

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

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Summary

Attacks by participants of conflicts against a third party are referred to as redirected aggression. Usually the third party is a conspecific — few documented cases of redirected aggression against other species exist. The Australian magpie (*Gymnorhina tibicen*), however, often attacks other species; the reasons for attacks are largely unknown. Some attacks occur after territorial disputes with conspecifics, suggesting that attacks are the result of redirected aggression. We subjected eight Australian magpie groups to simulated territorial intrusions. In one treatment an Australian magpie and rock dove (*Columba livia*) were presented in cages next to one another (5 m apart) on the territory for 30 min; the Australian magpie decoy was then covered and aggressive responses toward the rock dove by residents were recorded for a further 30 min (Treatment 1). Two additional treatments were presented in an identical manner on each territory where both decoys were either Australian magpies (Treatment 2) or rock doves (Treatment 3). We predicted that if Australian magpies regularly redirect aggression onto benign species after conspecific territorial intrusions, attack rates on the rock dove decoy in Treatment 1 would be higher than attack rates on the rock dove decoy in Treatment 3. Residents were seldom recorded close (<1 m) and not seen attacking rock dove decoys during tests. In contrast, Australian magpie decoys were often approached and attacked by residents. After a decoy was covered (following the first 30 min phase), residents spent little time in close proximity (on cage, <0.3 m, or 0.3-1 m) to the rock dove decoy in either Treatment 1 or Treatment 3; in contrast, residents were often recorded close to the Australian magpie decoy in Treatment 2. We found no evidence that Australian magpies redirect aggression onto other birds after territorial intrusions. The true proportion of territorial disputes leading to redirected attacks may be small, or only occur under highly specific contexts.

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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. The targets of displaced aggression include: (i) objects (e.g., great tits (*Parus major*) and blackbirds (*Turdus merula*) may aggressively peck the ground or twigs instead of an opponent during an aggressive interaction; Hinde, 1952; Tinbergen, 1966), (ii) conspecifics (e.g., primates may attack 'innocent' group members after losing conflicts with other conspecifics; Cheney et al., 1989; Aureli et al., 1993; Virgin & Sapolsky, 1997; Wittig & Boesch, 2003) and/or (iii) heterospecifics (e.g., male black-headed gulls (*Larus ridibundus*) have conflicting attack, escape and sex drives when visited by a female during pair formation, and often attack nearby gulls, other birds, or humans during the visit; Bastock et al., 1953). Our primary focus in the present study was on redirected aggression involving heterospecifics.

Several hypotheses have been developed to explain redirected aggression. For example, redirected aggression during competitive interactions may reduce aggression-induced stress (Bastock et al., 1953; Virgin & Sapolsky, 1997), potentially allowing the animal to improve its cognitive performance during the rest of the interaction. Alternatively, when attacking a provoking agent risks injury, animals may chastise weaker individuals to express their aggressive state more safely (Marcus-Newhall et al., 2000). 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) and may not have functional value. For example, domestic house cats (*Felis catus*) may attack their owners after seeing other cats through a window (Chapman & Voith, 1990; Beaver, 2004). An animal exposed to a highly threatening stimulus may become physiologically and mentally 'primed' to act; the inability to access the stimulus may eventually lead to the 'release' of an aggressive act as a form of vacuum behaviour (Craig, 1918; Lorenz, 1950).

Research investigating proximate processes associated with redirected aggression could have a profound impact on our understanding of why many species show displaced acts of aggression. Here we investigate processes that may explain why Australian magpie (*Gymnorhina tibicen*; magpie hereafter) regularly attack a wide range of non-threatening heterospecifics (McCaskill, 1945; Jones, 2002; Morgan et al., 2005); 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 (Morgan et al., 2005). Brown & Veltman (1987) report attacks on heterospecifics often occur after territorial disputes and suggest redirected aggression as a cause, but little detail on the interactions was provided. We used both live conspecific decoys and benign heterospecific decoys (rock doves, *Columba livia*) to 'prime' territory holders, and then measured their subsequent responses to another rock dove or magpie. If residents redirect aggression after territorial intrusions, rock doves should attract more aggression after residents were primed with a magpie decoy than with a rock dove decoy; however, if no difference is found, a priming effect associated with territorial intrusions could be dismissed as a proximate cause of redirected aggression in magpie and other causes would need to be explored.

