

Are there correlates of male Australian Magpie *Gymnorhina tibicen* reproductive success in a population with high rates of extra-group paternity?

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The reproductive success of a male bird is often correlated with measurable traits that predict his intrinsic quality. Females are thought to base their selection of mates on the latter's 'quality' in order to gain their 'good genes'. Male Australian Magpies *Gymnorhina tibicen* of the white-backed race *tyrannica* were trapped in two breeding seasons. Measurements were taken of morphometric and other characteristics in order to discover whether particular traits of males were associated with: (1) percentage of offspring sired in the territory, (2) number of fledglings produced in the territory per season and (3) whether females select males for their 'good genes'. There were no consistently significant correlations between any of the measured variables and male Magpie reproductive success within territories. In particular, none of the traits measured had any consistent correlation with the percentage of offspring sired in a territorial group. This was an unexpected result given that the species is strongly territorial but also engages regularly in extra-group copulations. These findings appear contrary to the predictions of the 'good genes' hypothesis. The general lack of correlation between the variables and level of genetic paternity may in fact be due to females engaging in extra-group mating primarily to avoid breeding with a close relative rather than to choose a high-quality male. In this case, males would not have to be 'high quality', but merely genetically different from the female's social mate.

Female choice of male partners is thought to be influenced by the female's search for 'good genes' to improve the quality of her offspring (Petrie & Kempenaers 1998). Females must be able to assess and select males that carry these 'good genes' using phenotypic or observable cues. These cues fall into five broad categories: (1) plumage characteristics such as structural colours (Doucet 2002), or ornament size (Hagelin & Ligon 2001); (2) behavioural aspects such as parenting ability (Ens *et al.* 1992); (3) aspects of territorial ownership (Beletsky & Orians 1993), or quality (Goodburn 1991); (4) physical characteristics such as weight, body size (Garnett 1981) and condition (Lozano 1994); and (5) indicators of condition or health, particularly those influenced by parasite loads, e.g. mites (Harper 1999), lice (Kose

et al. 1999) and haemoprotozoa (Sorci & Møller 1997), or heterozygosity as an indication of genetic 'good health' (Brown 1997). Studies that have found 'good genes' effects have examined characteristics such as weight, size and parasite loads (Kempenaers *et al.* 1992, Rätti *et al.* 1993, Lozano 1994).

The rates of extra-pair paternity in such studies (when calculated) were all moderate to low. When females mate outside the social pair bond, the quality of the genetic input from the extra-pair sire (or indirect benefits) is of paramount importance as these males contribute no direct benefits (Cordero 1998). The mating system of the Australian Magpie *Gymnorhina tibicen* displays an extremely high rate of extra-group paternity (EGP): 82% of young born in one population (Hughes *et al.* 2003) and 44% of young born in a second population (Durrant & Hughes 2005) were not the offspring of male territorial residents. It is useful to study this species to provide information on male quality and female choice when the system is extremely biased towards extra-group mating activity.

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Australian Magpies are large, group-living, omnivorous passerines that occupy permanent year-round territories. Non-territorial birds join large floater flocks in some races, and territory ownership is vital to reproductive success (Carrick 1963). Therefore, all territorial Magpies spend a large part of their time fighting and otherwise defending the territory (Farabaugh *et al.* 1992). EGP is a common occurrence in this species; however, the males responsible for EGP are rarely detected among the sample populations (Hughes *et al.* 2003, Durrant & Hughes 2005). In order to test whether female Magpies choose mates for their 'good genes', we measured indicators of the relative quality of cuckolded and non-cuckolded territory-owning male Magpies over two breeding seasons. We also compared territory-owning males that produced fledglings in their territory (regardless of paternity) with those that produced no fledglings. We used a variety of characteristics such as size, weight and parasite loads, selected from previous studies on other species that have been shown to have a positive effect on female choice. We also used only characteristics that we could apply readily to Australian Magpies; for example, plumage characteristics are not useful as White-backed Magpies *G. t. tyrannica* are not markedly sexually dimorphic (Simpson & Day 1999). Males have white backs and females have pale grey backs (in *G. t. tyrannica*), and males do not produce nuptial plumage (Simpson & Day 1999).

