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Multiple ornamentation, female breeding synchrony, and extra-pair mating success of golden whistlers (*Pachycephala pectoralis*)

Wouter F. D. van Dongen · Raoul A. Mulder

Abstract Considerable variation exists in rates of extra-pair paternity between species, and across and within populations of the same species. Explanations for this variation include ecological (e.g. breeding synchrony), morphological (e.g. ornamentation), and genetic (e.g. relatedness) factors, but it is rare for studies to simultaneously explore these factors within a single population. This is especially true for highly ornamented species, where mate choice based on ornamentation may be more complex than in less-adorned species. We conducted such a study in a migratory population of the highly ornamented golden whistler (*Pachycephala pectoralis*). We quantified male genetic reproductive success and related it to a range of factors putatively involved in determining extra-pair mating success. We found no effects of genetic factors (male heterozygosity and relatedness) on extra-pair success, nor of territory size, male age, or incubation effort. Instead, males possessing yellower breast plumage and large song repertoires enjoyed higher reproductive success. Additionally, we found a negative relationship between local breeding synchrony and male extra-pair mating success. This may be a consequence of mate guarding during the female fertile period and an inability of males to simultaneously mate-guard and pursue extra-pair fertilisations. In this species, the opportunity for extra-pair matings appears to vary temporally with an ecological variable (local breeding synchrony), while fine-scale, inter-male differences in mating success may be influenced by individual attributes (male ornamentation). The migratory nature of the study population and its lack of natal philopatry may mean that relatedness and inbreeding avoidance are less important considerations in mate choice.

Keywords Breeding synchrony · Extra-pair matings · Multiple ornamentation · Plumage · Bird song

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Introduction

Birds display a remarkable variety of different breeding strategies associated with varying levels of promiscuity, ranging from strict genetic monogamy through to polygyny and polygynandry (Andersson 1994). Considerable variation also exists within mating systems. For example, in a large proportion of socially monogamous bird species, males seek matings outside their pair bond (extra-pair fertilisation; EPF) at rates which vary dramatically from extremely few EPF (e.g. willow tit, *Parus montanus*, 0.9% of nestlings fathered by extra-pair males; Orell et al. 1997) to extremely high rates of EPF (e.g. superb fairy wren, *Malurus cyaneus*, 76% of nestlings; Mulder et al. 1994). Even within species, frequencies of extra-pair mating can vary dramatically between populations. For instance, a mainland population of the house sparrow (*Passer domesticus*) exhibited an extra-pair paternity frequency of 10.5%, and a study of an island population found almost no evidence of EPF (1.3% extra-pair paternity rate; Griffith et al. 1999). Finally, within populations, reproductive success is typically extremely skewed, with a small number of males siring most extra-pair young while the remaining

males sire few, if any, offspring (Blomqvist et al. 2005; Westneat and Mays 2005; Stewart et al. 2006).

Variation in the frequency of EPF seems to be driven by a wide variety of phylogenetic, ecological, morphological, and genetic factors, the relative importance of which continue to be the focus of debate (Westneat and Stewart 2003). Ecological factors that may influence the frequency of EPF include population density and local breeding synchrony (Estep et al. 2005; Carvalho et al. 2006; Kokko and Rankin 2006). The influence of local breeding synchrony is particularly controversial, because it can be argued that extra-pair matings should either increase with high levels of breeding synchrony (because females are better able to assess multiple potential extra-pair mates that are simultaneously displaying) or decrease (as fewer males are free from mate-guarding duties and available to pursue extra-pair matings). To date, the evidence for either hypothesis has been equivocal, with a small number of studies reporting positive (e.g. Stutchbury and Morton 1995; Stutchbury et al. 1997, 1998) or negative (e.g. Saino et al. 1997; Conrad et al. 1998) correlations and the majority reporting no relationship (e.g. Chuang-Dobbs et al. 2001; Johnsen and Lifjeld 2003; Arlt et al. 2004; Kraaijeveld et al. 2004; Westneat and Mays 2005; Stewart et al. 2006).

