**Australian Magpie *Cracticus tibicen* attacks on humans:
territoriality, brood defence or testosterone?**

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Abstract. Attacks on humans by Australian Magpies *Cracticus tibicen* are a significant human-wildlife conflict in Australia, especially in suburban environments. Despite the high frequency and widespread nature of these interactions, remarkably little is known about the phenomenon, significantly undermining attempts to develop sound management plans. Although many popular explanations of the causes and conditions influencing Magpie attacks exist, none have been studied empirically to date. Importantly, almost all attacks on intruders, including humans, are by males alone. In this study, we explored three common hypotheses – territoriality, brood-defence and testosterone – as potential and non-exclusive explanations for human-directed aggression in Magpies living in suburban areas of Brisbane, south-east Queensland. The response of ten pairs of aggressive Magpies to natural levels of human intrusion was compared to that of ten non-aggressive pairs. In addition, blood samples of all male Magpies were collected prior to breeding, during incubation and while nestlings were present to determine circulating plasma testosterone levels. Behavioural observations strongly supported the contention that attacks on humans resemble brood defence and did not support an association with territoriality. The study also found no support for the suggestion that testosterone levels correlated with aggressiveness toward humans; male testosterone peaked immediately prior to egg-laying and was significantly lower during the maximum period of human-directed attacks. Moreover, there were no differences in the testosterone levels of aggressive and non-aggressive male Magpies. The pattern of testosterone production over a breeding cycle closely resembled that of many other songbirds and appeared not to influence Magpie attacks toward humans.

Introduction

One of the notable effects of the rapid urbanisation currently underway globally has been an increase in human-wildlife conflicts (Marzluff 2010; Adams *et al.* 2006). While much discussion of the expansion of urban areas has focussed on the loss of biodiversity (Marzluff *et al.* 2001; Chace and Walsh 2006), more recent attention has turned to the small but significant number of species that thrive in the new anthropogenic landscapes of cities and suburbs (Catterall 2004; Bonier *et al.* 2006). Such species tend to be generalists with broad diets, the ability to exploit resources provided by urban environments and, axiomatically, a high tolerance for the presence of humans and their activities (Marzluff 2001; Low 2002). These characteristics are typical of many introduced species, although some notable native species also exhibit these features and have become abundant in urban areas (Jones 2003).

The coexistence of high densities of wildlife and humans is also resulting in an increase in the frequency of aggressive interactions between humans and some of these species (Decker and Chase 1999). This is a global phenomenon involving a wide range of species from large mammals (including bears and kangaroos) to small birds such as honeyeaters and even

hummingbirds (Conover 2001). While most of these interactions are relatively harmless, resulting in more alarm than injury, some are extremely dangerous and have resulted in serious injury and even death (Conover 2001; Adams *et al.* 2006). While the mitigation of such situations is obviously an important priority for urban wildlife agencies, the underlying causes of such attacks are often poorly understood, potentially undermining the development of informed approaches to management (Adams *et al.* 2006).

Aggression toward humans by Australian Magpies *Cracticus tibicen* is one of the best-known human-wildlife conflicts occurring in urban environments in Australia (Jones *et al.* 1980; Jones 2002; Jones and Neelson 2003; Jones 2008). Each year, thousands of people are swooped upon by aggressive birds, primarily during the late spring. Although major injuries (mainly involving damage to eyes; Horsburgh *et al.* 1992) are mainly infrequent, minor scratches and abrasions are common during most years (Jones *et al.* 1980). Considerable attention has been paid to many aspects of this conflict, including understanding the behavioural and ecological contexts of attacks, the effectiveness of management actions, and community support for different management options (Cilento and Jones 1999; Thomas and Jones 1999; Jones 2002; Jones and Neelson 2003). While our understanding of this phenomenon has increased markedly, the underlying causes of Magpie attacks on humans remains unresolved.

Although a large number of explanations for this form of aggression have been offered (see Jones 2002 for further details), the three most common relate to territoriality, brood defence and the hormone-influenced behaviour. Because management options are often influenced by topical explanations regardless of veracity (Adams *et al.* 2006), it is important that such ‘hypotheses’ are critically assessed.

