Behavioural interactions and reasons for aggression between Australian magpies (*Gymnorhina tibicen*) and other birds in New Zealand

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Abstract

The Australian magpie (*Gymnorhina tibicen*; magpie hereafter) was introduced to New Zealand from 1864 in an attempt to help control pest invertebrates in pasture. Since the introductions, magpie populations have gradually increased and they are now widely distributed throughout most of the country. In New Zealand there are many reports of magpies attacking and even killing many other birds; however, the reasons for the attacks are largely unknown. As such, the aims of this thesis were to: (1) document and describe aggressive interactions between magpies and other birds to determine the extent and context of this behaviour, and (2) examine potential explanations for the interspecific aggression displayed by magpies.

Accounts of magpie attacks on birds in New Zealand were collated from literature and a survey of the public, and then summarised to identify the frequency and characteristics of reported attacks on different species. Magpies were reported attacking 45 bird species. Species commonly found in rural habitats where magpies are abundant were attacked most; however, a directly proportional relationship between species abundance in rural habitats and reported attack frequency did not occur. Species consuming similar foods to magpies tended to be attacked more often, probably because these foods are more abundant in rural areas. Attacks on smaller birds regularly resulted in death, but deaths declined as victim weight increased. Non-contact and non-lethal contact attacks occurred throughout the year while attacks resulting in death occurred mainly during the magpie's breeding season (July to November).

Regular observations on six territorial breeding groups and three non-breeding flocks of magpies over a year indicated that a range of bird species actively avoided foraging close to both these social groups cf. adjacent magpie-free control areas; fewer birds were also recorded flying near territorial breeding groups but not non-breeding flocks. Excluding harriers (*Circus approximans*: see below), only 8% of birds recorded close to territorial breeding groups were observed being attacked. Attacks were most frequent when numerous birds occurred near magpies and species recorded in the highest frequencies were generally attacked most. Territorial breeding groups attacked 39% of passing harriers. All attacks consisted of the victim being swooped or chased; no physical contact was ever observed. Both adult male and female breeding magpies were seen attacking other birds; juveniles in breeding groups sometimes supported adults but never initiated attacks. Magpies in non-breeding flocks were not seen attacking other birds, except harriers (attacked in 17% of appearances).

Thirty-eight nests of seven species were continuously monitored in rural areas over two successive breeding seasons using time-lapse video recording to determine the proportion that were preyed on by magpies compared to other animals in this ecosystem. Twenty-two lethal events were recorded over the two breeding seasons; magpies were responsible for only one of these. A further eight scavenging events were also recorded; magpies were not responsible for any of these. Harriers, ship rats (*Rattus rattus*), and cats (*Felis catus*) were the main predators and were responsible for 36%, 32% and 23% of lethal events respectively. A pukeko (*Porphyrio porphyrio*) was also recorded preying on nest contents on one occasion. These results imply that magpies are not important nest predators in rural areas.

After territorial disputes with conspecifics magpies have been observed attacking other animals, suggesting that redirected aggression may be one reason for interspecific aggression. Residents from eight territorial groups were subjected to simulated territorial intrusions using live magpie and pigeon (*Columbus livia*) decoys. The magpie decoy was presented to subjects for 30min and then covered and aggressive responses toward the pigeon decoy by residents were recorded for a further 30min (Treatment 1). Two other experimental conditions were presented on each territory as controls; the two decoys were either both magpies (Treatment 2) or both pigeons (Treatment 3). No attacks on pigeon decoys were recorded during any test. In contrast, magpie decoys were always attacked by both male and female residents. In general, there was no difference in the percent of observations that residents were recorded at close proximity to the pigeon decoy between Treatment 1 and Treatment 3; however, both were lower than the percent of scans residents were recorded close to the magpie decoy in Treatment 2. From this experiment, there was no evidence that magpies redirect aggression onto other birds after territorial intrusions. It is possible, however, that the proportion of territorial disputes that result in redirected attacks are small, or only occur under highly specific circumstances, which were not recognised in this study.

Finally, the hypothesis that magpies currently attack birds in New Zealand partly because they evolved in an environment that rewarded such behaviour was investigated. Data were presented that suggest magpies had evolved in the presence of many predators, numerous dangerous resource competitors, and in areas where resource availability was limited. Therefore, individual magpies that displayed high levels of aggression towards a wide variety of species would have been more successful at obtaining and defending quality nesting and foraging sites against both conspecifics and other birds. Consequently, more aggressive magpies would have had higher levels of fitness and ultimately had a selective advantage over time. In New Zealand many of the environmental constraints from their evolutionary past no longer appear to be present, yet attacks on other birds still occur. It is suggested that the generalised, apparently unnecessary, attack regime is maintained by magpies in New Zealand because (1) interspecific aggression is still adaptive for magpies, (2) magpies have not been in New Zealand long enough for high levels of interspecific agonistic behaviour to be lost from the population, (3) magpies currently face no selection pressure to stop attacking other birds, or (4) interspecific aggression is a pleiotropic by-product of conspecific agonistic behaviour.

This research has determined that there are a range of mutually non-exclusive mechanisms that may explain interspecific aggression by magpies in New Zealand; however, circumstances under which attacks occur appear to be highly variable. Widely focused interspecific aggression by magpies may be best explained as a behaviour that was previously effective at securing resources or protection from threats during their evolution, which may no longer confer improved fitness in New Zealand magpie populations.

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Chapter 1: General Introduction

1.1 Understanding interspecific aggression

Why do members of one species attack members of another? What are they fighting over and how is the victorious species advantaged by winning the exchange? Moreover, have these species been aggressive towards each other over a long timeframe and how has behaviour associated with the exchange developed? These questions touch on the four main areas of ethology (Tinbergen 1963), namely: *mechanisms* (what are the underlying structural factors that cause the behaviour to occur?), *functions* (what is the survival value of the behaviour?), *evolutionary history* (how has the behaviour come about or been modified over evolutionary timeframes?), and *ontogeny* (how has the behaviour developed within the course of an individual's lifetime?). Furthermore, because these four types of questions are not mutually exclusive, experiments designed to discover why interspecific aggression occurs (and the adaptive benefits for species engaging in such behaviour) often attempt to test hypotheses addressing one or more of these areas. It is, therefore, not surprising that current research on interspecific aggression has a broad focus. Further, relationships between interacting species have been studied in both within and between invertebrate and vertebrate populations, under laboratory and field conditions (e.g., Wilson 1975; Huntingford and Turner 1987; Archer 1988).

Brown (1964) suggested that agonistic behaviour (including both intra- and interspecific) is generally employed by individuals in the acquisition of goals which tend to maximise survival and reproduction. This hypothesis was later echoed by Archer (1988) who stated that aggression could be viewed as 'a range of solutions to certain problems'. These are clearly functional explanations for aggression but the 'goals' or 'problems' may be associated with different proximate contexts. Proximate factors influencing interspecific aggression and the resulting functional benefits victors receive through winning conflicts may be divided into three main categories: (1) attacks associated with competition for limited resources (e.g., food or breeding sites), (2) attacks by predatory species hunting prey, and (3) anti-predator aggression (Wilson 1975; Huntingford and Turner 1987), although specialised mechanisms underlying these functional responses clearly also exist including: frustration-induced aggression (Haskell *et al.* 2000, 2004), pain-induced aggression (O'Kelly and Steckle 1939), or redirected aggression (Bastock *et al.* 1953; Marcus-Newhall *et al.* 2000).

1.1.1 Aggression and competition for resources

Aggression is frequently considered a specialised form of resource competition because individuals that are successful competitors will have access to greater amounts of food, optimal breeding sites, mates (if intraspecific competition), or other resources that will ultimately increase that individual's genetic contribution to future generations in comparison to less successful competitors (Maynard Smith and Price 1973; Wilson 1975; Archer 1988). Competition is usually greatest between conspecifics due to the requirement of similar resources; however, when two or more species with similar resource preferences have overlapping distributions (either naturally or through the introduction of one or more species to an area [see below]), high rates of interspecific aggression may subsequently be observed (Newton 1998).

Long-term competition for limited resources may ultimately affect interactions between individuals within and between species. For example, territoriality (both intra- and interspecific) may have evolved to regulate the density of competitors and allow residents exclusive access to a defended resource (Brown 1964; Wilson 1975). Consequently, numerous studies have demonstrated that interspecific territoriality can be a successful way for residents to secure access to resources required for survival and reproduction (e.g., insects, Lawton and Hassell 1981; *Tamias* chipmunks, Brown 1971; and birds, Wolf *et al.* 1976; Catchpole 1978; Reed 1982; Greenberg and Ortiz 1994; Robinson and Terbough 1995). Usually larger species dominate smaller species when competing for the same resources (Huntingford and Turner 1987; Shelley *et al.* 2004). In addition, interspecific competition can affect the foraging behaviour of coexisting species. For example, when great tits (*Parus major*), willow tits (*P. montanus*), and goldcrests (*Regulus regulus*) have overlapping ranges, subordinate species (goldcrests and willow tits) will use different foraging sites in the presence of the dominant great tit (Alatalo 1981). Thus, over evolutionary time natural selection will favour species that are successful competitors and those that are not as adept at securing sufficient resources will have to modify their behaviour (e.g., exploit different niches within a given habitat) or risk extinction (Newton 1998).

The intensity or rate of interspecific aggression may be correlated with resource availability; for example, attacks by the nectivorous golden-winged sunbird (*Nectarinia reichenowi*) on other nectar feeding birds were negatively correlated with the availability of *Leonotis nepetifolia* flowers (their primary food source) (Gill and Wolf 1975). Similarly, artificially increasing the apparent number of interspecific resource competitors in an area (through playback of vocalisations), thereby creating the perception to residents that resources may become limited, has been shown to increase rates of aggression in birds (measured by recording attack rates on playback speakers) (Catchpole 1978; Martin *et al.* 1996). Rates of interspecific aggression, however, do not continue to increase exponentially as the availability of the resources becomes more limited. Generally, defence of a resource can be viewed in an economic sense; the 'costs' associated with resource defence must be less than the 'benefits' obtained (Brown 1964).

1.1.2 Predatory aggression

Many animals need to hunt prey to secure sufficient amounts of food to survive and reproduce. In most cases, however, fighting between predatory and prey species does not occur. This is because many large predatory animals, such as birds, usually prey on small terrestrial or aquatic prey that can be captured without agonistic interactions (e.g, starlings *Sturnus vulgaris* prey on pasture invertebrates; Heather and Robertson 1996). In contrast, when prey species are also large and capable of inflicting injury [see below], the hunter may need to engage in agonistic acts to secure its quarry. For this reason, predators usually prey on species that are smaller to reduce the risk of injury; however, exceptions do occur (e.g., wolves *Canis lupus* hunting white-tailed deer *Odocoileus virginianus* or African lions *Panthera leo* hunting buffalo *Syncerus caffer*). When the risk of injury is high, predators may hunt in packs or select old or sick prey to minimise their risks (Curio 1976).

The effect that predators have on prey populations can be highly variable. For predators that are highly selective in their choice of prey or do not kill more than what would normally be removed by other mortality factors, the impact of predation on prey populations is small (Curio 1976; Newton 1998). For example, the sparrowhawk (*Accipiter nisus*) is the sole predator of several species of song bird in English woodlands. The nesting density and success rates of prey species close to hawk nests were lower than for birds that nested farther away across areas within the habitat (Newton 1992). In contrast, in woodlands where sparrowhawks were not present, there was no difference in the numbers of prey species counted (Newton 1992). Alternately, generalist predators with high fecundity can have devastating impacts on prey populations (King 1984; Holdaway 1989; Wiles *et al.* 2003).

1.1.3 Anti-predator aggression

Animals have developed many different defensive strategies to avoid being preyed on, including: avoiding areas where predators reside, sending visual or auditory signals to warn others of danger, employing different forms of escape behaviour (e.g., *stotting, zigzagging, scattering*), or altering life-history characteristics that minimise temporal or spatial overlap with predators (Edmunds 1974; Lewis and Murray 1993; Martin 1995; Norrdahl and Korpimäki 1998; Jullien and Clobert 2000; Caro *et al.* 2004; Palleroni *et al.* 2005). Attacking a predator is yet another behaviour that may reduce the probability of an individual being preyed on, albeit a more risky defensive strategy (Archer 1988). Although some prey species will attack predators at any time, it is when animals are raising offspring that direct aggression towards a predator is more likely to occur (Montgomerie and Weatherhead 1988; Caro *et al.* 2004).

Many prey species have developed attack strategies that may lower the potential risk of injury when attacking predators (e.g., mobbing) (Pavey and Smyth 1998). However, attacking a predator is often a last resort for a prey species and it is rare for the predator to be seriously or fatally injured during an attack (Edmunds 1974). For example, *Halictus* bees use their stings only as a defensive weapon; if they are caught in the web of an orb-web spider (*Araneus diadematus*), *Halictus* bees will deliver a sting that only paralyses the spider long enough for the bee to bite free of the web and escape (Edmunds 1974). Similarly, the primary defensive response of mice to a predation threat is to either freeze or flee; however, when cornered, subjects will bite predators before attempting to escape (Blanchard *et al.* 1998).

1.2 Ecological impacts of introduced species

After long periods of time, species are likely to develop behaviours that will maximise their survival and allow them to co-exist with other animals in an ecosystem (i.e., evolutionary stable system; Maynard-Smith and Price 1973). However, when animals are introduced to or colonise areas outside their normal range, the species composition changes and agonistic interactions (due to competition, predation, anti-predator responses, or other reasons) between introduced and native species may be enhanced.

Species (both animals and plants) can colonise new areas by either: (1) moving to the new area by their own means, or (2) by being deliberately or accidentally introduced by humans. There are many reasons why animals or plants have been deliberately introduced to areas outside their normal range including: provision of food or primary materials, creation of hunting opportunities, as biocontrol agents to control pest species, or for acclimatisation purposes (Thomson 1922; McDowall 1994; Pimentel 2002; Wilson 2004).

Most introduced species do not establish in new areas (Duncan *et al.* 2003). Generally, those species that do make successful colonists have either: (1) come from a similar ecosystem, (2) few or no resource competitors in their new range, (3) a large initial population size or multiple liberation sites, (4) large brains relative to body size that help them take advantage of novel environments, or (5) had humans modify new habitats to suit their resource requirements (Veltman *et al.* 1996; Duncan *et al.* 1999; Mack *et al.* 2000; Pimentel 2002; Sol *et al.* 2005).

Although many human societies rely on the production and harvesting of some introduced plants and animals (Pimentel 2002), the adverse impacts some introduced species may have in their new range can be enormous. These impacts include both financial losses and losses to biodiversity (Holdaway 1989; Mack *et al.* 2000; Clout 2002; Veitch and Clout 2002; Avery *et al.* 2005). Losses to biodiversity through the displacement, reduction or extinction of native species is of particular concern and the negative impact invasive species have on these native species may soon be more significant than the effect of habitat loss or degradation by humans (Vitousek *et al.* 1997; Chapin *et al.* 2000).

For animal populations, the main mechanisms by which introduced species limit the abundance or distribution of natives is through competition for resources or predation (particularly if they are generalist predators; Clout 2002). The impact of introduced predators can be particularly severe on islands and cases of extensive species extinction proceeding from accidental or deliberate animal liberations have been frequently documented (e.g., Guam, Wiles *et al.* 2003; Hawaii, Reynolds *et al.* 2003; New Zealand, see below). Recently, however, techniques have been developed, such as aerial toxic bait application, where it is becoming possible to eradicate or control to very low densities introduced pests to promote populations of native species (see Veitch and Clout 2002 for current progress in this field).

1.2.1 Introduced animals in New Zealand

New Zealand, like many other countries recently colonised by Europeans, has undergone extensive habitat modification (Taylor and Smith 1997; Kirkpatrick 2005) and been subjected to numerous liberations of exotic animals (Thomson 1922; McDowall 1994). However, unlike many other countries, New Zealand has been separated from other landmasses for at least 60 million years and was far enough away to prevent regular colonisation by animals from surrounding continents (Thornton 1985). Consequently, New Zealand's fauna has a high level of endemism and evolved in the near absence of land mammals; only three species of endemic bat were present (Wilson 2004). Terrestrial vertebrates were dominated by birds and reptiles, which were generally long-lived with low fecundity rates (Wilson 2004).

With the arrival of Maori (ca. 850 years ago), the kiore rat (*Rattus exulans*) along with the polynesian dog (kuri; *Canis familaris*) were introduced into New Zealand (Atkinson and Towns 2001; Wilson 2004), although there is some evidence that kiore may have first arrived about 1000 years earlier (Holdaway 1996, 1999; but see Anderson 2000). Kiore are generalist predators and will prey on animals up to the same size as themselves (60-80g) and will take eggs up to 68 mm in length (Wilson 2004). Consequently, kiore were probably responsible for limiting the abundance or recruitment of several species in many regions before the arrival of Europeans (Atkinson and Towns 2001). Ground nesting birds, such as petrels (*Pterodroma* spp.) and shearwaters (*Puffinus* spp.), were particularly vulnerable to predation; the breeding success of these species on islands has increased following the eradication of kiore (Atkinson and Towns 2001).

It was, however, not until the arrival of Europeans to New Zealand (ca. 200 years ago) that the majority of animal introductions occurred. Although many animal liberations were probably not recorded, introductions of over 195 different species have been documented; 76 currently maintain populations in the wild (see Thomson 1922; McDowall 1994; Wilson 2004 for summaries). Of these species, it was the mammals (especially ship rats *Rattus rattus*, Norway rats *R. norvegicus*, and cats *Felis catus*) that caused the most damage to native fauna (King 1984; Wilson 2004). These predators, along with three species of mustelids, possums (*Trichosurus vulpecula*), and eight species of deer (*Cervus* spp.) continue to endanger remaining native species populations on the mainland of New Zealand through predation and/or competition for resources (King 1984; Innes *et al.* 1999; Clout 2002).

Over 130 bird species were introduced to New Zealand but of these only 39 have self sustaining wild populations today (Wilson 2004). Most introduced birds are commonly found in agricultural or urban areas (Heather and Robertson 1996) as they are generally not as well suited for living in unmodified forested areas cf. native species (Diamond and Veitch 1981). Nevertheless, much of the rural landscape in New Zealand contains many native and exotic bush remnants that can sustain small populations of native birds. The impacts introduced birds are having on native birds in these areas are largely unknown (but see Innes *et al.* 2004), although there is anecdotal evidence that suggests some (predominantly larger) species, such as Indian myna (*Acridotheres tristis*), Australian magpie (*Gymnorhina tibicen*; see below), eastern rosella (*Platycercus eximius*) and starling may be having negative impacts (Oliver 1955; Barrington 1996a; Griffiths 2000; Wright and Clout 2001).

1.3 Study species in context

Australian magpies (magpies hereafter; Figure 1.1) are conspicuous crow-sized (ca. 41cm; 350g) birds that live predominantly in open areas with nearby tall trees for roosting and nesting (Robinson 1956; Carrick 1972; Heather and Robertson 1996). They mainly eat ground-dwelling invertebrates (Vestjens and Carrick 1974; Veltman and Hickson 1989) and for this reason were introduced to several regions in New Zealand from 1864 to help control pasture invertebrate pests (Drummond 1907; Thomson 1922). Magpie populations have successfully spread out from their original release points and are now common or abundant in most areas where suitable habitat exists (McCaskill 1945; McIlroy 1968; Bull *et al.* 1985; Heather and Robertson 1996; Figure 1.2).

Magpies are part of the Artamidae family, a group of passerines that also include currawongs (*Strepera*; 3 spp.), butcherbirds (*Cracticus*; 5 spp.), and woodswallows (*Artamus*; 6 spp.). The Artamidae family probably arose in Australia and all members are currently found in that country, although several have colonised or been introduced to surrounding countries (Sibley and Ahlquist 1985; Schodde and Mason 1999). Schodde and Mason (1999) describe Artamidae species as a 'text-book example of adaptive radiation', because of the different niches each species of this family exploits. For example, currawongs are largely omnivorous, feeding on insects, orchard fruits, birds, and small animals (MacDonald 1984; Schodde and Mason 1999; Bayly and Blumstein 2001). In contrast, butcherbirds are solitary predators and generally hunt prey (large insects, birds, and small animals) by pouncing on victims from a perch and holding down prey with their foot or impaling it onto a spike for dismembering (MacDonald 1984; Schodde and Mason 1999). Finally, woodswallows catch insect prey on the wing and usually hunt in groups (MacDonald 1984; Schodde and Mason 1999).

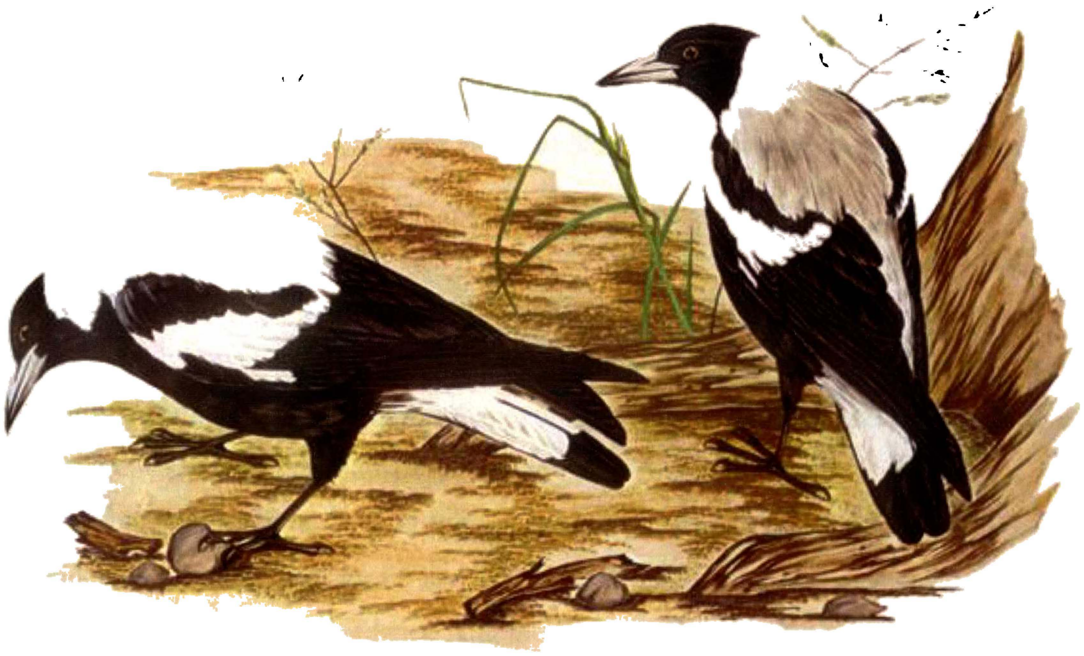

Figure 1.1. The Australian magpie (*Gymnorhina tibicen*). Displayed is the white-backed magpie, the most common variety in New Zealand; the female is on the right.

Adapted, with permission, from a drawing by Janet Marshall in: Kinsky, F.C.; Robertson, C.J.R. 1999. *The Reed Handbook of Common New Zealand Birds*. Reed. Auckland, New Zealand.

Up to eight subspecies of magpie have been identified in Australia that can differ considerably in size and plumage markings; however, interbreeding occurs in areas where subspecies meet and intermediate varieties are common (Burton and Martin 1976; Hughes 1982; Schodde and Mason 1999; Hughes *et al.* 2001). Despite the identification of eight different subspecies, magpies in Australia can be divided into three main classes based on back markings and geographic location: **western** (*Gymnorhina tibicen dorsalis*) are located in the south-east and males are white-backed while females are black-backed; **black-backed** (*G. t. tibicen*) are mainly in north-east and eastern Australia and both sexes are black-backed; and **white-backed** (*G. t. hypoleuca*) are located in south-east Australia and both sexes are white-backed although females also have distinct grey mottled back feathers (Schodde and Mason 1999; Jones 2002; Kaplan 2004). Most of the magpies introduced to New Zealand were collected from the Victorian region (McIlroy 1968). Accordingly, most magpies in New Zealand are white-backed, although black-backs make up to 95% of magpies in Hawke's Bay and North Canterbury regions (Heather and Robertson 1996).

There are arguments in Australia over whether the magpie should be classed as one species or several; however, it is generally accepted that only one exists because interbreeding occurs between varieties whenever they meet and there appears to be little genetic difference between the subspecies (although the western variety is more genetically divergent to white-backed and black-backed varieties; Hughes *et al.* 2001) (see Schodde and Mason 1999 for review). In New Zealand, only one species is accepted (OSNZ 1990); therefore, in accordance with these standards, magpies will be referred to as one species throughout this thesis.

Magpies have complex social systems and several different types of social groupings have been identified in Australia (Carrick 1963, 1972). Essentially these social groupings range from magpies that defend breeding territories all year round to those that live in semi-nomadic non-territorial flocks. Territories can be defended by monogamous pairs or up to 26 magpies (Robinson 1956; Carrick 1972; Hughes and Mather 1991; Baker *et al.* 2000). In Australia, pair-defended territories are more common among north-eastern populations compared to predominantly multiple member territories in the south-east and south-west (Robinson 1956; Carrick1972; Hughes and Mather 1991; Baker *et al.* 2000). The number of members in a territory appears to be positively correlated with rates of extra group paternity (Hughes *et al.* 2003; Durrant and Hughes 2005). Therefore, juveniles may be evicted from natal territories in areas with low rates of extra group

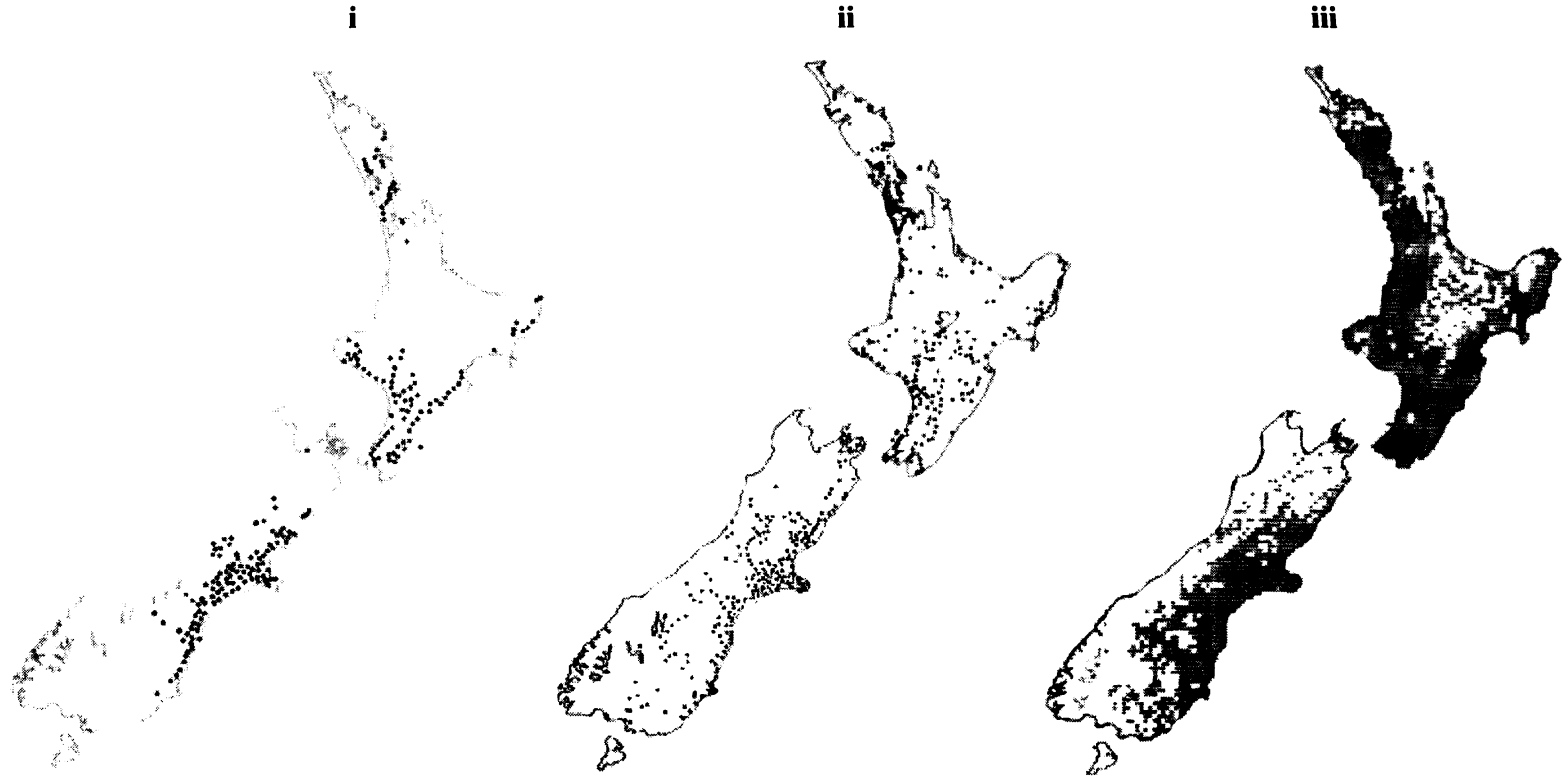

Figure 1.2. Reported distribution of magpies in New Zealand in: (i) 1945, (ii) 1968, and (iii) 1985. These distribution maps give no indication of magpie abundance in New Zealand. *Maps are adapted, with permission, from* (i) *a nationwide public survey* (McCaskill 1945); (ii) *a summary of McCaskill (1945), Classified Summarised Notes 1940-1962, the Ornithological Society of New Zealand Recording Scheme, and public reports up to 1968* (McIlroy 1968); *and* (iii) *data collected between September 1969-December 1979 as part of The Atlas of Bird Distribution in New Zealand* (Bull *et al.* 1985).

paternity, reducing inbreeding depression (Durrant and Hughes 2005). Rates of extra group paternity are currently not known for New Zealand magpies; however, territories defended by up to 10 magpies are common (McIlroy 1968; Veltman 1984; Farabaugh *et al.* 1992; Heather and Robertson 1996), suggesting extra pair copulations may be common. Magpies that live in non-territorial flocks consist of birds of both genders and varying age; generally flocks consist of previous breeding season birds evicted from natal territories and adults that have been displaced from territories or lost a partner (Carrick 1972; Veltman 1989b). Although non-territorial flocks can contain adult birds, no breeding takes place (Carrick 1972; Veltman 1989b). The precise reasons for the formation of non-breeding flocks are currently unknown; however, social bonds can be formed that may lead to an attempt by these magpies to obtain a breeding territory outside the flock (Carrich 1972; Veltman 1989b).

In New Zealand the magpie breeding season occurs between July and November; nest building begins in June (Heather and Robertson 1996). In territories defended by several magpies, breeding is generally conducted by only the dominant male and female, although nesting attempts are sometimes made by additional females (Veltman 1989b). On average, three or four eggs are laid and incubated for 20-21 days; chicks are reared in the nest and fledge at ca. 28 days (Heather and Robertson 1996). Incubation and brooding is conducted by only the breeding female, although chicks are fed by both parents (Veltman 1989b). Veltman (1989b) did not observe any non-breeding birds helping at the nest, although helping behaviour (feeding nestlings) by non-breeders was recorded by other researchers on the same population in New Zealand (Brown and Farabaugh 1991). In contrast, helping behaviour by non-breeders appears to be common in territories defended by several magpies in some Australian populations (Hughes *et al.* 1996).

1.4 Aims of the thesis

In both Australia and New Zealand there are many anecdotal and published reports of magpies attacking and even killing other birds (e.g., Chisholm 1910; Chandler 1944; McCaskill 1945; Moon 1956; Hall 1962; McIlroy 1968; Paton 1977a; Ashton 1986; Barr

1986; Tremont 1995; Barrington 1995, 1996b; Cox and Bauer 1997; Cilento & Jones 1999; Jones 2002; Kaplan 2004). Adaptive reasons for attacks by magpies on some species can be formulated; attacks on close resource competitors (e.g., white-winged choughs *Corcorax melanorhamphos*; Cox and Bauer 1997) or avian predators (McCaskill 1945; Kaplan 2004) may have direct fitness benefits. Other birds (e.g., black shags *Phalacrocorax carbo*; Hall 1962), however, that share little or no resource overlap and are not predators are also commonly attacked for no apparent reason.

In New Zealand, concerns have been raised over whether interspecific aggression by magpies has detrimental impacts on the abundance or distribution of native birds (e.g., McCaskill 1945; McIlroy 1968); furthermore, many people feel that magpies should be classed as a pest and controlled accordingly (e.g., Barrington 1995, 1996b). From a survey of 120 people in the South Island, New Zealand, 62% of respondants had been exposed to some form of negative experience involving magpies (i.e., either being divebombed by magpies or observing magpies harass other birds); accordingly, 29% of the total sample expressed concern over the possibility of magpies having debtrimental impacts on New Zealand's avifauna (McKay 1997). However, having a negative magpie experience heavily influenced the respondants' perception magpies (i.e., respondants were more likely to consider all magpies a 'pest' even if only one negative experience was reported) (McKay 1997).

In response to some of these concerns, Innes *et al.* (2004) quantified the impact magpies were having in rural New Zealand by culling magpies on five ca. 900ha blocks of farmland over three years and measuring the response of other birds to this control. Although significant, albeit small, increases in five introduced (blackbird *Turdus merula*, Indian myna, skylark *Alauda arvensis*, song thrush *Turdus philomelos*, and starling) and one native species (kereru *Hemiphaga novaeseelandiae*) were recorded, the high cost of controlling magpies in comparison to the small increases in bird abundance lead to the conclusion that magpie control operations should not be undertaken (Innes *et al.* 2004). The money could be better spent targeting mammalian pests.

The research presented in this thesis was conducted to complement the large-scale magpie removal trial co-ordinated by John Innes from Landcare Research (see Innes *et al.* 2004). Specifically, if magpie removal did influence bird numbers: what are the proximate reason(s) and adaptive benefit(s) for magpies conducting interspecific attacks on the species that increased? While much is known about the biology and ecology of magpies in both New Zealand (e.g., McIlroy 1968; Veltman 1984) and Australia (e.g., Robinson 1956; Carrick 1972; Kaplan 2004), behavioural interactions between magpies and other species have received comparatively little attention (but see Jones 2002 for a review of research on magpie attacks on humans in Australia). Furthermore, the reasons why magpies attack many species are generally unknown.

Therefore, the specific aims of this thesis can be divided into two parts:

1. To document interactions between magpies and other birds to determine (a) what species are attacked the most by magpies, (b) the proportion of passing birds that are attacked by magpies, (c) whether there are certain characteristics that predispose victims to being attacked, (d) whether certain categories of magpies are more aggressive (e.g., male vs. female, territorial vs. non-territorial), and (e) whether birds actively avoid flying or landing close to magpies.
2. To test or explore several reason(s) for interspecific aggression in magpies. These include (a) do magpies view other birds (including eggs, young, or adults) as a potential food source, (b) are magpies more likely to attack other birds after territorial disputes, and (c) were there reasons during the evolutionary past that promoted interspecific aggression in magpies?

Achieving these aims would greatly increase the amount of knowledge relating to the span and context of interspecific aggression by magpies in New Zealand. Furthermore, understanding the reasons for interspecific aggression will provide useful information to managers who may wish to minimise aggressive interactions between magpies and other birds.

1.5 Content of chapters

In **Chapter 2** reported accounts of magpies attacking other birds in New Zealand were collated from published sources and a survey of the public. These accounts were pooled and analysed to identify, (1) which species of bird were most commonly attacked, (2) whether overlap in diet or habitat requirements (foraging/nest location) might explain the frequency of magpie attacks, (3) if magpies alter attack intensity depending on the size of the victim to minimise their own risk of injury, (4) if the most attacked species are in greater numbers in rural areas (where magpies are most commonly found), and (5) if attacks in New Zealand are more frequent during certain times of the year.

In **Chapter 3** a field study was conducted to control several limitations identified in the collection of data from Chapter 2, specifically: (1) determining the proportion of passing birds that were attacked by magpies, and (2) identifying which categories of magpies are most aggressive [see above]. In addition, whether other birds actively avoid flying or landing close to territorial and flock magpies and the importance of magpies as a predator of adult birds was also determined in this chapter.

