti-predator behaviour that was described in Chapter 3 was also found to be lateralised (Chapter 6). Although the most common response of the magpies was to mob the predators (Chapter 4), they also performed predator inspection (Chapter 5). Indeed, there were significant differences between mobbing and 'inspection only' trials to lead to the conclusion that mobbing and predator inspection are functionally different and even processed by different hemispheres of the brain. An experiment was conducted in an attempt to elicit inspection behaviour by presenting model predators in unnatural postures. Indeed, the unnatural posture was found to elicit high levels of inspection behaviour in comparison to the same model in a natural posture. In the natural posture, the model predators elicited high levels of mobbing in magpies. Therefore, it seems that a function of predator inspection is to gather information about a potential predator, in novel contexts.

The experiments on the zebra finches were conducted in the laboratory under controlled conditions. The aim of these experiments was to determine whether predator inspection was functionally different from exploration behaviour. First, experienced finches that had been bred in conditions allowing some experience with predators were presented with a novel object and a model predator (Chapter 8). The finches habituated to the novel object but not to the model predator, which suggests that predator inspection is not simply a part of the birds' repertoire and tendency to explore its environment but rather a specific response to a potential predator. The second experiment compared naïve zebra finches and experienced birds. They were presented with a novel object and two model predators. The naïve zebra finches rapidly habituated to all stimuli while the experienced finches rarely inspected the novel object but constantly inspected both model predators.

9.2 Cognitive Process during Approach Behaviour

My data suggest that in different ways both magpies and zebra finches have complex anti-predator behaviour. This suggests that, while zebra finches were not observed mobbing any of the stimuli, in contrast to the powerful and proactive magpies, inspection behaviour elicited a number of subtle and consistent strategies during the presentations of the stimuli. Here it is timely to refer to a cognitive model of mobbing behaviour suggested by McLean and Rhodes (1991). Even though I agree with the model, I believe that it ought to be expanded to include the cognitive aspects of inspection behaviour and not be limited to just mobbing behaviour. The model suggests a seven stage process and is presented in Figure 9.1. First, the individual gathers perceptual information about the predator and then compares that information with previous experiences that it has had with predators. If the perceptual information and the stored information correspond with each other, then the stimulus is familiar. The next stage of the model process a semantic association. For example, the individual determines whether the predator is a ground or aerial predator. The semantic association provides a possible insight. Indeed, this has been found in studies on referential signalling (Evans, 1997). Once a semantic association has been formed, the individual determines the level of threat that the predator poses. There are a variety of factors that animals may need to consider when they assess threat levels. For example, they may assess various aspects of the predator's behaviour and recent activity (Hamerstrom, 1957; Csanyi, 1985; Brown and Cowan, 2000; Coss and Ramakrishnan, 2000; Brown and Dreier, 2002) while taking into account the vulnerability of other group members (Swaisgood *et al.*, 1999).

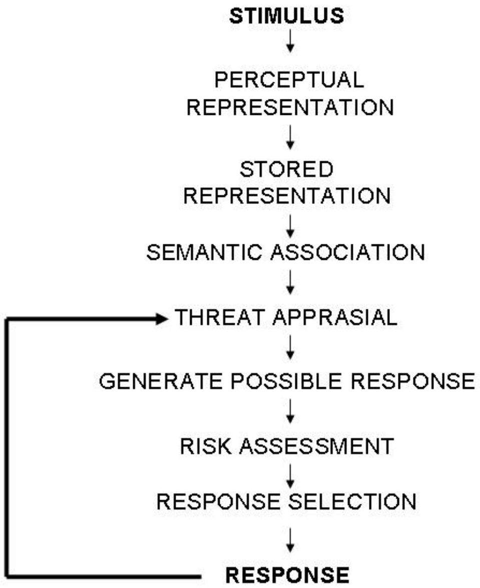


Figure 9.1. Cognitive model of the thought process required to decide appropriate primary defences. (Taken from McLean and Rhodes, 1991).

Following threat appraisal, the individual then generates possible strategies as to whether to avoid, approach, mob or attack the predator (McLean and Rhodes, 1991). The risk to the individual in performing these responses is then evaluated.

For example, confronting the predator may be a better response than avoiding the predator (Lingle *et al.*, 2005). Risk assessment leads to a selection of a specific response and the behaviour is then performed. The individual needs to continually evaluate the situation since the behaviour of the predator may change. Therefore, the stages from threat appraisal to the actual response are continually processed and these sequences are of necessity, performed very rapidly.