Territoriality is associated with behaviours directed at ensuring the exclusive use of an area – the territory – by a pair or group (Hinde 1956; Klopfer 1969). In a large number of species these behaviours are most evident at the start of the breeding season when nest sites are being selected and defended. Among songbirds this typically involves pronounced singing, usually by males, and the displacement of conspecifics perceived as potential competitors. For most species, this intensively aggressive phase is limited to a brief period early in a breeding attempt. Australian Magpies, however, are atypical in this regard, as they defend territories year-round: territory boundaries are patrolled continuously and any Magpies encountered are vigorously chased away, although there is also a pronounced peak in the intensity of this behaviour in early spring immediately prior to breeding (Robinson 1956; Carrick 1972; Farabaugh *et al.* 1992). Although territoriality typically refers to conspecific interactions, that is, between individual Magpies, it is nonetheless, the most common explanation invoked to explain aggression towards humans by both popular and scientific writers (e.g., Jones *et al.* 1980; Brown and Veltman 1987; Walraven 1990). Given that Magpie territoriality occurs year-round,

this explanation predicts that Magpie aggression toward humans should also occur year-round, with a peak early in the breeding season (Jones 2002).

The brood defence hypothesis emphasises the adaptive importance of parental protection of offspring. Nestling predation is recognised as the most important variable influencing fitness in birds (Ricklefs 1969). The central concept of the brood defence hypothesis asserts that parents attack potential predators to protect their young, and that the commonly observed increase in the intensity of this behaviour relates to the increasing fitness value of the developing young (Montgomerie and Weatherhead 1988; Curio 1993). Applied to aggressive Magpies, this explanation suggests that Magpies perceive intruding humans as threats to their nestlings, predicting that attacks would become especially evident while vulnerable young are in the nest. Moreover, this hypothesis further predicts a steady increase in attack intensity as with fledging, only waning with full independence (see Montgomerie and Weatherhead 1988).

Finally, aggression in animals is known to be mediated by various hormones, the most prominent being testosterone (T) (Wingfield *et al.* 1990; Wingfield *et al.* 1997). Testosterone is a primary androgenic steroid and plays a crucial role in the normal breeding behaviours of most vertebrates. High levels of circulating T are associated with increased aggression and a range of territorial behaviours such as singing and male-male fighting, as well as attacks on other species encountered nearby (Wingfield and Silverin 2002). Moreover, experimentally elevating T to high physiological levels has led to increased inter-pair aggression and reduced parental care, features unlikely to enhance reproductive success (also see Dufty 1989; Harding and Follett 1979). Thus, many biparental songbirds exhibit a peak in circulating T levels prior to nesting, followed by a significant reduction during incubation and especially during parental care, possibly to avoid conflicting behaviour and ensure adequate parental care (Wingfield *et al.* 1997). In the only known hormonal study of Australian Magpies, Schmidt *et al.* (1991) found T to be high prior to nest building but declined markedly after egg-laying. These Western Australian birds were apparently not aggressive toward humans. To support the testosterone hypothesis, elevated T levels in aggressive Magpies should coincide with the period of attacks on humans, and should therefore be higher during the later nestling and fledgling phases compared to T concentrations of non-aggressive birds.

These three explanations of Magpie attacks on humans are among the most widely discussed (see Jones 2002) and it is, therefore, important that these 'hypotheses' are evaluated in relation to readily observable behavioural patterns. Obviously, these explanations are not mutually exclusive (for instance, the relationship between territorial behaviour and heightened levels of circulating T is likely to be closely linked); effective hypothesis testing would ideally include experimental manipulations and is not attempted here. Nonetheless, when applied to aggressive Magpies, the predictions of these explanations are sufficiently distinct to demonstrate support or otherwise for the most tenable explanation.

We assessed these three explanations of Magpie attacks on humans by observing pairs of aggressive and non-aggressive Australian Magpies throughout the year in suburban Brisbane, south-east Queensland, Australia. Ten pairs of colour-banded Magpies from both categories were captured and circulating T levels determined from blood samples taken during pre-breeding, incubation and nestling phases.