Rural bird nests were monitored using continuous time-lapse recording techniques over two consecutive breeding seasons in **Chapter 4** to determine if magpies are important nest predators in comparison to other animals in this ecosystem.

Chapter 5 describes an experiment that examined whether magpie residents subjected to simulated territorial intrusions by magpie decoys will redirect attacks onto pigeon decoys or free-ranging birds. Anecdotal reports exist of magpies attacking other animals after the conclusion of territorial disputes (Brown and Veltman 1987), although whether this may explain why magpies attack some birds had not been tested.

Chapter 6 considers the hypothesis that magpies attack other birds because they have evolved in an environment outside of New Zealand that rewarded such behaviour. Although difficult to examine, Chapter 6 attempts to reconstruct the type of environment in which magpies may have evolved in Australia and identifies several limiting factors that may have influenced magpie behaviour. Individual magpies that displayed higher amounts of aggression may have had higher fitness levels and ultimately been selected for over time.

Chapter 7 summarises the main research findings from Chapters 2-6 and discusses their implications in terms of understanding the mechanisms and functions of interspecific aggression in magpies. Also, future areas of research that may be considered to further help understand the reasons for interspecific agonistic behaviour in magpies are discussed.

The research in the following chapters of this thesis is presented in the form of stand-alone manuscripts suitable for publication (although standardised formatting has been used throughout). As a result there is some repetition of basic information in sections of several chapters. Where possible, I have kept repetition to a minimum. In addition, Chapters 2-5 have been written with J.R. Waas and J. Innes as co-authors; as such, the manuscripts have been written to reflect their involvement (i.e., the terms 'we' and 'our' are used).

All aspects of this research were approved by the Waikato Animal Ethics Committee (protocols 576, 586); banding was conducted under permission from New Zealand Department of Conservation (permit no. 0423).

Chapter 2: Australian magpie interactions with other birds in New Zealand: results from a literature review and public survey[*]

2.1 Abstract

Accounts of Australian magpie (*Gymnorhina tibicen*) attacks on birds in New Zealand were collated from literature and a survey of the public, and then summarised to identify the frequency and characteristics of reported attacks on different species. Australian magpies were reported attacking 45 bird species. Species commonly found in rural habitats (e.g., harrier *Circus approximans*, blackbird *Turdus merula*) where Australian magpies are abundant were attacked most; however, a directly proportional relationship between species abundance in rural habitats and reported attack frequency did not occur. Species consuming similar foods to Australian magpie tended to be attacked more often, probably because these foods are more abundant in rural areas. Attacks on smaller birds (e.g., grey warbler *Gerygone igata*) regularly (66%) resulted in death, but deaths declined as victim weight increased. Non-contact attacks were most common for the largest species (e.g., kereru *Hemiphaga novaeseelandiae*). Non-contact and non-lethal contact attacks occurred throughout the year while attacks resulting in death occurred mainly during the Australian magpie's breeding season (July to November). This study indicates that Australian magpies can attack a wide range of species but fails to determine why (no one explanation satisfies all cases). Limitations of the dataset and future research to control these are discussed.

2.2 Introduction

The Australian magpie (*Gymnorhina tibicen*; magpie hereafter) was introduced to the Auckland, Wellington, Canterbury, and Otago regions of New Zealand during the 1860's and 70s in an attempt to help control pest invertebrates in pasture (McIlroy 1968). Since then, magpie populations have gradually increased and magpies are now widely

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distributed throughout North and South Islands up to low alpine levels, with their highest concentrations being in rural areas (Heather and Robertson 1996).

Public perception of magpies is often negative as they are undeniably aggressive and many anecdotal reports of attacks on other animals exist (McCaskill 1945; McIlroy 1968; Paton 1977b; Ashton 1986; Barrington 1995, 1996b; Cilento and Jones 1999). The possibility that magpies have negative impacts on the abundance and distribution of other birds, especially native New Zealand birds, is of particular concern (Barrington 1995,1996b). However, during one study of magpie involving over 2000 hours of observations, only one avian predation event was observed (a magpie killed a goldfinch *Carduelis carduelis* chick; Barrington 1995). Furthermore, aggressive behaviour by magpies may, at least in some cases, promote bird abundance; for example, magpies have been observed harassing predators such as harriers (*Circus approximans*).

Alone, these reports confirm that magpies interact with other species, but they fail to address important issues such as their impact on bird populations. If, however, many anecdotal reports are collated, it becomes possible to identify characteristics of the species targeted most frequently, the context of the attacks, and perhaps, even the reason for the attacks.

Some clues as to why magpies attack other species are available from studies conducted in Australia, where attacks on humans have become such a problem in cities that rangers are often employed to deal specifically with troublesome magpies (Jones and Thomas 1999). For example, attacks by male birds on humans increase during the breeding period (Jones *et al.* 1980; Jones and Thomas 1999) when increased levels of hormones like testosterone may lower their tolerance to other animals (Jones *et al.* 1980). However, in another Australian study, Carrick (1972) found that while territorial behaviour peaked during breeding, magpies defended territories rigorously all year round and that defensive behaviour was not explained wholly by gonadal state as caponised males still actively defended territories. Warne (2001) found that testosterone levels of male magpies aggressive towards humans were not different from those in magpies that did not attack humans. Attacks by female magpies on conspecifics and other animals have also been frequently observed (Veltman 1984; Jones 2002; pers. obs.). Thus, levels of aggression are not solely regulated by changes in gonadal state associated with breeding and territorial defence, leaving the mechanisms of interspecific aggression obscure.

The aim of our paper is to collate reported accounts of magpies attacking other birds from: (a) New Zealand publications and (b) a survey of the general public. These accounts are pooled and analysed to identify: (1) which species of bird were most commonly attacked, (2) whether overlap in diet or habitat requirements (foraging/nest location) might explain the frequency of magpie attacks, (3) if magpies alter attack intensity depending on the size of the victim to minimise their own risk of injury, (4) if the most attacked species are in greater numbers in rural areas (where magpies are most commonly found), and (5) if attacks in New Zealand are more frequent during certain times of the year. We used this information to develop specific testable hypotheses to explain why magpies attack other species of birds in New Zealand.

2.3 Methods

2.3.1 Data collection

Using the keywords “magpie”, “black-backed magpie”, “white-backed magpie”, “Cracticidae” and “Gymnorhina” in the NZ Superindex database (www.knowledge-basket.co.nz/superindex/welcome.html), a search of published accounts of magpies attacking other animals was conducted (1945-2001). The NZ Superindex was used because it is the only database to index the journal of the New Zealand Ornithological Society, *Notornis*, and its predecessor *New Zealand Bird Notes*, as well as other New Zealand based ecological journals (e.g., *New Zealand Journal of Ecology*, *New Zealand Journal of Zoology*). Popular articles, books, theses, Classified Summarised Notes (*Notornis*) and media reports were also consulted. Requests for published accounts of magpies attacking other birds can be made by contacting the first-named author.

The public was also invited to submit their personal observations of magpies attacking other birds. Requests for information (see below) were made through the magazine of the

Ornithological Society of New Zealand (*Southern Bird* September 2001), the annual newsletter updating the national magpie control programme (*Quardle Oodle Ardle* October 2001), Radio Pacific (16 February 2002), and major New Zealand newspapers including *The Dominion* (9 February 2002), *Otago Daily Times* (11 February 2002), *The Press* (12 February 2002), and *Waikato Times* (5 March 2002). Information requested from the public included (i) where and when the interaction took place, (ii) the species that were involved, and (iii) what actually happened during the attack. We considered attacks involving magpies that occurred long-ago to be as relevant as attacks that occurred recently; therefore, no limit on the date of interactions was set.

2.3.2 Data management

The relevant information (i.e. i-iii above) was entered into a database for both literature and public sources. Birds were ordered from most- to least-attacked and grouped into three "attack classes" according to the number of times the species was reported as being attacked by magpies (attack class 1 = ≥5 reports, attack class 2 = 2-4 reports, attack class 3 = 1 report). We also classified each report into one of three attack categories: non-contact, non-fatal contact, or kill. Non-contact attacks included magpies swooping at or chasing other birds without touching them. Non-fatal contact attacks included all interactions where physical contact occurred at least once during the encounter but did not result in the death of the target bird. All interactions where the loss of life was confirmed as the result of a magpie attack were classed as kills, including those where magpies were observed eating adult birds or chicks or preying on eggs.

In some instances, the reports sent to us did not include all the information we required. In these cases, we wrote back to the respondent. If the respondent could not provide the missing information (e.g., when an attack occurred), we entered missing values for that part of the analysis. Some published accounts also had information missing. In most of these cases it was not possible to write back to the author due to the age of the report; however, whenever possible attempts were made to gain the required data. Several reports were of magpies carrying away live adults or chicks but it was not possible to establish the final fate of the prey, or observers attempted to stop the magpie from killing the bird. In these instances, we assumed that the victim was killed by the magpie but formed no conclusions on whether consumption of the victim then occurred. Therefore, the proportion of prey listed as "consumed" may be under-estimated in our analysis.

We compared the number of reports for each attack type (non-contact, non-fatal contact, and kill) for each species between literature (*n*= 97) and public responses (*n*= 98) to determine if there were differences in the types of species reported between the two information sources. The only significant difference between the two sources was for non-fatal contact attacks (Wilcoxon's signed ranks test, *Z*= -2.76, *P*= 0.006; the public reported less non-fatal contact attacks), however, because there were no significant differences between the other two attack types (*Z*= -0.47, *P*= 0.64 [non-contact], *Z*= -1.53, *P*= 0.13 [kill]), or when attack types were combined (*Z*= -1.56, *P*= 0.12), we pooled all reports for analysis.

To examine "time of year" effects, magpie interactions were each assigned to a month of the year (when known; *n*= 33). When only the season was known, or the attack was reported to have occurred during the magpie breeding season (*n*= 12), the middle month for that season was assigned (January, April, July, and September for summer, autumn, winter and spring, respectively; September for magpie breeding season). When a species was reported as being attacked frequently, and at all times of the year (*n*= 11), an interaction was entered for each month. Likewise, when a species was reported as being attacked many times across the magpie breeding season (July to November; Heather & Robertson 1996) (*n*= 2), an interaction was recorded for each month during this period.

In some instances, the specific name of a bird was not known (e.g., observers only reported "duck" or "finch"). If, when re-contacted, the respondent could not give a species name, their observation was dropped from the analysis.

2.3.3 Ecological parameters

To investigate whether there were relationships between life history characteristics of the victims and the frequency, or type, of attack, the habitat preference, abundance in rural habitat, dietary preference, weight class and nesting preferences of attacked bird species were examined.

Habitat

We defined 'habitat' as the resources and conditions present in an area that produce occupancy by a species (Hall *et al.* 1997). Habitat types (rural, urban, coastal, native forest, exotic forest, forest edge and alpine; see Appendix 1) were defined broadly as the inclusion of too many categories prevented us from being able to identify general trends in the data set. While some of these categories were labelled on the basis of vegetation associations (e.g., native forest), vegetation type was not the only criterion for defining habitat because areas such as 'urban' or 'rural' often have a range of vegetation associations within them (Hall *et al.* 1997). Each species reported as being attacked by magpies was assigned a value from 0-3 depending on how commonly it occurred in each habitat type (see Appendix 1). No standardised system of quantifying the relative abundance of New Zealand bird species in different habitats currently exists. Therefore, we allocated values by using information on distribution and habitat for each species from contemporary ornithological texts (Marchant and Higgins 1990, 1993; Heather and Robertson 1996; Higgins and Davies 1996; Higgins 1999; Higgins *et al.* 2001). To determine if there was an association between habitat and attack frequency, victim preference within each habitat type was compared with the number of reports of them being attacked by magpies.

Bird occurrence in rural environments

Species occurrence at five-minute bird count sites in rural areas (where magpies occur most commonly) was derived from data supplied courtesy of Auckland Regional Council (ARC), Environment Bay of Plenty (BOP), Environment Waikato (EW), Wellington Regional Council (WRC) and Environment Southland (ES) (Figure 2.1). These Councils participated in a trial co-ordinated by Manaaki Whenua Landcare Research to examine the effect of magpie control on other bird species (Innes *et al.* 2004).

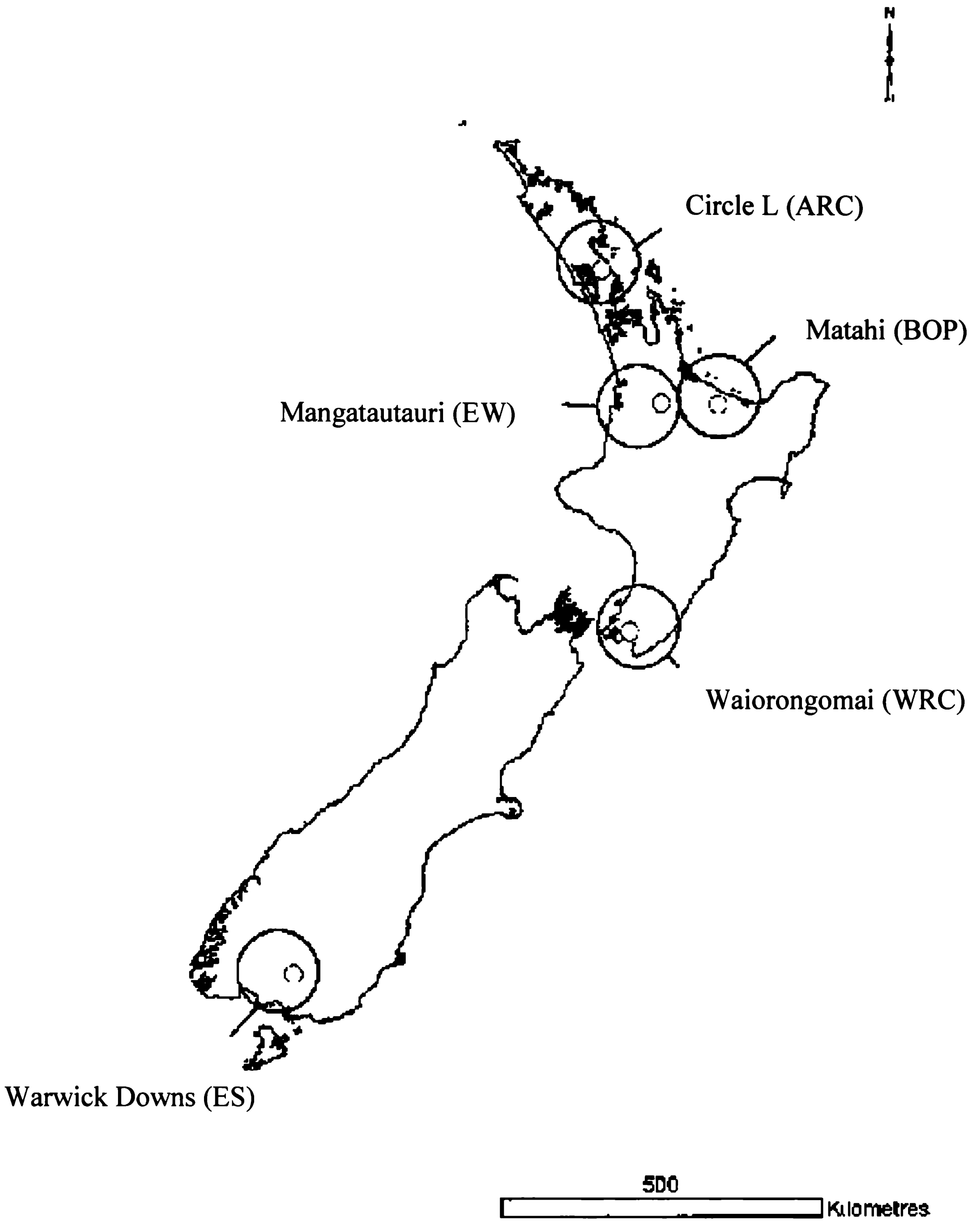

Figure 2.1 Locations of five-minute count blocks monitored by Regional Councils in New Zealand.

Five-minute bird counts (following Dawson and Bull 1975) were conducted in areas where magpies were common and not controlled (Circle L [ARC], Matahi [BOP], Mangatautari [EW], Waiorongomai [WRC], and Warwick Downs [ES]; Figure 2.1) by Landcare Research trained observers. Sample blocks were approximately 900 ha and 35-36 count sites were located in each. Six counts took place at each count site during December 1999 and January 2000, and during November and December 2000. The number of times that each species was observed (seen or heard) in each block was totalled and divided by the number of count stations for that site to provide a mean occurrence/five-minute count. The mean across-block occurrence of each species was then calculated.

We then averaged the mean occurrence of species at count sites for species in each of the three attack classes to determine if victims in attack class 1 (most attacked) were counted more often compared to victims in attack classes 2 or 3 (moderately or least attacked). We also used the five-minute count data to determine if there was a positive correlation between the frequency that victims were attacked and their mean occurrence at count sites.

Diet

Thirteen food categories were used to characterise the diet of all birds attacked by magpies (see Appendix 2). A ranking value (0-3) was assigned to each food type for each bird to characterise how important that component of the diet was to that species (see Appendix 2). Each rank was derived by interpreting information on the attacked species' diet from contemporary ornithological texts (Marchant and Higgins 1990, 1993; Heather and Robertson 1996; Higgins and Davies 1996; Higgins 1999; Higgins *et al.* 2001). We then compared diet preference with attack frequency to determine if species with particular food preferences were attacked more often, or if the most attacked species had dietary overlap with magpies.

Bird weights

Species were grouped into one of four weight categories (see Appendix 3) in order to determine whether a species' mean weight influenced the number and severity of attacks.

Information relating to the mean weight of each species was obtained from Heather and Robertson (1996). We then determined whether the frequency, or the type, of attack (i.e., non-contact, non-fatal contact, kill) differed across the four weight categories.

Nest type

In order to determine whether birds using magpie-like nesting sites were attacked more often, each species' nesting preference was assigned to one of six categories: above ground in open, above ground in tree hole (or cavity), ground nest in open area, ground nest in wetland, ground nest in burrow (or under cover), or varied nesting habits. All information regarding nest location was sourced from Heather and Robertson (1996). Two species were excluded from this analysis because they normally breed in captivity (canary *Serinus canaria*) or outside New Zealand (cattle egret *Bubulcus ibis*). We then compared nesting preference with attack frequency to determine if species with nesting preferences similar to magpie were attacked more often.

2.3.4 Analysis

The total number of attack reports per species, and species abundance in rural habitats (sighting/five-minute count), were square root transformed as a variance stabilising technique so that standard regression methods could be used.

Linear regressions on the transformed data were used to correlate the number of reported attacks on each species with their habitat and dietary preferences. Data from harriers were analysed separately as attacks on this species were much higher than other species, skewing the data set for each measured parameter.

We used a Kruskal-Wallis H test to detect differences in species occurrence from the five-minute counts in rural areas across the three attack classes. When a significant difference ($P < 0.05$) was identified, post-hoc multiple comparisons were conducted to investigate where the main differences occurred (*sensu* Siegel and Castellan 1988).

2.4 Results

Magpies were observed to attack harriers 2.6 times more frequently than the next most attacked species (Table 2.1). All birds that were reported as being attacked by magpies are listed in Table 2.1 (arranged from species attacked most to those least attacked).

2.4.1 Attack rates with respect to habitat preference

Species that were common or abundant (habitat rank 2 or 3) in rural areas (Appendix 1) were attacked more often than species that were rarely (habitat rank 0 or 1) found in these areas ($r^2 = 0.23$, $df = 43$, $P = 0.001$). All of the species (12/12) attacked most often (attack class 1; Table 2.1) and 94% (16/17) of species that were attacked at intermediate rates (attack class 2; Table 2.1) were commonly found or abundant in rural habitats (Figure 2.2). Only 38% (6/16) of species attacked at low rates (attack class 3; Table 2.1) were common or abundant in rural habitats (Figure 2.2).

Species commonly found (habitat rank of 2) on forest edges may also have been attacked more often than those rarely found near forest edges (habitat rank of 0 or 1) ($r^2 = 0.11$, df= 43, $P = 0.03$, Figure 2.2).

Species that were ranked as common or abundant in the other five habitat types were not attacked at higher rates than species that were ranked as rarely occurring there.

2.4.2 Attack rates with respect to occurrence in rural areas

Species occurrence at five-minute count sites varied significantly across the three attack classes ($H = 17.00$, df= 2, $P < 0.05$). On average, individuals of species in attack classes 1 and 2 were counted 0.22 (± 0.08 s.e.m) and 0.27 (± 0.08 s.e.m) times/five-minute count, a difference that was not statistically significant according to the post hoc comparisons. Birds in attack class 3, however, were only counted 0.03 (± 0.01 s.e.m) times/five-minute count, a value that was significantly lower than that for attack classes 1 and 2.

Table 2.1 Species attacked by magpies according to literature and a public survey, including the total number of reports per species, attack class (i.e., attack class 1 ≥5 reports, attack class 2= 2-4 reports per species, and attack class 3= 1 report), type of attack (non-contact, non-fatal contact or kill), and the mean frequency at which each species was counted in five-minute bird counts at five locations throughout New Zealand.

	Total	Attack class	Attack type			Species occurrence at five-minute count stations
			Non-contact	Non-fatal contact	Kill	
harrier hawk *Circus approximans*	37	1	30	6	1	0.07
blackbird *Turdus merula*	15	1	7	2	6	0.56
song thrush *Turdus philomelos*	14	1	5	3	6	0.48
kereru *Hemiphaga novaeseelandiae*	11	1	8	1	2	0.04
house sparrow *Passer domesticus*	11	1	2	3	6	0.84
white-faced heron *Ardea novaehollandiae*	9	1	4	2	3	0.01
bellbird *Anthornis melanura*	6	1	3	1	2	0.03
skylark *Alanda arvensis*	6	1	1	1	4	0.51
chicken *Gallus gallus domesticus*	5	1	3	1	1	0
kingfisher *Halcyon sancta*	5	1	2	0	3	0.09
pipit *Anthus novaeseelandiae*	5	1	2	1	2	0
tui *Prosthemadera novaseelandiae*	5	1	2	1	2	0.05
black-backed gull *Larus dominicanus*	4	2	2	1	1	0.01
goldfinch *Carduelis carduelis*	4	2	0	1	3	0.83
pheasant *Phasianus colchicus*	4	2	0	1	3	0.03
pukeko *Porphyrio porphyrio*	4	2	2	2	0	0.02
rock pigeon *Columba livia*	4	2	2	2	0	0.01
silvereye *Zosteropus lateralis*	4	2	0	0	4	0.41
starling *Sturnus vulgaris*	4	2	3	0	1	1.03
paradise shelduck *Tadorna variegata*	3	2	2	1	0	0.13
spur-winged plover *Vanellus miles*	3	2	1	1	1	0.09
black shag *Phalacrocorax carbo*	2	2	1	1	0	0
chaffinch *Fringilla coelebs*	2	2	0	1	1	0.6
fantail *Rhipidura fuliginosa*	2	2	0	0	2	0.27
little owl *Athene noctua*	2	2	1	1	0	0
grey warbler *Greygone igata*	2	2	0	0	2	0.36
mallard *Anas platyrhynchos*	2	2	0	1	1	0.01
morepork *Ninox novaeseelandiae*	2	2	1	1	0	0
yellowhammer *Emberiza citrinella*	2	2	0	0	2	0.74
banded dotterel *Charadrius binictus*	1	3	0	0	1	0
black-fronted tern *Sterna albostriata*	1	3	0	0	1	0.01
canary *Serinus canaria*	1	3	0	0	1	0
cattle egret *Bubulcus ibis*	1	3	1	0	0	0
Indian myna *Acridothesres tristis*	1	3	1	0	0	0.25
kaka *Nestor meridionalis*	1	3	0	1	0	0
kea *Nestor notabilis*	1	3	1	0	0	0
kokako *Callaeas cinerea*	1	3	1	0	0	0
long-tailed cuckoo *Eudynamys taitensis*	1	3	1	0	0	0
New Zealand dotterel *Charadrius obscurus aquilonius*	1	3	1	0	0	0

Table 2.1 cont.

New Zealand falcon *Falco novaeseelandiae*	1	3	1	0	0	0
California quail *Callipepla californica*	1	3	0	0	1	0
red-billed gull *Larus novaeseelandiae*	1	3	0	1	0	0
eastern rosella *Platycercus eximius*	1	3	1	0	0	0.16
spotted turtle-dove *Streptopelia chinensis*	1	3	0	0	1	0
tomtit *Petroica macrocephala*	1	3	0	0	1	0

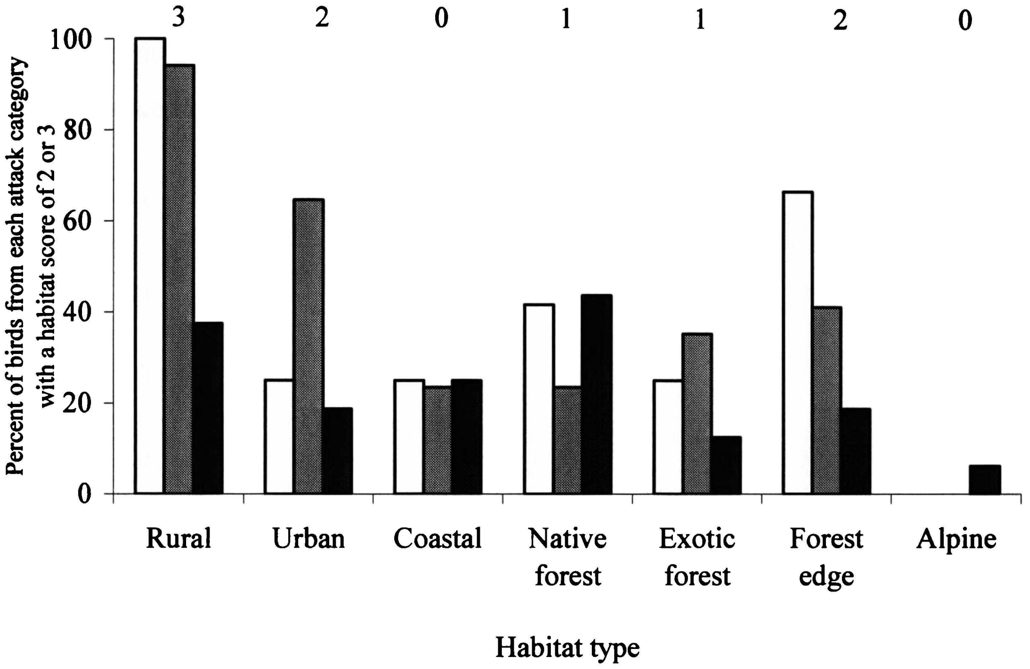

Figure 2.2 The proportion of species from each attack type that are common or abundant (habitat score of 2 or 3) in each habitat type (*numbers above bars represent magpie habitat rank from Appendix 1; open bars denote species in attack class 1, grey bars denote species in attack class 2, and black bars denote species in attack class 3*).

Attacks on species in attack class 1 made up 58% of the total reports on all species, however, species from this attack class only made up 35% of birds counted during five-minute bird counts, a variance that was significantly different (χ^2= 16.01, df= 1, P< 0.05; Figure 2.3). The percentage of total attacks on species in attack class 2 was 32% while these species made up 60% of birds counted in five-minute bird counts, also significantly different (χ^2= 13.07, df= 1, P< 0.05; Figure 2.3). There was no significant difference between the percentages of total attacks on species in attack class 3 (10%) and the proportion they made up of birds counted during five-minute counts (5%) (χ^2 = 3.68, df= 1, P> 0.05; Figure 2.3). Therefore, species in attack class 1 were reported as being attacked at rates higher than their occurrence would suggest, while species in attack class 2 were attacked at lower rates.

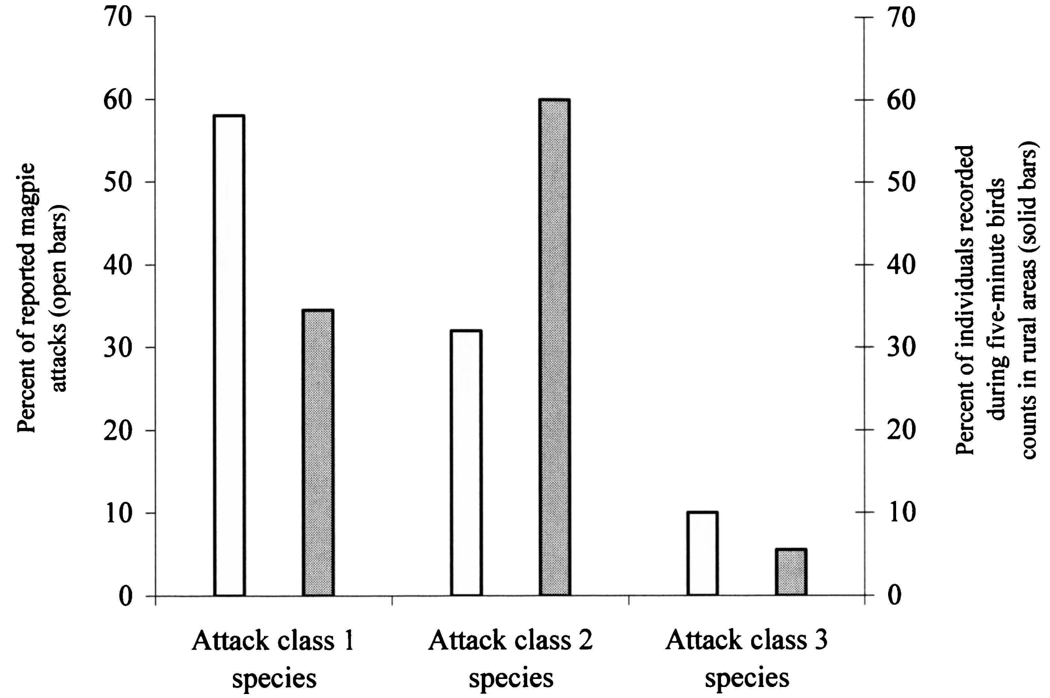

Figure 2.3 The percentage of birds from each attack class that were counted in five-minute bird counts in rural areas (solid bars) and the percentage of total attacks on birds in each attack class (open bars).

2.4.3 Attack rates with respect to dietary preference

Nine of 12 species (75%) in attack class 1 and 53% of species in attack class 2 commonly or mostly consumed open or pasture invertebrates (Figure 2.4). Only 19% (3/16) of species in attack class 3 commonly or mostly consumed this food type (Figure 2.4). Species that commonly or mostly consumed pasture invertebrates in their diet (diet rank 2 or 3), were attacked more often than species that rarely or never consumed this food type (diet rank of 0 or 1) (r^2= 0.13, df= 43, P= 0.02). When only the species that were common or abundant (habitat score of 2 or 3) in rural, forest edge and urban areas (n = 38) were included this difference was not apparent (r^2= 0.06, df= 37, P= 0.13).

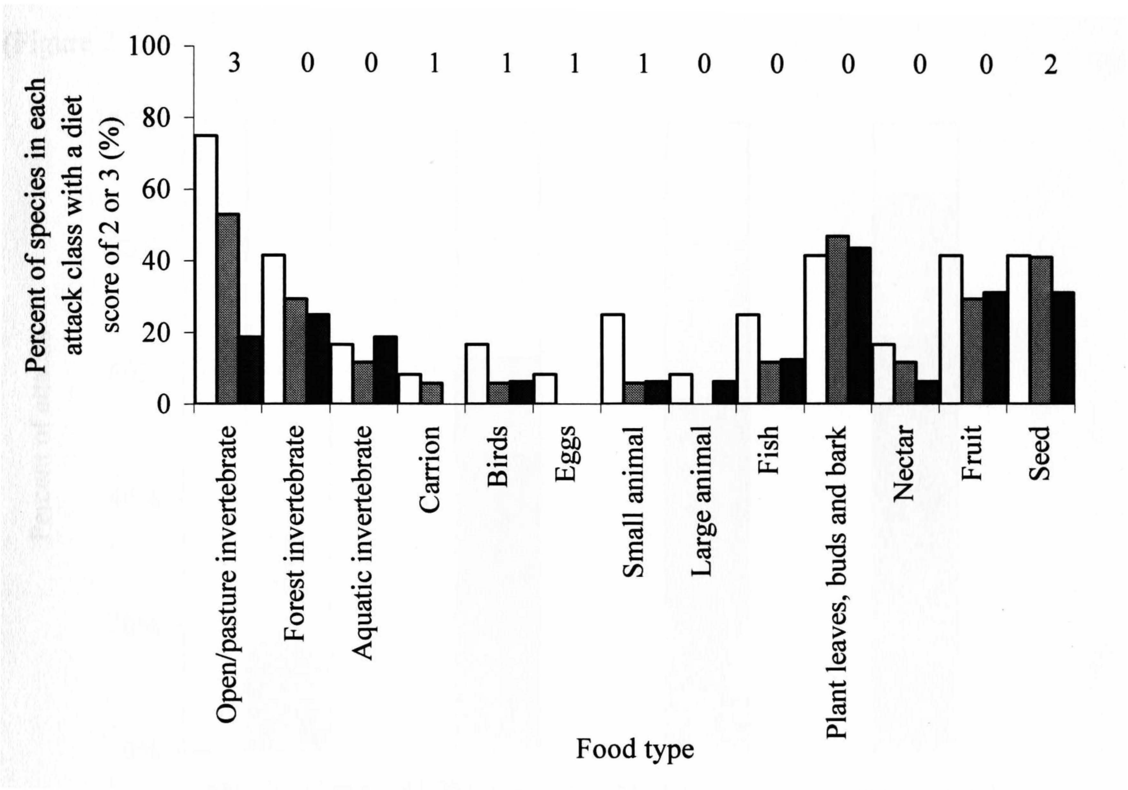

Figure 2.4 The proportion of the species from each attack category that have each food type as a common or main component (diet score of 2 or 3) of their diet (*numbers above bars represent magpie diet rank from Appendix 2; open bars denote species in attack class 1, grey bars denote species in attack class 2, and black bars denote species in attack class 3*).

No other significant correlations could be identified between reported attack frequency of species and the other food types.

2.4.4 Effect of weight

The probability of death when magpies attacked a species was associated with the victim's weight. An encounter between magpies and a bird in the lightest weight class (<60g) was more likely to result in death (66% of reports for this weight class) compared to non-contact (17% of reports) or non-fatal contact (17% of reports) (Figure 2.5). While the total proportion of non-fatal contact attacks was relatively constant over all weight categories (approximately 12-20%), kills significantly decreased and non-contact attacks significantly increased as the weight of the victim increased ($\chi^2 = 85.76$, df= 6, $P < 0.001$) (Figure 2.5).

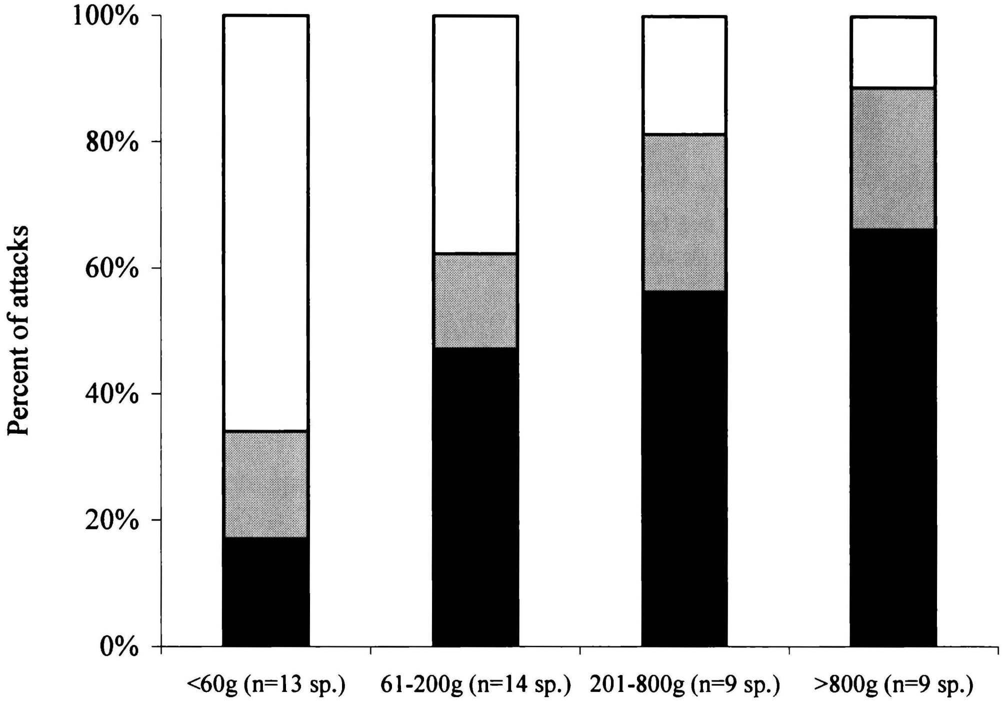

Figure 2.5 The proportion of different types of attacks (non-contact *black bars*, non-fatal contact *grey bars* or kill *open bars*) by magpies on birds in four different weight categories.