The purpose of this study was to test whether female Australian Magpies sought 'good genes' from their mates. If female Magpies were seeking 'good genes', from the characteristics we measured, we expected that males producing many territorial fledglings in which they achieved a high level of paternity would be physically large birds with low parasite levels and with high genetic diversity. We also expected these high-quality birds to sire some of the extra-group fledglings detected in territorial groups held by males of inferior quality. Given that this species has an extremely high rate of EGP (Hughes *et al.* 2003), this study would provide information on sexual selection and mate choice within an unusual mating system located in a region of the world whose avifauna has received little attention in this regard.

METHODS

Field and laboratory methods

The study site, observation and laboratory methods for paternity testing were as per Durrant and Hughes

(2005). The study site was a rural property 50 km west of Melbourne, Victoria, Australia (37°43'S, 144°24'E). We trapped members of 32 territorial groups, collecting blood samples and individually colour-banding a total of 221 birds between 2000 and 2002, as part of a larger study.

We observed birds in territories for 20 min at a time, 2–3 times per week throughout the breeding season (July–December). We recorded the identity of territorial group members, breeding activity (i.e. nest construction or provisioning of young), and demographic data such as number of females in a territory and number of fledglings produced in a breeding season. This gave an indication of a male's 'harem' size, as well as an indication of the potential quality of his territorial resources as estimated by the number of young surviving to fledging age each season. For information on morphology and parasite loads, all adult birds were trapped in 2001 ($n = 34$ males) and all adult males were trapped in 2002 ($n = 31$). The sample sizes of males differ between years because of the death or disappearance of some territorial males and failure to catch two males in the second year that were sampled in the first. We used a large wire 'walk-in' style trap (1.5 m in diameter), baited with grated cheese to catch the birds. On some occasions during 2002 a decoy bird was used. A non-territorial adult male was placed in a small wire cage (45 cm³), inside the larger walk-in trap to attract territorial residents. Birds were weighed using a 500-g Pesola spring balance (Weight). For each bird the length of the beak and left tarsus were measured using dial callipers (Beak and Tarsus variables). The bird was held by an assistant and assessed visually for feather-chewing lice (*Philopterus* sp. and *Brueelia* sp., see Hughes 1984) on the nape and back (Lice Total). The feathers of the nape were combed through layer by layer for 2 min and the back for 3 min using fingers and long forceps. We recorded the number of lice found in each region.

Finally, a blood smear on a microscope slide was made. Blood was extracted by clipping the smallest claw above the quick. The blood smear was air-dried, labelled and stored. Slides were fixed with 100% methanol for 2–7 min, and flooded with Giemsa's stain (R66 improved solution, Gurr, Biolab, Victoria, Australia, diluted 1 : 10 with phosphate buffer at pH 7.2) for 45 min. The slide was finally washed with distilled H₂O, blotted with filter paper and air-dried (method of R. Adlard, curator of the Queensland Museum's Avian Haemoproteoza collection, pers. com.). Slides were scanned on a Nikon Alphaphot-2

YS2 or an Olympus CH20 microscope, 1000 fields per slide under oil immersion ($\times 1000$). The presence or absence of three commonly found blood parasites was noted, but not the intensity of infection (variable Blood). The three parasites were two that use red blood cells as hosts, *Haemoproteus* sp. and *Plasmodium* sp., and one that invades white blood cells, *Leucocytozoon* sp. (Adlard *et al.* 2004).

For paternity analyses, eight microsatellite loci were analysed, using species-specific primers developed in the Molecular Ecology Laboratory, Griffith University (see Hughes *et al.* 2003, Durrant & Hughes 2005). Parentage was assigned (variables Sired and EGP Chick) using CERVUS 2.0 (Marshall *et al.* 1998); precise details of the methodology are given in Durrant and Hughes (2005).