Methods

Study area and selection of focal animals

The study was undertaken within suburban areas of Brisbane (153°03'E, 27°33'S), south-east Queensland. During earlier studies on Magpies conducted throughout Brisbane (O'Leary and Jones 2002; Jones and Neelson 2003), many pairs of both aggressive and non-aggressive Magpies had been located and colour-banded. Of these, ten aggressive (known to have attacked humans regularly) and ten non-aggressive ('controls') pairs were selected to serve as focal subjects in the present study. Previous behavioural studies (Warne and Jones 2003) had confirmed that while most suburban Magpies were thoroughly habituated to the presence of humans (Rollinson and Jones 2006) and tolerated even close encounters, a minority were distinctly aggressive towards people, though this behaviour was almost exclusively exhibited by males and limited to the nestling phase of the breeding season (see Jones 2002, 2008). Thus, observations of the male's reaction to naïve or experimental intrusions (Cilento and Jones 1999) during this phase provided rapid and unequivocal confirmation of whether pairs were 'aggressive' or 'non-aggressive'.

In the present study, all pairs classed as 'aggressive' had originally been reported as such by the public during a previous breeding season; this status was confirmed by subsequent observations for the present study. All focal pairs had been captured and coloured banded prior to the commencement of the present research. Moreover, in our experience of almost a decade of studies involving more than 200 captures, no non-aggressive male Magpie subsequently exhibited aggressive behaviour following its release (Jones 2002; Jones and Neelson 2003). Importantly, no nestlings or fledglings were captured and nest trees were avoided as far as possible so as to minimise any possible investigator influences (Knight *et al.* 1987). Study territories of all pairs were selected to be spatially independent and none were closer than 2 km of one another; in suburban environments, Magpie territories are almost fully contiguous with other territories and their relatively high density ensured that focal pairs were typically separated by several other pairs (Jones 2002). To ensure unhindered access to nests and facilitate observations, only birds with territories located primarily within parkland, recreational reserves or sporting grounds were included. Territories which encompassed school yards, childcare centres or other places of high human density were excluded (Warne 2001).

Note that although Australian Magpies in many mainly southern populations form long-lasting groups and may breed cooperatively, birds in northern New South Wales and Queensland generally do not (Brown *et al.* 1993); all of the focal pairs in the present study consisted entirely of strict pairs without attendant offspring.

Behavioural observations

Birds were observed regularly during six phases of the breeding season: Non-breeding (at least six weeks prior to any evidence of breeding behaviour); Incubation (a period of approximately 20 days, during which females brood eggs); three phases relating to the size of the nestlings: Small (first two weeks after hatch), Medium (weeks three and four after hatch), and Large (weeks five and six after hatch); and Fledgling phase (when young had permanently left the nest but were still accompanied by adults).

To assess the availability of human subjects potentially exposed to attack, the number of pedestrians walking within a 250m radius around the nest tree ('nest zone', see Jones 2002) and the duration of their presence in the zone were recorded during each 30 min observation period. Although some Magpies are known to attack cyclists and other types of intruders (Warne and Jones 2003), all of the aggressive birds in the present study targeted pedestrians only.

Observations of Magpie behaviour, almost always conducted from a stationary vehicle, were made during three periods of the day: morning (dawn to 09.00 hours), midday (09.00 to 15.00 hours) and afternoon (15.00 to dusk), with sessions randomised among focal pairs. Each observation period lasted 30 minutes during which generalised activities (perching, incubating, feeding young, foraging, singing, aggressive interactions and flying) of male and female separately were recorded at 30 second intervals. All events related to aggressive actions (see Cilento and Jones 1999) were noted opportunistically as they occurred throughout the session. At least 10 separate observation periods were conducted for most phases of the breeding season (number of observations sessions: Incubation, 33; Small nestlings, 18; Medium nestlings, 16; Large nestlings, 10) with the exception of the fledgling phase (Fledglings, 5) when locating these highly mobile groups proved difficult, and data averaged for each observation period.

Blood sampling and endocrinology

To determine plasma T levels, blood samples were obtained from all aggressive and non-aggressive male Magpies during each of three phases: Non-breeding; Incubation; and Medium (the central period of the nestling phase). Only males were sampled as this sex was overwhelmingly involved in aggression toward humans (Cilento and Jones 1999). Magpies were captured using a chicken-wire walk-in trap containing a live Magpie decoy confined to a small internal cage (see Jones 2002 and Jones and Neilson 2003 for further details). Once birds