Many male birds display conspicuous sexual signals such as colourful plumage or elaborate song, and these attributes may influence a male's success at obtaining EPF, because they reliably communicate aspects of his quality to females (for example, because they are costly to produce or maintain). Females may thus benefit from choosing males with the most elaborate signals to enjoy the genetic or phenotypic benefits associated with the expression of these signals (Andersson 1994). Likewise, females may choose males partly on the basis of genetic features such as male heterozygosity or relatedness (Tregenza and Wedell 2000). High heterozygosity may be beneficial if it correlates with individual fitness or viability (Hansson and Westerberg 2002). In this case, females benefit from mating with males with higher overall heterozygosity (because more heterozygous males will sire offspring with higher heterozygosity) or males that are genetically dissimilar to themselves, resulting in offspring with higher heterozygosity, thus avoiding the deleterious effects of inbreeding (Bensch et al. 1994; Foerster et al. 2003; Stapleton et al. 2007).

It remains unclear which of these ecological, morphological, and genetic factors most strongly influences levels of extra-pair paternity and which traits females pay attention to during mate choice. Much of our insight into the potential drivers of extra-pair paternity levels has come from comparative studies (e.g. Møller and Birkhead 1994; Stutchbury and Morton 1995; Petrie et al. 1998; Bennett

and Owens 2002), but these offer only modest insight into the factors that are likely to be important in a given study system. Ideally, the relevant factors should be quantified concurrently in a single species, but this has only rarely been attempted, and such studies have produced mixed results. For instance, in house sparrows, the number of extra-pair offspring sired by males was unrelated to most factors quantified, including breeding synchrony and density, relatedness, male ornamentation, and age (Stewart et al. 2006), whereas in another study, breeding synchrony, timing of breeding, habitat type, and male ornamentation had no effect of male extra-pair success in red-winged blackbirds (*Agelaius phoenicius*; Westneat and Mays 2005; Westneat 2006). Clearly, the fundamental question of how different life-history attributes influence the opportunity for extra-pair matings can only be resolved with more comprehensive studies that simultaneously quantify a broad spectrum of factors putatively influencing extra-pair mating success.

A particularly interesting area for such research concerns mating in species displaying multiple sexually-selected ornaments. Many bird species simultaneously possess a variety of both acoustic and visual ornaments, the presence of which can increase the complexity of mate choice decisions (Møller and Pomiankowski 1993). Despite many advances in our knowledge, the exact role of multiple ornaments in determining male reproductive success remains a debated issue (Candolin 2003). Each ornament type, for example, may differ in assessment costs, or conspecifics may be able to gain different information on signaller quality by paying attention to distinct ornaments. For example, in satin bowerbirds (*Ptilonorhynchus violaceus*) females pay attention to both a sexually-selected display structure and male plumage because each signal reflects a different aspect of male quality (Doucet and Montgomerie 2003), while female village weaverbirds (*Ploceus cucullatus*) initially base choice on an easily assessed signal (nest invitation displays), and then switch to more reliable cue (nest construction quality) to make a final choice of a subset of these males (Collias 1979).

Clearly, an important step in further increasing knowledge on the use of multiple ornaments in mate choice is to quantify both male display signals and a range of ecological and genetic factors in highly ornamented species. In many bird species, male ornamentation is correlated with other factors, for example genetic heterozygosity (e.g. Seddon et al. 2004; Reid et al. 2005), territory size (e.g. Evans and Hatchwell 1992a; van Dongen and Mulder 2007), or parental care (e.g. Sætre et al. 1995; Mitchell et al. 2007) and hence several traits should, ideally, be quantified to disentangle the effects of each trait on mating success.