Methods

Study area and subjects

Eight territorial groups located on two farms within the Waikato region, New Zealand (37°47'S, 175°20'E) were selected for study. Other territorial 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 60-100 m away where an observer could maintain visual contact throughout the test.

Magpies have a complex social system and year-round territories are defended against intruding conspecifics by groups of 2-26 birds (Robinson, 1956; Carrick, 1972; Veltman, 1989; Hughes & 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 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. All members of a territory can be involved in its defence; however, it is the most dominant individuals (i.e., the breeding male and most dominant female in our study) that are more aggressive in such exchanges (Farabaugh et al., 1992; Kaplan, 2004). Thus, we considered the groups to be our statistical unit for the main analyses. We later compared the male and female responses to provide additional detail on their individual roles during intrusions (see below). 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., <1 m; see below), and did not attack decoys. All territories were separated by at least one other magpie territory or distances of at least 500 m to reduce the possibility of pre-exposure of subjects to treatments.

Study design

Treatments were conducted between 23 Mar 2004 and 25 April 2004 on days that were not excessively windy or wet. At each territory, two cages ((a) and (b); 30 × 60 × 30 cm high) were placed 5 m apart, each containing either a live adult female magpie decoy or live adult rock dove decoy of unknown sex. Cages were placed in suitable areas (see above) as close to the centre of each territory as possible (note, however, that Farabaugh et al. (1992) found that magpies' response to an intrusion was similar regardless of where it occurred on the territory). Caged magpie decoys have been used previously to successfully provoke territorial responses in resident magpies (Farabaugh et al., 1992). Rock doves were used as controls because they: (1) are common birds in New Zealand (Heather & Robertson, 1996), which were likely to be familiar to resident magpies in our trial, (2) have been reported as being attacked by magpies in the past (Morgan et al., 2005) and (3) share little resource overlap with magpies (Heather & Robertson, 1996), so any observed attacks could not have been interpreted as defence of a resource. We used three different magpie and four different rock dove decoys in the study, rotating the animals used in each test to reduce the chances of subjects being exposed to the same decoys in subsequent tests. 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 60-100 m away, to cover decoy (a) during the

test. Each test lasted for 60 min, and was considered started when a resident magpie came within 15 m of either cage. After 30 min, decoy (a) was covered by the box, leaving decoy (b) exposed for the remaining 30 min.

To determine if magpies will redirect aggression towards a benign bird species, three variables (latency to respond, frequency of aggressive strikes, and percent of observations close the decoy (see below)) were measured. In Treatment 1, decoy (a) was a magpie and decoy (b) was a rock dove. Thus, residents were exposed to a 30-min phase where both a magpie and rock dove were present on their territory followed by a 30-min phase when only the rock dove was visible (Table 1). The function of the first phase of this treatment was to ‘prime’ residents into a highly aggressive state using a conspecific decoy and to determine if some of the aggression would be transferred to the neighbouring rock dove decoy. The function of the second phase was to determine if the ‘primed’ resident birds would direct aggressive acts towards the heterospecific in the absence of a magpie. In Treatment 2, the same protocol was followed but decoy (a) and (b) were both magpies while in Treatment 3, both were rock doves (Table 1). These additional treatments were conducted to determine if residents’ responses tended to wane across phases (Treatment 2) and the level of response elicited in the complete absence of conspecific intruders (Treatment 3).

All treatments were presented in a random order at each territory, with at least 48hr between tests. Cassette tapes (TDK) containing pre-recorded magpie vocalisations (distributed by Auckland/Waikato Fish and Game Council, R.D.9 Hamilton, New Zealand as audio lures to attract magpies into traps) were played for 5 min through a speaker (Sharp WQ-CH800; c. 72 dB at

Table 1. Treatments presented at each territory. In the first phase (0-30 min), both decoys were exposed to residents; after 30 min, decoy (a) was covered, and only decoy (b) was exposed for the remainder of the test (second phase; 30-60 min).