2.4.5 Nest location

Half (6/12) of the species that were attacked the most built open nests above the ground as magpies do (attack class 1), compared to 41% (7/17) and 36% (5/14) of species in the intermediate and least attacked classes, respectively (Figure 2.6).

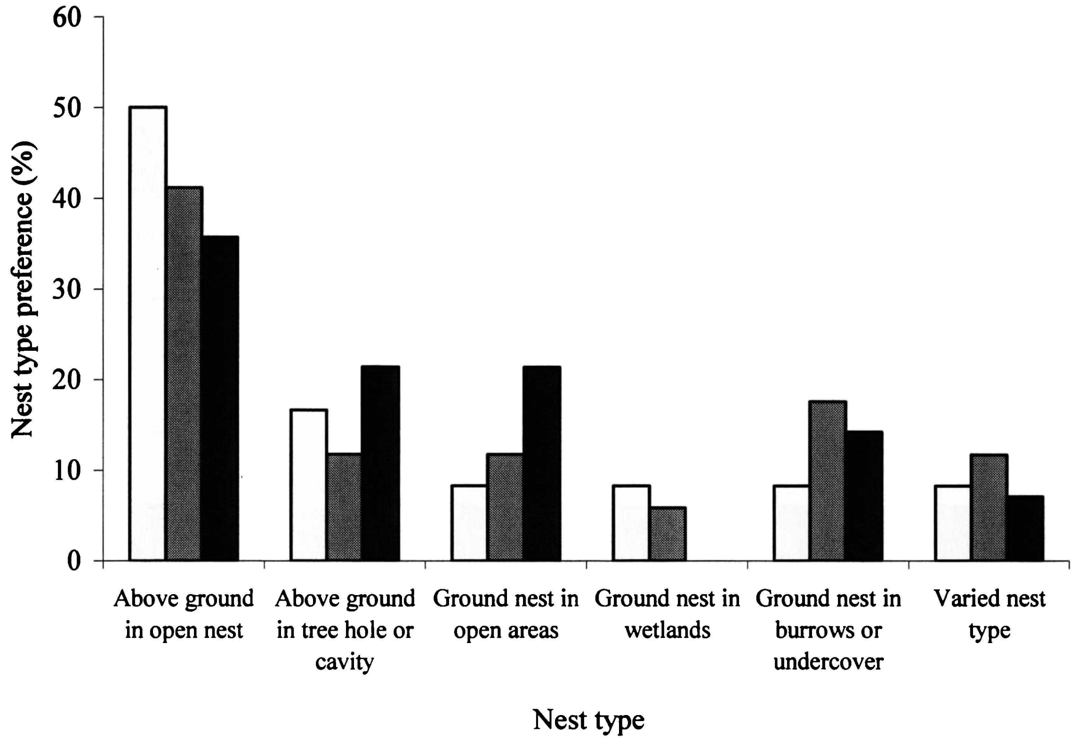

Figure 2.6 The proportion of birds from each attack category that have a specific type of nest (open bars denote species in attack class 1, grey bars denote species in attack class 2, and black bars denote species in attack class 3).

2.4.6 Timing of attacks

Non-contact and non-fatal contact attacks occurred evenly across the year (Figure 2.7). However, reported killings where dates were given (*n* = 12) occurred mainly during the magpie breeding season (July to November; Heather and Robertson 1996; Figure 2.7). Also reported were accounts of eggs or young birds being killed by magpies but no date given (*n* = 11). Although the month of these incidents could not be extrapolated from the available information, it is likely that most of these attacks occurred during the magpie breeding season.

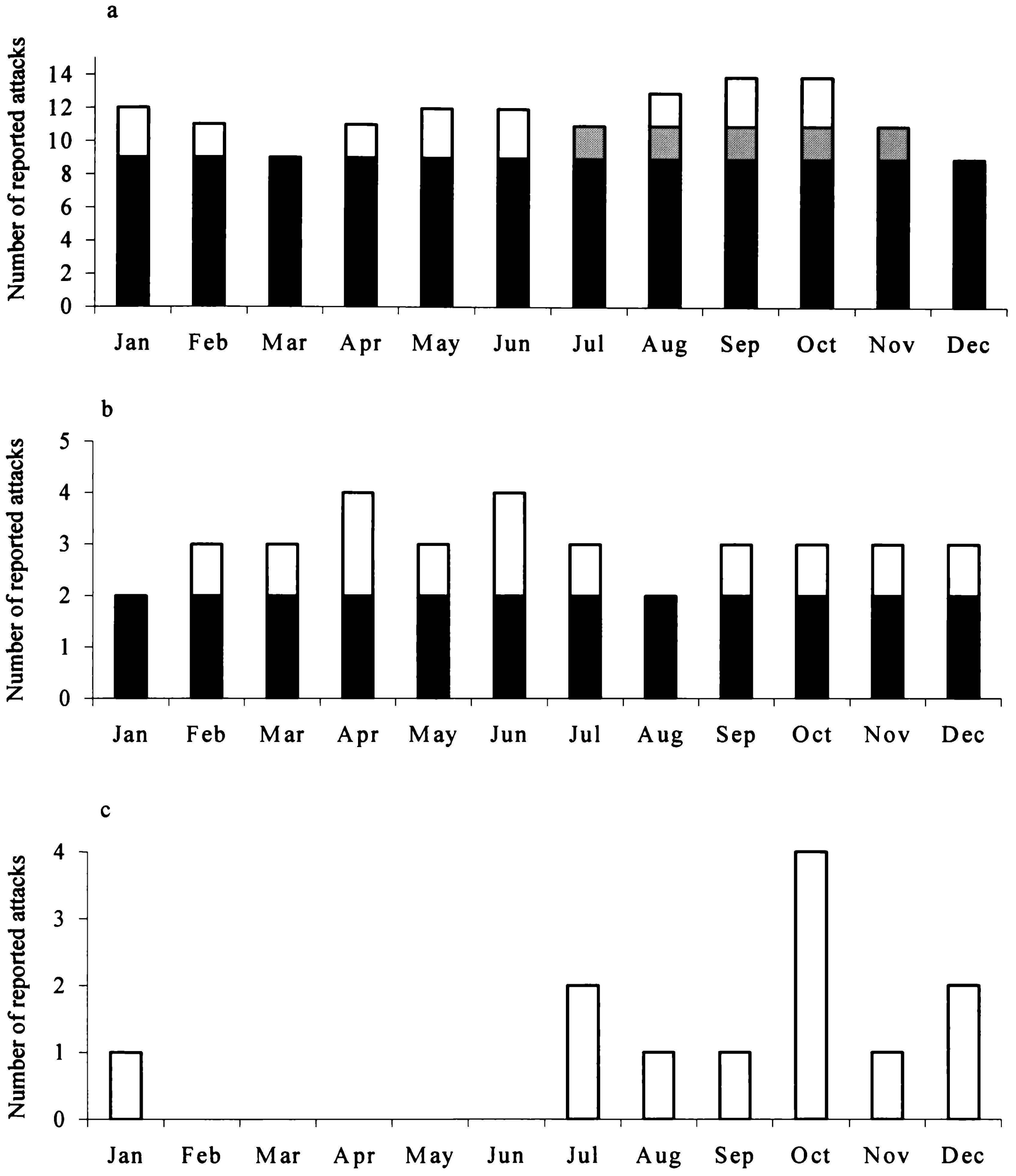

Figure 2.7 Number of (a) non-contact, (b) non-fatal contact, and (c) kill attacks per month for all attacked species (open bars denote attacks when month was known, grey bars denote attacks reported occurring frequently throughout the magpie breeding season, and black bars denote attacks reported as occurring frequently throughout the year).

2.4.7 Consumption of victims by magpies

Magpies were observed preying on eggs on five occasions (8% of kill attacks; Figure 2.8). Only a small proportion of attacks where victims were killed (17%) resulted in consumption of adult or young birds by magpies. Most birds that died as a result of being attacked (75%) were subsequently abandoned by the magpie.

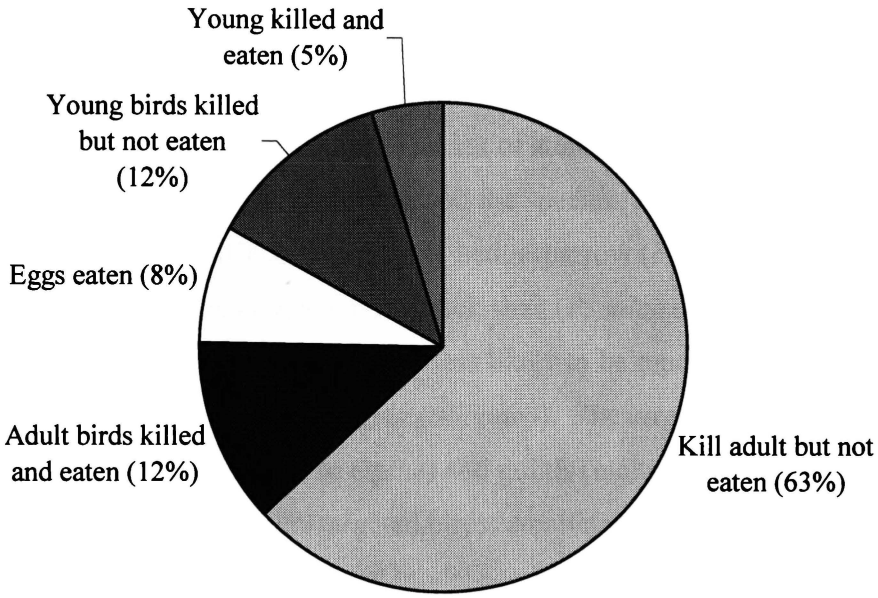

Figure 2.8 Fates of birds killed by magpies (*n*=65).

2.4.8 Place of attack

The majority of attacks (83%) were witnessed in rural areas (when the place was given; *n* = 87) with the rest of the interactions occurring in urban areas (9%), at forest edges or clearings surrounded by bush (7%), and coastal sites (1%).

2.4.9 Non-avian targets

Although not specifically investigated in the current study, we obtained a number of reports from the public and from the literature involving magpies harassing species other than birds, including sheep (*Ovis aries*), dogs (*Canis familiaris*), cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), horses (*Equus* spp.), possums (*Trichosurus vulpecula*), rabbits (*Oryctolagus cuniculus*), humans and inanimate objects such as automobiles and model aeroplanes.

2.5 Discussion

Magpies were reported attacking 45 bird species, although one (harrier) was attacked considerably more often than any other. The list of attacked species is virtually a complete list of New Zealand's rural birds, and the species missing (e.g., redpoll (*Carduelis flammea*), greenfinch (*C. chloris*), hedgesparrow (*Prunella modularis*), little shag (*Phalacrocorax melanoleucos*), little black shag (*P. sulcirostris*) tend to be less known to the general public, and so may be less likely to be reported. Perhaps the only well-known absentee is turkey (*Meleagris gallopavo*). The large range of sizes (7-1700g), preferred habitats (coastal to alpine) and guilds (including aerial insectivores, nectarivores and piscivores) of the targeted birds, combined with the known non-avian targets of magpies (including horses and model aeroplanes), confirm that magpies have a generalised attack regime, at least occasionally attacking many objects that move in the rural landscape.

2.5.1 Limitations of the dataset and analysis

Our collation of published and reported eye-witness accounts of magpie attacks, while describing the span of magpie behaviours, is limited as a database for quantitative exploration because of the unstructured way that observations were obtained.

Possible biases exist in whether an interaction between a bird and a magpie will firstly be observed, and secondly reported. Birds that are highly likely to be observed are probably those that are conspicuous, large, abundant, widespread, or common around farmhouses and other places where observers spend most time. Harriers were reported to be attacked nearly three times as often as the next most reported species (blackbird *Turdus merula* and song thrush *T. philomelos*), perhaps because they are large and conspicuous and would easily be seen from large distances or moving vehicles. Birds more likely to be reported may include easily recognised or highly valued species. People may be more inclined to report attacks on uncommon native birds such as kereru (*Hemiphaga novaeseelandiae*) and tui (*Prosthemadera novaseelandiae*) because they care for these species and hope that their report will trigger some conservation action. Finally, this study cannot determine what proportion of passing birds are attacked by magpies.

These biases can be overcome only by planning more scientifically structured observations in which trained observers undertake prolonged observations at a site where magpies and other species are common and are likely to interact. We undertook such observations for a year (October 2002-October 2003) at a field site in the western Waikato (Chapter 3). We also examined whether only territorial magpies attacked other species, which would suggest that attacks are linked with territorial defence in some way and will report on this research separately.

The largest response to the public surveys we describe here came from the Wairarapa, Wellington, Canterbury, and Otago regions of New Zealand, south of approximately 45° S. It is possible that some birds locally common or abundant north of 45° S (e.g., Indian myna *Acridothesres tristis*, eastern rosella *Platycercus eximius*, turkey; Heather and Robertson, 1996) are under-represented in the results.

2.5.2 Attributes of attacked bird species

Species with similar habitat preferences to magpies (i.e., predominantly rural birds) were reported to be attacked more frequently than birds typical of other habitats. This is unsurprising, because the majority of reported attacks were witnessed in rural habitats (cf. urban, coastal etc.) where magpies themselves are most abundant. Also, magpies would encounter more such birds because those birds are more abundant than others in rural areas. The mean counts of commonly attacked birds (attack classes 1 or 2; ≥ 2 reported attacks) in rural five-minute counts were significantly higher than for rarely attacked species (attack class 3; 1 reported attack). However, within attack classes 1 and 2, there was no evidence that magpies attacked the most abundant species most often (Table 2.1). Of the 12 most-attacked species (attack class 1; ≥ 5 reported attacks), only the house sparrow (*Passer domesticus*) was among the five most abundant species according to Regional Council counts (Table 2.1), while the most counted species (starling *Sturnus vulgaris*) was reported as attacked only four times.

After harriers, the most attacked species were middle-sized omnivores or insectivores e.g., blackbird, song thrush, house sparrow, skylark (*Alauda arvensis*), pipit (*Anthus novaeseelandiae*), kingfisher (*Halcyon sancta*), native frugivores and honeyeaters e.g., kereru, tui, bellbird (*Anthornis melanura*), a large insectivore and piscivore (white-faced heron), and a large omnivore (chicken *Gallus gallus domesticus*). Most of these species (and most attacked species overall) have at least some invertebrate intake at some time of the year, and so may be regarded by magpies as competitors for food. The two most attacked passerines (blackbird and song thrush) eat many pasture invertebrates, as magpies do. Magpies are also opportunistic feeders and will consume many other types of food ranging from carrion, eggs, juvenile and adult birds, mice, lizards, frogs, seeds and grass (Vestjens and Carrick 1974; Moeed 1976; Sanders and Maloney 2002), but usually only to supplement their diet when invertebrates are less abundant (Vestjens and Carrick 1974). Therefore, because magpies do occasionally consume these items nearly all birds in rural areas may be regarded as potential competitors. However, aggression towards such a wide array of species is rare as inter-specific aggression is usually between species with very similar resource requirements (Newton 1998). This is because the costs (energetic and risk of injury) of attacking another species are often very high but the benefit (exclusive use of a resource) is also high and generally results in fitness gains for the victor (Nuechterlein and Storer 1985; Newton 1998). The generalised attack pattern including birds that are not major food competitors would suggest that magpies are not highly focused on the main food competitors. Most targeted species (excluding harriers) pose little threat of injury to magpies. Therefore, any benefit, regardless of the size, would be obtained virtually risk free by the attacking magpie and would incur only an energetic cost.

2.5.3 Magpie chasing versus magpie killing

Most (66%) of the birds in the smallest weight-class (< 60 g) attacked by magpies were killed, whereas the proportion of non-contact attacks reported increased significantly as the weight of the victim increased. If smaller birds died more often due to frailty alone (rather than magpies attacking small birds more fiercely), we would expect to see the proportions of non-contact attacks similar for all weight classes; however, this did not occur (Figure 2.5). There were more reported non-contact attacks on heavier birds, suggesting that magpies perceived larger birds to be riskier to attack.

2.5.4 Beneficial effects of magpies

While magpie aggression has been thought to have detrimental impacts on the abundance and distribution of some birds (e.g., Barrington 1995, 1996b), such aggression may occasionally benefit other birds. For example, some respondents from the survey, and McIlroy (1968), suggested that magpies harassing harriers, a major avian predator (Heather and Robertson 1996), may promote the abundance of some species. Tryjanowski (2001) found that some rural bird species nest closer to raven (*Corvus corax*) roosts because they are known to chase away predators. It is possible that rural birds in New Zealand may gain from associations with magpies as well; the associated cost of occasional attacks by magpies may be out-weighed by the benefits of increased nesting success.

2.5.5 Why magpies attack other birds, mammals, and moving objects

Several non-exclusive hypotheses about why magpies attack birds and other objects can be explored using the results of this analysis:

1. Magpie eggs, chicks or adults are directly threatened by other birds, mammals and objects. This is true only for harriers and falcons, and to a lesser extent for kingfishers and moreporks, and arguably for humans who may shoot magpies. The high rate of magpie attacks on harriers may be substantially due to this threat, since harriers are a major predator at bird nests in rural areas (Chapter 4), making them a direct threat to breeding magpies. However, the vast majority of reported

attacks were against birds that do not threaten magpies, and the attacks occurred year-round, not just when magpies were nesting.

2. Magpies are themselves predators which kill and eat other birds. This is generally untrue. Although magpies occasionally ate small birds, most attacks occurred against birds and mammals which were far too large for them to eat, and two-thirds of adult birds killed by magpies were not eaten; even most young birds that were killed were not eaten (Figure 2.8). Magpies did not even come into contact with the birds they chased in about half of the reported attacks (Table 2.1, Figure 2.5), so predation was an unlikely intention.
3. Magpies are defending their invertebrate food supply or their nest site by driving food or nest site competitors away. This may be true as many attacked species are insectivores or seed-eaters and/or nest in open nests in trees. Also, magpies are opportunistic feeders and consume many other types of food when invertebrates are less abundant making nearly all birds potential competitors, if only in a small capacity.
4. Magpies attack others as a consequence of intra-specific territorial behaviour. Nearly all attacks where the victim was killed were observed during the magpie breeding season (July-November). Australian research has shown that magpies become more aggressive during the breeding season (Jones *et al.* 1980; Jones and Thomas 1999). Increased aggression during the breeding season is linked with hormone changes, especially in testosterone which is usually at its highest just prior to egg laying (Wingfield *et al.* 2001). Testosterone levels in magpies in Australia have been shown to increase from relatively low levels prior to breeding to a peak during the egg-laying period and then a decline during chick-rearing (Schmidt *et al.* 1991). Hormonal changes associated with territory defence against other magpie may explain the increased intensity in attacks during this period (Schmidt *et al.* 1991), but not *why* attacks occurred on other species. Also, magpies were observed attacking (non-contact/non-fatal contact) other birds equally at all times of the year (Figure 2.7). Furthermore, Australian research has shown that magpies with artificially lowered or naturally lower testosterone levels

display similar levels of aggression as those with normal or high concentrations of the hormone (Carrick 1963; Warne 2001).

5. Magpies may chase other birds to signal their "quality" to conspecifics. Inter-specific attacks not intended to kill avian prey may be performed to show mates or potential mates that they are willing to undertake risky behaviour in the future (e.g., warding off predatory species). Therefore, attacks may signal to potential mates that the actor has attributes of a successful breeder; alternatively, conspecific subordinates or neighbours may recognise the actor as a worthy adversary (Arnold 2000). Chasing other birds may also provide the actor with a net energy gain, especially for territorial holders, as the flying time would also double as a signal to neighbouring magpies that the territory is occupied, and the occupants alert.
6. Magpies attack other species because they have evolved in an environment that rewards such behaviour. This may be true as prior to European colonisation of Australia, suitable magpie habitat was limited and a greater proportion of closed woodland and forest existed (Taylor 1997). Therefore, it is likely that magpies evolved in a more competitive environment (both within and across species), and unlike New Zealand, Australia has many native species of predatory hawks, kites, eagles (family: Accipitridae), owls (family: Strigidae), and falcons (family: Falconidae) that prey on birds such as magpies and their eggs and chicks (Hill 1967; Blakers *et al.* 1984). Furthermore, other Artamidae species such as butcherbirds and currawongs, as well as ravens and crows (family: Corvidae) have diet and nesting overlap with magpies and are all noted for being aggressive (Hill 1967; Blakers *et al.* 1984). Clearly, being aggressive would have been an advantage for magpies in an environment with many avian predators and where food and nest sites were limited. In New Zealand where food and nest sites do not appear to be in short supply and there are comparatively few avian predators, being aggressive towards other species may not be as beneficial. Magpies, however, have only been in New Zealand around 120 years and the high rates of aggression may occur simply because they evolved in an Australian environment that rewarded such behaviour.

2.6 Acknowledgements

We thank members of the public who donated observations and the Northland, Auckland, Waikato, Bay of Plenty, Wellington and Southland Regional Councils for providing bird count data. We also thank Harold Henderson (AgResearch, Ruakura) for statistical advice and two anonymous referees for helpful comments on this paper. Figure 2.1 was drafted by Stephen Ferriss (Landcare Research, Lincoln).

Chapter 3: Do territorial and non-breeding Australian magpies influence the local movements of rural birds in New Zealand?*

3.1 Abstract

Australian magpies (*Gymnorhina tibicen*) sometimes attack and kill other birds in New Zealand. Here we assess how Australian magpie influence the local distribution of other birds in New Zealand and identify the members of an Australian magpie population that display the most agonistic acts. We conducted regular observations on six territorial breeding groups and three non-breeding flocks of Australian magpies for a year to determine (1) if other birds avoid flying or foraging close to Australian magpies, (2) the proportion of passing birds that were attacked and (3) which social subunits of the Australian magpie population are most aggressive. In comparison to adjacent magpie-free control areas, significantly fewer birds of a range of species (e.g., blackbird *Turdus merula*, skylark *Alsuda arvensis*, yellowhammer *Emberiza citrinella*) foraged close (i.e., ≤50m) to both territorial breeding groups and non-breeding Australian magpie flocks; fewer birds were also recorded flying near (i.e., ≤50m) territorial breeding groups but not non-breeding flocks. Excluding harriers (*Circus approximans*; see below), only 8% of birds recorded within 50m of territorial breeding groups were observed being attacked. Attacks were most frequent when numerous birds occurred near Australian magpies and species recorded in the highest frequencies were generally attacked most. Territorial breeding groups attacked 39% of passing harriers. All attacks consisted of the victim being swooped or chased; no physical contact was ever observed. Both adult male and female breeding Australian magpies were seen attacking other birds; juveniles in breeding groups sometimes supported adults but never initiated attacks. Australian magpies in non-breeding flocks were not seen attacking other birds, except harriers (attacked in 17% of appearances). Our results suggest that some birds avoid foraging and/or flying close to Australian magpies because they are sometimes chased by breeding

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adults of both sexes; however, the proportion of passing birds actually attacked was small. The numerous published observations of Australian magpie attacks are apparently biased heavily towards sensational events that are rare. Possible reasons why Australian magpies attack other birds are discussed.

3.2 Introduction

As humans have colonised new regions they have accidentally or deliberately released animal and plant species to areas outside of their normal range (Duncan *et al.* 2003). If introduced species become established in a new area, they may have serious impacts on the native flora and fauna. For example, the brushtail possum (*Trichosurus vulpecula*), that was deliberately introduced into New Zealand in the mid-1800's for the harvesting of its fur, has become a pest in that country because it damages indigenous forest ecosystems and is a vector for bovine tuberculosis (Cowan 2001). Other animals accidentally liberated into new areas, such as the brown tree snake (*Biolga irregularis*) in Guam, have gone on to cause the extinction of many native species (Wiles *et al.* 2003).

Introductions of birds to new areas have also been common and worldwide approximately 1400 attempts to introduce over 400 species have been documented (Blackburn and Duncan 2001). Birds are often introduced to either provide food for settlers, create game hunting opportunities, as biocontrol agents to control pest species, or simply to create a landscape with fauna similar to the countries where the colonisers had come (Thomson 1922; Wilson 2004). Introduced birds can compete with other species for resources (e.g., nest sites; Pell and Tidemann 1997) but are usually not as adept in unmodified new habitats as native birds and often have limited impact (Diamond and Veitch 1981). However, introduced birds often do well in highly modified habitats such as cities or farmland, and can become abundant (Day 1995; Innes *et al.* 2004). Some introduced birds also cause significant economic damage to agricultural and horticultural crops (Dawson 1970; Dawson and Bull 1970).

Australian magpies (*Gymnorhina tibicen*; magpie hereafter) are a conspicuous crow-sized bird that were introduced into New Zealand in the 1860's and 70's to control invertebrate pasture pests (Thomson 1922; McIlroy 1968). They prefer habitats with good amounts of short grass with nearby tall trees for nesting (Carrick 1972; Heather and Robertson 1996), making them well suited to rural areas in New Zealand. Consequently, they have spread widely from their original release points and are now abundant in most parts of the country where suitable habitat exists (McCaskill 1945; McIlroy 1968; Bull *et al.* 1985). Public perceptions of magpies in New Zealand are often negative as they are undeniably aggressive and many anecdotal reports of other birds being attacked and even killed exist (e.g., McCaskill 1945; Moon 1956; Porter 1993; Cox and Bauer 1997; Jones 2002). The possibility that magpies are having detrimental impacts on either the abundance or distribution of native birds in New Zealand is of particular concern (e.g., Barrington 1995, 1996b). In Australia, magpies have been shown to actively exclude white-winged choughs (*Corcorax melanorhamphos*; a bird with very similar resource preferences to magpies) from feeding grounds (Cox and Bauer 1997). In New Zealand, there is anecdotal evidence (e.g. Barrington 1996b) that native bird numbers increase after magpie control; however, the impact magpies may have on New Zealand birds has received little scientific study until recently [see below]. Furthermore, a literature review and public survey that collated and summarised cases of magpie attacks on other New Zealand birds reported that 45 different species had been targeted by magpies, nearly a complete list of New Zealand's rural birds (Chapter 2). Over half of these cases involved the target species being seriously injured or killed by the attacking magpie (Chapter 2). Although alarming, the impact magpies have on the abundance and/or distribution of New Zealand birds could not be determined because the review could not confirm how common the attacks really were; that is, instances where magpies seriously or fatally attack other birds may be reported at a much higher rate than less spectacular events.

Published accounts of magpies attacking other birds in scientific studies are rare. In a 2000 hr study of magpie behaviour conducted in New Zealand, only one instance of a magpie killing another bird was reported (Brown and Veltman 1987). Similarly, in a five year study of nest predators of ground nesting birds on braided river terraces in New Zealand, magpies were responsible for only one of 77 lethal events (Sanders and Maloney 2002). Few studies investigating the causes of nest mortality in pastoral areas (where magpies are most common) have been conducted in New Zealand (McLennan and MacMillan 1985), but recently time-lapse video cameras were used to identify predators at 38 nests on farmland; magpies were recorded preying on nest contents only once (Chapter 4).

A large-scale, national magpie control programme (1999-2002; Innes *et al.* 2004) investigated the impact that magpies may have on the abundance and/or distribution of birds in New Zealand (e.g., Barrington 1996b). The project assessed whether reducing magpie numbers on several large (900 ha) blocks of land altered the abundance of other birds. Significant, but 'unspectacular' increases were recorded for several introduced species (blackbird *Turdus merula*, Indian myna *Acridothesres tristis*, skylark *Alauda arvensis*, song thrush *Turdus philomelos* and starling *Sturnus vulgaris*) and one native species (kereru *Hemiphaga novaeseelandiae*) (Innes *et al.* 2004). The small improvements, coupled with the large cost of controlling magpies, lead to the conclusion that additional support for programmes targeting introduced mammalian predators would probably be more beneficial for promoting bird communities (Innes *et al.* 2004). However, the large scale project was not able to measure if magpies influenced bird movements or distributions at a more local scale. For example, anecdotal reports often suggest sharp decreases in bird numbers (especially native birds) when magpies first arrive in a given area, such as trees around a farmhouse (McCaskill 1945; McIlroy 1968; Barrington 1995). Furthermore, the behavioural events responsible for changes in the movements or distribution of birds interacting with magpies have not been documented.

Magpies live in one of two main social units: breeding groups or non-breeding flocks (Carrick 1972). Breeding groups defend territories and can consist of a single male and female, or a group of up to 26 mixed sex birds that may or may not be related (Robinson 1956; Carrick 1972; Hughes and Mather 1991; Baker *et al.* 2000). Non-breeding flocks consist of male and female magpies of all ages and are semi-nomadic (Carrick 1972). In Australia, attacks on humans are conducted by (usually male) magpies from breeding groups (Jones 2002), although it is currently not known if this is also true for attacks on other birds. Hypotheses for such agonistic behaviour could be formulated for both types of social group. For example, birds in breeding groups may exclude avian competitors to monopolise resources such as food and high quality nest sites (Newton 1998), or exclude avian predators such as harriers (*Circus approximans*; Innes *et al.* 1994, Sanders and Maloney 2002) to improve their own or their young's chances of survival. In non-breeding flocks, future breeding mates may be found (Carrick 1972; Jones 2002) and attacking other birds may advertise a willingness to undertake risky behaviour (e.g., chasing away predatory species), signalling that they would be a worthy partner (Arnold 2000). To assess these hypotheses, it would be useful to know if magpies of a given sex, status or social unit were responsible for most attacks.

Our aims were to collect observations of territorial magpie groups and non-breeding flocks over the course of a year in New Zealand to determine (1) the proportion of passing birds that magpies attacked and the context of attacks, (2) whether certain categories of magpies committed more attacks on other birds (e.g., territorial vs. flocking birds, males vs. females) and (3) if birds avoid flying near or foraging close to magpies compared to adjacent magpie-free control areas.

3.3 Methods

3.3.1 Study area

All fieldwork was conducted on the AgResearch Hill Country Farm at Whatawhata, western Waikato, New Zealand (37°50'S, 175°05'E). The agricultural research farm is approximately 840 ha and includes a sheep and beef unit with some agro-forestry. Several small (up to ca. 3 ha) and one large native bush remnant (27 ha) exist on the farm and stands of exotic trees are present, providing suitable nesting habitat for magpies (Carrick 1972; Heather and Robertson 1996). The total rainfall over the year of the study was 1636 mm (average 126 mm.month^{-1}) and the average monthly temperature ranged from 7.5°C in July 2002 to 19.3°C in January 2003 (data were collected from a climate station on the farm).

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3.3.2 Subjects and study design

Observations of magpie and other bird behaviour were conducted from October 2002 to October 2003 from 07:30-17:00 hours on six territorial breeding groups and three non-breeding flocks. The order in which each territory or flock was observed was altered each sampling day. The behaviour of birds was also observed on nine similar blocks of pasture where no magpies occurred, as controls. Observations were not done during excessively windy or wet conditions as birds often take cover in bad weather, making them less conspicuous and harder to count (Ratkowsky and Ratkowsky 1979).

Territorial magpies

All but two of the studied territories (Yoe and Yoe2) were separated by at least one other magpie territory that was not being observed. While there were no magpie territories between Yoe and Yoe2, there was an area ca.150 m wide between boundaries where no magpies occurred. Accordingly, no interaction was ever observed between the two groups. At the beginning of the study, two of the studied territories (Yoe2 and Barkers) were defended by monogamous pairs and one (Airstrip) was defended by an adult male and two adult females. Two groups (Long and Silo) were defended by an adult male, adult female and a sub-adult bird of unknown sex. The sub-adult bird in the Silo group was later found to be a female as it was seen nesting in September 2003. The last territory (Yoe) was defended by one adult male, three adult females and a sub-adult bird of unknown sex. Adult magpies are easily distinguished from sub-adults and juveniles in the field by plumage markings: they have an all black breast and a bill that is mostly white with a dark tip (sub-adults have a dark grey/brown breast and a bill that is mostly dark; Heather and Robertson 1996). Sexes of adult birds are also easily distinguished as males have pure white plumage on the neck and back in contrast to the finely barred grey female plumage (Heather and Robertson 1996). Sub-adult male and female magpies have very similar plumage markings and are difficult to distinguish in the field (Heather and Robertson 1996).

At the completion of the 2002 breeding season (November), Long, and Yoe successfully fledged one chick each and Silo fledged two chicks that remained within these territories for the rest of the study. Yoe2 successfully fledged two chicks of which one remained in the territory while the other was either evicted by the parents or left on its own accord in February 2003. Barkers and Airstrip did not successfully fledge any chicks during the 2002 breeding season. These reproduction rates are similar to other Australian and New Zealand studies where between 0.9-2.9 fledglings per group have been reported (Carrick 1972; Veltman 1989b; Hughes *et al.* 1996).

Before the study began (August and September 2002) subjects were captured and banded with unique colour combinations. Only three of the subjects (one adult and two sub-adults) were not banded, but they were from different groups, thus limiting the possibility of misidentification. Consequently, all birds were easily identified during observations. Fledglings were easily distinguished from other age classes by plumage markings and behaviour (underparts are brownish grey and they are usually close to adults when in the open begging for food; Heather and Robertson 1996). Where groups had more than one chick, at least one was banded so that they could be individually identified during observations.

Birds in each territory were observed once every 14 days weather permitting. Observations lasted 40 minutes and the observer (DM) was positioned 70-200m away, under a camouflage net, behind vegetation, or using a vehicle as a portable hide. Birdlife occurring within 50m of territory holders in view (treatment areas) was recorded using 8x32 field binoculars or a 25x scope mounted on a tripod. Magpies and other birds were observed while in open areas (i.e., on pasture, or in tress adjacent to pasture); therefore, behavioural observations and measures of bird abundance and diversity were not taken from bush remnants within territories as trees obstructed the observer's view. Magpies were usually close together (<20m) while sampling occurred; however if magpies in a group were dispersed more than 100m, recording bird life within 50m of them became difficult. When this occurred, only one cluster of magpies in the breeding group was selected as a focus. If magpies were separated by smaller distances (e.g., 20m) then birds flying within 50m of each magpie were recorded. Therefore, a larger area was often observed during observations on magpies than adjacent magpie-free areas (control areas), which were always a 100m diameter circle (see below); this provided us with a conservative measure of reductions in bird numbers that may be associated with the presence of magpies. Prior to the start and several times during the study, 50m transects were marked out for the observer to calibrate distance estimates.

Birds recorded within treatment and control areas were divided into two categories: (1) flying (hereafter referred to as "Flyovers"), and (2) landing (or hovering in the air) close to magpies for >10sec (hereafter referred to as "Landings"; hovering birds were usually either harriers or welcome swallows *Hirundo tahitica*). All birds recorded in treatment and control areas are listed in Appendix 4.

Observations of magpies and other species on their territory began when at least one of the territory holders was seen. The amount of time that each magpie on the territory was observed during each 40 minute session was recorded. Many sessions (100/135) included blocks of time when no members of the territory were visible, so only rarely was a full 40 minutes of data obtained.