I will now demonstrate how this model can be applied to my data.

9.2.1 Stimulus recognition and discrimination process

The process of recognition and discrimination between predators involves the first three stages of the cognitive model (perceptual representation, stored representation and semantic association). The magpies clearly recognised and discriminated between all model predators that were presented to them (Chapters 3, 4, 6 and 7). They rarely approached the model snake but consistently approached all other model predators depending on their posture. They did not approach the aerial predators, when they were presented upright in the natural posture, on the ground while they always approached the lizard on the ground. There were even subtle differences in their response towards the aerial predators. While there was little difference between the two eagles, magpies made crucial adjustments in their mobbing behaviour by performing different swooping flight patterns at the goshawk than at the eagles. My study, using solely avian species, is the first, to my knowledge, that demonstrates in detail that inspection behaviour is a distinctive behaviour. There are some other remarkable examples of a prey's ability to discriminate between predators but these have been found in mammals.

For instance, Californian ground squirrels discriminate between a large and small rattlesnake depending on the sound of the rattle. Moreover, they can also detect whether the snake is warm or cold (Rowe and Owings, 1990). Fish and some birds can discriminate between a predator that is statiated and one that has been fed (Hamerstrom, 1957; Csanyi, 1985; Walling *et al.*, 2004). Recently, Griesser (2008) found that Siberian jays not only discriminate between a predator that is perching, searching for prey or attacking, but they have distinct calls that communicate to conspecifics the behaviour of the predator. Hence, the level of discrimination can be quite specific.

The complexity of such a finite ability to recognise different predators and different predator behaviour would seem to be experience dependent since the prey needs to have had opportunities to recognise the predator's behavioural pattern and possibly even its specific weapons and strengths. For instance, avoidance of the tail used by the monitor lizard as an effective whip, or judging levels of agility and quickness of potential movements in a predator may all contribute to survival. Indeed, the zebra finch results suggest that experience is involved in approach behaviour. Zebra finches that had had some experience with predators were able to discriminate between a novel object and two model predators, whereas naïve zebra finches habituated to all of the stimuli without distinction. This result not only demonstrates that experience is required for recognition of predators by zebra finches but it also demonstrates that stored representations were categorised, i.e. semantic association (McLean and Rhodes, 1991). The habituation towards the novel object suggests that the experienced finches had classified this stimulus as non-threatening and, therefore, it required no more inspection. Mettke-Hofmann (2006) showed that birds that have had experience with a novel object, regardless of what the object is, tend to classify further novel objects much more quickly. Hence, the experienced zebra finches that were continually presented with novel objects quickly categorised this stimulus. To relate this to the cognitive model, the zebra finches process the visual information (perceptual representation) and relate it to previous exposures (stored representation). During each encounter, they classify the object (semantic associations). The more exposure they have had with the object the more rapid the process became. In other words, the duration of inspection decreased. This, of course, is not the case during the presentations of the model predators to the experienced finches. They inspected the predators on every presentation to the same extent. This suggests that the finches were continually monitoring the model predators. Habituation towards unrealistic model predators but not the realistic models of predators has also been observed in fish (Magurran and Girling, 1986; Brown and Warburton, 1997; Brown and Warburton, 1999; Walling *et al.*, 2004). The fish required continual assessment of the realistic models but, once they did not associate the unrealistic models with their stored representation of a predator, they ceased inspection.

9.2.2 Threat assessment of the stimuli

In most research on mobbing behaviour, the intensity of mobbing is usually indicated by the number of mobbing calls (Owings and Loughry, 1985; Graw and Manser, 2007). Mobbing intensity in the magpies cannot be analysed by determining only the number of mobbing calls, since they perform a range of agonistic behaviour towards the predators and these too must also be taken into account. This makes the magpies unique since they do not decrease or increase the intensity of mobbing; rather they perform completely different types of mobbing behaviour depending on the type of predator. For example, when the magpies were presented with aerial predators (in natural postures), they primarily swooped them and did not spend much time on the ground. By contrast, they approached the monitor lizard (and more instances than the snake) only on the ground and very rarely swooped it. They made even more subtle changes to the response to the various aerial predators. When they swooped the eagles, they performed looping and direct swoops but they rarely performed any looping swoops towards the goshawk. Hence, the intensity of their response can be measured by the number and types of behaviour they perform while type of approach may be indicative of risk assessment.