	First phase (0-30 min)		Second phase (30-60 min)	
	Decoy (a)	Decoy (b)	Decoy (a)	Decoy (b)
Treatment 1	Magpie	Rock dove	(Covered)	Rock dove
Treatment 2	Magpie	Magpie	(Covered)	Magpie
Treatment 3	Rock dove	Rock dove	(Covered)	Rock dove

1 m from speaker) placed 1 m 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 6 min after the equipment had been set up, which gave the observer enough time to move to a position 60-100 m away. All treatments were video-taped (Sony Hi8) using a video camera (Sony CCD-TRV89E) with a time stamp and later dubbed to standard VHS tape (Mitsubishi Black Diamond E180 using a Panasonic AG-6730 video recorder) for analysis. Video cameras were positioned on a tripod approximately 15-30 m away from the cages.

Magpies from two of the study groups had members that were colour-banded. However, it was safe in all cases 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 & 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.

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) <0.3 m from cage (i.e., <c. 1 magpie body length), (iii) 0.3-1.0 m from cage (i.e., c. 2-3 body lengths), or (iv) >1 m from cage) was recorded every 15 s. This gave 120 observations before decoy (a) was covered, and 120 after. Occasionally, the decoy was not covered on the 120th observation 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. At times the view of a resident magpie was partially obscured when reviewing video footage because the cage was between it and the camera. This was sometimes a problem when determining if the resident was <0.3 m or 0.3-1 m from the cage. If there was any confusion the greater distance was scored to give the most conservative distance measurement.

Aggressive behaviours directed towards decoys 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 &

Veltman, 1987) but we only measured instances when a resident magpie struck the cage with its bill or performed bill snaps (i.e., lunging at a victim and snapping the bill; Brown & 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 rock dove decoys or other free-ranging birds were also recorded in each test (e.g., aggressive postures close to rock dove 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., to approach within 15 m of the decoys) was recorded to the nearest second. When both decoys were initially presented in a territory, the arrival of a resident within 15 m signalled the start of the test as defined above. After decoy (a) was covered (which usually caused residents to temporarily flee the area), the amount of time residents took to return to decoys was also recorded to the nearest second. If subjects remained within 15 m of the decoys following the disturbance associated with covering decoy (a), the latency was considered 0 s and the time taken until the residents moved > 15 m of the decoys was also recorded.

Analysis

The percent of observations that residents were recorded at each proximity ((i)-(iv); see above) was calculated for both phases of each test. Aggressive strikes were calculated per minute. Differences between decoys (a) and (b) for measured variables (i.e., proximity to decoys; aggressive strikes) in the first phase of each treatment were tested using Wilcoxon signed-rank tests. Differences between Treatments 1, 2 and 3 for measured variables after decoy (a) had been covered (i.e., the second phase) were tested using a series of Friedman ANOVA tests.

Each 30-min period before and after decoy (a) was covered in all treatments was divided into six 5-min blocks and the number of aggressive strikes recorded in each block were compared (using repeated measures ANOVAs with the Greenhouse-Geisser epsilon correction factor) to determine if the intensity of aggression changed over time.

Wilcoxon signed-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 & Robertson, 1996).

Differences in the percent of observations that (1) males only, (2) females only, or (3) males and females together were recorded at close proximity to decoys were also tested using Friedman ANOVA tests, although only data from the tests involving two magpie decoys (Treatment 2) were used; there were insufficient responses to rock dove decoys during Treatments 1 and 3 to analyse statistically.

If significant differences were detected by Friedman tests, post-hoc tests (Wilcoxon signed-rank tests) were employed to identify where the differences occurred.

Ethical note

Four rock dove decoys were purchased from a local breeder in 2001 and housed together in an aviary (4.0 × 3.3 × 2.2 m high). Rock doves were provided with several perches, hay and an ad libitum diet of rock dove seed (with oyster grit), and water. In the first year of captivity two chicks were produced, so we removed eggs after this to keep the number of rock doves at six. Rock dove decoys were retained at the end of the trial for further research.