Either immediately before or after observing the bird life on a territory (selected randomly), observations were conducted in the control areas (i.e., similar patches of habitat adjacent to the focal territory [ca. 200-700m away] but free of magpies). This allowed a direct comparison of birdlife abundance and diversity in areas with and without magpies. For observations in control areas, a given point in the habitat was selected and all birds appearing within 50m of it were recorded for 40 minutes as described above; if a magpie came within 150m of the point, observations were stopped and another area free of magpies was selected. If a magpie entered the control area after 30 minutes of sampling had been completed, observations concluded. On occasions subjects in treatment or control areas were disturbed by farm workers; in these instances the observations were stopped and started again five minutes after the farmer had moved away. If the disturbance occurred before 30 minutes of sampling had been completed and the farmer did not move away, observations were either concluded (for treatment observations) or were moved to another area (for control observations). Furthermore, if a farmer disturbed an observation after 30 minutes, observations also concluded.

Non-breeding flocks

It was difficult to determine the exact sizes of the three study flocks because hilly topography prevented all members being viewed at the same time. By walking around the flocks we estimated that the largest flock (2nd Shed) was approximately 110 magpies, with the next largest (Heddon Road) being 65 and the smallest (NIWA) being 40.

There were only three non-breeding flocks located on the study farm. Therefore, they were observed once every 7-14 days (weather permitting) so that a comparable number of observations could be made in relation to breeding groups. The NIWA flock, however, either disbanded or relocated to an unknown area in February 2003 and no further observations were completed on that flock after 7/02/03. Flocks and associated control areas were sampled as described for territorial magpies (all birds recorded in treatment and control areas are listed in Appendix 4). A count of the number of magpies being observed was made at time 0, 10, 20, 30 and 40 minutes to determine the number of birds watched during observations.

3.3.3 Activities sampled

All interactions between magpies (groups or flocks) and other birds were classified into one of four different categories: (1) "Flushes"- magpies startled a bird causing it to suddenly interrupt its activities and fly to a new position (typically when a magpie flew over or landed near perching or foraging birds; no chasing by the magpie was associated with this behaviour); (2) Non-contact "Chases" or "Swoops"- magpies flew at speed toward other birds but did not come into physical contact with them; (3) "Physical Attacks"- magpies chased birds and came into contact with them (but did not kill them); and (4) "Kills" occurred when the attacking magpie was confirmed to have fatally injured the victim.

3.3.4 Analysis

Significant differences (*P*<0.05) in the number of birds counted in territorial and flock treatment areas with respect to control areas were detected using paired t-tests; counts for flyovers and landings were analysed separately.

The birds counted flying or landing in control areas as a percent of the total number of birds counted in combined control and treatment areas was calculated (for each session) by: (ctrl/(ctrl+trt))*100, where ctrl= birds (flying or landing) in control areas per unit time and trt= birds (flying or landing) in treatment areas per unit time. If no birds were counted either flying or landing in both control and treatment areas for a particular session then missing values were added. This criterion was only applied 13 times when no birds landed in control or treatment areas during observations on territorial groups. One-way ANOVA tests where used to determine if these proportions differed significantly between months of the study. If significant differences between proportions in different months were detected, Tukey HSD post-hoc tests were conducted to identify where these were.

Linear regressions were used to determine if species counted most often in treatment areas were also counted most often in control areas.

Four or more birds flying or on the ground together (<4m apart) in treatment or control areas were counted as a single report in the above analyses because we could not assume that group members were independent of each other. Birds may derive survival benefits from copying the behaviour of conspecifics in flocks (avoiding predation through early detection of predators or having 'safety in numbers'; see Jullien and Clobert 2000 for a review).

One-way ANOVA or Mann-Whitney tests (if datasets were non-parametric according to the Levene test after logarithmic transformation) were used to compare bird numbers within 50m of territorial groups during sessions with and without magpie attacks on other species. Linear regressions were used to investigate whether total species occurrence (flyovers and landings combined) in treatment areas was correlated with the frequency at which species was attacked. Birds flying or on the ground in groups of four or more were included in these analyses as they were the actual number of birds that the magpie would have seen and consequently responded to.

3.4 Results

On average, 23 observations of each of the six territorial groups (range 21-26) were made from Oct. 2002 to Oct. 2003 with mean duration 33.8 ±1.2 minutes (we present means ±s.e.m unless otherwise stated). Observations conducted in adjacent control areas lasted an average of 38.6 ±0.7 minutes.

Two of the studied flocks (Heddon Road and 2nd Shed) were observed 40 and 32 times respectively. The NIWA flock was observed 17 times up to February 2003 when the flock disbanded or left the study area. On average, observations of flocks lasted 38.8 ±0.7 minutes and observations in control areas adjacent to flocks lasted 39.4 ±0.3 minutes. Between one and 54 (mean: 10.9 ±0.3) magpies were in view during observations.

3.4.1 Are birds avoiding magpies?

On average, fewer birds were counted either flying or landing (including hovering) close to territorial magpie groups compared with adjacent control areas (Table 3.1). Significantly fewer birds were also counted landing close to non-breeding flock magpies (Table 3.1). However, there was no difference in the number of birds that flew near non-breeding flocks compared with adjacent control areas (Table 3.1).

Avoidance of magpies by other species of birds appeared to be generalised across all species. Species that were counted most often in areas with magpies were also usually most common in adjacent control areas for both territorial groups ($r^2 = 0.86$, $P<0.001$ flyovers; $r^2 = 0.71$, $P<0.001$ landings) and non-breeding flocks ($r^2 = 0.83$, $P<0.001$ flyovers; $r^2 = 0.62$, $P<0.001$ landings).

Birds counted in control areas as a percent of the total number of birds counted in control and treatment areas fluctuated slightly each month but, of all combinations, a significant difference was only detected for birds flying past territorial groups ($F=1.97$, $P<0.05$; Table 3.2). Flyovers in October were less common than in May or July.

3.4.2 Interactions between magpies and other birds

Birds attacked by territorial groups

The number of attacks on birds by magpies in territorial groups and the number of individuals and their location prior to being attacked are listed in Table 3.3. On average, an attack was observed every 1.9hrs. Attacks were seen during all months of the study except March and September.

When attacking species other than harriers, magpies from territorial groups chased the victim relatively short distances (50-100m) without making contact. In all but one attack the target animal evaded the pursuing magpie and flew into trees or out of the magpie's territory; the magpie(s) gave up the pursuit. On the one exception, a spur-winged plover (*Vanellus miles*) did not immediately depart and the magpie swooped it once before landing approximately 8-9 meters from the plover carolling loudly. The magpie remained there for approximately a minute without further vocalisation; it then flew into a tree leaving the plover where it was. During attacks when we did not directly observe the conclusion, the victim probably escaped injury as the magpie usually returned to view immediately. Harriers were repeatedly swooped as soon as they were detected in a territory until they left, although no contact was ever seen. A higher proportion (38.7%) of passing harriers were attacked by territorial magpies compared with other bird species (8.2%).

Most attacks by territorial magpies on birds involved a single individual (27/40), although on seven occasions the attacking magpie attacked two individuals. On two occasions three birds were chased, and on four occasions, four or more individuals were chased.

Table 3.1 Mean occurrence of birds flying and landing within 50m of (1) territorial magpie groups and adjacent control areas, and (2) non-breeding flocks and adjacent control areas. *P* is the probability level for the difference between areas using paired t-tests.

	Number of observations		Treatment areas (birds.hr^{-1})	Control areas (birds.hr^{-1})	s.e diff.	*P*
Territorial groups (n=6)	135	Flyovers	9.1	11.3	1.4	0.01
		Landings	2.6	6.2	1.4	<0.01
Non-breeding flocks (n=3)	89	Flyovers	11.6	11.3	0.6	0.49
		Landings	4.0	8.6	1.4	0.03

Table 3.2 The birds counted flying or landing in control areas as a percent of the total number of birds counted in control and treatment areas for each month; α, for (a) Territorial groups and (b) Non-breeding flocks. * indicates significant differences exist between months (one-way ANOVA, $P<0.05$); Flyovers in October were significantly less common than in May and July (Tukey HSD test, $P<0.05$).

	a. Territorial groups				b. Non-breeding flocks			
	Flyovers *		Landings		Flyovers		Landings	
Month	α (%)	s.e.m	α (%)	s.e.m	α (%)	s.e.m	α (%)	s.e.m
Oct 2002	53.8	4.5	62.7	11.0	49.2	6.6	69.4	7.1
November	51.6	3.4	66.7	7.6	48.7	2.1	71.0	6.9
December	54.1	2.7	73.0	7.1	44.0	3.6	69.0	9.5
Jan 2003	58.7	4.3	74.1	11.5	53.8	5.2	66.9	9.0
February	61.1	8.6	82.5	7.8	52.0	5.7	87.0	6.7
March	65.3	7.2	73.0	12.3	59.8	3.4	71.8	14.3
April	59.7	3.8	64.7	12.9	49.4	4.9	69.8	10.8
May	62.3	4.4	74.1	6.9	50.6	6.8	78.9	5.0
June	57.4	3.4	75.2	8.4	48.6	4.8	79.7	7.0
July	72.7	9.5	68.7	5.8	53.1	9.5	67.2	4.6
August	59.6	5.7	74.8	5.5	43.8	3.5	54.1	8.3
September	61.3	7.2	88.8	6.1	65.9	8.7	73.3	14.5
October	34.1	5.3	68.9	8.4	45.7	6.7	86.0	7.3
Mean	58.2	1.6	73.0	2.4	50.0	1.5	71.5	2.4

The majority of attacks (33/40) were conducted by a single magpie (22 by adult males, nine by adult females and two by sub-adults). Juvenile magpies were only seen attacking other birds when accompanying adults (three occasions). On seven occasions two or more magpies conducted attacks on other birds (six on harriers and one on an Indian myna).

More birds were counted in territorial magpie treatment areas when attacks occurred compared to observations when attacks were not observed (Figure 3.1). On average, 14.8 ±2.3 birds.hr^{-1} were counted flying in treatment areas during observations with attacks, significantly lower than the 8.7 ±0.6 birds.hr^{-1} when attacks were not witnessed ($P< 0.05$; Figure 3.1). During observations when attacks were seen, 8.8 ±2.2 birds.hr^{-1} were counted landing in treatment areas compared with 4.3 ±0.7 birds.hr^{-1} for observations without attacks ($P<0.05$; Figure 3.1).

There was a strong positive correlation between attack frequency and species occurrence, as species attacked the most were usually counted most often in treatment areas too ($r^2=0.48$, $P<0.001$; Figure 3.2a).

Table 3.3 The frequency of attacks by six territorial magpie groups on other species of bird, the number of each species attacked and the location of victims preceding attack. *1*= self introduced or native New Zealand species, *2*= introduced species, *3*= predatory species, *= predominantly introduced finch spp. and house sparrow.

			Location of victim(s) prior to attack				Number of attacks on species by territorial magpie groups					
Species attacked	Number of attacks on species	Number of each species attacked	On ground	Perching	Flying	Not seen	Long	Silo	Barkers	Yoe	Yoe2	Airstrip
harrier *Circus approximans*[1,3]	11	12	0	0	11	0	8	1	1	0	1	0
starling *Sturnus vulgaris*[2]	10	16	6	1	2	1	1	4	1	1	1	2
yellowhammer *Emberiza citrinella*[2]	4	5	2	1	0	1	0	4	0	0	0	0
goldfinch *Carduelis carduelis*[2]	3	10	2	0	0	1	1	1	0	0	0	1
Indian myna *Acridotheres tristis*[2]	3	4	0	1	1	1	0	0	1	0	0	2
greenfinch *Carduelis chloris*[2]	2	15	1	0	1	0	0	0	0	0	0	2
house sparrow *Passer domesticus*[2]	2	4	2	0	0	0	0	0	0	1	0	1
unknown species	2	3	2	0	0	0	1	0	0	1	0	0
kingfisher *Halcyon sancta*[1]	1	1	0	0	0	1	0	0	1	0	0	0
spur-winged plover *Vanellus miles*[1]	1	1	1	0	0	0	0	0	1	0	0	0
mixed flock*	1	30	1	0	0	0	0	0	0	0	0	1

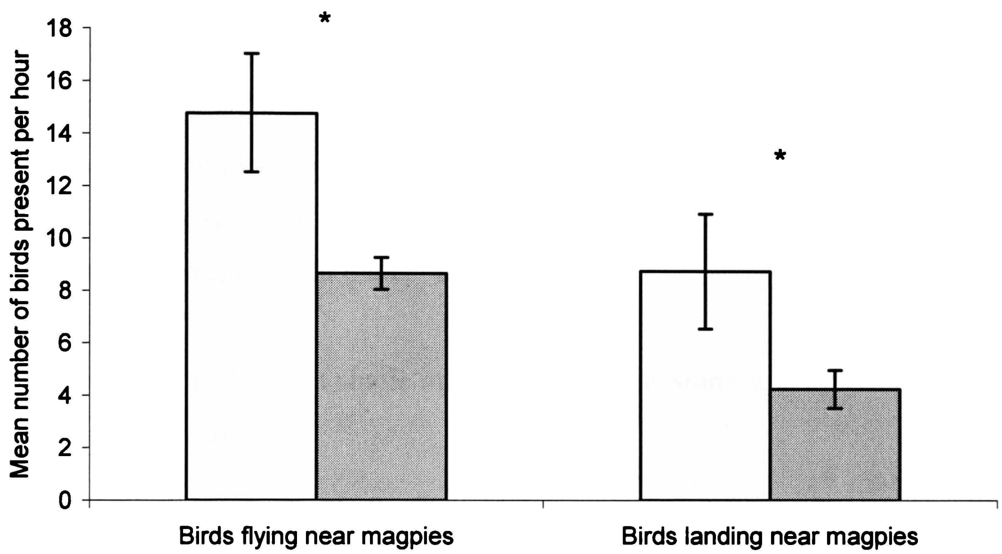

Figure 3.1 Mean number of birds within 50m of territorial magpie groups during observations with (open columns) and without (filled columns) magpie attacks on other species (* indicates significance difference between conditions [Mann-Whitney test; $P<0.05$]; bars are s.e.m).

Birds attacked by non-breeding flocks

We observed eight attacks by non-breeding magpies on other birds, all on harriers (an attack every 7.2 hrs [on 17% of passing harriers]). On each occasion only one harrier was attacked. During attacks the harrier was either chased or swooped by the non-breeding magpies; no contact was ever witnessed.

It was difficult to determine the sex or age class of the attacking magpie during most attacks because usually there were many birds being watched at a time and the attacker was in flight before identification could be made. Furthermore, the attacker would fly out of view after the event. On the one occasion when sex and age class of the attacker could be determined it was an adult male.

Attacks were conducted by a single magpie on five occasions, and by groups of two and four on one occasion each.

Birds flushed by territorial groups

The frequency of birds flushed and the total number of species flushed by territorial group magpies are listed in Table 3.4. A flush was observed every 4.1hr and occurred during all months of the study except December, March and July (range: 0-4 flushes/month).

Flushes (*n*=19) usually occurred in open pasture as a result of a magpie either flying near or landing close to the victim(s) on the ground; most birds would immediately fly away (12 occasions). On other occasions a magpie would fly past or land near bird(s) perched on tree branches; again, birds would immediately take flight (7 occasions). Generally, multiple victim flushes occurred in the open (9/11) while single victim flushes occurred in trees (6/8).

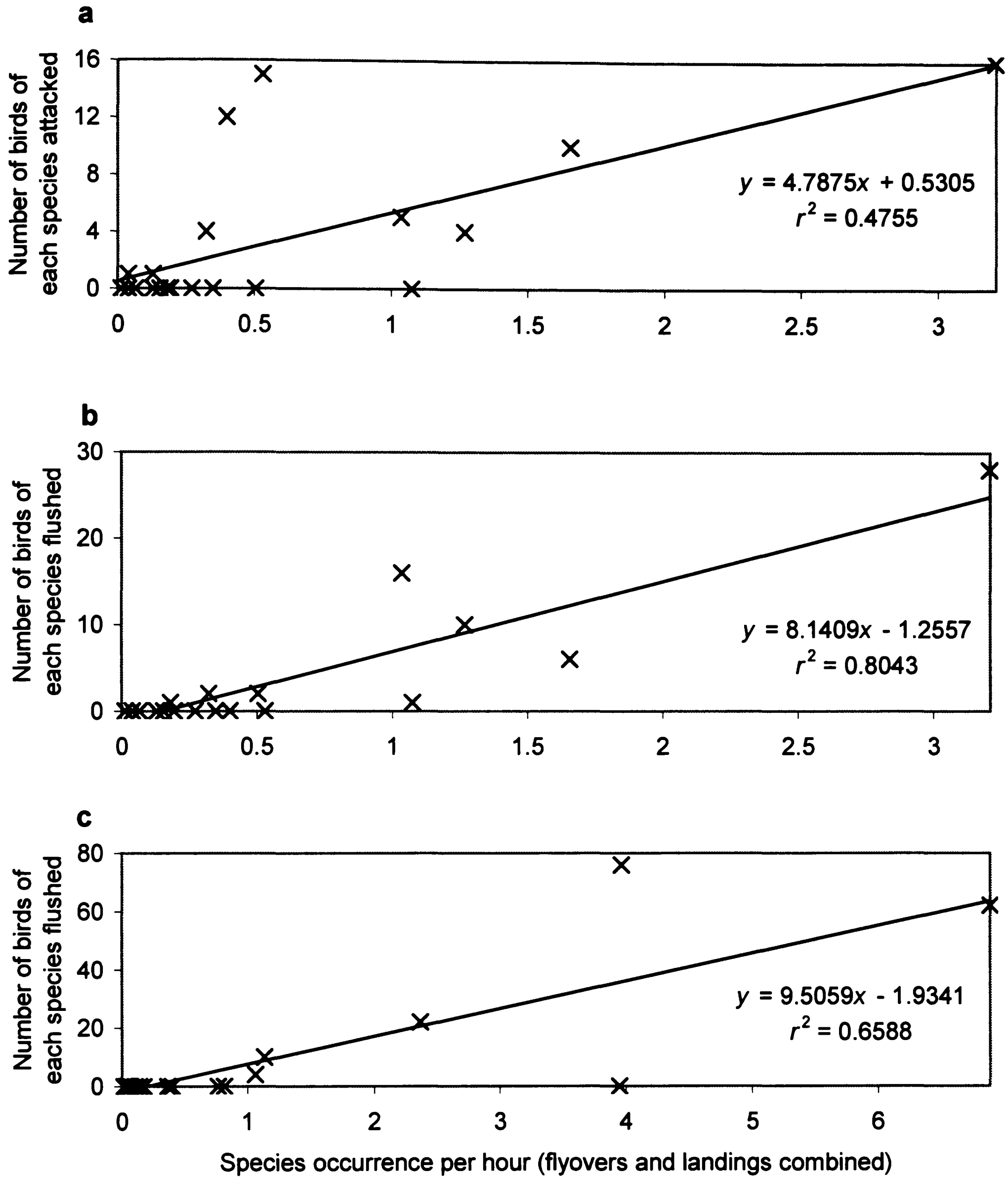

Figure 3.2 The number of individuals of a species (a) attacked, (b) flushed by territorial magpie groups and (c) flushed by non-territorial magpie flocks and their mean occurrence within 50m of these magpies. Each data point denotes a different bird species.

Table 3.4 The frequency of flushes on species and the number of each species flushed by six territorial magpie groups and three non-breeding magpie flocks. *1*= self introduced or native New Zealand species, *2*= introduced species, *= predominantly introduced finch spp. and house sparrow.

	Number of flushes on species			Number of each species flushed		Number of flushes on species by territorial groups						Number of flushes on species by non-breeding flocks		
Species flushed	Territorial groups	Non-breeding flocks	**Total**	Territorial groups	Non-breeding flocks	Long	Silo	Barkers	Yoe	Yoe2	Airstrip	Heddon Road	NIWA	2nd Shed
starling *Sturnus vulgaris*^{2}	6	8	**14**	28	62	1	0	0	0	2	3	1	4	3
goldfinch *Carduelis carduelis*^{2}	2	8	**10**	2	76	1	0	1	0	0	0	8	0	0
yellowhammer *Emberiza citrinella*^{2}	3	2	**5**	16	4	1	2	0	0	0	0	1	0	1
house sparrow *Passer domesticus*^{2}	1	1	**2**	10	10	0	0	0	0	0	1	0	1	0
fantail *Rhipidura fuliginosa*^{1}	2	0	**2**	2	0	0	1	0	0	1	0	0	0	0
mixed flock*	0	2	**2**	0	22	0	0	0	0	0	0	1	0	1
unknown Finch^{2}	2	0	**2**	8	0	0	0	1	1	0	0	0	0	0
kereru *Hemiphaga novaeseelandiae*^{1}	1	0	**1**	1	0	0	0	0	1	0	0	0	0	0
Indian myna *Acridotheres tristis*^{2}	1	0	**1**	2	0	0	0	0	0	0	1	0	0	0
welcome swallow *Hirundo tahitica*^{1}	1	0	**1**	1	0	0	1	0	0	0	0	0	0	0

Flushes involving only one individual were observed on eight occasions; on two occasions two victims were flushed and flushes involving four or more birds were witnessed nine times. On average, flushes involved 3.9 individuals.

Species that were most common in treatment areas were flushed more often than those that were recorded in low numbers ($r^2 = 0.80$, $P<0.001$; Figure 3.2b).

Birds flushed by non-breeding flocks

Table 3.4 lists all species flushed by magpies from non-breeding flocks. These flushes were seen every 2.7 hr and occurred during all months of the study except February, September and October 2003 (range: 0-4 flushes/month).

Most flushes (14/21) involved four or more victims while three individuals were flushed on three occasions and flushes involving one or two victims were each observed twice. On average, 8.3 individuals were involved in each flush.

Flushes occurred almost exclusively as a result of a magpie flying over or landing near the bird(s). Often birds would not depart the area but fly to a new patch of ground further from the magpie. This was seen on six of 21 occasions when the victims did not fly out of sight; however, this may have occurred on several other instances when victims flew out of view but could not be confirmed as the same when the same species returned into view a short time later.

There was a strong positive correlation between species flush rates and their occurrence during observations of non-breeding flocks ($r^2 = 0.66$, $P<0.001$; Figure 3.2c), indicating that the species flushed the most were also present in the highest densities.

On five occasions non-breeding magpies were flushed by harriers, an event never observed in territorial groups. During these events magpies would never remain on the ground, flying away from the approaching harrier either out of view or to a fencepost.

Increased vocal activity by magpies appeared to occur when harriers would be in the area, but this was not quantified.

3.4.3 Interspecific agonistic behaviour from species other than magpies

Of the 29 species seen during the study, spur-winged plovers were the only species other than magpies that were seen attacking other birds (on three occasions), although interspecific agonistic behaviour has been recorded in other species that were present in the study areas (e.g., blackbirds mobbing predators; Heather and Robertson 1996). Spur-winged plovers never came in contact with their targets, which were always harriers.

3.5 Discussion

Fewer birds were recorded landing in areas occupied by territorial groups and non-breeding flocks of magpies compared with adjacent control areas in similar habitat. Also, fewer birds were recorded flying past areas occupied by territorial magpies compared to control areas; however, this trend was not observed for birds flying past non-breeding flocks and their respective control areas. These results indicate that magpies can alter the immediate distribution of other birds in rural areas. Both territorial and non-breeding magpies were seen attacking other birds. However, only territorial magpies were observed attacking birds other than harriers and they do not appear to target specific species. As a result, attacks on species simply correlated with abundance. Only 8% of birds (excluding harriers) recorded in areas occupied by territorial groups were attacked suggesting that magpies are not as aggressive as some literature suggests (e.g., Barrington 1996b).

3.5.1 Why do birds avoid magpies?

Fewer birds were recorded close to magpies, probably because they are occasionally attacked by territorial males and females. Potential avian prey species have been shown to reside and nest in lower densities around predatory birds (Norrdahl and Korpimäki 1998). However, magpies were not seen killing or even making physical contact with their targets in the current study. Furthermore, studies identifying causes of nest failure in New Zealand have rarely (Sanders and Maloney 2002; Chapter 4) or never (Innes *et al.* 1994; Innes *et al.* 1996; Brown 1997) found magpies to prey upon bird nests suggesting that magpies are not serious predators of birds at nests. Despite this, other birds (excluding harriers) nearly always took flight to evade pursuing magpies. Only once was this was not observed, the species being a spur-winged plover, a bird of comparable size and also known for high levels of agonistic behaviour, including attacks on magpies (Le Huquet 1961; Heather and Robertson 1996). Apart from the spur-winged plover and harrier, all other attacked birds were much smaller in body weight (between ca. 8-125g; Heather and Robertson 1996) than magpies (ca. 350g; Heather and Robertson 1996). If these birds had not taken flight to escape attack, they potentially faced a serious threat of being injured by the much larger, stronger magpies, which sometimes do seriously wound or kill other birds (Moon 1956; Porter 1993; Chapter 2).

Most (84%) attacks on birds other than harriers started with the victim being either on the ground or perching. Accordingly, we found that birds appeared to be cautious about landing close to territorial magpies as significantly fewer birds were recorded landing within 50m of them. However, fewer birds were also recorded within 50m of non-breeding flocks even though these magpies were not observed to commit attacks on landing birds (except on harriers) during the study. This may indicate that the rural birds we observed do not distinguish different social units and as a result avoid landing close to all magpies. Even though not attacked by non-breeding magpies, birds observed within 50m of these magpies appeared to be wary as they often left an area or flew farther away when magpies passed over or landed close to them (i.e., they were flushed).

Fewer birds were recorded flying within 50m of territorial magpie groups but not non-breeding flocks. This discrepancy may be due to how conspicuous magpies in different social contexts are to other birds. A New Zealand study found that magpies in non-breeding flocks spent a high proportion of their time foraging and perching (Veltman 1984), behaviours that are not very conspicuous. In addition to foraging and perching, territorial groups also advertise and defend their territorial boundaries against conspecific neighbours (Veltman 1984). These behaviours can be very conspicuous as they involve low flights around territorial perimeters, carolling in prominent perches and fighting other magpies (Brown and Veltman 1987). Birds flying over a hill country farm may be able to detect territorial magpies performing these conspicuous behaviours sooner than non-breeding flocks and change course to avoid them.

3.5.2 Why do magpies attack birds?

Harriers

Attacks by magpies on harriers were most likely a response to a potential predator. Attacks on passing harriers by territorial magpies occurred at a higher rate than attacks on other birds (39% cf. 8%) and this was the only species attacked by non-breeding flocks (17% of passing harriers). For territorial groups, the attack regime for harriers was very different to attacks on other birds as this species was repeatedly swooped until it left the territory, sometimes for periods of more than one minute. Furthermore, harriers were the only species which were observed being attacked by more than one magpie and by juveniles accompanying adults. Attacks on harriers by flocking magpies were generally not as intense with the target being swooped only once or twice during an interaction. Harriers offer a serious threat to the survival of magpies and their offspring as they attack and kill other birds (Potter 1950; Small 1956; Gibb 1970) and are known nest predators (Innes *et al.* 1994; Sanders and Maloney 2002). In addition, flocking magpies were observed being flushed by harriers on five occasions, providing further evidence that magpies perceive this species as a survival threat.

The abundance of prey species has been shown to be lower in areas where avian predators are nesting (Norrdahl and Korpimäki 1998). Furthermore, Tryjanowski (2001) found that some birds nest closer to raven (*Corvus corax*) nests because they regularly chase away predators. Therefore, magpies harassing harriers may have had beneficial effects on other birds during the current study. Unfortunately, our data could not determine the effect magpies chasing harriers had on bird abundance as the distance between treatment and control areas was small (ca. 200-700m); it is possible that birds counted within control areas also benefited from magpie anti-predator behaviour.

Other birds

Protection of a resource, such as food, may explain why territorial magpies chase birds other than harriers away from their territory, although our results could not confirm this. Victims were usually foraging on the ground within a magpie territory prior to being chased and may have been perceived as reducing resources that could have been exploited by the resident territorial magpie. Magpies mainly consume pasture invertebrates supplemented with seeds. However, they can be opportunistic feeders and sometimes consume plant material, other birds (and their eggs), frogs and lizards (Vestjens and Carrick 1974, Veltman and Hickson 1989). Accordingly, most rural birds, including all birds that were seen attacked by magpies in the current study, could potentially compete with magpies for food. Competition for resources often causes agonistic behaviour between species, with the highest rates of aggression being between species with the most resource overlap (Newton 1998). In the current study, most birds had some dietary overlap with magpies but those with the highest rates of overlap are not always attacked the most (Chapter 2). Instead, the species that were counted in the highest numbers close to magpies were usually the most attacked, and attacks were more frequent during observations when more birds were counted. Magpies may consider other birds as potential food competitors but are willing to tolerate them in low frequencies within their territory because the energy obtained from the amount of food removed by birds in low density is less than the energy required to chase them away. However, when the numbers of birds counted close to groups increased, the amount of food being removed from the territory may have exceeded the energy required to conduct an attack.

Most (97%; 28/29) attacks on birds other than harriers resulted in the bird being chased a short distance, and not contacted physically; during most events the magpie lost interest quickly and the victim escaped uninjured. Therefore, predation was probably not the motivation for such attacks.

3.5.3 Are magpies having impacts on the distribution and abundance of birds in rural areas?

Our results indicate that magpies can influence the abundance and distribution of birds in rural areas. These impacts, however, were only measured on a local scale and we could not determine whether overall abundance of birds was affected by magpies on a larger scale. Observations on areas with and without magpies were separated by a relatively small distance (between ca. 200-700m). Therefore, the differences we detected in bird abundances between these two areas show that birds are wary of magpies and will actively avoid them.

The only large scale project designed to measure the impact magpies are having on the abundance of other birds in New Zealand (Innes *et al.* 2004) reported that reducing magpie numbers did increase the abundance of some species. However, the numbers of most other species did not change over the four years of the study (Innes *et al.* 2004). That study did not investigate local scale reports of birds 'disappearing' from areas when a pair of magpies establish a territory there (e.g., McCaskill 1945; McIlroy 1968; Barrington 1995). Results from the current study suggest that the findings from the large scale project and reports of changes on a smaller scale may both be correct as birds appear to avoid magpies but only by a few hundred meters. Such an effect may be too subtle to be detected in large scale magpie removal projects as increases in bird abundance were measured over ca. 900 ha blocks of land.

3.5.4 Is displacement of birds by magpies a problem?

Insectivorous and seed eating birds such as starling, blackbird and house sparrow (*Passer domesticus*) may not incur a large fitness cost when moving a few hundred metres to avoid magpies as suitable foraging and nesting areas are likely to be available at many locations. However, native New Zealand species such as kereru and tui (*Prosthemadera novaeseelandiae*) have more specialised habitat and dietary requirements (Heather and Robertson 1996) that may not be available nearby if displaced by magpies. Accordingly, large distances that may potentially incur a large fitness cost may have to be travelled by these species to find suitable nesting and foraging areas. Further research investigating the movement of both introduced and native birds after displacement is required to determine the impact magpies may have.

3.6 Acknowledgements

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Chapter 4: The relative importance of Australian magpies as nest predators of rural birds in New Zealand*

4.1 Abstract

Australian magpies (*Gymnorhina tibicen*) have been recorded as predators at nests of other birds in New Zealand but their importance as a predator in rural areas, where they are most common, has not been previously quantified. We continuously monitored 38 nests of seven species in rural areas over two successive breeding seasons using time-lapse video recording to determine the proportion that were preyed on by magpies compared to other animals in this ecosystem. Twenty-two lethal events were recorded over the two breeding seasons; magpies were responsible for only one of these. A further eight scavenging events were also recorded; magpies were not responsible for any of these. Harriers (*Circus approximans*), ship rats (*Rattus rattus*), and cats (*Felis catus*) were the main predators and were responsible for 36%, 32% and 23% of lethal events respectively. A pukeko (*Porphyrio porphyrio*) was also recorded preying on nest contents on one occasion. Other known nest predators such as Norway rats (*Rattus norvegicus*), possums (*Trichosurus vulpecula*), hedgehogs (*Erinaceus europaeus*) and ruru (*Ninox novaeseelandiae*) did not appear in any recorded frame although present in the study areas. Our results suggest that magpies are not serious nest predators in rural areas in comparison to ship rats, cats and harriers, and that controlling magpies in rural areas will not significantly improve the nesting success of other birds.

4.2 Introduction

The Australian magpie (*Gymnorhina tibicen*; magpie hereafter) is a conspicuous crow-sized bird introduced into New Zealand in the 1860's and 70's to help control pest invertebrates in pasture (McCaskill 1945; McIlroy 1968). Magpies often attack other birds, and have been accused of limiting the distribution or abundance of some New

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Zealand birds (e.g., Barrington 1995, 1996b). The reasons why they make these attacks on other birds are currently unknown. One hypothesis is that they see them as potential prey. Although there are few reports of magpies attacking and killing other birds or their young in Australia (Kaplan 2004), many exist in New Zealand (e.g., McCaskill 1945; Chapter 2). However, the relative importance of magpies as a nest predator in areas where they are most abundant (i.e., rural ecosystems; Heather and Robertson 1996) is unknown.

Predation on either eggs or chicks is a major cause of nesting failure in birds (Martin 1991; Newton 1993). This is especially true in New Zealand where introduced pest mammals are the most frequent predators of an endemic bird fauna that evolved with avian predators only (Holdaway 1989). Predation is the major cause of current declines of New Zealand forest birds (e.g., McLennan et al. 1996; Brown 1997; Innes *et al.* 1999; Powlesland *et al.* 2000; Moorhouse *et al.* 2003; Innes *et al.* 2004) and of endemic shorebirds (Dowding and Murphy 2001). Key predators of small forest birds in podocarp-broadleaved forests are ship rats (*Rattus rattus*), possums (*Trichosurus vulpecula*) and harriers (*Circus approximans*; Innes *et al.* 1996; Brown 1997; Powlesland *et al.* 2000). In beech (*Nothofagus* spp.) dominated forests, the main predators of birds are stoats (*Mustela erminea*) and (especially after masting) ship rats (Dilks *et al.* 2003; Kelly *et al.* 2005), while shorebirds and their nests are primarily damaged mainly by feral cats (*Felis catus*), stoats, ferrets (*Mustela furo*), hedgehogs (*Erinaceus europaeus*) and rats (*R. norvegicus* and *R. rattus*) (Dowding and Murphy 2001; Sanders and Maloney 2002). All of these predators are present in farmland, but nest predation has rarely been studied in farmland habitats.

On mixed farmland in one region of New Zealand, 40% of eggs and 31% of clutches of monitored greenfinch (*Carduelis chloris*) nests were preyed on, although the predators were not identified (MacMillan 1985).

Determining the impact that a suspected predatory species has requires that all predators in the study area are identified and the proportion of predation events caused by each is determined. It is also important to determine the extent of nest lost due to other causes; for example, Sanders and Maloney reported that flooding accounted for c.4% of nest failures in their study. Establishing the identity of predators by observational techniques alone is difficult due to the length of incubation and chick rearing and the fact that many predators hunt at night. Some early techniques to identify nest predators included: fast acting poisons injected into eggs to kill predators before they move away (McLennan and MacMillan 1985); fitting exclosures around artificial nests that allow access to only predators of a given size (McLennan and MacMillan 1985); placing double-sided tape around nests to collect hair or feathers of nest predators (Suckling 1978); placing footprint tunnels in the path of predators accessing a nest (Moors 1978); and automated still photography (Hussell 1974; Picman 1987; Savidge and Seibert 1988). Each of these techniques can provide useful information, but all have limitations that can bias results. One problem with these techniques is that predator behaviour is potentially altered because nests are artificially modified or decoy nests are used (see Major 1991 for review).

Linking predator species to sign left behind at the nest (e.g., faecal remains, eggshell or bird carcasses) is often possible (e.g., Moors 1975; Brown *et al.* 1996). In many instances, however, no sign is left at the nest; this potentially underestimates the incidence of predation because the total disappearance of nest contents is often classified as an 'unknown cause of egg loss' (e.g., Sagar *et al.* 2000). On other occasions the sitting bird may remove the remaining contents after a predation event, further limiting predator identification from nest sign (Brown *et al.* 1998). Similarities between the behaviour of different predators (e.g., ship rat and possum; Innes *et al.* 1994; Brown *et al.* 1996) may also make identification difficult, and adverse weather conditions can destroy evidence. Furthermore, identifying sign can only place a species at the nest and not determine if it was the predator as several species can visit a nest after a predation event occurs (Innes *et al.* 1994; Brown *et al.* 1998).