The intensity with which a species mobs a predator has been interpreted as a method of determining the perceived risk of predators on the mobbers (McLean and Rhodes, 1991; Graw and Manser, 2007). If mobbing intensity can be used to determine the perceived risk of predators, then the magpies seem to have made clear distinctions between threat levels posed by the model predators. From the data outlined in Chapters 3, 4 and 7, it is now possible to establish how the magpies perceived the predators based on the intensity of response to, and risk assessment of, each predator (Figure 9.2). This was evaluated using several measures which included whether or not they made contact with the model, whether they swooped the model and what type of swoop they performed (direct or looping) and whether they pecked or jumped at the stimulus. It was established in Chapter 4 that the magpies' behaviour was especially cautious and direct in encountering the goshawk. When presented with this model, they rarely spent time on the ground, mainly performed direct swoops and often made contact with model. The snake by contrast did not elicit such decisive actions. They usually neither approached nor avoided it as long as the snake was stationary. As shown in an earlier experiment, however, their behaviour towards a moving snake was similar to that given in response to the monitor lizard (Koboroff, 2004). In terms of risk assessment, it would appear that moving snakes are assessed as a greater risk than a stationary.

Figure 9.2. Perceived level of threats from the model predators by the magpies. 'NAT' refers to the model presented in a natural posture and 'UNNAT' indicates that it was presented in an unnatural posture. The hierarchy was based on the following behaviours: swooping, type of swooping flight (direct or looping), pecking, jumping and how often the magpies made physical contact with the models.

There was not much difference in strategy in the response of the magpies between the little eagle and wedge-tailed eagle but the little eagle was struck more often by direct contact than the wedge-tailed eagle. Indeed, from the dietary habits of either eagle species we already know that little eagles are regular hunters of birds but not wedge-tailed eagles. When the little eagle was presented in the unnatural posture it was not swooped as often and the magpies spent most of the time on the ground. One may deduce from this response that, in this posture, it was considered less of a threat than the aerial predators presented in an upright posture. The little eagle in the unnatural posture elicited more agonistic behaviour than the lizard and the lizard in the natural posture elicited more agonistic behaviour compared to the presentations of it in an unnatural posture. By evaluating the mobbing strategy that the magpies performed, an understanding of the magpies threat appraisal can be established. Moreover, this demonstrates that the magpies adopt different mobbing strategies mainly based on the perceived risk of the predator and not just the based on the species of the predator since they varied their anti-predator behaviour towards one and the same model predator depending on the posture in which the model predator (the little eagle) was presented to them.

It is interesting that factors such as the vulnerability of juveniles (Chapter 4) and previous experience with a predator (Chapter 7, Part II) did not seem to influence threat appraisal by magpies. For example, the little eagle was perceived as a similar threat to them across various stages of juvenile vulnerability. Also, a simulated predatory event involving the little eagle did not affect their response towards it. As I have already argued, this is not to say that magpie anti-predator behaviour is one-dimensional (Hennessy, 1992) because the evidence presented here strongly identified variations of mobbing approaches, i.e. they have strategies with multiple dimensions. Therefore, the magpies seem to identify characteristics of a predator for threat appraisal and approach rather than act defensively in protection juveniles or base their behaviour on a previous encounter with a predator.

Threat assessment thus appears to be a complex and sophisticated process and it perhaps needs to be so in order for an individual to survive. For example, fish vary their anti-predator behaviour depending on the diet of the predator (Brown and Cowan, 2000; Brown and Schwarzbauer, 2001; Brown and Dreier, 2002) or whether the predator has just fed or not (Csanyi, 1985a). There is evidence that birds also adapt their response to a predator depending on the predator's posture (Hamerstrom, 1957).

9.2.3 Decision making

Once an animal has recognised the predator and has assessed the risks associated with it, it processes this information and formulates a response. McLean and Rhodes (1991) suggested that animals generate possible responses and then assess the risk involved about performing such a response. Indeed, the data presented here produced evidence that the magpies perform such risk assessment prior to responding to the model predators. The different swooping flight patterns performed by the magpies indicates risk assessment must have been made since the magpies perform a slow flight towards the slower aerial predators and a direct, fast flight to the more agile aerial predator. Hence, the magpies have perceived the goshawk as a greater threat.