Magpies are commonly controlled as 'introduced pests' in New Zealand because they are thought to have negative impacts on other birds (Morgan et al., 2005); no government permits are required to capture or hold magpies in New Zealand. Three wild magpies were captured in 'Larsen'-style live-traps (i.e., a trap containing four c. 35 × 25 × 35 cm high compartments, each able to catch one bird, and a central c. 62 × 70 × 35 cm high compartment containing a live conspecific 'call bird'). The birds were collected at least 30 km away from our study sites. They were housed together in an aviary identical to that housing the rock doves from c. 7 days before tests started until the end of the trial. While in captivity, magpies were provided with perches and hay, and supplied a diet that mainly consisted of a c. 50:50 mix of crumbled dog roll and bread crumbs (minced beef was occasionally added as well), along with ad libitum water. Food was replaced every 1-2 days and although we did not weigh the amount given, it was rarely all consumed between feeding

episodes. Aviaries were cleaned and had fresh hay added every 1-2 weeks, or as required. Following the study, the magpies were humanely destroyed by stunning with a blunt object following standard procedures developed by pest managers (e.g., Environment Southland, 2006).

No decoys were injured during any test as the cages were large enough for occupants to easily move to avoid strikes by resident magpies. On only one occasion was a decoy physically attacked; however, the decoy was not injured during the exchange (see below). If resident magpies were seen making physical contact with decoys, or decoys appeared exhausted (e.g., ceased movements around the cage to avoid residents), we intended to abandon tests; however, this never occurred. Residents spent less than 37% of their time positioned on cages and only a small proportion of that time was devoted to directing agonistic acts toward the decoys (see below). Furthermore, no change in behaviour, appetite or condition was observed when decoys were returned to holding aviaries between tests. All procedures were approved by the University of Waikato Animal Ethics Committee (Protocol 586).

Results

Resident magpie responses to decoys

Resident magpies seldom approached (<1 m) and never attacked rock dove decoys during the first or second phase of any tests (Figure 1; Tables 2, 3, 4). However, during the first phase of two separate tests when both a magpie and rock dove decoy were exposed at the same time (Treatment 1), residents 'charged' the rock dove decoy (i.e., lunged forward 1m, stopping <0.3 m from the cage) a total of five times (twice during one test 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 rock dove decoys.

During the first phase of Treatment 1, when residents were exposed to both magpie and rock dove decoys, significantly more aggressive strikes and observations where residents were close (on cage, <0.3 m) to the magpie decoy were recorded (Tables 2, 3); residents were also recorded in fewer observations at distances >1 m to the magpie decoy cf. the rock dove decoy (Table 2). During the first phase of treatments when both decoys were only