We examined ecological, morphological, and genetic correlates of male extra-pair reproductive success in the highly ornamented golden whistler, *Pachycephala pectoralis*, a small passerine inhabiting Australian forests. Male golden whistlers display several plumage ornaments, incorporating melanin-based (black), carotenoid-based (yellow), and unpigmented (white) plumage, and are also highly vocal, with large song repertoires (van Dongen 2006). We examined patterns of paternity in relation to ecological (local breeding synchrony and territory size), morphological (male song, plumage ornamentation, and paternal care) and genetic effects (male relatedness and heterozygosity). This allowed us to explore the potentially complex mechanisms temporally and spatially controlling intrapopulation mating success patterns in this species.

Methods

Study site and species

This study was carried out between September 2001 and February 2004 at Toolangi State Forest, Victoria, Australia (37°31′S, 145°32′E). The study area covered 106 ha from a continuous stretch of forest covering approximately 38,000 ha. The predominant vegetation is a mountain ash (*Eucalyptus regnans*) canopy with a variable understorey dependent on local topography (van Dongen and Yocom 2005).

The golden whistler is a socially monogamous passerine. Males attain full adult plumage in their third year, but these males can often be distinguished from older males by traces of juvenile plumage. Adult males display bright yellow breast plumage, a yellow nape band and a white throat patch. Black plumage totally surrounds this throat patch, including a narrow black chin stripe, which separates the white throat patch from the yellow breast plumage. In contrast with adult males, females and sub-adult males have uniform grey-brown plumage.

The study population is migratory. Individuals arrive in early to mid-September and depart in late April. Both sexes within a pair vigorously defend their territory throughout this time (van Dongen and Yocom 2005). Natal philopatry appears to be rare in this population, as no offspring were sighted at the study site in subsequent years (van Dongen and Yocom 2005).

Capture methods and morphometric measures

Individuals were captured upon arrival at the study site or at the onset of breeding. Birds were caught in mist nets and fitted with a metal ring supplied by the Australian Bird and Bat Banding Scheme and a unique combination of three coloured leg rings. The approximate age of adult males was estimated on the basis of the presence (first year adult males) or absence (all other adult males) of traces of juvenile plumage. We took standard measurements including head–bill length (distance from the tip of the beak to the back of the head, to the nearest 0.1 mm, using dial callipers), tarsus length (nearest 0.1 mm, callipers), and body mass (nearest 0.1 g, spring balance). The length and width (in mm) of the elliptical throat patch was measured using dial callipers ensuring the male's head was fully outstretched to minimise variation in patch size because of the angle of the head relative to the body (van Dongen and Mulder 2007). Throat patch area was then calculated using the equation throat patch area $= \pi(\text{width}/2)(\text{length}/2)$. Average chin-stripe width was calculated by averaging three width measurements taken from the left, middle, and right sides of the chin-stripe. Nape-band width was measured in the same way. We also took a small blood sample (50 μl) from the brachial vein of each bird for subsequent genetic analysis.

Spectrophotometric quantification of plumage colour

In 2001 and 2002, spectral reflectance properties of the yellow breast was measured using a S2000 spectrometer, PX-2 pulse xenon light source, a fibre-optic reflectance probe, and OOIBase32 software (Ocean Optics, Dunedin, USA). Before measurement of each bird the spectrophotometer was calibrated against a Spectralon white reference (Labsphere). A dark calibration reference was also used to minimise electrical noise. We took four replicate measurements from the breast plumage region of each bird, placing the probe with its machined 45° angle end flat against the feathers. Reflectance measurements were taken at 3-nm increments from 300 to 700 nm.