Continuous video recording of nests is one method that can conclusively determine the identity of predators and provide information regarding interactions between predators and their prey (Innes *et al.* 1994). The camera can be quickly set up to film the nest, and is connected to a time-lapse video cassette recorder (VCR) unit some distance away ensuring that the nest itself does not have to be visited again throughout the monitoring period (Innes *et al.* 1994). There is also no need to handle the nest at any stage during monitoring, further reducing disturbance to the sitting bird. Infra-red (IR) diodes, that can be triggered to switch on after dark, mean that nests can be illuminated for night recording. However, recording equipment is expensive and labour intensive to maintain in the field, hence achieving large sample sizes is often difficult (Sanders and Maloney 2002).

Magpies have not been reported preying on nest contents in any forest-based study, and were responsible for only one of 77 lethal events on braided river terraces (Sanders and Maloney 2002). These are not preferred magpie habitats in New Zealand (Heather and Robertson 1996). Only McLennan and MacMillan (1985) have attempted to identify nest predators in a rural setting, where magpies are most common in New Zealand (Heather and Robertson 1996). In their study, however, continuous video recording techniques were not used to identify predators. Instead, experimental nests were fitted with wire meshing and predator identity was inferred by excluding larger animals and analysing marks left on tracking papers (McLennan and McMillan 1985). Consequently, the role of magpies or other avian species as nest predators could not be determined by McLennan and McMillan (1985). The aim of the current study was to determine if magpies are serious predators of nesting birds in rural areas by comparing the proportion of nests preyed on by magpies compared with other predators.

4.3 Methods

4.3.1 Study sites and species

Nests were monitored on orchards and farms on the outskirts of Hamilton in the Waikato, New Zealand (37°47'S, 175°20'E) over two successive breeding seasons, 2002 (September 2002-January 2003) and 2003 (September-December 2003). Different locations were used for each season to capture some variation among sites. Data from both seasons were pooled and analysed together. Nests were mainly found within exotic hedgerows, exotic or native trees, and (in 2002) within blueberry bushes. No predator control or magpie trapping was done before or during the study in any area where cameras were placed.

Initially we planned to monitor as many different species of nesting bird in the study sites as possible, as most birds within these areas have been reported as being attacked by magpies (Chapter 2). However, most of the nests recorded in the current study belonged to either blackbirds (*Turdus merula*) or song thrushes (*T. philomelos*) as these species were generally the most abundant and their nests easily found (Table 4.1). Other species whose nests were video monitored included greenfinch, goldfinch (*Carduelis carduelis*), pukeko (*Porphyrio porphyrio*), chaffinch (*Fringilla coelebs*) and mallard duck (*Anas platyrhynchos*) (Table 4.1). Nests of species such as house sparrows (*Passer domesticus*), silvereyes (*Zosterops lateralis*), welcome swallows (*Hirundo tahitica*) and starlings (*Sturnus vulgaris*) were also found; however, they were in locations where it was either impractical or unsafe to place a camera. Nests of other species seen within the study areas such as yellowhammers (*Emberiza citrinella*) and kingfishers were never found.

4.3.2 Recording protocols

Monitoring was done using small (65x65x120mm; 430g) black and white, fixed-focus, weatherproof cameras (Jaycar AVC 307R) with infra-red diodes for night illumination. Cameras were mounted onto the end of 30cm 'F'-clamps that were fastened to branches, tree trunks or fence posts to film nests. Cameras were usually set up 1-2m away from nests, unless vegetation obscured the camera shot, in which case closer distances (i.e., 0.4-1.0m) were used. Branches or leaves were occasionally trimmed to improve the field of vision when cameras were placed. Camera units and clamps were also spray painted in camouflage colours to reduce conspicuousness. Cameras were connected by a 20-50m cable to time-lapse VCRs (Gyyr 1800-X1; Panasonic AG-1070DC, AG-6730, AG-TL550; Sanyo TLS-1600P) placed 15-45m from nests on the ground in a weatherproof housing. VCR units were set to record on either 24 or 48-hour time-lapse mode, although 72 and 96-hour modes were trialled during 2002 so that battery and tape changes could be done on every third or fourth day. Because 72 and 96-hour recording modes resulted in fewer frames per second, predator identification became more difficult during analysis and these slower speeds were not continued. Either 24 or 48-hour time-lapse mode permitted easy identification of predators in most instances. Cameras and VCR units were powered by multiple 36Ah or 63Ah dry cell rechargeable batteries connected in parallel; batteries were changed every 24 or 48 hours along with VHS tapes, depending on the recording mode being used.

Nests were found by searching hedgerows and trees or by observing the behaviour of breeding birds from a distance. Once found, cameras were set up on nests as quickly as possible to minimise disturbance (always <10 min). Nests were usually not disturbed again until an outcome had been achieved, as camera performance could be checked by viewing a portable monitor connected to the VCR. After video monitoring had commenced, nests were disturbed only if the camera had moved between battery and tape changes and had to be aimed at the nest again, or a malfunction required the camera to be replaced.

After a final nest outcome had been observed, the recording unit was dismantled and moved to the next closest nest to start monitoring. If the observer was aware of the location of a nest held by species other than blackbirds or song thrushes, then that would usually be selected next even if not the closest. This was done because we wanted to monitor as many other species as possible.

There were 1-4 recording units monitoring nests at any one time during 2002 and 1-3 during 2003.

4.3.3 Video analysis

A nest was classified as 'active' if the sitting bird was seen at the nest after recording had commenced. If a nest had been deserted [see below] or was empty after the contents had been destroyed or chicks had fledged, then it was classified as 'inactive'. Occasionally a predator removed only a proportion of the nest contents, leaving the rest viable. If this happened and the adult bird holder continued to sit or brood, then the nest remained 'active'.

A visit by an animal other than the holders of a nest was classed as either (1) a lethal event: where death of eggs or chicks was caused by the visitor, (2) a non-lethal event: where the appearance of any animal in a recorded frame of footage at a nest did not result in a lethal event, or (3) a scavenging event: where subsequent visits were made to an inactive nest by the visitor to inspect, consume or remove eggshell or chick remains. A nest abandoned for an unknown reason was classified as 'deserted', and subsequently became inactive. Therefore, removal of deserted nest contents by predators was considered scavenging events.

Often predators would leave the camera field of view during an event, only to return a short time later. However, visits to a nest by the same species of predator spaced >30 minutes apart were classed as separate events, as it could not be assumed that they were made by the same individual (Sanders and Maloney 2002). If the predator was a cat, however, repeat visits to a nest were classed as the same event if pelage markings indicated it was probably the same individual cat, even if the visits were spaced >30 minutes apart. This standard was used only twice, as most cats did not go out of view or visited nests only once during lethal events. Video footage was initially viewed in fast-forward mode through section of tape without any of the above events; when significant movement became apparent, the recording was viewed in real time or slowed down further to determine details (e.g., identifying a predator or behavioural interactions).

4.3.4 Predator surveys

Rodents

A tracking tunnel survey was conducted at the end of each breeding season (March 2003 for 2002 season; November 2003 for 2003 season) to determine if rats and mice (*Mus musculus*) were present in the study areas. We used a modified tracking tunnel protocol developed by Gillies and Williams (2001, unpubl. DOC report). The placement and direction of lines could not be randomised in the current study as tunnels placed on open paddocks would have got in the way of stock or farmers. Instead, tracking tunnel lines were set along existing hedgerows or fence lines. Furthermore, if the end of the hedgerow or fence line was reached before all tunnels had been placed in a line, then an adjacent hedgerow or fence line would be followed until all tunnels were out. Seven and six tracking tunnel lines (10 tunnels/line; spaced 50m apart) were used during 2002 and 2003 respectively. Tunnels were placed in the field at least two weeks before the survey was done to get target animals acclimatised to them (Gillies and Williams 2001, unpubl. DOC report). Tunnels were baited with approximately one teaspoon of peanut butter at either entrance. Tracking papers were collected one night after the tunnels were set, and species (to genus level) that tracked through tunnels were identified from their footprints. The mean percent of tunnels tracked by rodents per line was calculated (see Gillies and Williams 2001, unpubl. DOC report).

Trapping for rats using standard rat snap and Fenn traps (totalling 220 trap nights) was conducted at the completion of the 2002 breeding season (in April 2003) to determine whether the rats recorded in the rodent index were ship or Norway rats. Footprints of these species can be very similar, so identification of rats from tracking tunnel indices can only be made to the genus level (Ratz 1997).

Mustelids

A tracking tunnel survey was also conducted at the end of each breeding season (March 2003 for 2002 season; November 2003 for 2003 season) to confirm the presence of mustelids in the study areas. The protocol was developed by Gillies and Williams (2001, unpubl. DOC report) and modified as described above. The same lines were used as in the rodent surveys, except that only every second tunnel was set (Gillies and Williams 2001, unpubl. DOC report). Tunnels were baited with approximately 5g of fresh rabbit meat placed in the middle of the tunnel. Tracking papers were collected after three nights of tunnels being set, and abundance indices were calculated (see Gillies and Williams 2001, unpubl. DOC report).

Possum indexing was not done at any stage in the study areas, but their presence was assumed from sightings and as no possum control had been conducted in the areas. Some other known or suspected predators such as cats, and harriers were regularly seen by observers during battery and tape changes, although no indices of abundance were calculated. While exact indices of magpie abundance were not taken, at least 12 territorial groups were identified in or around the study sites in 2002 and five in 2003. Additional magpies from non-breeding flocks may have also visited study sites; this type of magpie is semi-nomadic and may move around the landscape (Carrick 1972).

4.4 Results

4.4.1 Nest outcomes

Thirty-eight nests were monitored during the 2002 (20 nests) and 2003 (18 nests) breeding seasons. Cameras were usually set up to film nests during the egg stage (30 nests) but occasionally monitoring started after hatching (8 nests). On average, nests were monitored for 12.1 (± 1.4 s.e.m) days before an outcome was observed.

Of the 38 nests, nine (24%) successfully fledged one or more chicks while not being subject to any lethal events (Table 4.1). In 18 nests (47%), all contents were removed by predators (Table 4.1). Five nests (13%) were deserted for unknown reasons; one of these nests may have been deserted because one of its three eggs was removed by a predator two days previously (Table 4.1). Farm workers clearing branches from a hedgerow where another nest was being monitored may have also caused the holder to desert its clutch. Equipment malfunctions (five occasions) or lethal events completed too quickly for the predator to be identified (one occasion) meant that the final fate of six nests (16%) were unknown (Table 4.1). Five additional nests that were abandoned on the day monitoring started were assumed to have been disturbed by the camera setup and were dropped from the analysis.

Table 4.1 Final outcomes of 38 monitored rural bird nests, 2002-2003.

Nest outcome	blackbird	thrush	goldfinch	greenfinch	chaffinch	pukeko	mallard	Total (%)
Egg predation	4	3	0	0	0	0	1	8 (21)
Chick predation	3	5	1	1	0	0	0	10 (26)
Fledged with no lethal events	5	3	0	0	1	0	0	9 (24)
Deserted	2	2	1	0	0	0	0	5 (13)
Missed/unknown events[†]	2	3	0	0	0	1	0	6 (16)
Nests monitored of each species	16	16	2	1	1	1	1	38

[†] events missed because of equipment malfunction, or the predator could not be identified from footage.

On four of the five occasions when the recording equipment malfunctioned, a lethal event was almost certainly missed; an empty nest was present when the tape and battery change took place, but the last recorded frames of the recorded video footage showed that nests were still active. In the fifth case, we were not sure whether to record a lethal event or not, since the eggs in a pukeko nest may have hatched when the cameras were not operating. Pukeko chicks are precocial and they could have left the nest before the batteries and tapes were changed.

On the only occasion when the lethal event happened too quickly for the predator to be identified, we suspected that an avian species was probably responsible because the victim (a 14 day old song thrush chick) was removed from the nest during daylight hours and between two recorded frames of video footage (i.e., in <0.4s). A harrier was the likely predator in this event, because mammals would have been recorded climbing to the nest, and other birds such as magpies or pukekos almost certainly could not remove a large chick of this age so quickly. Furthermore, during other lethal events caused by harriers that were caught on tape, a similar sequence of events was recorded (i.e., quick removal of contents, and a short time at nest; see below).

4.4.2 Who were the predators?

Video monitoring identified five species as nest predators: harrier, ship rat, cat, magpie and pukeko (Figure 4.1), and they were responsible for 36%, 32%, 23%, 4.5% and 4.5% of 22 lethal events, respectively (Table 4.2). The magpie was identified as an adult female from bill and plumage markings. Norway rats, possums, hedgehogs and ruru (*Ninox novaeseelandiae*) did not appear in any recorded frame, although known to be in the study areas.

Table 4.2 Lethal, non-lethal and scavenging events recorded at rural bird nests, 2002-2003.

Species	Non-lethal event	Scavenge event	Lethal event		
			Egg	Chick	Total (%)
magpie	0	0	1	0	1 (4.5)
harrier hawk	0	3	2	6	8 (36.4)
ship rat	2	5	5	2	7 (31.8)
cat	0	0	1	4	5 (22.7)
pukeko	0	0	0	1	1 (4.5)
mouse	1	0	0	0	0
blackbird	1	0	0	0	0
Total	4	8	9	13	22

Figure 4.1 Images of predators filmed preying on rural bird nests: (a) magpie, (b) ship rat, (c) harrier, (d) cat, (e) pukeko.

Techniques used by predators to locate nests could not be determined, as cameras were usually setup too close to the nest to see their approach. However, on one occasion a camera was setup some distance from the nest, a cat was recorded walking past the nest, seemingly unaware of its presence until the sitting bird was flushed and flew away. The cat appeared to be momentarily startled but then investigated the nest, removed the contents (three eggs), and consumed them on the ground.

Predation of adult birds was never observed during the present study. On one occasion, adult blackbird feathers were found in and around a blackbird nest containing one chick, suggesting that it had been attacked while brooding. Unfortunately, due to the equipment malfunctioning, we were unable to determine what happened. The large chick being raised in the nest, however, was seemingly uninjured during this incident and successfully fledged two days later.

Ship rats always consumed nest contents at the nest, whether the contents were eggs or chicks. Harriers consumed eggs at the nest but removed chicks, while cats always removed both eggs and chicks from nests. Both the magpie and pukeko removed their prey from the nest.

Only six nests were visited on more than one occasion by potentially different individual predators (i.e. when visits were separated by >30 minutes; Table 4.3). Two other nests were visited by cats >30 minutes apart, but, unique pelage markings allowed identification of the same cat both times and the two visits were consequently classified as the same event. The apparent reason for repeat visits was to remove or consume remaining eggs or chicks, although subsequent visits were made to empty nests on three occasions and accordingly classified as non-lethal events (Table 4.3). Ten nests were visited more than once, but the duration between visits was <30 minutes and the visitor was always the same species; therefore, we assumed that on these occasions the same individual was recorded. Evidence to support this appeared on two separate video clips when the predators (a harrier and a cat) were recorded removing some of the contents, moving to the ground at a distance that would normally be out of camera shot to eat, and then returning to the nest a short time later.

Table 4.3 Monitored nests visited more than once (>30min apart) by predators or potential predators.

Nest holder	Stage of nest at first visit		Visitor	Visit outcome	Date and time
goldfinch	Inactive	Visit 1:	ship rat	Scavenge event	18 Dec 2059hr
	(deserted: 1 dead chick in nest)	Visit 2:	ship rat	Non-lethal event (empty nest)	19 Dec 0022hr
thrush	Active	Visit 1:	ship rat	Lethal event	30 Nov 0109hr
	(chicks)	Visit 2:	ship rat	Scavenge event	30 Nov 0253hr
		Visit 3:	ship rat	Scavenge event	30 Nov 0406hr
thrush	Active	Visit 1:	ship rat	Lethal event	17 Oct 2133hr
	(eggs)	Visit 2:	ship rat	Scavenge event	17 Oct 2351hr
mallard	Active	Visit 1:	ship rat	Lethal event	10 Sept 2307hr
	(eggs)	Visit 2:	ship rat	Scavenge event	11 Sept 0036hr
		Visit 3:	harrier	Scavenge event	11 Sept 0852hr
		Visit 4:	harrier	Scavenge event	11 Sept 1118hr
		Visit 5:	harrier	Scavenge event	13 Sept 1755hr
thrush	Active	Visit 1:	harrier	Lethal event	18 Sept 1203hr
	(chicks)	Visit 2:	harrier	Lethal event	18 Sept 1353hr
blackbird	Inactive	Visit 1:	ship rat	Non-lethal event	15 Oct 0155hr
	(chicks fledged)	Visit 2:	mouse	Non-lethal event	15 Oct 1203hr

Nests were usually left intact by predators after a lethal event with only minor disruption to the nest lining, although a cat and harriers destroyed nests on one and two occasions respectively.

Total time spent at the nest by predators varied greatly depending on species and nest content. Generally, rats consumed prey in the nest and, therefore, spent the most time at the nest during predation events (Table 4.4). Harriers and cats, which usually removed prey items, spent much less time at nests; however, harriers preying on eggs were present longer because the contents were consumed at the nest (Table 4.4). The lethal events caused by magpie and pukeko both resulted in nest contents being removed, and accordingly the time spent at nests by these species was small (Table 4.4). During all but one lethal event captured on tape, only one predator was recorded at the nest. The only exception was an occasion on which two ship rats were recorded together preying on blackbird eggs in the same nest.

Table 4.4 Time (minutes) spent at nests containing either eggs or chicks during lethal events by predators.

Predator	Egg stage			Chick stage		
	Mean	s.e.m.	*n*	Mean	s.e.m.	*n*
ship rat	27.2	10.0	4[†]	5.4	1.2	2
harrier	3.5	1.5	2	0.5	0.3	6
cat	0.1	n/a	1	1.7	1.5	4
magpie	0.2	n/a	1	-	-	-
pukeko	-	-	-	0.4	n/a	1

[†] duration of one lethal event not available

Predation events were recorded at all times of the day, although ship rats always hunted at night (7/7), while harriers (8/8), magpie (1/1), and pukeko (1/1) hunted during the day. Cats were recorded preying on nest contents both during the day (2/5) and at night (3/5).

Predator species responsible for more than one lethal event were recorded taking both eggs and chicks (Table 4.5). Species responsible for only one lethal event, i.e., magpie and pukeko, preyed on eggs and chicks respectively (Table 4.5).

Table 4.5 The frequency of lethal events recorded at different nest types in rural areas, 2002-2003.

Nest type	Nest stage at event	Predator species				
		magpie	ship rat	harrier	cat	pukeko
blackbird	eggs		1	2	1	
	chicks			1	2	1
thrush	eggs	1	3			
	chicks		2	3	2	
goldfinch	eggs					
	chicks			1		
greenfinch	eggs					
	chicks			1		
mallard	eggs		1			
	chicks					

Four non-lethal events were also recorded (Table 4.2). Most non-lethal events (3/4) were recorded at nests that were empty (i.e., inactive) at the time of the visit because chicks had recently fledged or the contents of the nest had previously been removed by a predator. During these visits the animals (a mouse on one occasion and ship rats on the other two) were in the nest a short time (mouse =4.1 min; ship rats =2.7 and 2.6 min). On the only occasion when a non-lethal visit to an active nest was recorded, a male blackbird was observed at a song thrush nest containing three chicks. The blackbird appeared to investigate the contents of the nest, and contact between its beak and a chick was recorded; however, the chicks did not appear to be injured, and they eventually fledged. The blackbird was at the nest for 39 seconds, and its arrival caused the sitting thrush to leave the nest; the thrush returned 2.5 minutes after the blackbird left.

4.4.3 Bird behaviour

Sitting birds were seen defending their nests on only two occasions. During both events, ship rats approaching at song thrush nests appeared to be pecked by the sitting birds several times. This did not, however, deter the rats and the sitting bird eventually flew from the nest leaving the contents to be preyed on. During one of these events the ship rat appeared to lunge at the bird, and both went out of camera field of view, but the rat returned 17 minutes later to eat the nest contents. The fate of this bird could not be determined, although a thrush was recorded at the nest 160 minutes after the event removing eggshell, and was assumed to be the same individual that had been previously seen.

Eighteen nests failed as a result of predator activity (Table 4.1), and of these nests the presumed sitting bird was recorded returning on all but two occasions. When eggshell or uneaten chick remains were left in the nest after a lethal event (eight occasions), they were always removed by the returning bird.

4.4.4 Potential predators in study areas

Mice were present at 32% and 20% of tunnels in 2002 and 2003 respectively, and rats at 18% and 10% respectively. Kill trapping (220 trap nights) at the completion of 2002 showed that both Norway and ship rats were present in the study areas; 75% (6/8) of trapped rats were Norway rats. Hedgehog prints were recorded at low rates (3%) during the rodent tracking tunnel survey in 2002 and not at all in 2003. In addition, six hedgehogs were caught during rat trapping in 2002. At the end of the second breeding season, kill traps were not used to identify rat species although the presence of both was established by other means. Norway rats were seen in the study area by farmers, and ship rats were videoed at nests. Possums were seen and heard in the study areas during both breeding seasons, although no indices to establish their density were taken. Harriers and magpies were seen during nearly all visits to study areas in both breeding seasons. Cats were also regularly seen during both breeding seasons. Mustelids were not recorded during mustelid tracking tunnel surveys conducted in either 2002 or 2003. The presence of ruru was not recorded by us in either year although they are known to reside around the study areas.

4.5 Discussion

4.5.1 Are magpies serious predators?

Although many anecdotal reports exist of magpies robbing the nests of other birds in New Zealand (e.g., Chapter 2), up until now the importance of magpies as rural nest predators has not been determined by systematic observation. Magpies were common in the study areas during both breeding seasons and they were seen during almost all visits to sites by observers. Several groups of magpies were known to hold territories in and around the study areas in both breeding seasons, and they were seen during almost all visits to sites by observers. Yet, magpies were responsible for only one of 22 lethal events, and no scavenging events. Although we present a relatively small sample size, if magpies were a serious predator of nests in rural areas we would have expected to see more than one lethal event caused by them.

Our results are consistent with other nest predator identification studies in New Zealand that report low or no lethal events caused by magpies (Brown 1997; Innes *et al.* 1999; Sanders and Maloney 2002). These studies, however, have not been conducted in rural areas, where magpies are most common (Heather and Robertson 1996). It is, therefore, possible that the low reported incidents of nest predation attributed to magpies in other studies may be due to their comparatively low density in these ecosystems in relation to the other predators. In the only other published study of nest predators in rural areas in New Zealand, McLennan and MacMillan (1985) included magpies in a list of suspected predators that were present in their study areas but failed to assess their true importance as large birds, such as magpies, were excluded from experimental nests.

4.5.2 Predators in rural versus other areas

Studies during which authors have been able to identify nest predators have largely been conducted in native forest blocks (James and Clout 1996; Brown 1997; Innes *et al.* 1999; Innes *et al.* 2004; Kelly *et al.* 2005; I. Flux, DOC, unpubl. data; R. Powlesland, DOC, unpubl. data) or braided rivers (Sanders and Maloney 2002). Hedgehogs were found to be important predators of some ground nesting birds (Sanders and Maloney 2002) and although they were present in our study sites, we concentrated on monitoring above-ground nesting sites that would have been difficult for hedgehogs to reach. Damage to recording equipment by farm stock meant that cameras were set up on only one nest at ground level, and this was preyed on by a ship rat and then scavenged by a ship rat followed by harriers (Table 4.3). Therefore, our data could not rule out hedgehogs as being important predators of ground nesting birds in rural areas. In beech-dominated forests, when stoats are in high densities, they are an important nest predator of hole-nesting birds (O'Donnell 1996a) and of kiwi (*Apteryx* spp; McLennan *et al.* 1996). In our study, we detected no evidence of the presence of stoats, and they were not recorded preying on nest contents, although mustelids have been linked to nest predation by sign left at the nest in another rural-based study (McLennan and MacMillan 1985).

4.5.3 Predators at rural nests

Harriers, ship rats and cats were the main predators of nesting birds in the rural areas of the Waikato near Hamilton. In contrast to Sanders and Maloney (2002) who found that harriers were responsible for only one of 77 predation events at nests in braided river systems where they were very common. Other researchers have concluded that harriers are important predators at nests of kokako (*Callaeas cinerea wilsoni*) and tui (*Prosthemadera novaeseelandiae*) (Innes *et al.* 1999; J. Innes, Landcare Research, unpubl. data). Our data indicate that harriers are important predators of birds in rural areas, as both eggs and chicks were regularly taken. The reason(s) for the difference in the relative importance of harriers as nest predators between studies is unclear, but one explanation may be associated with the availability of other prey, especially rabbits (*Oryctolagus cuniculis*), in each ecosystem.

Ship rats are major predators of birds in forested areas, and reducing their numbers has been shown to significantly improve the breeding success of tree nesting birds (e.g., Innes *et al.* 1999). They have also been linked to the local extinction or decline of other native New Zealand birds (O'Donnell 1996a; Dilks *et al.* 2003). McLennan and MacMillan (1985) determined that ship rats were responsible for predation events at experimental nests in rural areas. Ship rats are abundant in forests and urban parks throughout New Zealand; they are strong climbers and live in trees (Innes 1990). Rat tracking indices measured in this study during both seasons were low (18% and 10% respectively), and 75% of the total records were probably Norway rats (judging by the snap-trapping at the end of 2002). However, we found that 32% of known lethal events were caused by ship rats, targeting both eggs and chicks, indicating that they are a serious predator in rural areas, even if not abundant.

Cats were responsible for 23% of lethal events at nests, and they preyed on both eggs and chicks. Cats are regarded as important predators in forested, island, and braided river habitats (Veitch 2001; Sanders and Maloney 2002), although their importance in rural areas was unknown. Cats are difficult to control, as they are extremely mobile and can have large home ranges, meaning that they can potentially reach many breeding birds even when cats live in low densities (Moller and Alterio 1999). Furthermore, birds are often caught by domesticated cats (Gillies and Clout 2003) and cats are regarded as important nest predators in areas populated by people as they can have similar hunting qualities and diets as feral cats (Fitzgerald 1990; Catt 1996). Several farmhouses were situated in and around the study sites in both breeding seasons, and it was impossible to determine whether feral or domesticated cats preyed on monitored nests. Sanders and Maloney (2002) found that cats were the only predator that they recorded preying on adult birds. No evidence of this was found in the current study, although in most cases the camera was set up at a distance that did not show the fate of the sitting bird leaving the nest before the predator arrived. On the one occasion that the camera was able to record an entire feline predation event without the subject moving out of view, the sitting bird left the nest before the cat could attack and it was not pursued.

Pukekos are known to occasionally consume other small birds and nest contents (Carroll 1966; Heather and Robertson 1996). To our knowledge, however, this is the first time a pukeko has been filmed preying upon young chicks. Although counts were never conducted, pukekos were present in study sites in both years, but were responsible for only one of 22 lethal events.

Possums are an important predator in some New Zealand forests and have been shown to be a major cause of nest failure in the North Island kokako (Innes *et al.* 1999) and kukupa (New Zealand woodpigeon; Innes *et al.* 2004). Conversely, Sanders and Maloney (2002) found that possums were not responsible for any lethal events and are not serious predators in braided river systems. Anecdotal evidence suggested that possums were common in our study areas during both breeding seasons, although measurements of density were not taken. Possums were never filmed at any nest during the current study.

Mice and Norway rats were not filmed preying on nest contents, although a mouse was recorded at an empty nest on one occasion. McLennan and MacMillan (1985) found that experimental nests in a rural area surrounded with mesh that excluded all animals except mice suffered no losses, and concluded that mice were probably not an important predator. Video monitoring in forested and braided river ecosystems did not reveal nest predation by mice either (Innes *et al.* 1996; Brown 1997; Innes *et al.* 1999; Sanders and Maloney 2002), confirming that this species is not a serious predator. Norway rats are known to prey on nest contents of some burrowing birds (Gaze 2000) but are not strong climbers compared with ship rats (Moors 1990). All nests monitored except one were situated above ground, which may help explain why Norway rats did not appear on film. However, in other studies it has been found that Norway rats did not prey on nest contents, even if nests were located on the ground (Sanders and Maloney 2002).

4.5.4 Limitations of video monitoring

Video monitoring can provide undisputable proof identifying nest predators and, therefore, is a valuable conservation tool. Sanders and Maloney (2002) discuss a number of assumptions and limitations that are made regarding the video monitoring method that also applied to our study. For example, video monitoring may alter bird or predator behaviour, and monitored nests may not be truly independent as predators can sometimes visit more than one; further, predators may be able to perceive the IR light sources that illuminate nests at night. In their study, Sanders and Maloney (2002) tested some of these assumptions and found that failure rates of nests monitored with and without IR video equipment were not significantly different, indicating that continuous video monitoring may not have a major impact on bird or predator behaviour. They did, however, recommend that further research be undertaken to quantify potential observer effects (Sanders and Maloney 2002).

Independence between nests monitored could not always be assumed because sometimes relatively short distances separated them (e.g., 15-20m). Therefore, predators (e.g., cats and harriers) in the area may have had access to more than one nest, as their movements can range over large areas. Nests in different study areas were monitored to help control this potential source of bias.

In the current study, only seven bird species were monitored, with blackbirds and song thrushes making up a combined 82% of sampled nests. Nests of other birds such as silvereyes, house sparrows and welcome swallows were present in the study areas but could not be successfully monitored because they were often located on thin branches or in areas that were too dangerous to reach. It is possible that predators of these species may be different from the species we monitored. We tried to find nests of as many different species as possible, and thorough searches were regularly made in the study areas. The proportion of each species' nests monitored reflected the numbers that were found.

Finally, continuous video monitoring is an expensive and time consuming method to monitor nests, albeit able to provide excellent results. Moisture, battery failure and wildlife can all cause breakdowns of equipment that can result in missed events. These factors contributed to our relatively small sample size of confirmed nest outcomes. However, in the present study the number of lethal events captured on video was large enough to identify the main species preying on arboreal nests in our study sites. In this study, magpies were responsible for only 4% of recorded lethal events, the same as pukekos and considerably lower than ship rats, harriers and cats. Our results suggest that magpies are not serious nest predators in farmland habitats, and controlling this introduced species would not considerably increase the nesting success of other birds in rural areas.

4.6 Acknowledgements

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Chapter 5: Can redirected aggression explain interspecific attacks by Australian magpies on other birds?

5.1 Abstract

Attacks by participants of agonistic conflicts against a third party are referred to as redirected aggression. Usually the third party is a conspecific and relatively few documented cases of redirected aggression against other species exist. The Australian magpie (*Gymnorhina tibicen*), however, often attack other species, although the reasons for attacks are largely unknown. Some attacks occur after territorial disputes with conspecifics, suggesting that redirected aggression may be one reason for interspecific aggression in Australian magpies. In the present study, we subjected residents of eight territorial Australian magpie groups to simulated territorial intrusions. In one treatment an Australian magpie and pigeon (*Columbus livia*) were presented in cages next to one another on the territory. After 30min, the Australian magpie decoy was covered and aggressive responses toward the pigeon by residents were recorded for a further 30min (Treatment 1). Two additional treatment combinations were presented in an identical order on each territory as controls where both decoys were either Australian magpies (Treatment 2) or pigeons (Treatment 3). It was predicted that if Australian magpies regularly redirect aggression onto benign species after conspecific territorial intrusions, attack rates on the pigeon decoy in Treatment 1 would be higher than attack rates on the pigeon decoy in Treatment 3. The Australian magpie decoys in Treatment 2 were expected to be attacked at the highest rates during both 30min phases. No attacks on pigeon decoys were recorded during any test. In contrast, Australian magpie decoys were always attacked by both male and female residents. After a decoy was covered (following the first 30min phase), the percent of observations that residents were recorded at close proximity (on cage, <0.3m, or 0.3-1m) to the pigeon decoy in Treatment 1 was not significantly different (*P*>0.05) from that recorded for the pigeon decoy in Treatment 3. The percent of observations residents were recorded close to pigeon decoys in Treatment 1 and 3 were both significantly lower (*P*<0.05) than that recorded for the Australian magpie decoy in Treatment 2 (except 0.3-1m class that was not different between Treatments; *P*>0.05). We found no evidence that Australian magpies redirect

aggression onto other birds after territorial intrusions. It is possible that the proportion of territorial disputes that result in redirected attacks are small, or only occur under highly specific circumstances, which were not recognised in the current study.

5.2 Introduction

After agonistic encounters with conspecifics, subjects sometimes attack a third party that was not the initial source of provocation. This type of behaviour is often referred to as 'displaced' or 'redirected aggression' (Bastock *et al.* 1953; Marcus-Newhall *et al.* 2000). In humans, redirected aggression has been well documented (see Marcus-Newhall *et al.* 2000 for review), but it has also been identified in other wild and captive animals. For example, several species of primates have been shown to attack 'innocent' group members after losing agonistic conflicts with other conspecifics (Cheney *et al.* 1989; Aureli *et al.* 1993; Virgin and Sapolsky 1997; Wittig and Boesch 2003) and rainbow trout, when briefly exposed to larger and more aggressive fish, have been found to react with increased aggression toward smaller individuals (Øverli *et al.* 2004).

Often it is the loser of aggressive interactions that are observed redirecting aggression onto a third party, possibly as a means of reducing aggression-induced stress (Virgin and Sapolsky 1997), or because continuing to attack the provoking agent risks injury (Marcus-Newhall *et al.* 2000). However, winners of agonistic interactions may also have increased stress or anxiety levels (Aureli 1997; Øverli *et al.* 1999; Summers *et al.* 2003), and attacking another conspecific may reduce this. In other situations, animals may redirect aggression because the object of provocation is unobtainable; this has been referred to as 'frustration-induced aggression' (Haskell *et al.* 2000; 2004). For example, domestic hens (*Gallus gallus*) will often attack conspecifics when food or water is withheld (Haskell *et al.* 2000), while domestic house cats (*Felis catus*) may attack their owners after seeing other cats through a window (Chapman 1990; Beaver 2004).

Redirected aggression has also been identified in wild birds, and aggression can be directed toward on both inanimate objects and other individuals. For example, great tits (*Parus major*) and blackbirds (*Turdus merula*) will aggressively peck the ground or twigs instead of an opponent during an aggressive interaction (Hinde 1952; Tinbergen 1966). Male black-headed gulls (*Larus ridibundus*) have conflicting attack, escape, and sex drives stimulated when visited by a female during pair formation, and will often attack nearby gulls, other birds, or humans during the visit (Bastock *et al.* 1953). Furthermore, nesting prairie falcons (*Falco mexicanus*) that are disturbed by human intruders will physically attack other passing birds instead of directing their aggression towards the provoking agent (Bastock *et al.* 1953). However, documented cases of birds redirecting aggression onto other species after a conflict are relatively rare.

The Australian magpie (*Gymnorhina tibicen*; magpie hereafter) is a crow-sized bird that is an excellent subject for studies of redirected aggression as they have been observed attacking other animals after territorial disputes with conspecifics (Brown and Veltman 1987). However, it is unknown if reported attacks were triggered by the previous dispute, or another undocumented reason. Moreover, magpies can be highly aggressive and many reports of them attacking birds and other animals exist (McCaskill 1945; Jones 2002; Chapter 2), regardless of whether attacks were preceded by a territorial dispute. Magpies from territorial breeding groups appear to be more aggressive towards a wide range of other bird species in comparison to magpies from non-breeding flocks, suggesting that protection of a resource may be a possible reason why other birds are attacked (Chapter 3). Conversely, at least 45 species have been reported as attacked by magpies in New Zealand alone, many of which have no apparent resource overlap with magpies, leaving the reason(s) for attacks obscure (Chapter 2).

Breeding magpies defend territories year round and territorial intrusions by conspecifics occur at all times (Carrick 1972; Brown and Veltman 1987; Jones 2002; Kaplan 2004; pers. obs.). Territorial disputes can be lengthy (e.g., >30min) and may involve all members of a territorial group, although physical fighting between groups seldom happens (Carrick 1972; Brown and Veltman 1987; Kaplan 2004; pers. obs.). In other birds, territorial intrusions can result in a marked increase in levels of some hormones and enzyme activity that have been associated with aggression (e.g., testosterone [T] and luteinizing hormone [LH]: Butterfield and Crook 1968; Crook and Butterfield 1968;

Wingfield 1985; Wingfield and Wada 1990; aromatase activity [AA]: Silverin *et al.* 2004, dehydroepiandrosterone [DHEA]: Hau *et al.* 2004). Increases in such hormones that are induced through territorial challenges may help maintain high rates of aggression or enhance responsiveness to further challenges (Wingfield and Lewis 1993). However, levels of hormones, such as T in other species, are often not affected by simulated territorial intrusions (Wingfield and Lewis 1993; Moore *et al.* 2002; Hau *et al.* 2004).