The intention was to trap all the birds at the beginning of the breeding season. Owing to the nature of the trapping method, it was not possible to catch all birds at the same point in the season, and trapping continued once a week throughout the 2001 breeding season. In the 2002 breeding season, after some analysis of the previous year's data, only blood smears and feather louse loads were obtained from the males trapped, in addition to the standard observational data and paternity study on fledglings produced that season. Overall, however, 79% of males were trapped and assessed during the first month of the breeding season, July, when mate selection is likely to be occurring. Using the microsatellite data generated during the parentage study (Durrant & Hughes 2005), an assessment of genetic diversity (Mean d^2) was made by averaging the repeat unit distances between

the two alleles at each of eight loci (Otter *et al.* 2001). This method gives an indication of how 'outbred' an individual is. It assumes a stepwise mutation model of microsatellite evolution, i.e. microsatellite alleles that are similar in size are assumed to be more closely related than two alleles that are many repeat units apart (Goldstein & Schlötterer 2001). This model of single-step mutation has yet to be proven, and some modelling data have led to the rejection of this hypothesis (Nielsen & Palsbøll 1999). Therefore, another measure of heterozygosity was estimated (Hetero) by averaging the number of alleles per locus across all eight loci. This method assumes that, as in the infinite alleles model, all alleles are equally related to each other (Goldstein & Schlötterer 2001).

Statistical methods

All tests were performed in SPSS version 11.5. The variables measured and their abbreviations are explained in Table 1. Multivariate analyses followed Tabachnick and Fidell (2001). Shapiro–Wilk's tests of normality were performed on each variable. Parametric tests were used wherever possible. The majority of variables were non-normally distributed and for them non-parametric tests were used. Univariate comparisons between mean and median values for two groups of males (e.g. Group 1, males that owned territories that produced fledglings; Group 0, males that owned territories that did not produce fledglings) used one-tailed *t*-tests or Mann–Whitney *U*-tests as appropriate for each breeding year. We did this to test whether any variables influenced the

Table 1. Variables measured among the male White-backed Magpie population and the abbreviated titles used in this paper for statistical tests. A few males were only measured in one of the two seasons, owing to mortality or disappearance between breeding seasons.

Variable name	Variable measured	Years collected
Weight	The weight of the male during the breeding season (g)	2001
Tarsus	The length of the right tarsus (to the nearest mm)	2001
Beak	The length of the beak from between the nares on the dorsal surface to the tip (mm)	2001
Lice Nape	The number of feather-chewing lice on the nape (white part of the back of head)	2001 & 2002
Lice Back	The number of feather-chewing lice on the white part of the back to the base of the tail	2001 & 2002
Lice Total	The total of Lice Nape and Lice Back	2001 & 2002
Blood	The presence or absence of any of three genera of haemoprotozoa	2001 & 2002
Female	The number of resident adult females within the territorial group	2001 & 2002
Terr. Chick	The number of fledglings born within the territory, regardless of genetic paternity	2001 & 2002
Sired	The percentage of territorial fledglings that were the genetic offspring of that male, assessed using microsatellites	2001 & 2002
EGP Chick	The number of fledglings sired outside the territorial group, assessed using microsatellites	2001 & 2002
Mean d^2	The average repeat unit distance between alleles of eight microsatellite loci	Constant across years
Hetero	The average number of different alleles across eight microsatellite loci	Constant across years

production of fledglings within a male's territory (regardless of paternity) in the first instance. As it would have been inappropriate to compare the level of paternity gained between males when some males did not even nest in that season, males that owned territories that produced fledglings were treated separately in an additional analysis. To test whether any variables influenced the level of paternity gained once fledglings had been produced, Pearson's or Spearman's correlation coefficients were calculated individually for the following variables: Weight, Tarsus, Beak, Lice Total, Female, Terr. Chick, EGP Chick, Mean d^2 and Hetero against Sired for each year that data were collected. Mann–Whitney U -tests were used to test for an effect of Blood on Sired, and Blood on Terr. Chick.