The multiple spectral curves for each male were averaged and used to derive the three colour variables: brightness, hue, and chroma, which were calculated as described in van Dongen and Mulder (2007). Briefly, plumage brightness (spectral intensity) was estimated from the sum of reflectances between 300 and 700 nm ($R_{300-700}$). Plumage hue (spectral location or "yellowness") was estimated from $\lambda(R50)$: the midpoint wavelength between the wavelength of maximum (R_{max}) and minimum (R_{min}) reflectances. Plumage chroma (spectral saturation) was estimated by dividing the reflectance between the wavelengths at which yellow reflects maximally (450–700 nm) by total reflectance ($R_{450-700}/R_{Total}$). These measures of colour were moderately repeatable for the four replicates taken from each plumage region (brightness: $r = 0.713$, $F_{1,36} = 12.58$, $P = 0.001$; chroma: $r = 0.663$, $F_{1,36} = 7.68$, $P = 0.009$; hue: $r = 0.828$, $F_{1,36} = 31.11$, $P < 0.001$) and are in

accordance with other studies reporting similar measurement repeatability estimates (e.g. Perrier et al. 2002).

Daily census and nest monitoring

The population was monitored via daily censuses throughout the breeding season. We monitored 25 pairs in 2001, 27 in 2002, and 24 in 2003. After locating an individual, we noted its position in relation to a set of fixed reference points spread throughout the study site (97 reference points over 106 ha). Male territories were mapped using the geographic information system software package ArcView GIS 3.2 (Environmental Systems Research Institute 1999). We mapped territories for males in 2001 and 2002. Territory sizes were calculated where we had a minimum of eight fixes per male from different days (mean number of fixes per male: 2001: 11.1 ± 3.0 SD, $n = 18$, 2002: 12.4 ± 4.0, $n = 20$). Using ArcView, we implemented minimum convex polygons to delineate the boundaries of territories by outlining the outermost territory fixes for each individual (Southwood 1966). Nests were located for each pair and monitored every two or three days. A blood sample was taken from nestlings via brachial venipuncture for paternity analysis.

Behavioural observations

In 2001, recordings were made using a Sony TCD-D8 Digital Audio Tape recorder and Sennheiser ME67 unidirectional microphone. We opportunistically recorded song time budgets throughout the breeding season in order to obtain information on male song repertoires and singing rates (mean song time budget duration: 21 min 19 s $\pm$ 11 min 34 s SD). In 2002, we documented individual variation in singing rates by following an individual for a 30-min period and counting all songs sung. We performed these counts during nest building (commencing when the female was first seen collecting nesting material for a nest and ending when the penultimate egg was laid) and incubation (commencing after the final egg was laid in a clutch until egg hatching) stages. In 2003, recordings were made in conjunction with simulated territory intrusion experiments using live caged decoy birds and song broadcast from speakers (van Dongen and Mulder 2008). We made recordings using a Sony TC-D5 pro-stereo cassette recorder and Sennheiser ME67 microphone. We were thus able to estimate male singing rates in 2001 and 2002 and male repertoire sizes in 2001 and 2003. Male song repertoires were determined by calculating the total number of different song-types sung by an individual male for all recordings in a given year (see van Dongen (2006) for details on how different song-types were identified). Repertoire exhaustion curves were constructed to ensure that most song-types were logged for each male (van Dongen 2006).

We quantified parental effort at the nest by conducting nest watches during the incubation period during 2001. One 90-min incubation observation was completed for each male during which time we were hidden from view at a distance of 8–12 m from the nest. During the observation, we recorded the number of incubation bouts and the duration of each incubation bout for each sex. Males usually did not assist in incubation until five days after the complete clutch had been laid, so all watches occurred after this time (van Dongen and Yocom 2005).

Nestling paternity assessment using polymorphic microsatellites

DNA was extracted from all blood samples using a salting out procedure (Bruford et al. 1992) and stored in TE buffer (10 mM Tris pH 7.5, 0.1 mM EDTA). All nestlings and adults were genotyped at six microsatellite loci (Ppm1, 3, 7, 8, 10 and 11) using procedures described in van Dongen and Mulder (2005). These six loci resulted in a high probability of unambiguously identifying the genetic father of each nestling (exclusion probability = 0.9997).