The aim of the current study was to determine if territorial magpies were more likely to attack other birds after stimulated territorial intrusions. We used both live conspecific decoys and benign heterospecific decoys (pigeons *Columbus livia*) to 'prime' territory holders, and then measured their subsequent responses to another pigeon or magpie. If increased levels of aggression (either towards other species or conspecifics) were observed after priming with a magpie decoy, further research investigating the function and underlying mechanisms (e.g., changes in the levels of hormones linked to aggression) would be justified.

5.3 Methods

5.3.1 Study area and subjects

Eight territorial breeding groups located on two farms within the Waikato region, New Zealand (37°47'S, 175°20'E) were selected for study. Other territorial breeding groups were present on both study farms, but the landscape in which these groups lived made it difficult to access them for our experiment. Suitable topography within a magpie territory included a flat area close to nesting trees where our equipment could be set up and an inconspicuous area 60-100m away where an observer could maintain visual contact throughout the test.

Magpies have a complex social system and territories can be defended by groups of 2-26 birds (Robinson 1956; Carrick 1972; Veltman 1989b; Hughes and Mather 1991; Baker *et al.* 2000). In the current study, three territories were defended by a monogamous pair while another two consisted of a monogamous pair with one juvenile bird of unknown sex. One group consisted of a breeding pair with one sub-adult bird of unknown sex, while another consisted of one adult male and two adult females. The final group was comprised of one adult male, three adult females and one juvenile of unknown sex. Data from juvenile magpies were excluded from the analysis because they were only present in three territories, were seldom recorded close to decoys (i.e., ≤1m; see below), and did not attack decoys. All territories were separated by at least one other magpie territory or distances of at least 500m to reduce the possibility of pre-exposure of subjects to treatments.

5.3.2 Study design

Treatments were conducted between 23/3/04 and 25/4/04. At each territory, two cages ([a] and [b]; 0.3x0.3x0.6m) were placed 5m apart, each containing either a live adult female magpie decoy or live adult pigeon decoy of unknown sex. A large box was placed on its side adjacent to decoy [a]; the box had a string attached that could be pulled by an observer, positioned 60-100m away, to cover decoy [a] during the test. Each test lasted for 60min, and was considered started when a resident magpie came within 15m of either cage. After 30min, decoy [a] was covered by the box, leaving decoy [b] exposed for the remaining 30min.

To determine if magpies will redirect aggression towards a benign bird species, three variables (latency to respond, frequency of aggressive strikes, and percent of scans close the decoy [see below]) were measured. In Treatment 1, decoy [a] was a magpie and decoy [b] was a pigeon. Thus, residents were exposed to a 30min phase where both a magpie and pigeon were present on their territory followed by a 30min phase when only the pigeon was visible (Table 5.1). In Treatment 2, the same protocol was followed but both decoy [a] and [b] were magpies while in Treatment 3, both were pigeons (Table 5.1). If magpies redirect aggression toward other species, we expected pigeons exposed to residents in Treatment 1 to attract more aggression than those in Treatment 3. The caged magpies in Treatment 2 should receive high levels of aggression across both phases of these tests.

Table 5.1 Treatments presented at each territory. In the first phase (0-30min), both decoys were exposed to residents; after 30min, decoy [a] was covered, and only decoy [b] was exposed for the remainder of the test (second phase; 30-60min).

	First phase (0-30min)		Second phase (30-60min)	
	decoy [a]	decoy [b]	decoy [a]	decoy [b]
Treatment 1	magpie	pigeon	(covered)	pigeon
Treatment 2	magpie	magpie	(covered)	magpie
Treatment 3	pigeon	pigeon	(covered)	pigeon

Treatments were presented in a random order at each territory, with at least 48hr between tests. Magpie vocalisations, recorded onto an analogue cassette tape (TDK), were played for 5min through a speaker (Sharp WQ-CH800; c.72db at 1m from speaker) placed 1m from decoy [a] at the start of all tests. This was done to draw residents into the area (they usually flew away while the observer set up experimental equipment); the playback was used to alert residents to the presence of the decoys after the observer had moved away from the cages. Magpie playback started automatically 6min after the equipment had been set up, which gave the observer enough time to move to a position 60-100m away. All treatments were video taped using a handheld video recorder (Sony CCD-TRV89E) with a time stamp to the video tape (Sony Hi8) and later dubbed onto standard VHS tape (Mitsubishi Black Diamond E180 using a Panasonic AG-6730 video recorder) for analysis. Video cameras were positioned on a tripod approximately 15-30m away from the cages.

Magpies from only two study groups had members that were colour banded. However, it was safe to assume that the same magpies were seen during each test because: (1) territories are defended year round by the same birds (Carrick 1963, 1972; Brown and Veltman 1987), (2) the tests were conducted well inside the territory, and (3) group composition (i.e., gender and age-class) did not change in any group over the course of the study.

5.3.3 Activities sampled

From the start of each test the proximity of the closest resident magpie to the decoys (i.e., either [i] on cage, [ii] <0.3m from cage, [iii] 0.3-1.0m from cage, or [iv] >1m from cage) was recorded every 15s. This gave 120 scans before the decoy [a] was covered, and 120 scans after. Occasionally, the decoy was not covered on the 120th scan due to the time taken to draw slack on the string attached to the box, resulting in 1-2 extra intervals being added to the first half of some tests. On these occasions the same number of intervals was also added to the second half of the test.

Aggressive behaviours directed towards decoys or other birds were measured continuously throughout each test. This was easily accomplished because the aggressive behaviours we measured were obvious and had a very short duration. Magpies have a large repertoire of aggressive behaviours (Brown and Veltman 1987) but we only measured instances when a resident magpie struck the cage with its beak or performed bill snaps (i.e., lunging at a victim and snapping the beak; Brown and Veltman 1987); these acts were the most extreme forms of agonistic behaviour and were most likely to cause injury to an unprotected victim. We pooled occurrences of these two behaviours as it was not always possible to clearly distinguish between them (hereafter referred to as ‘aggressive strikes’).

Any additional aggressive behaviour by resident magpies towards the pigeon decoys or other free-ranging birds were also recorded in each test (e.g., aggressive postures close to pigeon decoys, boundary disputes with neighbouring conspecifics, or chases of other free-range species). Similarly, reactions of other species to the decoys were recorded as well (e.g., instances of free-ranging species approaching or attacking decoys).

The amount of time residents took to respond (i.e., approaching within <15m of the decoys) was recorded to the nearest second. When both decoys were initially presented in a territory, the arrival of a resident within 15m signalled the start of the test as defined above. After decoy [a] was covered (which usually caused residents to temporally flee the area), the amount of time residents took to return to decoys was also recorded to the nearest second. If subjects remained within 15m of the decoys following the disturbance associated with covering decoy [a], the latency was considered 0s and the time taken until the residents moved >15m of the decoys was also recorded.

5.3.4 Analysis

The percent of scans that residents were recorded at each proximity ([i]-[iv]; see above) were calculated for both phases of each test. Aggressive strikes were calculated per minute. Significant differences ($P<0.05$) between treatments for measured variables (i.e., proximity to decoys; aggressive strikes) were calculated using a series of Friedman ANOVA tests. Differences in the percent of scans that (1) males only, (2) females only, or (3) males and females together were recorded at close proximity to decoys was also calculated using Friedman ANOVA tests using only data from the tests involving two magpie decoys (Treatment 2); residents were not recorded close to pigeon decoys enough during Treatments 1 and 3 for statistical analyses to be conducted. If significant differences were detected by any Friedman tests, post-hoc tests (Wilcoxon sign-rank tests) were employed to identify where the differences occurred.

Each 30min period before and after decoy [a] was covered in all treatments were divided into six 5min blocks and the number of aggressive strikes recorded in each block were compared (using repeated measures ANOVAs with the Greenhouse-Giesser epsilon correction factor) to determine if the intensity of aggression changed over time. Wilcoxon sign rank tests were used to compare aggressive strike rates between males and females. Behavioural data from all sub-adult magpies were dropped from all analyses comparing sexes as the sex of these birds could not be assessed from plumage markings (Heather and Robertson 1996).

5.4 Results

5.4.1 Resident magpie responses to decoys

Residents did not attack pigeon decoys during the second phase of any test (Figure 5.1). However, during the first phase of two separate tests when both a magpie and pigeon decoy were exposed at the same time (Treatment 1), residents 'charged' the pigeon decoy (i.e., lunged forward 1m, stopping <0.3m from the cage) a total of five times (twice during one and three times during the other test). This behaviour, however, was seen many times at cages containing magpie decoys and was usually followed by an aggressive strike, which did not occur at pigeon decoys.

When two magpie decoys were present during the first phase of Treatment 2, they each received about the half the as many strikes as the single magpie exposed with a pigeon during Treatment 1 (i.e., the total number of strikes during the first phase of Treatments 1 and 2 are similar; Figure 5.1).

No significant differences were detected in the frequency of aggressive strikes/min across the 5min blocks that comprised the two 30min phases (all repeated measures ANOVAs, $P>0.05$; Figure 5.1). Therefore, aggressive strikes were pooled and are presented as the mean number of aggressive strikes/min for each period (hatched bars in Figure 5.1). Differences in attack rates on magpie decoys between Treatments 1 and 2, or between phases of treatments, were not apparent (Friedman test, $P>0.05$; Figure 5.1).

Both male and female residents from all groups were recorded attacking magpie decoys. Over all periods when magpie decoys were exposed to residents (i.e., the first phase of Treatment 1 and both phases of Treatment 2), males generally scored more aggressive strikes on decoys than females (1.1 strikes/min ±0.2s.e.m cf. 0.5 ±0.2); however, these scores were highly variable (range: 0-3.1 strikes/min for males and 0-3.5 for females) and often female members of a group delivered more strikes. Accordingly, no significant differences in the number of aggressive strikes/min between sexes were detected (all Wilcoxon sign rank tests, $P>0.05$).

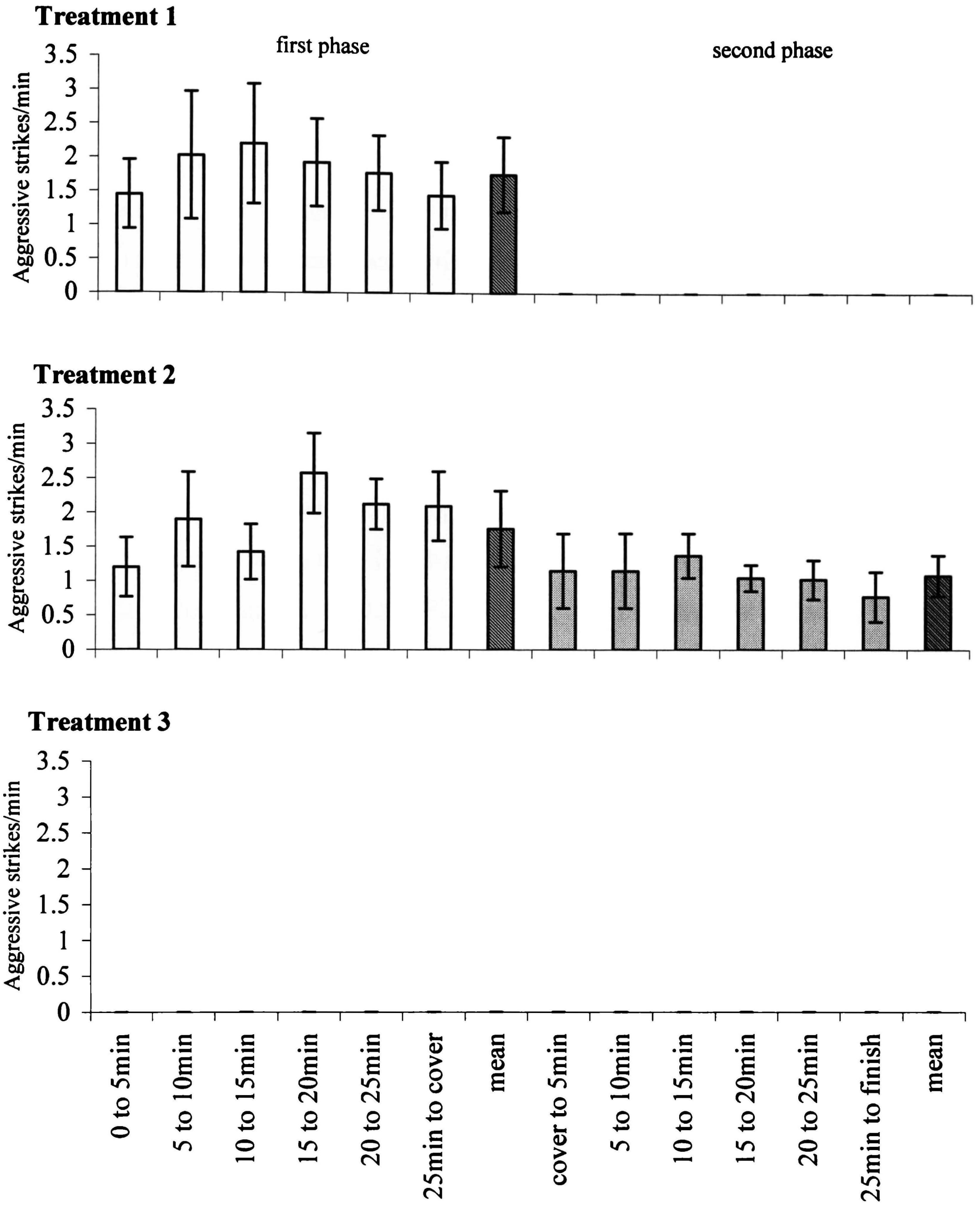

Figure 5.1 The mean number of aggressive strikes by resident magpies on decoys per 5min block before (first phase) and after (second phase) decoy [a] was covered (see Table 5.1 for decoy combinations). There were no significant differences in the number of aggressive strikes/min between 5min blocks (all repeated measures ANOVAs, *P*>0.05). The mean number of aggressive strikes/min for each phase of each treatment are also presented as hatched bars. Error bars are s.e.m.

Residents were recorded more often at close distances (on cage, <0.3m) to the magpie decoy [b] during the second phase Treatment 2 than when pigeon decoys [b] were in place in the second phase of Treatments 1 and 3, (all Friedman tests, *P*<0.05; Table 5.2). There was no difference between the percent of observations residents were recorded at 0.3-1m between the second phases of all Treatments (Friedman test, *P*>0.05; Table 5.2). Additionally, residents were recorded during fewer scans at distances >1m from the magpie decoy during the second phase of Treatment 2 compared with the second phases of Treatments 1 and 3 when only a pigeon decoy was presented (Friedman test, *P*<0.05; Table 5.2).

Males and females were recorded together within close proximity to the magpie decoy [b] significantly more often when together than when on their own during the second phase of Treatment 2 (Friedman test, *P*<0.05; Figure 5.2). During the first phase of Treatment 2, when residents were exposed to two magpie decoys at the same time, males tended to be recorded close to one of the decoys while females was recorded at the other (Figure 5.2).

Table 5.2. Mean percent of observations that residents territorial groups (*n*=8) were recorded at different distances to decoy [b] after decoy [a] was covered (see Table 5.1 for decoy combinations for each treatment).

		Proximity to decoy (mean % of scans ±s.e.m)			
	decoy [b]	on cage*	<0.3m*	0.3-1m	>1m*
Treatment 1	(pigeon)	0.1 ±0.1	1.1 ±0.7	0.2 ±0.1	98.6 ±0.9
Treatment 2	(magpie)	29.8 ±8.1	20.1 ±7.2	0.8 ±0.3	49.3 ±11.6
Treatment 3	(pigeon)	0 ±0	0.2 ±0.2	0.3 ±0.2	99.5 ±0.4

* indicates that significant differences exist between treatments (Friedman test, *P*<0.05; post-hoc tests confirmed that Treatment 2 was always significantly different to Treatments 1 and 3, which were not different from one another).

After the magpie decoy [a] was covered during Treatment 1, resident magpies returned to the pigeon decoy [b] five of the eight tests (Table 5.3). In Treatment 2, residents always returned to magpie decoy [b] after the magpie decoy [a] was covered (Table 5.3). The response to pigeon decoys in Treatment 3 was highly variable with three groups not approaching decoys during either the first or second phase, two groups only during the first 30min phase, and another two groups only in the second 30min phase (Table 5.3). Only once during a Treatment 3 test were residents seen within 15m of pigeon decoys both before and after decoy [a] was covered (Table 5.3); however, at no time were these residents scored at distances <1m to either decoy. Although residents remained <15m of decoy [b] after [a] was covered during three tests (twice during Treatment 2 and once in Treatment 1), residents took longer to leave the test arena when decoy [b] was a magpie cf. a pigeon (Table 5.3).

5.4.2 Resident magpie response to other birds

Free-range birds of different species were often seen flying over or landing near (e.g., <20m) decoys during tests, although residents were not seen attacking or chasing birds except other magpies or harriers (*Circus approximans*). Territorial disputes between conspecifics and resident magpies were observed during five trials: three times (at different territories) during Treatment 1 tests and once (at different territories) during Treatment 2 and 3 tests. Intruding magpies were quickly detected by residents and were never recorded close to decoys; therefore, attacks on decoys by intruders did not occur. In addition, because territorial disputes occurred away from the decoys, the number of aggressive strikes and proportion of scans where residents could be scored close to decoys were probably lower than if a boundary dispute did not occur, although this did not affect the overall trends that were observed (i.e., the proportion of scans that residents were >1m from decoys during tests with boundary disputes were not significantly different than tests without; Mann-Whitney U test, $P>0.05$). Residents did not attack pigeon decoys at the completion of territorial disputes that took place during Treatment 1 tests, although the disputes always occurred before the magpie decoy had been covered. However, at the completion of the territorial dispute recorded during a Treatment 3 test, no attacks on pigeon decoys or any other free-range birds were observed. The behaviour of intruding magpies after the each territorial dispute could not be determined because they always flew out of view.

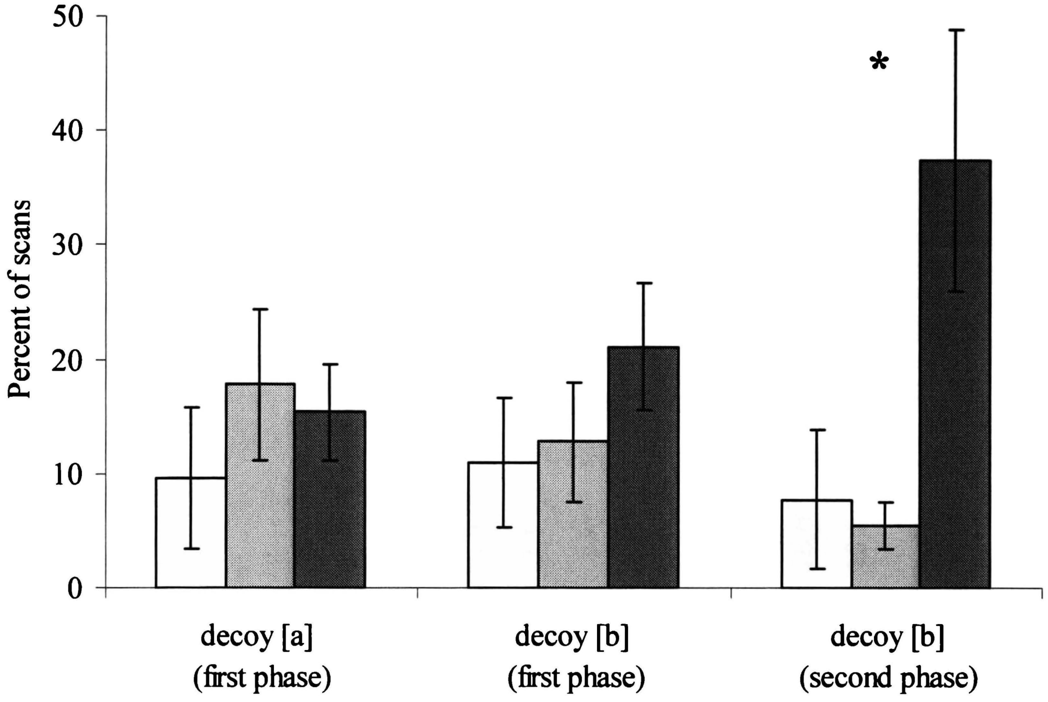

Figure 5.2 The mean percent of scans that males only (white), females only (light grey), and males and females combined (dark grey) were recorded at distances <1m to magpie decoys [a] and [b] during the first phase of Treatment 2 and decoy [b] only during the second phase of Treatment 2. * indicates that significant differences between columns exist (Friedman's test, $P<0.05$; post-hoc tests confirmed that males and females combined were present significantly more often than males only and females only). Error bars are s.e.m.

Table 5.3 Latency (min) of resident magpies from territorial groups to be recorded within 15m of decoys at the start of each test (first phase) and after decoy [a] had been covered [b] (second phase) (see Table 5.1 for decoy combinations for each treatment). If residents were not recorded within 15m of decoys during an experiment then no latency data were collected and 'no response' is presented. If subjects remained within 15m of the decoys following decoy [a] being covered the time it took for birds to move >15m of decoy [b] is presented in parentheses.

	Treatment 1		Treatment 2		Treatment 3	
territorial group	first phase	second phase	first phase	second phase	first phase	second phase
1	5.2	0.9	9.9	3.0	no response	3.0
2	6.1	3.4	2.1	(30.0)	no response	no response
3	6.4	no response	23	11.0	no response	no response
4	6.7	(1.3)	1.9	(28.6)	no response	no response
5	4.6	no response	9.1	13.8	no response	6.7
6	5.3	12.8	0.5	0.8	0.8	no response
7	3.1	26.2	16.6	3.5	21.4	1.7
8	14.5	no response	18.8	3.5	18.7	no response

Harriers were seen being chased during two different tests: once during a Treatment 1 test and once during a Treatment 2 test. On both occasions the harrier was repeatedly swooped by residents until it left the territory, although contact was never seen between the birds. Before being chased away during the Treatment 1 test, the invading harrier circled around the decoys at low altitude before landing on the cage containing the pigeon, reached inside and seized the bird in its talon. It then tried to fly away with the pigeon but could not get the bird out of the cage. The resident magpies continued to swoop the harrier and it quickly gave up its attempt to remove the pigeon and flew away. The residents returned to the cages in <2min after chasing the harrier away to continue attacking the magpie decoy; the pigeon decoy was uninjured during this exchange. No other instances of free-ranging birds approaching (i.e., <1m) decoys were recorded.

5.5 Discussion

Although reports of redirected aggression by magpies after territorial disputes exist, this type of behaviour in magpies has not previously been investigated experimentally. The few published reports of redirected aggression in magpies that exist (e.g., Brown and Veltman 1987) do not include important information such as when the attacks took place, the sex or age of attackers, whether intruding or resident magpies were responsible for attacks, or how long territorial disputes lasted before redirected attacks took place. It is, therefore, possible that redirected attacks are in fact rare and take place under very specific circumstances. We found no evidence of redirected aggression in territorial magpies after simulated territorial intrusions. Resident magpies never attacked and were seldom recorded within close proximity of pigeon decoys during tests, regardless of being exposed to magpie decoys. Furthermore, free-ranging birds or animals were not seen being attacked during any stage of the tests except harriers and other magpies. In contrast, the mean number of attacks and the percent of observations residents spent close to magpie decoys were always constantly high over the duration of tests.

Redirected aggression has mainly been studied in gregarious animals such as primates, although the motivation for such attacks by these species is probably very different from magpies. This is because conflicts resulting in redirected aggression in primates occur between members of the same species within the same social group (Cheney *et al.* 1989; Aureli *et al.* 1993; Virgin and Sapolsky 1997; Wittig and Boesch 2003). Nevertheless, conflicts within primate groups nearly always result in a clear winner and loser (Aureli *et al.* 1993). Often, it is the loser of such conflicts that redirects aggression onto 'innocent' group mates, possibly to divert further aggression from the former aggressor onto a new target, or the victim may try to involve the former aggressor in the redirected attack, which may function as a type of reconciliation (Aureli and van Hooff 1993). In contrast, increased stress levels in winners may occur as a result of conflict (Aureli 1997; Øverli *et al.* 1999; Summers *et al.* 2003) and attacking another conspecific may reduce this too. Like primates, territorial magpies live in complex social groupings (Carrick 1972), but reported attacks after territorial disputes were not targeted at conspecifics but at other birds and animals (Brown and Veltman 1987). During magpie territorial disputes in the wild, winners are ultimately either the residents that repel intruders or the intruders that evict residents. In the current study, it could not be clearly determined whether resident magpies were winners or losers. Moreover, residents we subjected to simulated territorial intrusions could be classed as both. For example, residents were able to attack the decoy magpies with little personal risk and at no time was their territory ownership compromised, suggesting that they could be classed as a winner. In contrast, 'intruding' magpies were unable to be driven from the territory as they were inside a cage, which also protected the decoy from any injury, suggesting that residents could be classed as losers. Published accounts of redirected attacks by magpies may have been conducted by only winners or only losers. Therefore, it is possible that our experimental design did not fully exploit this detail: providing one explanation for our result.

Some animals that are prevented from attacking opponents or barred from a food source will sometimes attack other animals as a means of venting frustration-induced aggression (in cats: Chapman 1990; Beaver 2004; in chickens: Haskell *et al.* 2000). Although resident magpies in the current study would probably have had elevated frustration levels at not being able to physically attack or drive away magpie decoys, they did not attack pigeon decoys and were not seen attacking other free-range birds (except other magpies and harriers) at any stage in the response. Attacks on other magpies and harriers, however, are not unusual (Brown and Veltman 1987; Kaplan 2004; Chapters 2+3) and probably occurred because these species are strong resource competitors or predators (Heather and Robertson 1996; Chapter 4). Furthermore, one of the attacks on a harrier occurred during a test with only pigeon decoys present, a situation when redirected aggression should not have occurred. Territorial disputes during the current study could have potentially increased the likelihood of residents redirecting aggression against other species as it is after these types of interspecific conflicts that redirected aggression was initially reported (Brown and Veltman 1987). Because no attacks were seen after normal territorial intrusions, further credence can be provided for the hypothesis that redirected attacks occur infrequently or under unusual circumstances.

Endocrine responses to territorial intrusions have received little study in magpies and it is possible that changes in hormones and enzymes associated with aggressive behaviour (as observed in other species; e.g., T, DHEA, LH, AA [see Introduction]) may also apply to magpies. In magpies, circulating plasma T levels are usually very low with a marked increase during the breeding season (Schmidt *et al.* 1991; Warne 2001). In addition, Warne (2001) found that basal levels of circulating plasma T were similar between magpies that were extremely aggressive towards humans and those that were not. To date, only one study has investigated hormone changes in magpies in response to territorial intrusions. In his study, Rollinson (2004) reported that levels of corticosterone in territorial male magpies positively correlated with the number of intrusions. This indicated that intrusions may be stressful to magpies as corticosterone has been shown to increase in many species during stressful situations (Creel 2001). In the current study, we found no evidence of redirected aggression towards other animals regardless of whether hormones associated with supporting or maintaining aggression fluctuate in magpies after intrusions. Therefore, it is unlikely that reported accounts of redirected aggression can be explained by hormonal changes alone.

Territorial defence in magpies is often highly organised and several different strategies adopted by group members have been documented (Kaplan 2004). All members of a group can be involved in a given attack but it is usually the highest ranking members that play the most important roles (Robinson 1956; Brown and Veltman 1987; Kaplan 2004). We found that both males and females were regularly recorded close to magpie decoys. Furthermore, there was no significant difference in the number of aggressive strikes/min between sexes. There was, however, a large amount of variability in the number of aggressive strikes/min between sexes across tests. High variation in attack rates between sexes within groups is not unusual in magpies and has been reported in other studies (e.g., Farabaugh *et al.* 1992). Moreover, our study was conducted during the non-breeding season; therefore, the proportion of time allocated to territorial defence by males and females at other stages of the year may be different. For example, during the breeding season females spend more time incubating eggs or tending young while males undertake more of the territorial defence (Robinson 1956; Brown and Veltman 1987). Juveniles can take part in territorial defence but their involvement can be highly variable; some juveniles will display high levels of territoriality while others show none at all (Farabaugh *et al.* 1992). Juvenile birds during the current study did not attack and were seldom recorded close to any of the decoys, although they were only present in three territories and the lack of response to decoys may not be representative of juveniles in other groups.

Despite reported accounts to the contrary, we found no evidence that magpies redirect aggression onto other birds after territorial intrusions. Protection of a resource (Chapters 2 and 3), chasing away potential nest predators (Chapter 4), or strong selection for aggressive individuals over evolutionary time spans (Chapter 6) may better explain why magpies attack other birds. It is possible, however, that the proportion of territorial disputes that result in redirected attacks are small, or only occur under highly specific circumstances, which were not recognised in the current study. We suggest that further work in this field should focus on identifying perceived winners and losers and measuring their behaviour towards other animals after territorial disputes under normal field conditions or by manipulating parameters, such as food availability, to promote interactions between neighbouring groups.

5.6 Acknowledgements

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Chapter 6: Can the evolutionary past of the Australian magpie help explain current patterns of interspecific aggression in New Zealand?

6.1 Abstract

In this chapter the hypothesis that Australian magpies (*Gymnorhina tibicen*) currently attack birds in New Zealand partly because they evolved in an environment that rewarded such behaviour is investigated. Data are presented that suggest Australian magpies have evolved in the presence of many predators, numerous dangerous resource competitors, and in areas where resource availability was limited. If this hypothesis is correct, individual Australian magpies that displayed high levels of aggression towards a wide variety of species would have been more successful at obtaining and defending quality nesting and foraging sites against both conspecifics and other birds. Consequently, more aggressive magpies would have had higher levels of reproductive success and ultimately been selected for over time. Australian magpies were introduced into New Zealand from 1864 and many of the environmental constraints from their evolutionary past no longer appear to be present, yet attacks on other birds still occur. It is suggested that the generalised, apparently unnecessary, attack regime may be maintained by Australian magpies in New Zealand because (1) interspecific aggression is still adaptive for Australian magpies in some contexts, (2) Australian magpies have not been in New Zealand for long enough for high levels of unnecessary interspecific agonistic behaviour to be lost from the population, (3) Australian magpies currently face no selection pressure to stop attacking other birds, or (4) interspecific aggression is a pleiotropic by-product of conspecific agonistic behaviour.

6.2 Introduction

Conflict between species is common and has been the basis of much research (e.g., Huntingford and Turner 1987). Agonistic behaviour is generally employed by individuals in the acquisition of goals which tend to maximise individual survival and reproduction (Brown 1964). Thus, species with very similar resource requirements generally display the highest levels of interspecific agonistic behaviour (Newton 1998).

In some species, however, reasons for interspecific attacks are largely unknown. For example, steamer-ducks (*Tachyere* spp.) often commit apparently unprovoked attacks on other species (Nuechterlein and Storer 1985; Livezey and Humphrey 1985a). Nuechterlein and Storer (1985) suggested that male steamer-ducks may commit attacks to demonstrate quality to potential mates or to reduce competition for food; however, several species that are attacked by steamer-ducks show little resource overlap with them. In addition, males with long-term breeding partners continue to commit attacks, and the presence of other birds in steamer-duck territories does not always elicit an aggressive response (Livezey and Humphrey 1985a,b). However, there may be little selective pressure for discrimination between targets as the risk associated to a steamer-duck during most interspecific attacks is negligible; steamer-ducks are large birds with protruding bony knobs on each wing that they use as weapons (Nuechterlein and Storer 1985). Livezey and Humphrey (1985a) suggest that interspecific aggression may not simply reflect resource competition, but instead represents a host of secondary adaptations for the protection of offspring, defence of food resources from marginal competitors, sexually selected rituals for assessment of males by females, and practices for intrageneric fighting. However, this inclusive list of adaptive benefits has remained untested.

Behaviours that may appear to be non-adaptive in a contemporary context could have been adaptive during a species' evolutionary past. For example, New Zealand's avifauna evolved in the absence of terrestrial mammalian predators with the main predation threat coming from diurnal avian raptors (Holdaway 1989; Wilson 2004). Therefore, many endemic birds are cryptically coloured, have nocturnal behaviours, or remain motionless when threatened to avoid these predators (e.g., Merton *et al.* 1984; Pierce 1986), although proving this was indeed the function of such adaptations is largely impossible as many of the avian predators are now extinct (Holdaway 1989; Wilson 2004). What is clear, however, is that many of the behavioural adaptations New Zealand birds developed during their long period of isolation were no longer effective after the introduction of mammalian predators; consequently, many species are now extinct or endangered (Holdaway 1989; Maloney and McLean 1995; Bunin and Jamieson 1996). Therefore, investigating a species' evolutionary past in order to identify ultimate reasons for behavioural traits may be more appropriate than trying to identify current functional mechanisms.

The Australian magpie (*Gymnorhina tibicen*; magpie hereafter) is a crow-sized bird that can display high levels of aggression towards other birds. Interspecific aggression may be the consequence of selective pressures magpies experienced during their evolutionary past. Alternately, their aggressive nature may reflect a relatively recent development in response to new environmental conditions (e.g., arrival of Europeans to Australia; being introduced into New Zealand). Interspecific attacks are not just carried out by magpies in New Zealand as there are many reports of Australian birds also being targeted (e.g., Chisholm 1910; Chandler 1944; Paton 1977a; Barr 1986; Tremont 1995; Cox and Bauer 1997; Jones 2002), indicating that this behaviour must have been present in magpies before they were introduced into New Zealand. There may be adaptive reasons for some interspecies aggression by magpies; for example, attacks on predators or close resource competitors may have direct survival benefits. However, many birds that are neither predators nor close resource competitors are sometimes attacked as well (Chapter 2), leaving reasons for attacks on these species obscure.

In this chapter it is argued that magpies were likely to have always displayed the high levels of aggression observed during historic times because the environment in which they evolved rewarded such behaviour. If magpies have evolved in an environment where there was a strong selection pressure for widely focused aggression, this behaviour may be maintained in the current behavioural repertoire of magpies in New Zealand. Therefore, reasons for some interspecific attacks by magpies in New Zealand may be better explained as previously adaptive traits that may no longer be necessary but maintained in (or not yet lost from) current populations. In order to do this (1) attributes of the environment in which magpies evolved before the arrival of Europeans to

Australia, and (2) the species that they may have coexisted with, are explored. The main goal is to determine why aggression is currently maintained in New Zealand magpie populations (cf. current Australian populations [see below]) because magpies have been accused of having negative impacts on the abundance or distribution of some New Zealand birds (e.g., McCaskill 1945; Barrington 1995, 1996b). While this has been shown to be largely untrue on a large-scale level (Innes *et al.* 2004), magpies do appear alter the distribution of rural birds on a local level (i.e., birds avoid landing or flying close to magpies in preference to adjacent magpie-free areas; Chapter 3). As indicated above, magpies are still reported attacking other birds in Australia, but they have not been implicated as having major impacts on species diversity or abundance (but see Cox and Bauer 1997).

6.3 Past and present magpie distribution and species coexistence

The ecological conditions of an environment will ultimately determine the behavioural traits that are favoured over evolutionary time. Accordingly, through natural selection, individuals that have adapted their behaviour to suit the environment are generally more successful; for example, birds that that live in the midstorey of forests usually produce lower-pitched songs than those in the understorey or canopy; low frequency vocalisations are able to travel greater distances in dense vegetation, which may be useful in attracting potential mates or advertising territorial boundaries (Seddon 2005). Therefore, where a species has evolved, or the species that they evolved with, would have had a large influence on how a species' behavioural repertoire has developed. In this section, the location of magpie populations and the species that they coexisted with during their evolution are compared with current magpie populations in New Zealand.