9.3 Defining predator inspection

9.3.1 Inspection and exploration

The fact that animals explore their environment suggests that predator inspection may simply be a part of exploration and not a specific behaviour to monitor the predator (Dugatkin and Godin, 1992). My data suggests that this is not the case. Zebra finches with experience of predators habituated to the novel object and not to the model predator. Hence, predator inspection is functionally different from exploration as found in other species (Magurran and Girling, 1986; Brown and Warburton, 1997; Brown and Warburton, 1999; Walling *et al.*, 2004). Moreover, it seems that there is an experienced-based component to predator inspection since naïve zebra finches responded to the model predators in the same way as they responded to the novel object, whereas the experienced finches constantly inspected the model predators but not the novel object.

If experience influences the occurrence or frequency of predator inspection then, presumably, more experienced animals should respond differently to predators than naïve animals. Using wild caught three-spine sticklebacks (*Gasterosteus aculeatus*) from areas either containing or not containing predators, Walling *et al.* (2004) showed a distinct difference between the two populations. Fish that were taken from a habitat with predators were considered to be experienced fish and the other populations from habitats without predators were considered to be predator naïve. The experienced fish inspected more often than the naïve fish. Age in the experienced population of sticklebacks had no effect on the results. These results suggest that experience with predators *enhanced* predator inspection behaviour, not the opposite. I found that experienced finches consistently inspected the model predators while the naïve finches soon lost interests in the model predators. Hence, experience with predators seems to be essential across a variety of taxa.

9.3.2 Predator Inspection and Mobbing

Even though the literature does not state that mobbing and predator inspection form a continuum, it is often implied. For instance, Simmons (1952) classified mobbing behaviour along a continuum from fleeing to attacking. Shedd (1982) categorised approach behaviour by American robins (*Turdus Migratorius*) as either (1) silent approach, (2) vocal approach, (3) mobbing or (4) attack, thus suggesting that silent approaches were low risk and mobbing and attack high risk. This invites one to place mobbing and inspection on a continuum.

My data suggest that there is in fact no such continuum between mobbing and predator inspection. In Chapter 5, I demonstrated the differences between predator inspection and mobbing by analysing the response of magpies to the monitor lizard when they approached it alone or in a group. The response of the magpies, when alone, was notably different from that of magpies that approached the lizard in a group. Moreover, the visual information obtained during predator inspection is processed in the right hemisphere, whereas visual information during mobbing is processed in both hemispheres. This is strong evidence to suggest that mobbing and predator inspection are functionally different since they are processed in different areas of the brain. Predator inspection and mobbing, it seems, may be discretely different. The two types of approach behaviour, inspection and mobbing were also shown to serve different functions and hence cannot form a continuum.

This is not to say that there are not degrees of inspection or mobbing. Predator inspection and mobbing can increase in intensity depending on the situation. For example, in Chapter 7, I found that inspection increased but mobbing decreased during presentations of the little eagle placed face down compared to the presentations of it in an upright position. The magpies performed primarily jumping during the presentations of the little eagle face down, whereas they swooped at the little eagle when it was presented face down perhaps suggesting a change in mobbing strategy. Indeed, there are many examples of degrees of mobbing to different predators. These results confirm Coss and Ramakrishnan' findings (2000). The latter researchers presented two model leopards (*Panthera pardus*) to bonnet macaques (*Macaca radiata*). One of the models had markings familiar to the macaques and the other had markings that were unfamiliar to them. Both models were presented in an upright and upside down postures. It is possible that the presentations of the models upright were more of a threat than the same mode presented upside down. Moreover, they measured whether or not individual macaques looked at their neighbours to assist in assessing risk during presentations of the model predators. The upside-down posture of the familiar predator elicited more 'information seeking' than the same model upright. However, the unfamiliar model presented upright elicited more information seeking than the model presented upside-down. In fact, the upside down model of the unfamiliar model was ignored by the macaques. The resemblance of my results to those of Coss and Ramakrishnan (2000) suggests that animals, across various taxa, that encounter predators in an unfamiliar posture perform inspection behaviour. This supports the hypothesis that animals monitor and assess threats during predator inspection. Hence, predator inspection increases if the individual is uncertain about the predator or if the circumstances require some monitoring or continual assessment (Dugatkin and Godin, 1992). Mobbing increases or adapts depending on the threat imposed by the predator.