had entered the outer cage, two researchers immediately approached the trap, and transferred the bird into a cloth bag for further handling. Blood was collected from the alar vein (from the underside of the wing) by puncturing with a 25 ga needle and collected into heparinized capillary tubes, which were placed on ice in a small cooler (Buttemer and Astheimer 2000). All samples were collected within 5 min of capture, minimising any effects of capture on circulating hormone levels (Buttemer and Astheimer 2000) and all were within 10 min of the focal bird sighting the decoy (Wingfield and Farner 1993). Blood samples were kept on ice for no longer than 4 h before being centrifuged (at 7000 rpm) and resulting plasma stored at -20°C. Plasma T content was determined by double-antibody radioimmunoassay kit (Pantex, CA) adjusted to maximise sensitivity (Buttemer and Astheimer 2000). All samples were run within one assay; intra-assay variation (c.v. of 11%) was assessed by inclusion of standards at the beginning and end of the assay. Levels of testosterone during the non-breeding period were almost all undetectable in the assay and for statistical purposes were assigned a value of less than 0.001 ng/ml.

Statistical analyses

Behavioural data for each pair was averaged before collation for statistical comparisons of means. Due to the unequal sample sizes and the lack of normality, non-parametric techniques were used to assess behavioural data (Zar 1996). Arcsine transformation was employed for proportional data (Martin and Bateson 1993), which subsequently resembled a normal distribution. Friedman's ANOVA was used to compare means for breeding phases and Mann-Whitney U-tests used when comparing aggressive and non-aggressive Magpies.

Testosterone levels, which were normally distributed, were analysed using two-factor ANOVA to compare means between breeding phases and Student's T-tests to compare aggressive and non-aggressive birds. Pearson's correlation was used to assess relationships between T levels and aggressiveness towards humans, using mean number of swoops per intrusion. All means are presented as $\pm$ standard error (SE).

Results

Human intrusions and attacks by Magpies

All 20 pairs of focal Magpie pairs maintained territories situated primarily in suburban parks. Overall, both non-aggressive and aggressive pairs experienced a fairly regular stream of human intruders, with typically between four and 11 pedestrians passing within the 'nest zone' (250 m radius area of the nest tree) during each 30-minute observation period. This rate of human intrusion remained relatively consistent through each of the breeding phases (Table 1). Observations spanned the months of June to November and overall there were no significant

differences in the mean number of pedestrians per observation period experienced by non-aggressive (4.90 ± 8.75) and aggressive Magpies pairs (3.89 ± 6.38).

None of the males classed as 'non-aggressive' attacked any human intruders at any time during the study. In contrast, all males classed as 'aggressive' exhibited some form of regular swooping or attack except during the fledgling phase, although only a small proportion of all human intruders were attacked (Table 1). Only about 1.5% of human intruders were attacked during the non-breeding phase, while 11-12% were attacked during the incubation and small chick phases (Table 1). A significantly higher proportion (approximately 19-29%) of human intruders were attacked during the medium and large chick phases ($X^2 = 18.67$, d.f. = 4, $P < 0.01$). The intensity of attacks, measured as the number of swoops per minute of observation, ranged from an average of 1.65 swoops per minute during incubation to 2.55 swoops per minute averaged for the three nestling phases (Fig. 1). There was, however, no statistical difference in mean attack frequency between these phases. Attacks on human intruders ceased completely during the fledgling phase for both groups (Fig. 1).

Testosterone levels

The range of T levels obtained for aggressive Magpies during the incubation phase was extremely variable, ranging from 0.001 to 3.08 ng/ml (Fig. 2). There were no significant differences between non-aggressive and aggressive Magpies in any of these groups.

The most important finding was that T levels during the incubation phase were significantly higher ($F = 8.285$, d.f. = 2, 46, $P = 0.001$) than any of the periods when nestlings were present. Interestingly, a two-factor ANOVA found an interaction between aggressive category and phase ($F = 5.747$, d.f. = 1, 46, $P = 0.001$), apparently due to mean T levels during the incubation phase being higher for non-aggressive Magpies. Of the five birds having T levels above 1 ng/ml, three were non-aggressive males, one of these having the highest level observed (3.52 ng/ml).

Discussion

Our results support the predictions of the brood defence hypothesis as an explanation for Magpie aggression towards humans. We dismiss territoriality as a valid explanation for such attacks and we found testosterone levels to be low during periods when attacks were occurring, discounting an influential role for the hormone in aggression towards humans. This study is the first attempt to assess the three most prominent explanations for Magpie aggression (Jones 2002) and is a valuable step towards the improving our understanding of this serious conflict and its management.