We used logistic regression to check if any of the variables had an effect on the probability of producing offspring within the territory during each breeding season (Group 1 vs. Group 0). Logistic regression was also used to detect which variables had an effect on the probability of gaining at least some paternity of each brood of fledglings produced by those males that had territorial fledglings in each season (Some vs. Zero). These variables were placed into a model to test their predictive power of group membership (Group 1, Group 0) (Some, Zero) based upon their distributions between groups. The variable Beak was found to be highly correlated with the variable Tarsus, and was dropped from the analyses, as tarsus length has been found to be a much better estimator

of body size in other species of birds (Dufour & Weatherhead 1998). Variables entered into each equation were Hetero, Mean d^2 , Weight, Tarsus, Lice Total, Blood, EGP Chicks and Females for males producing or not producing territorial fledglings in 2001, and Hetero, Mean d^2 , Lice Total, Blood and Females for males that produced or did not produce territorial fledglings in 2002. EGP Chicks was excluded from analysis for the 2002 males as none of them was detected as being the father of an extra-group fledgling and the value was a constant. Variables entered into each equation for males achieving some or zero paternity of a brood of fledglings were Hetero, Mean d^2 , Weight, Tarsus, Lice Total, Blood, Females and Terr. Chick in 2001 (EGP Chick was a constant for this group), and Hetero, Mean d^2 , Lice Total, Blood, Terr. Chick, EGP Chick and Females for 2002 males.

RESULTS

Comparisons of the means or medians of each variable between the two groups of males (those that owned territories that produced fledglings and those that owned territories that did not) produced non-significant differences for most of the variables examined (Table 2). The number of lice found on males was significantly higher in the group of males that did not produce territorial fledglings in 2001 but not in 2002. There were also significantly higher louse loads on territory-owning males that did not produce

Table 2. Mean, standard error and Mann–Whitney U - or t -test results (one-tailed) for each variable measured between males that owned territories that produced fledglings (Group 1) and males that owned territories that did not produce fledglings (Group 0). Results are presented for each season. Results in bold type are significant at the $\alpha = 0.05$ level. Test statistics that are underlined are parametric t -tests based on normally distributed data.

	Weight (g)	Tarsus (mm)	Beak (mm)	Lice Total	Female	EGP Chick	Mean d^2	Hetero
2001								
Group 1 – Mean	378.82	63.70	54.84	7.71	1.94	0.00	89.14	1.78
($n = 17$) se	5.55	0.45	0.54	2.27	0.13	0.00	12.26	0.03
Group 0 – Mean	369.71	64.08	54.72	18.41	1.65	0.06	65.51	1.73
($n = 17$) se	4.03	0.44	0.58	4.79	0.12	0.06	12.32	0.03
Test statistic	–1.28	<u>0.61</u>	<u>–0.14</u>	–1.40	–1.53	–1.00	–1.72	–1.04
P value	0.10	0.27	0.44	0.04	0.06	0.16	0.04	0.15
2002								
Group 1 – Mean	n/a	n/a	n/a	10.53	1.79	0.05	66.83	1.75
($n = 19$) se				2.38	0.12	0.05	8.61	0.03
Group 0 – Mean	n/a	n/a	n/a	21.92	1.83	0.08	82.09	1.75
($n = 12$) se				7.51	0.17	0.08	20.75	0.04
Test statistic	n/a	n/a	n/a	–0.69	–0.20	–0.33	–0.32	–0.38
P value				0.25	0.42	0.37	0.37	0.35

Table 3. Correlations between measured variables and the percentage of fledglings sired by a male within a territory (Sired) for groups that produced territorial fledglings. One-tailed significance values are given beneath the r -values in parentheses. Values that are underlined were calculated using Pearson's r correlation as they were from variables that were normally distributed, otherwise Spearman's r correlation was used. Significant correlations are indicated in bold type.