To determine the genetic father of each nestling ($n = 130$) we first established whether the social father was also the genetic sire of that nestling. The genotype of the nestling's sire was determined by subtracting the maternal alleles from the nestling's genotype. We then compared the genotype of the putative sire to that of the social father. Nestlings that matched their social father's genotype at all loci were considered within-pair ($n = 80$). One-allele mismatches between social father and offspring occurred in 25 cases. We conservatively assumed these were mutations or typing errors because all other loci matched the nestling to the social father and no other males in the population provided a better match. Although these mismatches could potentially be a result of extra-pair fertilisations, a similar degree of mismatches occurred between mothers and offspring ($n = 15$ mismatches; degree of offspring mismatching between mothers and fathers: $\chi^2 = 2.50$, df = 1, $P = 0.114$). This good agreement in mismatch rates between the sexes supports the assumption that father–offspring one-allele mismatches were because of mutations or typing errors and not extra-pair matings.

We assigned nestlings as extra-pair in cases where nestling genotypes differed at more than one locus from that of the social father ($n = 25$). To determine the genetic father of these nestlings, we searched a database of all genotyped males present in that year for individuals that possessed all the paternal alleles of the nestling. In 15 cases, only a single male matched the offspring at all loci and was assumed to be the extra-pair sire. In another five

cases, the putative genetic extra-pair sire mismatched the offspring at one locus. Consistent with our exclusion protocol, we assumed this to be due to mutation or typing error, because no other males provided a better match. However, no male genotypes within the database matched the paternal alleles of an additional five nestlings. These individuals were presumably sired by extra-pair males we did not capture. In all cases where we assigned a father ($n = 125$), we were confident in our assignment of paternity because only one male matched the non-maternal genotype of nestlings at a minimum of five loci. Paternity assignment was later confirmed using the maximum likelihood procedure in the computer software Cervus 2.0 (Marshall 2001), setting the minimum confidence level of correctly assigning paternity to 80%. In all cases, the most likely fathers determined by use of the exclusion method were identical with those nominated by Cervus 2.0.

Genetic diversity and relatedness

Variation in genetic diversity between social and extra-pair mates and between within-pair and extra-pair young was calculated using individual heterozygosity (number of heterozygous loci divided by the total number of typed loci). Paired t-tests were used to compare differences in heterozygosity between cuckolding males and the males they cuckolded, and between extra-pair and within-pair offspring within the same nest. Relatedness between females and their social and extra-pair mates was estimated from allele variation between individuals at each locus using the relatedness software MER 3.0 (Wang 2002).

Quantification of female breeding synchrony

Studies of sperm usage in birds indicate that females can store sperm for subsequent egg fertilisation for more than ten days before the first egg is laid (Birkhead and Møller 1992). Because no data on fertility in golden whistlers exist, we conservatively defined the female fertile period for this species as the time extending from ten days before the date of first egg laying until the penultimate egg was laid.

Successful extra-pair sires are typically immediate neighbours of the cuckolded male, although in some cases males up to three territories away successfully sired extra-pair young (see Results). For the purposes of this study, we therefore quantified female breeding synchrony by determining the number of females within a radius of three territories that were simultaneously fertile with the focal female (mean number of neighbouring territories: 8.0 ± 1.0 territories SE, $n = 10$, range $= 5$–13). All focal pairs were neighbours of each other and therefore included in each other's three-territory radius.

Statistical analysis

We tested whether ornament size is consistent within individuals but between years (i.e. ornament repeatability) and whether ornaments, and hence reproductive success, can be influenced by male age. Repeatability of ornament expression was estimated following Lessells and Boag (1987), where repeatability is given by $r = S_A^2/(S_W^2 + S_A^2)$ (S_A is the among-groups variance component and S_W is the within-group variance component). Age effects on ornamental size was analysed for ornaments for which we had two years of data for a large sample of males. Changes in ornament size with age were then tested for via pairwise t-tests.