6.3.1 Magpie distribution

In Australia

Modern accounts describe magpies' preferred habitat in Australia as predominantly open areas with good amounts of short grass for foraging and tall trees for nesting (Robinson 1956; Carrick 1963, 1972; Brown and Veltman 1987). Although magpies are found in nearly all areas of Australia (Barrett *et al.* 2003), the largest concentrations are in areas that possess these features (Schodde and Mason 1999). Since Europeans colonised Australia in 1788, approximately 43% of forest, which is generally regarded as poor magpie, habitat has been lost. In addition, closed woodland (32%) and low (76%) and tall (37%) shrubland have all been drastically reduced (Noble *et al.* 1996). Much of this vegetation was cleared for agricultural or urban development, which has been credited with increasing the magpie population size and range, so that they have become common in these regions (Schodde and Mason 1999; Jones 2002).

Records of magpie distribution in Australia prior to the formation of the ornithological journal *Emu* (pre-1901) are few, and thus their distribution before European arrival can only be inferred by comparing what is now preferred magpie habitat with where this type of habitat was formerly available. The vegetation structure in Australia prior to European arrival largely reflected the moisture gradient (i.e., wetter regions were mainly found in the coastal regions and conditions became progressively drier towards the centre of the continent) (AUSLIG 1986). If magpie habitat prior to European arrival in Australia was similar to that today, then it is likely that much of the coastal regions, where they are currently abundant, would not have been occupied as these areas would have been covered by forest (AUSLIG 1990; Figure 6.1). Most magpies would have been restricted to the open woodland and grassland habitats that were generally found inland (AUSLIG 1990), with smaller populations possibly occupying clearings surrounded by forest (Schodde and Mason 1999; see also Jones 2002). Much of the early research and anecdotal evidence suggests that this may be correct as many reports indicate that magpies were often very fast at invading and colonising areas soon after forest clearance (e.g., Macarthur 1930; Robinson 1956). In contrast, other researchers have suggested that the white-backed magpie (*Gymnorhina tibicen hypoleuca*) variety may have also occupied forested areas (Kallioinen *et al.* 1995; Hughes *et al.* 2002). However, many reports published in the early 1900's make no reference to this variety being common in forested areas, classing them as open country birds (e.g., Littler 1903; Campbell 1905; Batey 1907; Campbell 1909). For the purpose of this Chapter it is assumed that magpies mainly occupied similar habitats during their evolutionary past as they do today.

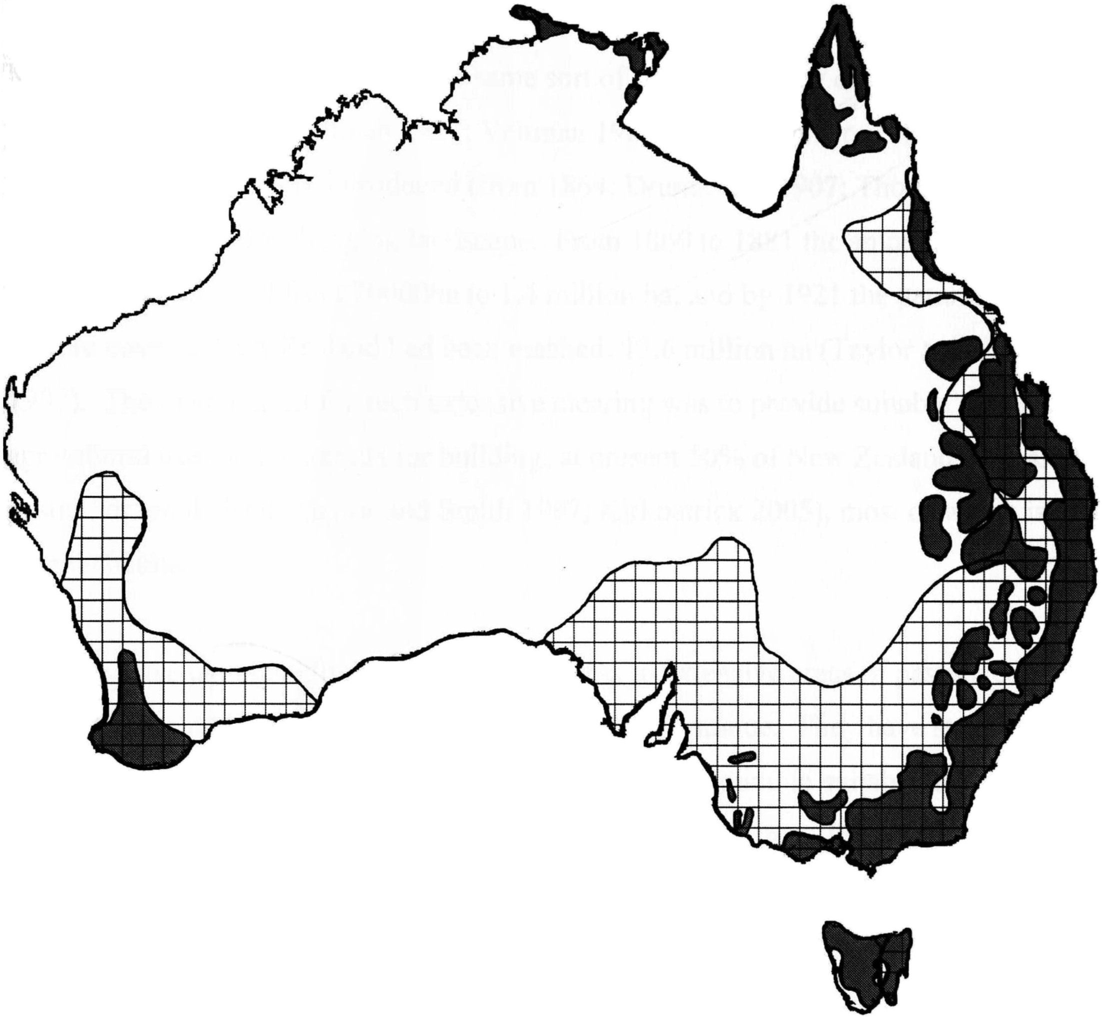

Figure 6.1 The current main breeding distributions of Australian magpies in Australia (tiled) and the estimated coverage of open, closed, tall open, and tall closed forest in the 1780's (grey). Much of the areas covered in forest before 1780 would have been unsuitable magpie habitat, restricting them to woodlands and grasslands that were mainly found in drier inland regions.

(data sources: AUSLIG 1990; Barrett *et al.* 2003)

In New Zealand

Magpies in New Zealand occupy the same sort of habitats as they currently do in Australia (Brown and Veltman 1987; Veltman 1989b; Farabaugh *et al.* 1992). At the time when magpies were introduced (from 1864: Drummond 1907; Thomson 1922), New Zealand had a rapidly changing landscape. From 1860 to 1881 the amount of grassland and pasture increased from 70000ha to 1.4 million ha, and by 1921 the natural limit of pasture cover in New Zealand had been reached: 17.6 million ha (Taylor and Smith 1997). The main reason for such extensive clearing was to provide suitable land for agricultural uses and materials for building; at present 50% of New Zealand is classed as pasture or arable land (Taylor and Smith 1997; Kirkpatrick 2005), most of which is ideal magpie habitat.

Magpies have undoubtedly benefited from access to extensive areas of pasture combined with a fragmented landscape created through forest clearance. They have steadily dispersed from their original release points and are now found in suitable habitat in most parts of the country (McCaskill 1945; Westersov 1954; McIlroy 1968; Bull *et al.* 1985; Heather and Robertson 1996). Only the far north, the west coast of the South Island, and Stewart Island have low or no magpie populations (Bull *et al.* 1985; Heather and Robertson 1996).

6.3.2 Coexistence with other species

In Australia

It is difficult to determine exactly which species coexisted with magpies prior to European arrival. This can only be hypothesised from known distributions and historical habitat preferences. It is likely, however, that many native Australian birds that currently live in open areas, forest edges, and forest remnants also inhabited these areas prior to European arrival, and so coexisted with magpies. Magpies liberated into New Zealand were mainly collected from Victoria (Thomson 1922; McIlroy 1968). Therefore, published surveys and summaries of Australian birds commonly recorded with magpies that were conducted in Victoria between 1912 and 1983 (i.e., Cheney 1915; Brown 1950;

Loyn 1985) were chosen to estimate which birds may have coexisted with magpies prior to European arrival. Table 6.1 lists all birds that were commonly recorded in these surveys, although introduced and aquatic birds (except aquatic birds that have overlapping ranges with magpies; e.g., maned duck *Chenonetta jubata*) have been excluded as they would have not interacted with magpies. Aside from Loyn (1985), surveys did not include quantitative counts of bird abundance; therefore, 'common' birds were classed as those species that were recorded as being 'regularly observed'.

Magpies have been extensively studied in many regions in Australia and there are large amounts of behavioural overlap between magpies from different regions; for example, breeding magpies hold territories, the breeding cycle is similar, and non-breeding magpies usually aggregate in flocks (excluding Western Australia) (Robinson 1956; Carrick 1972; Jones 2002; Kaplan 2004). Therefore, it is appropriate to include findings from magpie behavioural studies conducted outside the Victorian region.

Most (97/134; 72%) birds that coexisted with magpies also may have competed for either food or nesting sites, indicating that high levels of competition for resources existed (Table 6.1). In addition, 67% (24/36) of species the same size or larger than magpies were also resource competitors. Moreover, 10 large avian predators were commonly recorded in surveys, seven of which had resource overlap with magpies (Table 6.1). Thirteen additional predatory birds of varying sizes were also recorded (Table 6.1); although most of these birds probably did not threaten adult or juvenile magpies, but may have preyed on magpie eggs or nestlings (Blakers *et al.* 1984; Morcombe 2000).

In New Zealand

Most of New Zealand's endemic land birds are forest dwellers (Holdaway 1989), since ca. 85% of the country was covered in forest prior to Maori arrival (Taylor and Smith 1997; Kirkpatrick 2005). The fragmented farmland ecosystem that was created through the burning of forests, coupled with the introduction of small mammalian predators, had profoundly negative impacts on the abundance and distribution of bird populations and many became endangered or extinct (King 1984; Wilson 2004).

Table 6.1 Species commonly counted in three reported surveys conducted in Victoria between 1912-1983 (Cheney 1915; Brown 1950; Loyn 1985). Birds are ordered from largest to smallest. † represent species that are approximately the same weight or heavier (i.e., ≥300g) than magpies, 'f' indicates some dietary overlap with magpies (i.e., consume ground invertebrates as part of their diet), 'n' indicates competition for nesting sites (i.e., above ground tree nesters not including birds that nest in hollows), 'pa' indicates potential predator of fledglings or adult magpies, 'pn' indicates potential nest (i.e., egg or chick) predator. Aquatic birds that have no habitat overlap with magpies and introduced species have been excluded.

Species	Weight (g)				
brolga *Grus rubicunda*†	8700	f			
wedge-tailed eagle *Aquila audax*†	4200			pa	pn
straw-necked ibis *Threskiornis spinicollis*†	1500	f			
grass whistling-duck *Dendrocygna eytoni*†	1400				
purple swamphen *Porphyrio porphyrio*†	1050	f			
little eagle *Hieraaetus morphnoides*†	1000		n	pa	pn
sulphur-crested cockatoo *Cacatua galerita*†	975				
yellow-tailed black cockatoo *Calyptorhynchus funiereus*†	900				
peregrine falcon *Falco peregrinus*†	890			pa	
Pacific heron *Ardea pacifica*†	860		n		
harrier hawk *Circus approximans*†	850			pa	pn
whistling kite *Haliastur sphenurus*†	850		n	pa	pn
maned duck *Chenonetta jubata*†	800				
Australian kestrel *Falco cenchroides*†	800	f		pa	pn
spotted harrier *Circus assimilis*†	750		n	pa	pn
dusky moorhen *Gallinula tenebrosa*†	700				
grey goshawk *Accipiter novaehollandiae*†	680		n	pa	pn
Australian raven *Corvus coronoides*†	675	f	n		pn
bush stone-curlew *Burhinus grallarius*†	625	f			
brown falcon *Falco berigora*†	625		n	pa	pn
brown goshawk *Accipiter fasciatus*†	570		n	pa	pn
coot *Fulica atra*†	570				
little raven *Corvus mellori*†	567	f	n		
white-faced heron *Ardea novaehollandiae*†	550	f	n		
pied currawong *Strepera graculina*†	428	f	n		pn
spur-winged plover *Vanellus miles*†	400	f			
laughing kookaburra *Dacelo novaeguineae*†	380				pn
barn owl *Tyto alba*†	380				pn
white-winged chough *Corcorax melanorhamphus*†	371	f	n		
grey currawong *Strepera versicolor*†	365	f	n		pn
tawny frogmouth *Podargus strigoides*†	350	f	n		pn
common bronzewing *Phaps chalcoptera*†	350		n		
galah *Cacatua roseicapilla*†	330				
silver gull *Larus novaehollandiae*†	315	f			
boobook owl *Ninox novaeseelandiae*†	315	f			pn
black-shouldered kite *Elanus axillaris*†	300		n		pn

Table 6.1 cont.

Australian hobby *Falco longipennis*	290	f	n	pa	pn
king parrot *Alisterus scapularus*	275				
brush bronzewing *Phaps elegans*	260		n		
gang-gang cockatoo *Callocephalon fimbriatum*	250				
collared sparrowhawk *Accipter cirrhocephalus*	240		n	pa	pn
buff-banded rail *Gallirallus philippensis*	230				
Australian snipe *Gallinago hardwickii*	230				
banded plover *Vanellus tricolor*	200	f			
nankeen night-heron *Nycticorax caledonicus*	185	f	n		
crimson rosella *Platycercus elegans*	150				
dollarbird *Eurystomus orientalis*	143				
noisy friarbird *Philemon corniculatus*	122	f	n		
red wattlebird *Anthochaera carunculata*	120		n		
white-throated needletail *Hirundapus caudacutus*	120	f			
brown quail *Coturnix ypsilophora*	120	f			
magpie-lark *Grallina cyanoleuca*	118	f	n		
spotted quail-thrush *Cinclosoma punctatum*	114	f			
black-faced cuckoo-shrike *Coracina novaebollanandiae*	112	f	n		
eastern rosella *Platycercus eximius*	110				
stubble quail *Coturnix pectoralis*	110	f			
lewan water-rail *Rallus pectoralis*	100				
plains wanderer *Pedionomus torquatus*	95				
olive-backed oriole *Oriolus sagittatus*	95	f	n		
grey butcherbird *Cracticus torquatus*	92		n		pn
pallid cuckoo *Cuculus pallidus*	85	f			
noisy miner *Manorina melanocephala*	80		n		
grey-crowned babbler *Pomatostomus temporalis*	80	f	n		
musk lorikeet *Glossopsitta concinna*	70				
eastern whipbird *Psophodes olivaceus*	68	f	n		
red-backed parrot *Psephotus haematonotus*	65				
grey shrike-thrush *Colluricincla harmonica*	65				pn
sharp-tailed sandpiper *Calidris acuminata*	65				
crested bellbird *Oreoica gutturalis*	63	f	n		
blue-winged parrot *Neophema chrysostoma*	60				
fan-tailed cuckoo *Cacomantis flabelliformes*	50	f			
brown songlark *Cincloramphus cruralis*	50	f			
regent honey eater *Xanthomyza phrygia*	45		n		
white-browed babbler *Pomatostomus superciliosus*	42	f	n		
sacred kingfisher *Todiramphus sanctus*	40	f			pn
fork-tailed swift *Apus pacificus*	40				
little lorikeet *Glossopsitta pusilla*	40				
dusky woodswallow *Artamus cyanopterus*	39		n		
singing honeyeater *Lichenostomus virescens*	35		n		
white-browed woodswallow *Artamus superciliosus*	35		n		
Australian bee-eater *Merops ornatus*	30				
budgerigar *Melopsittacus undulatus*	30				
azure kingfisher *Alcedo azurea*	30				
Australian pipit *Anthus novaeseelandiae*	30	f			
crested shrike-tit *Falcunculus frontatus*	27		n		
white-eared honeyeater *Lichenostomus leucotis*	25		n		
golden whistler *Pachycephala pectoralis*	25	f	n		
shining bronze-cuckoo *Chrysococcyx lucidus*	25	f			
rufous whistler *Pachcyephala ruflventris*	25	f	n		
Horsfield's bronze-cuckoo *Chrysococcyx basalis*	23	f			
red-browed treecreeper *Climacteris erythrops*	23				
hooded robin *Melanodryas cucullata*	22	f	n		

Table 6.1 cont.

white-throated treecreeper *Cormobates leucophaeus*	22		
willie wagtail *Rhipidura leucophyrys*	21	f	n
New Holland honeyeater *Phylidonyris novaehollandiae*	20		n
eastern yellow robin *Eopsaltria australis*	20	f	n
striated fieldwren *Calamanthus fuliginosus*	20	f	n
restless flycatcher *Myiagra inquieta*	20	f	n
satin flycatcher *Myiagra cyanoleuca*	20		n
singing bushlark *Mirafra javanica*	20	f	
white-plumed honeyeater *Lichenostomus penicillata*	18.5		n
yellow-faced honeyeater *Lichenostomus chrysops*	17		n
fuscous honeyeater *Lichenostomus fuscus*	16		n
leaden flycatcher *Myiagra rubecula*	15		n
jacky winter *Microeca fascinans*	15		n
diamond firetall *Stagonopleura guttata*	15	f	
tree martin *Hirundo nigricans*	15		
welcome swallow *Hirundo neoxena*	14	f	n
white-naped honeyeater *Melithreptus lunatus*	14		n
brown-headed honeyeater *Melithreptus brevirostris*	14		n
flame robin *Petroica phoeicea*	13	f	n
scarlet robin *Petroica multicolor*	13	f	n
silvereye *Zosterops lateralis*	13		n
varied sittella *Daphoenositta chrysoptera*	13		
white-browed scrubwren *Sericornis frontalis*	13	f	n
white-fronted chat *Epthianura albifrons*	13	f	
southern whiteface *Aphelocephala leucopsis*	12.5	f	
superb fairy-wren *Malurus cyaneus*	12		n
striated pardalote *Pardalotus striatus*	12	f	
eastern spinebill *Acanthorhynchus tenuirostris*	11		n
tricoloured bush-chat *Epthianura tricolor*	11	f	n
grey fantail *Rhipidura fuliginosa*	10	f	n
rufous fantail *Rhipidura rufifrons*	10	f	n
fairy martin *Hirundo ariel*	10	f	n
red-browed firetail *Neochmia temporalis*	9	f	n
mistletoebird *Dicaeum hirundinaceum*	9		n
red-capped robin *Petroica goodenovii*	9	f	n
yellow-rumped thornbill *Acanthiza chrysorrhoa*	9	f	n
spotted pardalote *Pardalotus punctatus*	9		n
buff-rumped thornbill *Acanthiza reguloides*	8	f	
white-throated gerygone *Gerygone olivacea*	7		n
brown thornbill *Acanthiza pusilla*	7	f	n
striated thornbill *Acanthiza lineata*	7		n
yellow thornbill *Acanthiza nana*	7		n

Many exotic bird species were introduced, by the same societies responsible for the introduction of magpies, for the purpose of creating game hunting opportunities, helping control pest invertebrates, or making New Zealand resemble a landscape more closely aligned with the countries from which the colonisers had come (McDowall 1994; Wilson 2004). Over 130 bird species were introduced to New Zealand but of these only 39 have self-sustaining wild populations today (Wilson 2004). Most of these species are either large game birds or small passerines. Table 6.2 lists the common species (both introduced and native but excluding aquatic birds with little habitat overlap with magpie [see above]) counted in five rural locations across New Zealand, where magpies were also present and not controlled (i.e., at normal density), over four consecutive years (see Innes *et al.* 2004 for detailed survey methods). Two additional locally common species from regions not surveyed during Innes *et al.*'s (2004) study but known to contain magpies are also included in Table 6.2.

Most (22/26; 85%) rural New Zealand birds have some resource overlap with magpies (Table 6.2). Unlike Australia, however, just seven common rural species are magpie size or larger and only the harrier is a serious avian predator (Table 6.2). Harriers have been recorded taking mammalian prey up to c.3kg and birds up to c.800g (Marchant and Higgins 1993); however, there are no published accounts of adult magpies being taken. Smaller birds such as moreporks (*Ninox novaeseelandiae*) and kingfishers (*Halcyon sancta*) may occasionally prey on nest contents (Heather and Robertson 1996), although this was not recorded in a study designed to identify nest predators in rural areas (Chapter 4).

6.4 Adaptive significance of interspecific aggression

Attacking a wide range of other birds may have been adaptive for magpies during their evolutionary past and in this section three non-exclusive arguments are proposed to support this hypothesis.

1. Location of magpie habitat and its effect on territorial behaviour

Open woodland and grassland habitats prior to European arrival were predominantly found inland between the dense forest found at the margins of Australia and the arid centre (AUSLIG 1990). The location of these regions would have been affected by climatic variables such as lower annual rainfall, higher average temperatures, and frosts in winter (AUSLIG 1986). Magpies primarily forage on ground invertebrates (Vestjens and Carrick 1974; Veltman and Hickson 1989). Drier conditions often result in the decline of some invertebrate communities; for example, subterranean invertebrates such as earthworms will burrow deeper into the soil to avoid the dry top layer (Falk 1976;

O'Leary and Jones 2002). In addition, Carrick (1972) noted that during periods of hard frosts in his inland Australian study sites, the mortality rates of magpies that occupied open areas increased because they were unable to forage on the frozen ground while territorial birds that occupied areas with vegetation cover were largely unaffected.

Areas where there were an unpredictable, limited, or patchy distribution of food may have forced magpies to increase the size of breeding territories to ensure an adequate food supply was always maintained to support all group members and offspring. In other birds, territory size has been shown to fluctuate with food availability (e.g., nuthatches *Sitta europeae*; Enoksson and Nilson 1983). Although food addition experiments have been conducted on magpie populations (e.g., Veltman 1989a; Rollinson 2004), these studies did not examine the impact on territory size. Therefore, the effect of food availability on magpie territories is currently unknown. Several studies in Australia have attempted to measure territory size; however, results both within and across studies are highly variable and sizes between 2.2-24.3ha have been recorded (Carrick 1972; Shurcliff and Shurcliff 1974; Hughes *et al.* 1983; Hughes *et al.* 1996; Cox and Bauer 1997; Rollinson 2004). The proportion of available short grass has been suggested as an important factor that may influence magpie territory size (Hughes *et al.* 1983); for example, smaller territories generally have a high proportion of short grass (Rollinson 2004). This is probably because short grass provides suitable habitat for invertebrates and magpies are well adapted morphologically to forage on the ground. Long grass can also sustain high invertebrate densities (Falk 1976; Rollinson 2004), but magpies are generally not adept foragers in this habitat (Kaplan 2004; Rollinson 2004). Furthermore, Carrick (1972), who measured the size of magpie territories in an inland setting near Canberra, found that within his study sites the smaller territories (excluding those held by 'marginal groups') were those that had good feeding pasture (i.e., short grass) with moist and shade areas; this implies that these areas offered superior foraging opportunities. Carrick (1972) also noted that these smaller territories were always held by 'permanent groups' that were the most successful breeders. Although Australia has always had large grazing mammals (e.g., kangaroos), it is still likely that long grass was more common in open areas prior to the advent of agricultural practises and urbanisation, further suggesting that magpie territories were probably larger so residents could secure sufficient suitable foraging sites.

In addition, magpies are opportunistic feeders and are known to occasionally consume non-invertebrate food items including: seeds, frogs, house mice (*Mus musculus*), carrion, and bird eggs and nestlings (Vestjens and Carrick 1974; Brown and Veltman 1987; Sanders and Maloney 2002), although these non-preferred food items usually only supplement magpie diet (Vestjens and Carrick 1974). O'Leary and Jones (2002) found that during periods of drought discarded human food make up a significant proportion of food items (ca. 32%) consumed by urban magpies in Brisbane, Australia, presumably because their normal invertebrate food supply was scarce. This suggests that territory sizes may no longer have to be as large because magpies are currently able to exploit previously unavailable alternative food supplies in times when normal food supplies are scarce.

Bigger territories often require residents to spend a greater proportion of time defending longer boundaries, finding food, or in locomotion; often at the expense of maintenance behaviours such as preening or resting (Godfrey *et al.* 2003). Small, high quality territories may require similar amounts of time dedicated to defence as they would be highly valued by competitors because of superior food availability (Ens 1992). However, holders of such territories would not need to spend as much time foraging or searching for food, and so could spend more time on maintenance, defence, or raising young (Ens 1992; Godfrey *et al.* 2003). Magpies that displayed higher levels of aggression towards both conspecifics and other resource competitors would have been more successful at defending larger territories (or obtaining smaller high quality territories). Accordingly, this behavioural trait may have been selected for in magpie populations due to the associated adaptive advantages.

In New Zealand, only Veltman (1984) has measured magpie territory size; an average size of 5ha was reported. Although tentative due the small amount of data available in New Zealand, Veltman's (1984) findings are comparable with other contemporary

Table 6.2 Common rural birds recorded in five-minute bird counts from five regions in New Zealand (Innes *et al.* 2004). Species with * represent birds that are locally common in rural areas not surveyed by Innes *et al.* (2004). Birds are ordered from largest to smallest. † represent species that are approximately the same size or heavier (i.e., ≥300g) than magpies, ‘f’ indicates some dietary overlap with magpies (i.e., consume ground invertebrates as part of their diet), ‘n’ indicates same nest preference to magpie (i.e., above ground tree nesters not including birds that nest in hollows), ‘pa’ indicates potential predator of fledglings or adult magpies, ‘pn’ indicates potential nest (i.e., egg or chick) predator. Aquatic birds with habitat overlap with magpies have been included.

Species	Weight (g)				
paradise shelduck *Tadorna variegata*†	1700				
pheasant *Phasianus colchicus*†	1400	f			
mallard *Anas platyrhynchos*†	1300				
harrier hawk *Circus approximans*†	850	f		pa	pn
kereru *Hemiphaga novaeseelandiae*†	650		n		
pied oystercatcher* *Haematopus ostralegus finschi*†	550	f			
spur-winged plover *Vanellus miles*†	370	f			
morepork *Ninox novaeseelandiae*	175	f			pn
Indian myna *Acridothesres tristis*	125	f			
tui *Prosthemadera novaseelandiae*	120		n		
eastern rosella *Platycercus eximius*	110				
blackbird *Turdus merula*	90	f	n		
starling *Sturnus vulgaris*	85	f			
song thrush *Turdus philomelos*	70	f	n		
kingfisher *Halcyon sancta*	65	f			pn
skylark *Alanda arvensis*	38	f			
house sparrow *Passer domesticus*	30	f	n		
greenfinch *Carduelis chloris*	28		n		
yellowhammer *Emberiza citrinella*	27	f	n		
chaffinch *Fringilla coelebs*	22	f	n		
goldfinch *Carduelis carduelis*	16	f	n		
welcome swallow *Hirundo tahitica*	14				
silvereye *Zosteropus lateralis*	13		n		
redpoll* *Carduelis flammea*	12	f	n		
fantail *Rhipidura fuliginosa*	8		n		
grey warbler *Greygone igata*	6.5		n		

Australia studies (e.g., Hughes *et al.* 1996). The proportion of magpie territories in New Zealand that consist of short grass is currently is unknown; however, because most rural areas are under agricultural or horticultural management regimes [see above], the proportion of short grass (i.e., high quality foraging sites) in these areas is likely to be high, reducing the need for magpies to hold large territories to secure enough food.

2. Magpies evolved with many resource competitors

Many of the birds that coexisted with magpies during their evolutionary past probably competed for many of the same resources (Table 6.1). Competition would be exacerbated if resources were limited or distributed in patches. This may explain why breeding magpies defend territories all year. Economic explanations for why species become territorial state that the benefits acquired by defending a territory must outweigh the costs (Brown 1964). It would undoubtedly require a lot of energy for a magpie to defend a territory year round but this may have been necessary to ensure that access to sufficient resources was secured during the breeding season.

Table 6.1 indicates that magpies evolved in the presence of many large avian competitors. In addition, several predatory birds also competed with magpies for nesting sites (Table 6.1). This could have had major impacts on the foraging or nesting success of magpies as confrontations between individuals of different sizes generally results in the larger being the victor (Huntingford and Turner 1987). Recent experimental evidence has also shown that magpies usually lose confrontations with larger species over food but win against smaller species (Shelley *et al.* 2004). Evolving in a habitat shared by a number of large (and therefore dangerous) competitors suggests that magpie access to food or nest sites would have been restricted. Attacks on smaller birds to chase them out of a territory could have been very important for breeding magpies in order to secure the remaining resources not exploited by larger birds.

Many large avian competitors (along with several introduced species) still coexist with magpies in Australia, indicating that competition for resources at inland areas may continue to be a limiting factor, and reports of magpies attacking other resource competitors exist (e.g., Cox and Bauer 1997). However, in areas closer to the coast of Australia cleared of forest after European colonisation, competition for resources may no longer be as great because more favourable conditions provide increased amounts of available food (or alternative food sources), although it is unknown if rates of interspecific aggression are lower for these populations cf. inland populations. In addition, forest fragmentation and planted trees in many coastal areas has increased the amount of area suitable for magpies to hold breeding territories [see above].

In New Zealand, most of the birds that inhabit the same areas as magpies are smaller (Table 6.2). Territorial magpies attacked several different bird species on farmland west of Hamilton, New Zealand; magpies in non-breeding flocks were observed attacking only the predatory harrier (Chapter 3). Moreover, attacks were more frequent as the number of other birds in magpie territories increased, suggesting that defence of a resource (e.g., food) may have triggered agonistic encounters; most victims shared some degree of resource overlap (Chapter 3). However, other researchers have found that food availability is probably not a limiting factor in New Zealand; foraging success and food supply between flock and territorial magpies were found to be no different (Veltman and Hickson 1989), and the addition of food did not delay the dispersal of juveniles to nearby flocks or increase the reproductive success of breeding females (Veltman 1989a). Therefore, the adaptive benefit territorial magpies currently receive by attacking other birds in New Zealand would be minor if the amount of food removed by other birds was small when compared with the total amount of food available.

3. Response to predation threat

Although birds of all age classes are susceptible to predation, it is at the nesting stage that predators can cause the most significant losses (Martin 1991; Newton 1993). While eggs and young are particularly vulnerable, sitting birds are also in danger of being preyed on (O'Donnell 1996b; Sanders and Maloney 2002). Species that have evolved in the presence of high levels of predation often develop behaviours or alter certain life-history characteristics to reduce or minimise the effect predators have; for example, many species camouflage or lay nests inside tree cavities, possibly to reduce conspicuousness to potential predators; reducing clutch size or incubation time may mean nesting birds are able to relay multiple times over a season if initial nests are preyed on (Martin 1995).

Magpies have undoubtedly evolved in the presence of many avian predators that not only threaten eggs and offspring (e.g., currawongs *Strepera* spp. and grey goshawks *Accipiter novaehollandiae*) but also adult birds (e.g., wedge-tailed eagles *Aquila audax* and hawks *Circus* spp.) (Table 6.1). Predation has been implicated as a major cause of nesting failure in magpies in Australia, especially by the Australian raven (*Corvus coronoides*) and pied currawong (*Strepera graculina*) (Robinson 1956; Carrick 1972; Bayly and Blumstein 2001). Carrick (1972) also noted that adult and young magpies were also preyed on by raptors. Magpies have developed a number of anti-predator behaviours; for example, magpies unable to obtain a breeding territory often aggregate in non-territorial flocks (Carrick 1963, 1972; Brown and Veltman 1987), rather than living singly between territories. Birds may benefit from living in flocks through quicker detection of predators and the reduced probability of an individual being preyed on (Jullien and Clobert 2000). In addition, mobbing is common in magpies, and is a way in which much larger predators can be chased from a territory (Pavey and Smyth 1998). The risk of injury to a magpie associated with attacking a large raptor is high, especially as raptors can 'roll over' in flight to capture prey in their talons. Consequently, magpies have developed a coordinated attack strategy where birds will often remain on either side of raptors when mobbing so if the predator does roll to one side to capture a magpie, the opposing magpie can then counter-attack (Kaplan 2004).

The presence of avian predators may have influenced how magpies interact with other birds. Predators often aggregate in areas where high prey densities occur, to improve foraging success. Consequently, secondary or non-preferred prey may be taken incidentally when primary prey is abundant, or intentionally when the primary prey population becomes over-exploited (Schimdt 2004). Secondary prey species may try to reduce the risk of being taken by moving to areas where predators are not present, or by dispersing to reduce prey density (Lewis and Murray 1993). An area where prey density is below a forager's threshold level of patch acceptance is often referred to as 'enemy-free space' (Charnov 1976; Schimdt 2004). In some instances, however, it may not be possible for a prey species to move to areas with lower predation levels (e.g., if a species is territorial or breeding), in which case they may try to create an enemy-free space by excluding or reducing other prey species (i.e., 'apparent competition'; Holt 1977). Magpies may have attacked other birds simply because reducing the density of prey species could have resulted in fewer predatory species aggregating in their territory. For example, attacks on species such as rosellas (*Platycercus* spp.) and mallards (*Anas platyrhynchos*), which have little resource overlap with magpies but are regularly preyed on or have nests depredated by avian predators (Kaplan 2004; Chapter 4), could be explained by apparent competition. However, differentiating between agonistic behaviour caused by apparent and resource competition is often difficult (Begon *et al.* 1996) and this may be true for magpies (i.e., many species that share common predators with magpies also compete for the same resources).

High predation levels may have also made competition for resources between magpies and other birds more intense, especially during periods such as incubation and brooding. Female magpies generally do not receive help during incubation or chick rearing from other non-breeding group members (Veltman 1989b: but see Hughes *et al.* 1996). Therefore, it is important that when the female leaves the nest to either forage or collect food for chicks, she is able to locate these items quickly to reduce the amount of time the nest is undefended against predators. If many avian predators are in the area then being able to locate food items quickly has added importance. The presence of food competitors in a territory could further reduce the amount of food available or increase the amount of time that the female needs to spend away from the nest searching for food; thus, increasing the risk of predation to either herself or the nest contents. Reducing the numbers of competing species from a territory could increase food availability close to the nest, resulting in the female being able to spend more time protecting offspring at the nest.

6.5 How much can 'evolutionary conditioning' explain current magpie behaviour in New Zealand?

Magpies probably diverged from other Artamidae lineages 10MYA (Sibley and Ahlquist 1985). Several glacial and inter-glacial periods have occurred over this time, but for most of the Holocene the climate in Australia has been fairly constant with only gradual warming that has resulted in very slow changes in vegetation composition, although Aboriginal burning regimes promoted the fire tolerant species such as *Eucalyptus* spp. (AUSLIG 1990; Dodson 2001). However, Dodson (2001) points out that the speed of vegetation composition change caused by Aboriginal burning was comparatively slow compared with after European arrival. Determining the areas where magpies were most common and the species with which they shared these habitats during their evolutionary past is highly speculative. The above summary has been extrapolated by interpreting existing information on distribution and behaviour and assuming that magpie resource preference was similar in the past. This summary may be subject to criticism as not all research confirms the assumption that magpies were predominantly open habitat birds prior to European arrival (e.g., Kallioinen *et al.* 1995). Nevertheless, the current findings suggest that in New Zealand there were fewer avian predators and that resources may not have been as limiting as they were in Australia when magpies were first introduced. Moreover, the development of improved agricultural practices may have further increased food availability to magpies through the maintenance of well irrigated pasture. Consequently, the need for magpies to be especially aggressive towards a wide range of species, which was probably highly effective at securing adequate resources during their evolution, is not as great in New Zealand because: (1) most of the birds that coexist with magpies do not offer a serious injury threat to magpies (Table 6.2), and (2) resource availability (e.g., food) does not appear to be a limiting factor (Veltman and Hickson 1989). Therefore, the risk of injury to magpies attacking most other birds in New Zealand is low, the energy required to commit attacks would probably not exceed availability, and there are fewer avian predators in New Zealand, reducing the need for magpies to chase away other prey species to create an enemy-free space.