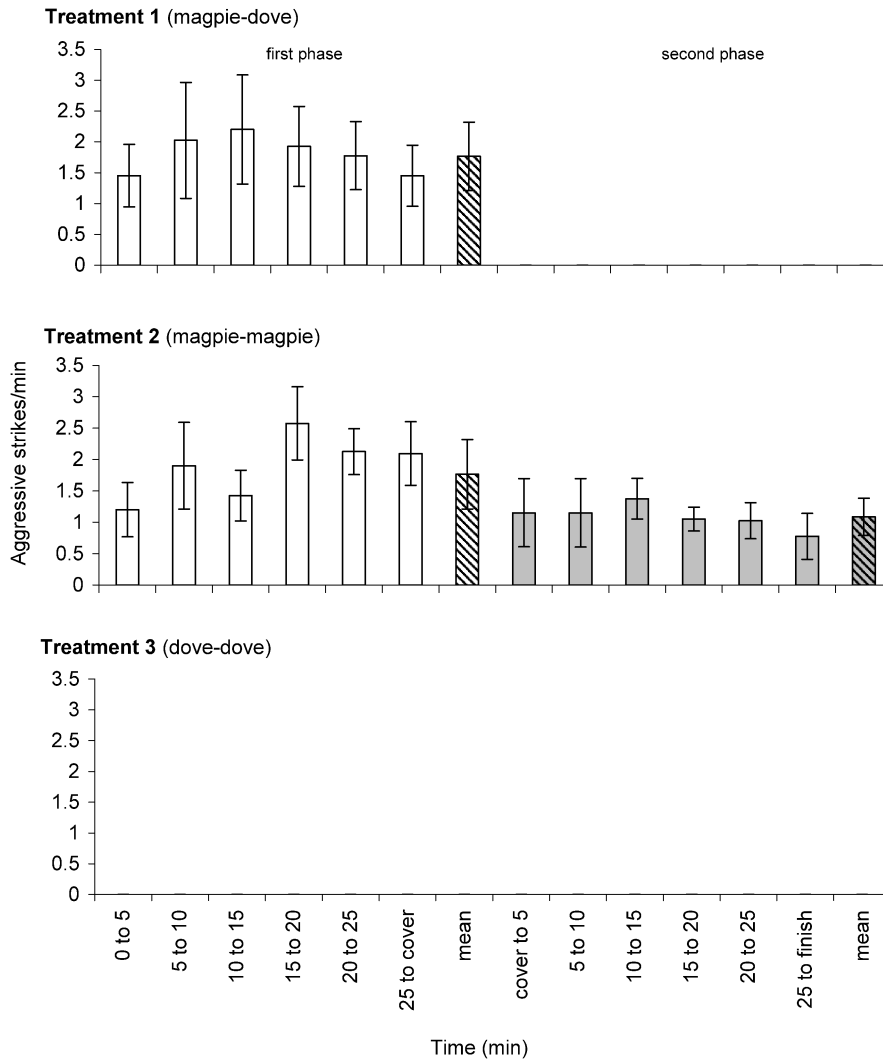


Figure 1. Mean \pm SE number of aggressive strikes/min by resident magpies from territorial groups ($N = 8$) on decoys per 5 min block before (first phase) and after (second phase) decoy (a) was covered (see Table 1 for decoy combinations). No attacks on rock dove decoys were recorded in any test that they were presented; therefore, all data represent attacks on magpie decoys. Attacks on both magpie decoys in the first phase of Treatment 2 have been combined. There were no significant differences in the number of aggressive strikes/min between 5-min blocks ($p > 0.05$; see text); therefore, the mean numbers of aggressive strikes/min for each phase of each treatment are also presented as hatched columns.

Table 2. Mean percent of observations that resident territorial groups ($N = 8$) were recorded at different distances to decoy (a) and (b) during the first phase of each treatment.

	Decoy (a) (mean (SE))	Decoy (b) (mean (SE))	Wilcoxon Z	p
Treatment 1 (magpie-rock dove)				
On cage	36.2 (11.0)	1.2 (0.8)	1.99	0.046
<0.3 m	21.2 (6.2)	1.9 (0.7)	2.38	0.017
0.3-1 m	2.3 (0.6)	3.1 (1.0)	1.05	0.295
>1 m	40.2 (11.9)	93.6 (1.9)	2.38	0.017
Treatment 2 (magpie-magpie)				
On cage	12.2 (4.0)	30.2 (7.4)	1.54	0.123
<0.3 m	19.8 (7.4)	19.0 (5.7)	0.42	0.674
0.3-1 m	5.4 (1.9)	6.4 (2.9)	0.31	0.753
>1 m	63.5 (10.0)	44.4 (8.1)	1.40	0.161
Treatment 3 (rock dove-rock dove)				
On cage	0 (0)	0 (0)	*	
<0.3 m	0.1 (0.1)	0.4 (0.4)	*	
0.3-1 m	0.3 (0.2)	0.2 (0.2)	*	
>1 m	99.6 (0.3)	99.4 (0.7)	*	

*Not enough variation in the measured parameters between decoys for statistical analyses to be conducted.

Table 3. Mean number of aggressive strikes/min on decoy (a) and decoy (b) by resident territorial groups ($N = 8$) during the first phase of each treatment (see Table 1 for decoy combinations for each treatment).

	Decoy (a) (mean (SE))	Decoy (b) (mean (SE))	Wilcoxon Z	p
Treatment 1	1.8 (0.6)	0 (0)	2.52	0.012
Treatment 2	0.5 (0.3)	1.2 (0.3)	1.12	0.263
Treatment 3	0 (0)	0 (0)	*	

*Not enough variation in attack rates between decoys for a statistical analysis to be conducted.

magpies (Treatment 2) or only rock doves (Treatment 3), there were no significant differences in the percent of observations at each proximity (i.e., (i)-(iv); see above) to, or number of aggressive strikes/min on, each decoy by residents (Tables 2, 3).