Year	Weight	Tarsus	Beak	Lice Total	Female	Terr. Chick	EGP Chick	Mean d^2	Hetero
2001 ($n = 17$)	0.22 (0.20)	<u>-0.31</u> (0.12)	<u>-0.01</u> (0.48)	-0.17 (0.26)	0.13 (0.32)	-0.26 (0.16)	Constant	-0.34 (0.09)	0.23 (0.19)
2002 ($n = 19$)	n/a	n/a	n/a	-0.05 (0.42)	0.17 (0.24)	0.49 (0.02)	-0.19 (0.21)	-0.01 (0.48)	0.28 (0.12)

territorial fledglings in either breeding season than on males that produced fledglings in both seasons (means (se): 'territorial fledglings' males ($n = 11$) = 6.77 (1.61); 'no fledglings' males ($n = 9$) = 23.56 (6.73); test statistic = -1.94; $P = 0.03$). The variable Mean d^2 was significantly higher among males that owned territories that produced fledglings in 2001, but not in 2002. Correlations between the measured variables and Sired were mostly not significant, with one exception: Sired vs. Terr. Chicks was significantly positively correlated for males that produced territorial fledglings in the 2002 breeding season, but not in 2001 (Table 3). This suggests that males that had many fledglings produced within their territorial group were more likely to father a large proportion of them. Comparison of the proportion of males infected with one or more forms of haemoprotozoans (Blood) showed that in 2001, 17.6% of males that produced territorial fledglings were infected compared with 23.5% of those that produced none; in 2002, 15.8% of males that produced territorial fledglings were infected, compared with 0% of those that produced none. The tests of proportions of haemoprotozoan infection were non-significant in both years for males that owned territories that either did or did not produce fledglings (Group 1 vs. Group 0). Likewise, none of the Mann-Whitney U -tests for an effect of presence or absence of haemoprotozoa on the level of paternity gained in territories that did produce fledglings (a continuous variable) was significant in either year.

Logistic regression failed to produce any significant models for predicting group membership at the $\alpha = 0.05$ level for any of the categories of males examined. The parameter estimates produced from the model indicate that for 2001 ($P = 0.076$; parameter estimate for Lice Total 2001 = -0.052), there was a slight tendency for males that had high feather louse loads to be less likely to produce fledglings within their territory. However, this was non-significant.

DISCUSSION

The lack of clear or consistent correlations between any of the measured variables and male paternity level is an unexpected result for a species with a mating system that displays such a high rate of extra-group mating. Under the 'good genes' hypothesis, females are expected to select extra-group mates that are superior in quality to their social mate (Petrie & Kempenaers 1998). Given that extra-group males are only likely to contribute indirect, or genetic, benefits (Cordero 1998), and that females may be taking a risk to engage in such copulations (Poiani & Wilks 2000, Arnold & Owens 2002), we expected that there would be a large difference between territory-owning males that maintained paternity and those males that were cuckolded. This, however, was clearly not the case.

The lack of correlation of variables indicating size and weight with paternity were particularly surprising. In a highly territorial bird that invests a large amount of time in fighting (Farabaugh *et al.* 1992), we expected that indicators of large body size and high weight would positively influence female mate choice. Male Tree Swallows *Tachycineta bicolor* that owned territories were found to be heavier than floater males (Lozano 1994). This was believed to be because they would win in intrasexual conflict more often and so might be chosen by females. The body-size of territory-owning males influenced female choice in the Blue Tit *Cyanistes caeruleus*, cuckolded males had significantly shorter tarsi than non-cuckolded males (Kempenaers *et al.* 1992). However, there was no body size or weight difference between territory-owning and floater Red-winged Blackbirds *Agelaius phoeniceus* (Eckert & Weatherhead 1987, Shutler & Weatherhead 1991), or male Marsh Wrens *Cistothorus palustris* (Leonard & Picman 1988). Male Australian Magpies do not differ in weight or size between those

that were cuckolded and those that were not. This suggests that females did not select males in order to acquire the 'good genes' necessary for producing large offspring that will be capable of defending a breeding territory.