If interspecific aggression is no longer as important to magpies in New Zealand, why is this behaviour still very common? Several hypotheses are suggested that could be explored to examine why this behaviour persists:

1. Interspecific aggression is still adaptive for magpies

It has been suggested in this chapter that because of a wetter climate (most regions receive at least 800mm of rainfall per year; Kirkpatrick 2005) and modern agricultural practices that suit magpie habitat requirements, food is more readily available to magpies in New Zealand than during their evolutionary past in Australia. However, territorial magpies were more likely to chase away other birds (mainly small passerines) when increased numbers were recorded in their territory (presumably foraging) (Chapter 3). Accordingly, magpies may only tolerate high densities of other birds when the amount of food being removed from the territory was less than that amount required for an attack (Chapter 3). Further research, where food availability in magpie territories is manipulated and subsequent rates of interspecific aggression are measured, would help clarify the role competition for food has in causing attacks. That is, if magpies attack birds simply to defend a resource then rates of aggression should be negatively correlated with resource availability.

2. Magpies have not been in New Zealand for long enough for high levels of interspecific agonistic behaviour to be lost from the population

If no adaptive advantage is currently gained through attacking most other birds in New Zealand then over time magpies that are not aggressive may experience higher reproduction success and there could be a measurable change in rates of interspecific aggression. Lynch (1980) demonstrated that extreme levels of aggression can be selectively bred for in laboratory breeding trials involving mice. This experiment, however, was conducted over 15 continuous generations of mice (mice reach breeding maturity at 50 days), and only individuals displaying the most extreme levels of aggression were interbred. For magpies in New Zealand, breeding usually does not occur until at least three years of age (Heather and Robertson 1996) and in the wild many environmental variables may limit the speed that widely focused interspecific aggression is selected against. Magpies have only been in New Zealand since 1864 (Drummond

1907; Thomson 1922), which may not be long enough for this behaviour to be lost from the population.

3. Magpies currently face no selection pressure to alter their behaviour

This may be true if the environmental pressures magpies faced during their evolutionary past are no longer present, or are less prevalent, in current New Zealand populations. Species with the ability to adapt to changing environmental conditions will only do so if there is an appropriate selection pressure (i.e., increased fitness). Adaptive benefits that may be gained by magpies through the abstinence of conducting interspecific attacks on New Zealand birds appear to be few. This is probably because the costs of such exchanges are small. For example, attacks usually result in other birds being swooped or chased short distances; most New Zealand birds can be attacked with very little chance of the magpie being injured (Chapter 3). The benefits associated with attacking other birds [see above], even if very small, would be gained at little cost to the magpie. Therefore, magpie aggression may be close to neutral in evolutionary terms.

4. Interspecific aggression is a pleiotropic by-product of conspecific agonistic behaviour

Breeding magpies are highly territorial year round and regularly have to defend boundaries against intruding conspecifics (Robinson 1956, Carrick 1972; Brown and Veltman 1987). Clearly, individuals that were adept fighters would be more successful at defending a territory and would consequently be able to produce more offspring. Furthermore, territorial magpies attacked other birds; non-breeding magpies within flocks (which included magpies of all age classes) were only ever observed attacking the predatory harrier (Chapter 3). Individuals that are able to obtain and subsequently defend a breeding territory may be those that are generally better at fighting than those magpies of similar age that remain in a non-breeding flock. Accordingly, if the same genes responsible for maintaining conspecific aggression also promote interspecific aggression, regardless of whether this behavioural trait is currently unnecessary in New Zealand, it would be maintained because the net pleiotropic effect is beneficial (de Belle 2002).

6.6 Conclusion

Species adapt to environmental pressures through natural selection, which shapes the physiology, anatomy, and behaviour of individuals to maximise their fitness over very long periods of time (Wilson 1975). If magpies evolved in an environment where widely focused aggression was adaptive, this behaviour would have been selected for over many thousands of years. It is unlikely that magpies have lost the ability to reduce levels of interspecific aggression in New Zealand; however, if this behaviour has been selected for over evolutionary timescales, the relatively short amount of time since their introduction into New Zealand may mean that this behaviour has not had enough time to be lost from the population, especially if there is little selective pressure for magpies to stop interspecific attacks (i.e., the cost of aggression is very small). Therefore, if high levels of interspecific aggression are largely unnecessary in New Zealand magpie populations the number of attacks on other birds should eventually decline over time. Alternatively, if widely focused interspecific aggression is still adaptive in New Zealand magpie populations, or is a pleiotropic by-product of conspecific aggression, then this behaviour would be maintained.

6.7 Acknowledgements

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Chapter 7: Summary

Magpies are aggressive birds. Although it has been claimed that magpies have had a negative impact on the abundance and distribution of other birds, this claim was largely based on anecdotal evidence and has since been shown to be largely unfounded (Innes *et al.* 2004). Nonetheless, magpies have been frequently observed attacking other birds for reasons that are generally unknown. As such, this thesis aimed to: (1) document and describe interspecific aggression in magpies in order to identify ecological aspects of this behaviour, and (2), investigate possible mechanisms that may explain why magpies attack other birds.

7.1 Describing interspecific aggression in magpies

Collating published reports and accounts from a public survey (Chapter 2) revealed that 45 bird species have been observed being attacked by magpies; this is nearly an entire list of New Zealand's rural birds, as well as many other birds not common in this habitat. In addition, I also found or received accounts of other animals (e.g., livestock, domestic pets) and inanimate objects (e.g., cars, model aeroplanes) being attacked. Aggressive encounters between species are not uncommon, but usually occur between competitors for the same resource (Newton 1998), predators hunting prey (Curio 1976), or prey defending themselves from predatory attacks (Caro *et al.* 2004). Such a generalised attack regime, as observed in magpies, is highly unusual and has not been documented in many other species (but see Nuechterlein and Storer 1985).

In Chapter 2, species with similar habitat preferences to magpies were reported as being attacked more often. These findings are unsurprising as most reported attacks were observed in rural areas where magpies are most abundant. Furthermore, reported attacks occurred at all times of the year, although most fatal attacks occurred during the magpie breeding-season.

While the accounts of magpie attacks in Chapter 2 are valuable to describe the span of magpie behaviours, as a database it has several limitations for quantitative exploration because of the unstructured way that observations of attacks were obtained. Observed attacks were generally made by chance; therefore, attacks on large or conspicuous birds may have had a greater probability of being seen (and consequently reported) than attacks on smaller or cryptic birds. For example, the large number of reported attacks on harriers (*Circus approximans*) may have simply occurred because this species is highly visible in a rural landscape. Furthermore, species such as tui (*Prosthemadera novaeseelandiae*) and kereru (*Hemiphaga novaeseelandiae*) are relatively uncommon rural birds (Innes *et al.* 2004), but were in Attack Class 1; people observing attacks on these species may have been more motivated to send in accounts if they thought it may trigger some conservation action. I also had concerns that reported attacks may be biased toward the sensational as a high proportion of reported attacks involved the victim being seriously injured or killed. Moreover, I had no way of determining whether the proportions of each attack type were equally reported in the literature or public survey. In addition, I could not determine the proportion of birds that were not attacked by magpies from these reported accounts. It was therefore unclear if magpies attacked all birds in their territory, as Barrington (1995, 1996) has claimed. If this is indeed the case and over half of magpie attacks result in the victim being either seriously injured or killed: the impact magpies have on New Zealand's avifauna would be enormous. Finally, the reported accounts of magpie attacks could not identify which type(s) of magpies were committing attacks (e.g., male vs. female, adult vs. juvenile, territorial vs. flocking). Attacks on humans are nearly always conducted by males from territorial groups; territorial females sometimes join males in attacking humans but magpies from non-breeding flocks do not perform this behaviour (Jones 2002). This type of information relating to magpie attacks on other birds was previously unknown.

To address some of these concerns, in Chapter 3, I measured the proportion of birds that were attacked in comparison to the number of birds that flew or landed close to magpies from both territorial groups and non-breeding flocks. In addition, the context of magpie attacks was also investigated to determine the proportion of aggressive interactions that were non-contact, non-fatal contact, or fatal. I found that harriers were attacked more often than any other species by both territorial and flocking magpies (in 39% and 17% of appearances respectively), confirming this similar finding from Chapter 2. Harriers are the only important avian predator in rural areas (Heather and Robertson 1996) and attacks on this species by magpies were undoubtedly an anti-predator response [see below]. Harriers have also been observed being attacked or mobbed by other species in New Zealand (e.g., blackbirds *Turdus merula*, spur-winged plovers *Vanellus miles*, Indian myna *Acridotheres tristis*; Le Huquet 1961; Heather and Robertson 1996); however, of these, only the spur-winged plover was seen attacking harriers in Chapter 3.

Several other species were also observed being attacked by magpies during the research described in Chapter 3; however, attacks on these species were only conducted by territorial magpies and in just 8% of appearances. In addition, contact was never seen between magpies and any other species (including harriers) during any attacks. During interspecific attacks (excluding harriers) a single magpie would generally chase the victim short (50-100m) distances, which ended when the target flew out of the territory or into trees. Attacks on harriers, however, were usually longer in duration (sometimes >1min) and involved the target being repeatedly swooped by several magpies. This mobbing strategy has also been observed in other magpie populations and has been suggested as a way of reducing individual risk during attacks on dangerous species (Kaplan 2004). Both sexes were observed individually attacking other birds, but male magpies were responsible for about two thirds of attacks (when the sex could be determined). Juvenile birds were not seen initiating attacks, but sometimes joined adults during attacks on harriers. The results presented in Chapter 3 suggested that there was a bias for the public to report attacks that were 'sensational' as incidents where magpies seriously or fatally attacked other birds were in fact rare.

In Chapter 3, I also found that birds actively avoided landing close to both social groupings of magpies in comparison to adjacent control areas; fewer birds were recorded flying close to territorial magpies but there was no difference in birds flying close to non-breeding flocks compared with adjacent control areas. Birds may have avoided territorial magpies because both male and female magpies sometimes chased them. It should be noted that the cost of changing flight paths or foraging in areas 200-700m away to avoid territorial magpies is probably small for most species. However, birds also actively avoided foraging (but not flying) near non-breeding flocks, even though these magpies were never seen committing attacks (except on harriers). This finding suggested that birds were unable to distinguish between magpie social classes and avoid magpies equally. The finding that there was no difference between the number of birds flying close to flocks compared with control areas may be explained by these magpies few conspicuous behaviours cf. territorial magpies (Veltman 1984). Therefore, birds flying over a hilly farm may not be able to detect magpie flocks as quickly and adjust their flight paths to avoid them.

7.2 Reasons for interspecific aggression in magpies

7.2.1 Competition for resources

Competition for resources that are limited or have a patchy distribution has been shown to increase rates of interspecific aggression (Newton 1998). Accordingly, it is between species with large amounts of resource overlap that the highest rates of interspecific aggression are usually observed (Newton 1998). My research could not rule out competition for resources, such as food or nest sites, as a proximate cause for interspecific aggression in magpies. Magpies are tree nesters and generalist foragers that will exploit many other types of food when pasture invertebrates are less abundant (Vestjens and Carrick 1974; Brown and Veltman 1987). As such, most rural birds in New Zealand that were reported as attacked are potential resource competitors with magpies, if only in a small capacity (Chapter 2). In addition, interspecific attacks were only observed being committed by territorial magpies and attacks occurred more often when numerous birds were observed within magpie territories, further suggesting that competition for, or protection of, resources may have been a proximate cause for interspecific attacks (Chapter 3). Data presented in Chapter 6 indicated that magpies evolved in habitats where competition for limited resources was probably much greater than it is in New Zealand and individual magpies that displayed a highly generalised attack regime would have ultimately been more successful.

Conversely, I found that some birds with very little resource overlap have also been observed being attacked by magpies, including species that are generally not found in rural areas (Chapter 2). Detailed observations of magpie behaviour indicated that only small proportions (8%) of passing birds were actually attacked by territorial magpies (Chapter 3). If competition for resources was a main reason for interspecific aggression in magpies, then the proportion of attacks on species with very high amounts of resource overlap (e.g., starlings *Sturnus vulgaris*) would have outweighed those with less overlap (e.g., greenfinches *Carduelis chloris*). For example, least flycatchers (*Empidonax minimus*) were more likely to aggressively approach playback speakers broadcasting a resource competitor's song than a non-competitor's when the different vocalisations were played the same number of times to subjects (Martin *et al.* 1996). Close resource competitors, however, was not necessarily attacked more often by territorial magpies during the study described in Chapter 3. The abundance of species in rural areas appeared to be a better predictor of which birds were attacked the most; species that were most abundant were those attacked more often (excluding harriers) (Chapter 3).

Further research is needed to determine what role resource competition has in regulating rates of interspecific aggression in magpies. If resource availability was limited during the magpies' evolutionary past, then aggression associated with resource competition may have been selected in magpies for so long that the relatively short time they have been in New Zealand is not enough time for the behaviour to be lost from populations. Experiments where nest site or food availability is artificially increased would probably not reduce attacks because food availability does not appear to be a limiting factor in New Zealand as it may be in parts of Australia (see Veltman and Hickson 1989). Instead, artificially decreasing the availability of these resources may be a better way to test the impact resource competition has on regulating rates of interspecific aggression.

7.2.2 Predatory aggression

Although many accounts of magpies fatally injuring victims during interspecific attacks in New Zealand exist (Chapter 2), it is likely that these reports are biased toward the sensational and instances of such extreme aggression are rare. While magpies were occasionally observed eating their victims, two-thirds of adult birds killed were not consumed (Chapter 2), suggesting attacks on other birds were not motivated by predatory aggression. When territorial and flocking magpies were observed regularly over a year (ca. 114 observation hours), interspecific attacks on other birds by magpies never had a fatal conclusion (Chapter 3). My findings in Chapter 3 support previous research where, over 2500 magpie-hours of observation, magpie predation on adult birds was not seen (Barrington 1995).

While in Chapter 3, I found that the predation threat magpies presented to other adult birds in rural areas is small, that study could not determine if magpies were a serious threat to the nesting success of other birds. Although members of the public have sometimes observed magpies preying on nest contents (Chapter 2), scientific studies have shown that magpies are not important nest predators in New Zealand (e.g., Brown 1997; Innes *et al.* 1999). However, these studies were not conducted in rural ecosystems where magpies are most abundant. Sanders and Maloney (2002) reported that in their braided river terrace study areas, magpies were not abundant but were recorded preying on a banded dotterel (*Charadrius bicinctus*) nest containing chicks, implying that if magpies were in larger numbers then they may have been responsible for more lethal events. In Chapter 4, I monitored 38 rural bird nests over two consecutive breeding seasons and 22 lethal events were filmed; magpies were only responsible for one of these. Accordingly, I concluded that it was unlikely magpies are serious predators in rural areas, although this result may be tentative because of the small sample size. Only by conducting further nest monitoring trials in rural areas where all bird nests in an area are filmed will the importance of magpies as a nest predator be better understood (Brown 1997).

7.2.3 Anti-predatory aggression

In New Zealand, attacks by magpies on most birds can not be explained as an anti-predator response because harriers are the only important avian predator in rural areas, although moreporks (*Ninox novaeseelandiae*), kingfishers (*Halcyon sancta*), and pukeko (*Porphyrio porphrio*) occasionally prey on nest contents or small birds (Marchant and Higgins 1993; Heather and Robertson 1996; Chapter 4). Furthermore, of the 45 species reported as attacked by magpies, the only other important predator was the New Zealand falcon (*Falco novaeseelaniae*) (Chapter 2). Most of the birds attacked do not threaten magpies and attacks occurred at all times of the year, not just when magpies were nesting (Chapters 2 and 3).

Magpies have undoubtedly evolved in the presence of many avian predators (Chapter 6). Consequently, many of their current behaviours may reflect this previous predation threat; for example, co-ordinated mobbing attacks on raptors (Kaplan 2004; Chapter 3), a higher proportion of attacks on harriers (cf. other species) (Chapter 3), and non-breeders aggregating in flocks (Veltman 1989b; Chapter 3). In addition, in Chapter 6, I explored the hypothesis that high predation rates may have promoted attacks on other prey birds in order to create enemy-free spaces (Charnov 1976; Schmidt 2004) for territorial magpies. Reducing prey density may have had adaptive benefits for sedentary magpies as it would have also reduced the number of avian predators that aggregated in their territories. Moreover, many prey species that evolved with magpies were also resource competitors. Reducing the density of these species within magpie territories would therefore not only increase food availability but also enable residents to locate food items quickly to further help avoid avian predators or spend more time protecting offspring at the nest (Chapter 6).

7.2.4 Redirected aggression

After agonistic encounters with conspecifics, subjects sometimes attack a third party that was not the initial source of provocation; often referred to as 'displaced' or 'redirected aggression' (Bastock *et al.* 1953; Marcus-Newhall *et al.* 2000). Magpies have been observed chasing and attacking other birds and mammals after territorial disputes (Brown and Veltman 1987), but whether these reported attacks were triggered by the previous dispute, or another undocumented reason was unknown. In Chapter 5, I tested whether attacks on benign species occurred more often after simulating territorial intrusions using caged magpie decoys. While magpie decoys were always attacked by both male and female residents, attacks on pigeon decoys or other free-ranging birds (excluding other magpies and harriers) were never observed. It was possible, however, that the proportion of territorial disputes that result in redirected attacks are small, or only occur under highly specific circumstances, which were not recognised in the current study.

7.3 Conclusion

My research has determined that there are several different and mutually non-exclusive mechanisms that may explain interspecific aggression by magpies in New Zealand. Resource competitors, avian predators, and benign species are all occasionally attacked by magpies in New Zealand; however, circumstances under which attacks occur appear to be highly variable. Therefore, widely focused interspecific aggression by magpies may be best explained as a behaviour that was previously effective at securing resources or protection from threats during their evolution. This behaviour may or may not still confer improved fitness in New Zealand magpie populations.

7.3.1 Further research on magpie interspecific aggression in New Zealand

It is currently unknown if there are differences in rates of interspecific aggression between New Zealand and Australian magpie populations. Farabaugh *et al.* (1992) found that the aggressive response to simulated conspecific territorial intrusions was higher for rural Queensland, Australia, magpies than rural magpies in Manawatu, New Zealand; however, the response to hetrospecific intruders was not measured in her study. Therefore, conducting a comparative behavioural experiment where rates of interspecific aggression are compared between magpie populations in New Zealand and Australia may help determine if the apparent increase in resource availability in New Zealand (see Chapter 6) has affected magpie behaviour.

Manipulating magpie resources (e.g., food, nest sites) may be another way to further investigate the reason(s) why magpies attack other birds. Although magpies appear to no longer have as many environmental limitations in New Zealand (Chapter 6), attacks on other birds still occur; accordingly, increasing the availibility of resources would probably not stop interspecific attacks. However, if resource availibility in magpie territories was artificially reduced and subsequent rates of interspecific aggression measured, the role that competition for resources has in causing attacks could be clarified. In additition, the hypothesis that indivduals expressing high rates of interspecific aggression have higher reproductive success than less aggressive individuals could also be tested through resource manipulation.

7.4 Implications for magpie management

In New Zealand, magpies are easily recognisable due to their large size and highly conspicuous behaviours (Brown and Veltman 1987). When magpies do chase or attack other birds, the probability of the event being observed by a member of the public is high. In contrast, attacks by other introduced species often go unnoticed due to the culprit being cryptic, stealthy, or nocturnal (e.g., mustelids, cats, rodents). Furthermore, many people enjoy magpie carolling, magpies can become attentive pets, and they are perceived to help control pasture invertebrate pests. As such, the public's perception of magpies as a pest species is often divided and they have both advocates and enemies throughout New Zealand.

7.4.1 Further research on magpie impacts in New Zealand

Innes *et al.* (2004) recommended that large-scale magpie control programs should not be undertaken to promote bird communities in rural areas as most (18/24; 75%) monitored species did not increase after magpie removal; changes of those species that did increase were small, and the result may have reflected a 'conspicuousness' change rather than a change in abundance. In other New Zealand ecosystems, significant increases in the survival and recruitment of numerous bird species have been recorded following control operations where specific introduced mammalian pests were targeted (see Veitch *et al.* 1992). Clearly, the observed avifauna response to magpie removal reported by Innes *et al.* (2004) was unexceptional when compared with mammalian control operations, indicating that magpies are not currently as significant a threat to other New Zealand birds.

I found that on a local-scale (200-700m), birds do actively avoid magpies. The detrimental impact that localised displacement may have on rural birds is currently unknown; however, for most rural species it is likely to be negligible (Chapter 3). In contrast, native species such as tui and kereru, that have more specialised resource requirements, may incur large fitness costs due to displacement as suitable foraging or nesting areas may be long distances away. Further research is required to determine the impact magpies are having on both introduced and native birds in localised areas (e.g., in bush remnants or at forest edges). One possible way of measuring magpie impact on a small-scale would be to intensively control magpies only around small bush remnants or forest edges adjacent to pasture; thus, providing suitable magpie-free nesting and feeding habitat to highly valued species such as tui and kereru. In order to quantify the effect localised magpie removal has on bird communities, monitoring should also be concentrated at a localised level (i.e., only around areas where control has been done). Additional monitoring of bird movements after localised magpie control had ended would be useful in determining displacement rates (and where displaced birds go) as magpies recolonise these areas. Thus, information on appropriate levels of magpie management could be provided to managers in areas where magpies are currently not present or in low numbers (e.g., northwest South Island).

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Appendices

Appendix 1 Abundance of all birds reported as being attacked by magpies in various habitats. Species are ordered from most to least attacked. Magpies are also listed at bottom of table. (*Key: 3=where largest numbers are found, 2=commonly found, 1=reported as occurring, but not common, 0=very rarely or never found here; rural= developed farmland/hedgerows/wetlands/small settlements, urban= cities/city parks/ towns, coastal= beaches/estuary, native forest= predominantly native forest, exotic forest= predominantly exotic forest, forest edge= edge of forests or small patches of bush/trees* [*i.e. remnants*], *alpine= above the tree line*).

	Habitat type						
	Rural	Urban	Coastal	Native forest	Exotic forest	Forest edge	Alpine
harrier hawk *Circus approximans*	3	1	0	1	1	2	0
blackbird *Turdus merula*	3	3	0	2	2	2	0
song thrush *Turdus philomelos*	3	3	0	1	2	2	0
kereru *Hemiphaga novaeseelandiae*	2	0	0	3	1	2	0
house sparrow *Passer domesticus*	3	3	1	1	1	2	0
white-faced heron *Ardea novaehollandiae*	3	1	2	0	0	0	0
bellbird *Anthornis melanura*	2	1	1	3	1	2	0
skylark *Alanda arvensis*	3	1	0	0	0	1	0
chicken *Gallus gallus domesticus*	3	0	0	0	0	0	0
kingfisher *Halcyon sancta*	3	1	2	2	2	2	0
pipit *Anthus novaeseelandiae*	3	1	2	0	0	1	1
tui *Prosthemadera novaseelandiae*	2	1	1	3	1	2	0
black-backed gull *Larus dominicanus*	2	1	3	0	0	0	0
goldfinch *Carduelis carduelis*	3	3	0	0	0	2	0
pheasant *Phasianus colchicus*	3	0	0	0	2	1	0
pukeko *Porphyrio porphyrio*	3	2	1	0	0	1	0
rock pigeon *Columba livia*	1	3	1	0	0	0	0
silvereye *Zosteropus lateralis*	2	3	0	3	3	2	0
starling *Sturnus vulgaris*	3	2	1	1	1	2	0
paradise shelduck *Tadorna variegata*	3	0	1	0	0	0	0
spur-winged plover *Vanellus miles*	3	2	2	1	1	1	0
black shag *Phalacrocorax carbo*	2	1	3	0	0	0	0
chaffinch *Fringilla coelebs*	3	2	0	1	2	1	0
fantail *Rhipidura fuliginosa*	2	2	0	3	2	2	0
little owl *Athene noctua*	3	2	0	0	0	2	0
grey warbler *Greygone igata*	2	1	0	3	2	2	0
mallard *Anas platyrhynchos*	3	3	2	0	0	1	0
morepork *Ninox novaeseelandiae*	2	1	0	3	3	2	0
yellowhammer *Emberiza citrinella*	3	2	0	0	0	1	0
banded dotterel *Charadrius binictus*	2	0	3	0	0	0	0
black-fronted tern *Sterna albostriata*	1	0	3	0	0	0	0

Appendix 1 cont.

canary *Serinus canaria*	0	0	0	0	0	0	0
cattle egret *Bubulcus ibis*	3	0	1	0	0	0	0
Indian myna *Acridothesres tristis*	3	3	1	1	1	1	0
kaka *Nestor meridionalis*	0	0	0	3	1	1	0
kea *Nestor notabilis*	0	0	0	3	0	1	3
kokako *Callaeas cinerea*	0	0	0	3	0	1	0
long-tailed cuckoo *Eudynamys taitensis*	0	0	0	3	1	1	0
New Zealand dotterel *Charadrius obscurus aquilonius*	0	0	3	0	0	0	0
New Zealand falcon *Falco novaeseelandiae*	1	1	1	3	1	2	1
California quail *Callipepla californica*	3	0	0	0	2	1	0
red-billed gull *Larus novaeseelandiae*	2	2	3	0	0	0	0
eastern rosella *Platycercus eximius*	3	1	0	2	2	2	0
spotted turtle-dove *Streptopelia chinensis*	1	3	0	0	0	0	0
tomtit *Petroica macrocephala*	1	1	0	3	1	2	0
magpie *Gymnorhina tibicen*	3	2	0	1	1	2	0

Appendix 2 Diet of birds reported as being attacked by magpies. Species are ordered from most to least attacked. Magpies are also listed at the bottom of table. (Key: 3= *main component of diet, 2= commonly consumed, 1= known to consume, but not common, 0= not known to consume; "aquatic invertebrates" includes both freshwater and marine invertebrates, "small mammal and reptile" include mammals and reptiles ≤2kg, "large mammal" includes mammals >2kg).*

	Food Type												
	Open/pasture invertebrate	Forest invertebrate	Aquatic invertebrate	Carrion	Birds	Eggs	Small mammal and reptile	Large mammal	Fish	Plant leaves, buds, bark	Fruit	Nectar	Seeds
harrier hawk *Circus approximans*	2	0	0	2	3	2	3	3	2	0	0	0	0
blackbird *Turdus merula*	3	2	0	0	0	0	0	0	0	3	3	0	3
song thrush *Turdus philomelos*	3	2	0	0	0	0	0	0	0	3	3	0	3
kereru *Hemiphaga novaeseelandiae*	0	0	0	0	0	0	0	0	0	2	3	1	1
house sparrow *Passer domesticus*	2	0	0	0	0	0	0	0	0	1	1	0	3
white-faced heron *Ardea novaehollandiae*	3	0	3	0	0	0	2	0	2	0	0	0	0
bellbird *Anthornis melanura*	0	2	0	0	0	0	0	0	0	2	2	3	2
skylark *Alanda arvensis*	0	0	0	0	0	0	0	0	0	0	0	0	0
chicken *Gallus gallus domesticus*	2	0	0	0	0	0	0	0	0	1	0	0	0
kingfisher *Halcyon sancta*	3	3	2	0	2	0	2	0	2	0	0	0	0
pipit *Anthus novaeseelandiae*	3	0	0	0	0	0	0	0	0	0	0	0	0
tui *Prosthemadera novaseelandiae*	0	2	0	0	0	0	0	0	0	2	2	3	2
black-backed gull *Larus dominicanus*	2	0	2	2	0	0	0	1	2	0	0	0	0
goldfinch *Carduelis carduelis*	2	0	0	0	0	0	0	0	0	0	0	0	0
pheasant *Phasianus colchicus*	2	0	0	0	0	0	0	0	0	3	2	0	2
pukeko *Porphyrio porphyrio*	2	0	1	0	1	1	1	0	1	3	1	0	1
rock pigeon *Columba livia*	0	0	0	0	0	0	0	0	0	1	0	0	0
silvereye *Zosteropus lateralis*	0	3	0	0	0	0	0	0	0	2	2	2	2
starling *Sturnus vulgaris*	3	0	0	0	0	0	0	0	0	3	3	2	3
paradise shelduck *Tadorna variegata*	1	0	1	0	0	0	0	0	0	3	1	0	1
spur-winged plover *Vanellus miles*	3	0	1	0	0	0	1	0	0	1	0	0	0
black shag *Phalacrocorax carbo*	0	0	0	0	0	0	0	0	3	0	0	0	0
chaffinch *Fringilla coelebs*	2	2	0	0	0	0	0	0	0	3	2	0	2
fantail *Rhipidura fuliginosa*	1	3	0	0	0	0	0	0	0	2	2	0	2
little owl *Athene noctua*	3	0	0	0	1	0	1	1	0	0	0	0	0
grey warbler *Greygone igata*	0	3	0	0	0	0	0	0	0	1	1	0	1
mallard *Anas platyrhynchos*	1	0	0	0	0	0	0	0	0	3	0	0	3
morepork *Ninox novaeseelandiae*	1	3	0	0	2	0	2	0	0	0	0	0	0
yellowhammer *Emberiza citrinella*	2	0	0	0	0	0	0	0	0	0	0	0	0
banded dotterel *Charadrius binictus*	2	0	3	0	0	0	0	0	0	0	1	0	1
black-fronted tern *Sterna albostriata*	1	0	3	0	0	0	0	0	2	0	0	0	3
canary *Serinus canaria*	0	0	0	0	0	0	0	0	0	0	0	0	0
cattle egret *Bubulcus ibis*	3	0	0	0	0	0	1	0	0	0	0	0	0

Appendix 2 cont.

Indian myna *Acridothesres tristis*	3	0	0	0	1	1	1	0	0	3	3	0	3
kaka *Nestor meridionalis*	0	3	0	0	0	0	0	0	0	2	3	3	3
kea *Nestor notabilis*	0	0	0	1	0	0	0	0	0	3	3	0	3
kokako *Callaeas cinerea*	0	2	0	0	0	0	0	0	0	3	3	0	3
long-tailed cuckoo *Eudynamys taitensis*	0	3	0	0	1	1	1	0	0	0	0	1	0
New Zealand dotterel *Charadrius obscurus aquilonius*	0	0	3	0	0	0	0	0	1	0	0	0	0
New Zealand falcon *Falco novaeseelandiae*	0	0	0	0	3	0	3	3	0	0	0	0	0
California quail *Callipepla californica*	1	0	0	0	0	0	0	0	0	2	0	0	3
red-billed gull *Larus novaeseelandiae*	1	0	0	1	0	1	0	0	3	0	0	0	0
eastern rosella *Platycercus eximius*	1	0	0	0	0	0	0	0	0	3	3	0	3
spotted turtle-dove *Streptopelia chinensis*	0	0	0	0	0	0	0	0	0	0	0	0	0
tomtit *Petroica macrocephala*	0	3	0	0	0	0	0	0	0	2	0	0	0
magpie *Gymnorhina tibicen*	3	0	0	1	1	1	1	0	0	0	0	0	2

Appendix 3 Weight categories of all birds reported as being attacked by magpies.

<60g	60-200g	201-800g	>800g
banded dotterel *Charadrius binictus*	blackbird *Turdus merula*	cattle egret *Bubulcus ibis*	black shag *Phalacrocorax carbo*
bellbird *Anthornis melanura*	black-fronted tern *Sterna albostriata*	kaka *Nestor meridionalis*	black-backed gull *Larus dominicanus*
canary *Serinus canaria*	California quail *Callipepla californica*	kereru *Hemiphaga novaeseelandiae*	chicken *Gallus gallus domesticus*
chaffinch *Fringilla coelebs*	eastern rosella *Platycercus eximius*	kokako *Callaeas cinerea*	harrier hawk *Circus approximans*
fantail *Rhipidura fuliginosa*	Indian myna *Acridotheres tristis*	New Zealand falcon *Falco novaeseelandiae*	kea *Nestor notabilis*
goldfinch *Carduelis carduelis*	kingfisher *Halcyon sancta*	red-billed gull *Larus novaeseelandiae*	mallard *Anas platyrhynchos*
grey warbler *Gerygone igata*	little owl *Athene noctua*	rock pigeon *Columba livia*	paradise shelduck *Tadorna variegata*
house sparrow *Passer domesticus*	long-tailed cuckoo *Eudynamys taitensis*	spur-winged plover *Vanellus miles*	phesant *Phasianus colchicus*
pipit *Anthus novaeseelandiae*	morepork *Ninox novaeseelandiae*	white-faced heron *Ardea novaehollandiae*	pukeko *Porphyrio porphyrio*
silvereye *Zosterops lateralis*	New Zealand dotterel *Charadrius obscurus aquilonius*		
skylark *Alauda arvensis*	song thrush *Turdus philomelos*		
tomtit *Petroica macrocephala*	spotted turtle-dove *Streptopelia chinensis*		
yellowhammer *Emberiza citrinella*	starling *Sturnus vulgaris*		
	tui *Prosthemadera novaseelandiae*		

Appendix 4 Mean occurrence (birds.hr^{-1}) of each bird species recorded flying and landing in areas with (trt) and without (crtl) magpies from territorial breeding groups and non-breeding flocks.

	Territorial groups				Non-breeding flocks			
	flyovers		landings		flyovers		landings	
	trt	crtl	trt	crtl	trt	crtl	trt	crtl
black shag *Phalacrocorax carbo*	0.02	0.02	0	0	0.02	0	0	0.02
blackbird *Turdus merula*	0.30	0.38	0.07	0.27	0.12	0.19	0.02	0.15
chaffinch *Fringilla coelebs*	0.37	0.43	0.10	0.23	0.28	0.27	0.09	0.12
eastern rosella *Platycercus eximius*	0.07	0.32	0.19	0.09	0.07	0.10	0	0
fantail *Rhipidura fuliginosa*	0.26	0.2	0.42	0.78	0	0.12	0.03	0.48
goldfinch *Carduelis carduelis*	1.43	2.29	0.14	0.88	1.41	1.59	0.36	0.51
greenfinch *Carduelis chloris*	0.30	0.38	0.03	0.27	0.28	0.32	0.24	0.09
grey warbler *Greygone igata*	0	0.02	0	0.03	0.07	0	0	0
harrier hawk *Circus approximans*	0.49	0.47	0.05	0.15	0.59	0.22	0.23	0.07
house sparrow *Passer domesticus*	0.54	0.9	0.14	0.78	0.36	0.67	0.17	0.55
Indian myna *Acridothesres tristis*	0.33	0.34	0.10	0.14	0.16	0.29	0.02	0.07
kereru *Hemiphaga novaeseelandiae*	0.21	0.14	0.03	0.17	0	0.10	0	0
kingfisher *Halcyon sancta*	0.10	0.08	0.07	0.26	0.02	0.05	0	0.24
mallard *Anas platyrhynchos*	0	0.06	0	0	0	0	0	0.02
New Zealand falcon *Falco novaeseelandiae*	0.02	0	0	0	0	0	0	0
paradise shelduck *Tadorna variegata*	0.14	0.11	0.07	0	0.23	0.09	0.10	0.02
pheasant *Phasianus colchicus*	0.03	0.02	0.02	0.03	0	0	0	0.02
pukeko *Porphyrio porphyrio*	0	0	0	0.05	0	0.03	0	0.09
silvereye *Zosteropus lateralis*	0.03	0.06	0.02	0.15	0	0.03	0	0.02
skylark *Alanda arvensis*	0.02	0.06	0	0.14	0.07	0.27	0.07	0.68
song thrush *Turdus philomelos*	0.05	0.05	0.03	0.11	0.05	0.03	0	0.05
spur-winged plover *Vanellus miles*	0	0.02	0.05	0.02	0	0.10	0.10	0.19
starling *Sturnus vulgaris*	2.49	2.62	0.71	1.11	2.85	1.66	0.85	1.06
tui *Prosthemadera novaseelandiae*	0	0.02	0	0.02	0	0.03	0	0
welcome swallow *Hirundo tahitica*	1.05	2.61	0.31	0.85	2.59	3.42	0.76	2.09
white-faced heron *Ardea novaehollandiae*	0	0	0	0	0	0	0	0.02
yellowhammer *Emberiza citrinella*	0.92	1.34	0.21	0.81	0.78	0.72	0.21	0.96
unknown	1.86	1.25	0.19	0.14	0.89	0.74	0.02	0.39
unknown finch	0.49	0.37	0.02	0.02	0.43	0.07	0.02	0