No significant differences were detected in the frequency of aggressive strikes/min across the 5-min blocks that comprised the two 30-min phases (repeated measures ANOVA; Treatment 1, first phase, $F_{1.9,13} = 0.48$, $p = 0.625$; Treatment 2, first phase, $F_{3.9,27} = 1.80$, $p = 0.16$; Treatment 2, second phase, $F_{2.2,16} = 0.45$, $p = 0.67$; Figure 1). Therefore, aggressive strikes were pooled and are presented as the mean number of aggressive strikes/min for each period (hatched columns in Figure 1). Differences in attack rates by residents on magpie decoys between the first phase of Treatment 1 and both phases of Treatment 2 were also not apparent (Friedman, $df = 2$, $S = 3.25$, $p = 0.197$; Figure 1); although, when two magpie decoys were present during the first phase of Treatment 2, they each received about half as many strikes as the single magpie exposed with a rock dove during Treatment 1 (i.e., the mean number of strikes per minute during the first phase of Treatments 1 and 2 are similar; 1.77 strikes/min ± 0.55 (SE); Figure 1).

Residents were recorded significantly more often at close proximity (on cage, <0.3 m) to the magpie decoy (b) during the second phase of Treatment 2 than when rock dove decoys (b) were in place in the second phase of Treatments 1 and 3 (Table 4). There was no difference between the percent of observations in which residents were recorded at 0.3-1 m between the second phases of all Treatments (Table 4). Additionally, residents were recorded

Table 4. Mean percent of observations that residents in territorial groups ($N = 8$) were recorded at different distances to decoy (b) in the second phase of each treatment (see Table 1 for decoy combinations for each treatment).

	Treatment 1 (mean (SE))	Treatment 2 (mean (SE))	Treatment 3 (mean (SE))	Friedman S	p
On cage	0.1 (0.1)	29.8 (8.1)	0 (0)	15.44	$<0.001^\dagger$
<0.3 m	1.1 (0.7)	20.1 (7.2)	0.2 (0.2)	15.08	$<0.001^\dagger$
0.3-1 m	0.2 (0.1)	0.8 (0.3)	0.3 (0.2)	2.70	0.259
>1 m	98.6 (0.9)	49.3 (11.6)	99.5 (0.4)	14.00	0.001^\dagger

On cage	Wilcoxon			Wilcoxon			Wilcoxon		
	Z	p	<0.3 m	Z	p	>1 m	Z	p	
Trt 1 vs. Trt 2	2.52	0.012	Trt 1 vs. Trt 2	2.52	0.012	Trt 1 vs. Trt 2	2.52	0.012	
Trt 1 vs. Trt 3	*		Trt 1 vs. Trt 3	*		Trt 1 vs. Trt 3	1.28	0.201	
Trt 2 vs. Trt 3	2.52	0.012	Trt 2 vs. Trt 3	2.52	0.012	Trt 2 vs. Trt 3	2.52	0.012	

*Not enough variation in the measured parameters between treatments for post-hoc comparisons to be conducted.

during significantly fewer observations at distances >1 m from the magpie decoy during the second phase of Treatment 2 compared with the second phases of Treatments 1 and 3 when only a rock dove decoy was presented (Table 4).

There was considerable variation across the eight territories in terms of how the resident groups responded to the magpie decoys. For example, the number of strikes on, and the percent of scans >1 m of the magpie decoy during the second phase Treatment 2 tests ranged from 0.13–3.77 strikes/min and 0–83%, respectively. The observed variation across the groups was not due to differences in group composition; for example, attack rates on magpie decoys by monogamous pairs were very similar to those recorded in territories defended by multiple birds (all Mann-Whitney tests, $p > 0.05$). This was probably because the dominant individuals (i.e., the breeding male and most dominant female in our study) are primarily responsible for territory defence (Carrick, 1972; Kaplan, 2004).