Territory or brood defence?

In the present study, males alone were responsible for all attacks on humans. Other studies (Cilento and Jones 1999; Jones and Neelson 2003) have reported some human-directed attacks by females but these were rare exceptions to the typical pattern and almost always involved females becoming aggressive immediately after the capture and removal of their dangerous mate (Jones and Neelson 2003). We also confirmed that even among male Magpies classified as 'aggressive', the proportion of available human intruders actually attacked was highly variable but never above about 20% percent of all pedestrians. This confirms other work indicating that Magpie aggression towards humans is typically varied in intensity: Jones and Thomas (1999) found that an average of only about 12% of males breeding in suburban environments exhibited human-orientated aggression.

This variability of response to human intruders contrasts markedly with the reaction of breeding Magpies to intrusions by conspecifics and potential predators, both of which are typically attacked immediately upon detection throughout the year (Cilento and Jones 1999; Warne 2001; Rollinson and Jones 2006). Moreover, there were no significant differences in the proportion of such intruders attacked by either non-aggressive and aggressive Magpies (Warne 2001). The main seasonal influence occurs during the early spring when territory boundaries are being tested and defended and Magpie-Magpie interactions peak due to an increase in territorial intrusions by conspecifics (Robinson 1956; Farabaugh *et al.* 1992). Thus, territoriality is more evident during this pre-breeding period because of the increase in the rate of intrusions by other Magpies (Carrick 1972).

The territorial explanation predicts that human-directed aggression by Magpies should mirror that of attacks on conspecific intrusions, with the number of attacks being proportional to intrusions. In the present study, both non-aggressive and aggressive Magpies were exposed to similar levels of human intrusion throughout the breeding season yet attacks by aggressive birds occurred mainly when chicks were in the nest (Fig. 1); this prediction was clearly not supported.

If Magpie aggression towards humans is better understood as a form of brood defence, we would first expect more aggression during the nestling phases and, second, that the intensity of the attacks should increase as the chicks increased in size (Montgomerie and Weatherhead 1988). The first of these predictions was mainly supported by the present study although a small number of attacks were also noted during both the non-breeding and incubation phases (Fig. 1). Such attacks appear to be relatively unusual; almost all other relevant studies (Jones *et al.* 1980; Cilento and Jones 1999; Jones and Thomas 1999) reported attacks only when chicks were present in the nest, although other studies similarly found a complete cessation of aggression upon fledging.

Cilento and Jones (1999) found that attack frequency did exhibit a discernable increase with nestling age, as predicted by several models of avian brood defence and demonstrated by numerous studies (see Montgomerie and Weatherhead 1988; McLean and Rhodes 1991). This

trend was less apparent in the present study, largely because the birds observed appeared to reach a high level of attack frequency earlier in the nestling phases than expected. This may have been due to the high average number of pedestrian intruders, a variable not quantified in any other Magpie studies to date.

Despite these minor variations in the predicted results, the overall findings clearly support the contention that Magpie aggression toward humans conforms to a general pattern of brood defence: the style and patterns of Magpie attacks on human intruders are consistent with behaviours aimed at defending nestlings (see Cilento and Jones 1999).

The influence of testosterone

Testosterone is associated with behavioural expressions of aggression in most vertebrates although its role in regulating and mediating a wide range of other behaviours is far more complex than popularly presented (Wingfield and Farner 1993). Its various influences on the reproductive cycle of songbirds are reasonably well understood, and numerous observational and experimental studies have investigated many aspects of this phenomenon (Wingfield *et al.* 1997). Of particular interest is the regulation of T in species in which early territorial aggression associated with high T levels is followed by a dramatic reduction in hormone levels, apparently facilitating the expression of parental care of nestlings by males (Hau *et al.* 2000; McDonald *et al.* 2001). Prolonged elevations in T have important and potentially deleterious physiological impacts (Dufty 1989) and are largely incompatible with most forms of chick care (Vleck and Brown 1999).