There was also no consistent correlation between indicators of heterozygosity or health (as parasite loads) and paternity among Australian Magpies, although this is perhaps less unexpected. Among Blue Tits, extra-pair young were found to be more heterozygous than within-pair young, but the males that lost paternity did not differ in heterozygosity with males that were not cuckolded (Foerster *et al.* 2003). Red-winged Blackbird males that were more heterozygous were neither in better condition nor did they have lower parasite loads (Weatherhead *et al.* 1999). Furthermore, male Red-winged Blackbirds that were parasitized with haemoprotozoans did not sire fewer offspring (Weatherhead & Boag 1995). It may be that the haemoprotozoans we found are only pathogenic to their hosts at very high densities, and none of the infected males carried a sufficient load of parasites to provide cues to females choosing a mate. The same may also apply to the feather-chewing lice we looked at.

There was a correlation between high feather louse loads and males that produced no young within their territories for the season, both when breeding seasons were combined and just in 2001. It may be that male Magpies that struggle to hold a territory, possibly from high intrusion rates, will neglect to preen and also invest less time in reproductive effort. These males may be of inferior quality, although the other variables measured do not appear to support this. The correlation between louse loads and reproductive output was also not consistently significant over all the breeding seasons.

As Australian Magpies that reside in a territory are known to be heavier and to have lower mortality rates than flock-living Magpies (Carrick 1972), perhaps we should not expect much variation in these traits when all sampled males are territory-owning birds. There is also a potentially confounding effect of the timing of the sampling for weights. Owing to the passive nature of the trapping method, males were sampled across the entire breeding season. Weights of birds may fluctuate across the breeding season (Takagi 2002). However, the majority of males (79%) were sampled in the first month of the breeding season. The remainder (seven males), which were sampled towards the end of the season, represented all classes of males that were examined

(two males that produced no fledglings within their territories, three males that were cuckolded, two males that maintained high levels of paternity). We therefore do not believe that the timing of capture affected our conclusions.

Heterozygosity may still be an important characteristic for female Magpies, but given that we examined functionally neutral microsatellites (Goldstein & Schlötterer 2001), rather than a marker under selection such as the avian major histocompatibility complex (MHC) that determines immune function (Hess & Edwards 2002), we may not have been able to detect it. Foerster *et al.* (2003) also mentioned this point: the heterozygosity of microsatellites may not reflect the heterozygosity of the overall genotype. In the future, examining variation in the MHC or other functional genes may prove to be of value.

The fact that very few significant results were produced for any of the tests could be explained in two ways. First, none of the variables measured had a strong influence on the paternity level or reproductive success of a given male, or second, there were high levels of variation in the data and the sample sizes of male birds were too small to detect any influence. However, the sample sizes in this study ($n = 9-19$) fall within the range used in other similar studies that obtained positive results. Kose *et al.* (1999), in a study that related sexual selection to a feather characteristic, used 15-18 male Barn Swallows *Hirundo rustica* per treatment. Female Blue Tits were found to mate assortatively with respect to a male's ultraviolet radiance of the crown patch, using a sample size of 18 pairs (Andersson *et al.* 1998).

If females do not base mate choice on quality indicators, then other factors unrelated to intrinsic quality must drive mate selection, particularly extra-group mate selection. Other hypotheses that do not depend on females assessing and selecting high-quality males with which to mate are inbreeding avoidance (Pusey & Wolf 1996), enhancement of genetic diversity (Blomqvist *et al.* 2002) and reduction of the risk of genetic incompatibility (Zeh & Zeh 1996). The population of Australian Magpies studied was characterized by high EGP rates (Durrant & Hughes 2005). Because some of the offspring may remain in the natal territory until adulthood, they have a small chance of breeding with a close relative within their territorial group. Therefore, female Magpies that seek extra-group mates may avoid the negative effects of inbreeding depression among their brood (Durrant & Hughes 2005). The frequency of EGP in this species may explain the lack of a strong correlation

between reproductive output, paternity and classic indicators of male quality. This study has largely dismissed the 'good genes' hypothesis for this species. The inbreeding avoidance hypothesis may be more appropriate to explain the unusual mating system and the extremely high rate of EGP found among Australian Magpies (Hughes *et al.* 2003, Durrant & Hughes 2005).

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