Both male and female residents from all groups attacked 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 did females (1.1 ± 0.2 (SE) strikes/min, 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 (Wilcoxon, $Z = 0.70$, $N = 8$, $p = 0.484$).

Males and females were generally recorded together within close proximity to the magpie decoys more often than when on their own during both phases of Treatment 2 tests; however, this trend was only significant during the second phase (Table 5).

After the magpie decoy (a) was covered during Treatment 1, resident magpies returned to the rock dove decoy (b) in five of the eight tests (Table 6). In Treatment 2, residents always returned to magpie decoy (b) after the magpie decoy (a) was covered (Table 6). The response to rock dove 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 30 min phase, and another two groups only in the second 30 min phase (Table 6). Only once during a Treatment 3 test were residents seen within 15 m of rock dove decoys both before and after decoy (a) was covered (Table

Table 5. Mean percent of observations that males only, females only, and males and females together were recorded at distances <1 m to magpie decoy (a) or (b) in the first phase of Treatment 2, and decoy (b) in the second phase of Treatment 2.

	Females only (mean (SE))	Males only (mean (SE))	Males and females together (mean (SE))	Friedman <i>S</i>	<i>p</i>
First phase	9.2 (4.5)	13.0 (9.5)	39.4 (11.1)	4.75	0.093
Second phase	5.4 (2.1)	7.8 (6.1)	37.6 (11.5)	7.55	0.023 [†]
†Post-hoc tests			Wilcoxon <i>Z</i>	<i>p</i>	
Females vs. males			0.68	0.499	
Females vs. males + females			2.24	0.025	
Males vs. males + females			1.96	0.050	

6); however, at no time were these residents scored at distances <1 m to either decoy. Although residents remained <15 m 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 rock dove (Table 6).

Magpie decoys never attacked residents. Generally, decoys emitted distress vocalisations (mainly when residents were conducting aggressive strikes), adopted submissive postures and moved around the cage to distance themselves from residents.

Resident magpie response to other birds

Free-range birds of different species were often seen flying over or landing near (e.g., <20 m) decoys during tests, although residents were not seen attacking or chasing birds except other magpies or Australasian 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

Table 6. Latency (min) of resident magpies from territorial groups to be recorded within 15 m of decoys at the start of each test (first phase) and after decoy (a) had been covered (second phase) (see Table 1 for decoy combinations for each treatment). If residents were not recorded within 15 m of decoys during an experiment then no latency data were collected and ‘no response’ is presented. If subjects remained within 15 m of the decoys following decoy (a) being covered the time it took for birds to move >15 m from decoy (b) is presented in parentheses.

Territorial group	Treatment 1		Treatment 2		Treatment 3	
	1 st phase	2 nd phase	1 st phase	2 nd phase	1 st phase	2 nd 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	23.0	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		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

observed (i.e., the proportion of scans that residents were >1 m from decoys during tests with boundary disputes was not significantly different than tests without; Mann-Whitney, $U = 35.50$, $N_{1(\text{tests with boundary disputes})} = 5$, $N_{2(\text{tests without boundary disputes})} = 19$, $p = 0.406$). Residents did not attack rock dove 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 rock dove decoys or any other free-range birds were observed. The behaviour of intruding magpies after each territorial dispute could not be determined because they always flew out of view.

Australasian harriers were 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 harassed 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 rock dove, reached inside and seized the bird in its talon. It then tried to fly away with the rock dove

but could not get the bird out of the cage. Before we could reach the cage to protect the rock dove, the resident magpies chased off the harrier. The residents returned to the cages <2 min after chasing the harrier away to continue attacking the magpie decoy; the rock dove decoy was uninjured during this exchange. No other instances of free-ranging birds approaching (i.e., <1 m) the decoys were recorded.