Australian Magpies are noteworthy in exhibiting unambiguously territorial behaviour throughout the year, yet having an otherwise typical spring-based breeding cycle (Robinson 1956; Rollinson and Jones 2002). Despite this year-round conspecific aggression, Schmidt *et al.* (1991) found high levels of T during the early breeding period and low levels during all other times of the year. The results of the present study were similar, with an obvious peak in the incubation phase, though the variation among individual males was also marked. This peak coincides with both the period of increased intrusions by conspecifics (Brown *et al.* 1993; Farabaugh *et al.* 1992) and a major increase in testes size and spermatogenesis (Carrick 1972; Schmidt *et al.* 1991). Similar year-round territorial defence occurs in other sedentary passerine species and, in those where T has been studied, birds have substantially reduced T during non-breeding periods (e.g. Wingfield and Soma 2002). Some tropical residents maintain very low T levels year-round, even during breeding (e.g. Hau *et al.* 2000). Initially, such examples suggested that the underlying driver for territorial aggression was of cognitive origin, independent of T. However, blocking T production and its aromatisation in non-breeding sparrows (Wingfield and Soma 2002) and tropical antbirds (Hau *et al.* 2000) decreased territorial behaviour, suggesting some dependence on T, perhaps from non-testicular sources, in

facilitating this behaviour. The underlying mechanisms for this hormone-behaviour relationship have yet to be described. However, in the context of Magpie attacks, low T activity may be permissive, with the expression of aggression most dependent on motivation to protect offspring.

Thus, despite their overt and continuous territorial behaviour, Australian Magpies do not maintain elevated T levels. Indeed, the peak in this hormone is entirely typical of most spring-breeding passerines (Wingfield *et al.* 1990) and appears aimed at mediating appropriate behavioural responses to the increased territorial ‘challenges’ by other Magpies experienced at that time (Wingfield *et al.* 1990). Of particular relevance to the present study, however, is the fact that this peak in T, and in conspecific aggression, occurs prior to the presence of young in the nest, while aggression toward humans is primarily associated with the nestling period. This again supports the contention that human-oriented aggression resembles a form of brood defence and suggests strongly that territoriality is an inappropriate explanation.

Previous studies have suggested that Magpie attacks toward humans may be strongly influenced by hormone levels, with the implication being that higher T levels are correlated with increased aggression in specific birds (e.g., Jones *et al.* 1980). Furthermore, if this link could be confirmed, this may suggest that the administration of a chemical blocker or reversing agent could potentially be used to mitigate this form of aggression in Magpies (see discussion in Jones 2002). The findings of this study, however, unequivocally show that T has little or no influence in the manifestation of Magpie aggression towards humans and that the option of a chemical solution is not warranted. Furthermore, recent investigations have indicated that the stress hormone corticosterone may have a role in mediating Magpie aggression (Rollinson 2003). These results and related endochronological studies (Wingfield and Farner 1993) indicate that the relationship between animal behaviour, hormones and environment is exceptionally complex, especially in for species living in urban environments (Bonier *et al.* 2006). We hope this modest study to be a small step toward a better understanding of an important urban human-wildlife interaction (Jones 2008).

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Table 1. Mean number of pedestrian intruders and the percentage attacked by non-aggressive and aggressive male Australian Magpies during the non-breeding period and four phases of the breeding season in Brisbane

Phase	Non-aggressive		Aggressive	
	Mean number intruders (+ S.E.)	Percent intruders attacked	Mean number intruders (+ S.E.)	Percent intruders attacked
Non-Breeding	3.96 $\pm$ 4.25	0	3.04 $\pm$ 4.75	1.5
Incubation	6.12 $\pm$ 7.75	0	4.03 $\pm$ 6.30	11
Small Nestlings	6.17 $\pm$ 5.55	0	6.12 $\pm$ 5.00	12
Medium Nestling	3.54 $\pm$ 8.90	0	3.12 $\pm$ 9.70	19
Large Nestlings	4.25 $\pm$ 8.06	0	3.08 $\pm$ 6.74	29
Mean	4.90 $\pm$ 10.22	0	3.89 $\pm$ 5.89	14.5

Figure Captions

Fig. 1. Mean (+ S.E.) intensity of attacks (measured as swoops per minute) per human intruder by Australian Magpies within 250m radius of nest trees during 30 minute observation sessions for each phase of breeding cycle.

Fig. 2. Mean (+ S.E.) level of circulating plasma testosterone (ng/ml) in non-aggressive (open bars) and aggressive (solid bars) Australian Magpies during non-breeding, incubation and nestling (medium nestling) phases. Note: Undetectable T levels were ascribed as 0.001ng/ml.

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