9.4 Conclusion

My data show that approach behaviour by avian species is comprised of two distinct strategies: mobbing and predator inspection. While animals perform exploration of their environment, the function of predator inspection is qualitatively different from exploration. A distinction was also made between mobbing and inspection behaviour. Although, mobbing and predator inspection are similar in that they both involve animals approaching a predator, my data show that mobbing and predator inspection are two vastly different strategies. Hence, they do not form part of a continuum. I suggest that any study investigating approach behaviour discriminates between predator inspection and mobbing elements since they seem to have very different functions.

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APPENDIX I

Data from Experiment 1

A

Measure	**Little eagle**	**Wedge-tailed eagle**	**Brown goshawk**	**Monitor lizard**	**Chi-Square** (Friedman's test)	**p-value**
Swooping	4.6 (1.6 and 11.65)	3.3 (1.5 and 6.9)	3.1 (0.4 and 4.5)	0.0 (0.0 and 0.0)	20.326	**0.000**
Physical Contact	0.0 (0.0 and 0.5)	0.0 (0.0 and 0.2)	0.0 (0.0 and 0.1)	0.0 (0.0 and 0.0)	7.138	0.068
Pecking	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	N/A	N/A
Jumping	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.0 (0.0 and 1.0)	N/A	N/A
Circling	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.2)	0.0 (0.0 and 0.0)	2.0 (0.0, 9.0)	11.821	**0.008**
Stationary Viewing	0.0 (0.0 and 0.6)	0.0 (0.0 and 0.6)	0.0 (0.0 and 0.0)	8.5 (0.0 and 11.1)	8.486	**0.037**

These data show the medians with the 25th and 75th quartiles in parentheses during Stage 1 (September 2005 and January 2006). Each value is standardised by the number of magpies present. Friedman's test was used to analyse these data with stimulus as the repeated measure. N/A indicates that no tests were conducted on these data since few events of these measures were scored. Significant p-values are in bold. The total number of presentations per model predator N = 14. These data were reposted in Chapter 4.

B

Measure	**Little eagle**	**Wedge-tailed eagle**	**Brown goshawk**	**Monitor lizard**	**Chi-Square** (Friedman's test)	**p-value**
Swooping	2.8 (0.0 and10.5)	2.9 (0.5 and 6.0)	4.4 (1.6 and 8.2)	0.0 (0.0 and 0.0)	15.08	**0.002**
Physical Contact	0.2 (0.0 and 0.7)	0.0 (0.0 and 0.0)	0.1 (0.0 and 0.8)	0.0 (0.0 and 0.0)	13.31	**0.004**
Pecking	0.1 (0.0 and 0.8)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.7)	0.0 (0.0 and 0.0)	N/A	N/A
Jumping	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.3)	0.1 (0.0 and 1.1)	9.77	**0.021**
Circling	0.0 (0.0 and 0.6)	0.00 (0.0 and 0.1)	0.0 (0.0 and 0.0)	2.4 (0.0 and 5.9)	N/A	N/A
Stationary Viewing	0.0 (0.0 and 1.5)	0.0 (0.0 and 0.0)	0.00 (0.0 and 1.2)	8.9 (2.0 and 16.9)	N/A	N/A

These data show the response of the magpies towards the model predators during Stage 2 (February to April 2006) as presented in Table A.

C

Measure	**Little eagle**	**Wedge-tailed eagle**	**Brown goshawk**	**Monitor lizard**	**Chi-Square** (Friedman's test)	**p-value**
Swooping	6.6 (4.7 and10.5)	8.3 (0.6 and 11.9)	3.4 (0.3 and 7.0)	0.0 (0.0 and 0.0)	20.05	**0.000**
Physical Contact	0.1 (0.0 and 1.2)	0.0 (0.0 and 0.5)	0.7 (0.0 and 1.6)	0.0 (0.0 and 0.0)	13.54	**0.004**
Pecking	0.0 (0.0 and 3.2)	0.0 (0.0 and 0.0)	0.0 (0.0 and 2.2)	0.0 (0.1 and 1.0)	0.78	0.885
Jumping	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.8 (0.0 and 3.8)	N/A	N/A
Circling	0.0 (0.0 and 0.8)	0.0 (0.0 and 0.0)	0.0 (0.0 and 0.0)	0.5 (0.0 and 5.2)	N/A	N/A
Stationary Viewing	1.1 (0.0 and 2.7)	0.0 (0.0 and 0.5)	0.0 (0.0 and 0.9)	3.3 (0.1 and 19.3)	7.68	0.053

These data show the response of the magpies towards the model predators during Stage 3 (June to August 2006) as presented in Table A.