Discussion

Although reports of redirected aggression by magpies after territorial disputes exist, the issue has not previously been investigated experimentally. We found little evidence of redirected aggression in territorial magpies after simulated territorial intrusions. Resident magpies were seldom recorded close to and never attacked rock dove decoys during tests, regardless of being exposed to magpie decoys. In contrast, the mean number of attacks and the percent of observations residents spent close to magpie decoys were always high. Redirected attacks may be rare and may only occur under very specific circumstances. Certainly, we provide no support for the idea (Brown & Veltman, 1987) that a priming effect associated with interacting aggressively with conspecific intruders facilitates attacks on benign species like the rock dove. Future researchers investigating redirected aggression should focus on obtaining field observations on the sex and age of attackers, the timing of attacks, whether intruding animals or residents instigate attacks, and how long disputes lasted before redirected attacks took place. This information could then be used to direct further experimentation.

Redirected aggression is often investigated in gregarious animals like macaques (*Macaca* spp.; Aureli, 1997), where the losers of conflicts with conspecifics may attack benign or weaker members of the group to 'vent' aggression-induced stress (Virgin & Sapolsky, 1997) or because attacking the provoking agent risks injury (Marcus-Newhall et al., 2000); increased levels of stress or anxiety may also occur in winners as a result of conflict (Aureli, 1997; Øverli et al., 1999; Summers et al., 2003). Territorial magpies also live in complex social groupings (Carrick, 1972). During magpie territorial disputes in the wild, winners are ultimately either: (1) the residents that repel intruders or (2) the intruders that evict residents. In our experiment, it was difficult to assess whether the resident magpies we tested would view

themselves as winners or as losers. For example, while residents were able to attack the decoy magpies with little risk, the 'intruding' magpies were unable to be driven from the territory as they were inside a cage, which also protected the decoy from any injury. If redirected aggression is tied to a specific type of contestant (e.g., a winner or loser), future experiments may need to create specific outcomes for each contestant (e.g., by removing the decoy following an initial attack and then recording responses directed at the heterospecific) to identify the context and perpetrators of redirected acts.

Some animals, prevented from attacking opponents, will attack other animals as a means of venting frustration-induced aggression (e.g., Chapman & Voith, 1990; Beaver, 2004). Although resident magpies in the current study would be expected to have had elevated frustration levels due to an inability to physically attack or drive away magpie decoys, they did not attack rock dove decoys and were not seen attacking other free-range birds (except other magpies and Australasian harriers; these species were probably attacked because they are competitors and/or predators; Heather & Robertson, 1996; Morgan et al., 2006). Thus, our experiment provides little support for the frustration-induced aggression hypothesis. Furthermore, the experiment may have triggered several territorial disputes with neighbouring magpies which would be expected to increase the likelihood of residents redirecting aggression against other species as a result of the priming effect considered above (Brown & Veltman, 1987) — this did not occur either. It would appear, therefore, that none of the current hypotheses for redirected aggression fits well with the magpie scenario. Perhaps redirected attacks are rare, spontaneous acts triggered by unusual circumstances and have no functional value.

Territorial defence in magpies can be highly organised and a range of strategies can be adopted by group members (Kaplan, 2004). All group members can participate in attacks, but usually dominant males and females play the most important roles (Carrick, 1972; Kaplan, 2004). We found dominant males and females were regularly recorded close to magpie decoys and that there was little difference in the number of aggressive strikes/min across sexes; there was, however, a large amount of variability which is not unusual in magpies (e.g., Farabaugh et al., 1992). Also, our study was conducted during the non-breeding season (magpies aggressively defend territories all year) — during the breeding season, territories are defended more vigorously and gender differences develop. 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 & Veltman,

1987; Kaplan, 2004). Perhaps only these peaks in male territorial behaviour (during the breeding season) instigate the redirected aggression observed in magpies; future researchers examining links between aggressive interactions with conspecifics and redirected aggression should focus on these points of the breeding cycle.

Despite accounts to the contrary, we found no evidence that magpies redirect aggression at a benign species after territorial intrusions. Protection of a resource (Cox & Bauer, 1997; Morgan et al., 2005), deterring potential nest predators (Morgan et al., 2005, 2006), or strong selection for aggressive individuals in previous evolutionary landscapes may better explain why magpies attack other birds (i.e., a non-discriminating attack regime may have been adaptive if numerous heterospecifics competed for resources with magpies in early Australian ecosystems; Morgan, 2006). Alternatively, the rare cases of magpies attacking benign species may simply represent spontaneous acts triggered by unusual circumstances and have no functional value.

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