We used general linear models (GLM) or generalised linear mixed models (GLMM) depending on the nature of the data. GLMs were used for data that were only collected in one season. However, our data on male reproductive success were potentially non-independent because of males re-nesting several times within a year or being present for more than one breeding season (twelve males were present for two consecutive seasons, and an additional five males returned to the study site each year during the three-year study period). We therefore utilised GLMMs, incorporating male identity as a random factor. Models were produced by entering all variables into the full model and dropping non-significant factors and interactions in order of increasing significance (i.e. from those factors that were highly non-significant to those that were only marginally non-significant), until only significant variables remained in the model. We then assessed the excluded variables for their lack of significant contribution to the model by re-entering them one by one. The values for these re-entered terms were then used to report the non-significant variables. The model containing all the significant factors and interactions was termed the "final model".

Several measures were used to estimate male reproductive success within a season: the number of within-pair young (WPY) sired, the number of extra-pair young (EPY) sired, and the total number of offspring sired (WPY + EPY). Within-pair success was quantified via the proportion of extra-pair nestlings in all the males' nests during a single season. Similarly, extra-pair success was measured as the total number of extra-pair young sired within that season. Total reproductive success was estimated using both the total number of young sired and the total number of fledglings sired.

Our analyses involved a relatively large number of variables ($n = 13$), increasing the chance of type I errors. We nevertheless did not use Bonferroni corrections in the analyses of male reproductive success because of the high likelihood of losing biologically meaningful relationships because of the low sample sizes (Nakagawa 2004). To be

confident that any associations between male traits and reproductive success were indeed biologically significant, we expected consistent associations between particular traits with different measures of reproductive success. This pattern was confirmed (see Results) and thus we consider the likelihood that our results are statistical artefacts to be small. By contrast, in our analysis of intercorrelations between different male traits (Table 1), we performed a very large number of tests ($n = 61$) and had no clear predictions as to which traits would be intercorrelated. In this case, we applied Bonferroni corrections to this subset of analyses. To reduce the subsequent increased risk of type II errors because of low sample sizes in this analysis, we increased the alpha level to 0.1 for this test only (Wright 1992; Chandler 1995).

Sample sizes for different analyses varied considerably, depending on the number of males for which each ornament was quantified. For example, over the three-year study period, song repertoire size was quantified for 30 males and breast brightness for 34 males (figures include repeated measurements of same males in different years) but only 17 males had both ornaments quantified in the same year (sample size of quantified ornaments between years: song repertoire size—2001: 18, 2002: 0, 2003: 12; breast brightness—2001: 20, 2002: 14, 2003: 0). In all analyses involving male song repertoire size we included male age in the model, as older males are known to possess larger song repertoires (van Dongen 2006).

All GLMs were analysed using SPSS 12.0 (SPSS, Chicago, Illinois, USA) and all GLMMs using GenStat 7.0 (Lawes Agricultural Trust, 2003). We tested data for normality and conducted transformations where necessary. Data are reported as means and standard errors unless otherwise stated.

Results

Intercorrelations between male traits

A small number of male traits were intercorrelated (Table 1). However, most of these intercorrelations disappeared after applying Bonferroni corrections (Bonferroni-corrected critical value for 61 correlations is $P = 0.002$, with a relaxed alpha-level of 0.1).

Individual variability in male traits

To identify sources of inter-individual variation in ornamental traits, we documented repeatability in ornament size between years. Repeatability of ornamental trait between years was low (Table 2). Only song repertoire size and territory size were marginally and non-significantly repeatable between years. Similarly, most traits did not vary predictably with age, with the exception of song repertoires and the width of the chin-stripe, both of which tended to increase across successive years (Table 2).

Golden whistler mating system

Overall, 19.2% of all offspring genotyped were sired by a male other than the social father and 23.1% of all nests

Table 1 Pearson correlation matrix for male golden whistler ornamental traits measured within a single season

	Throat Patch	Chin Stripe	Nape Band	Breast Brght	Breast Chrm	Breast Hue	Song Rep	Sng Rte (NB)	Sng Rte (INC)	Male Inc	Terr Size
Chin Stripe	−0.097										
Nape Band	−0.373	0.118									
Breast Brght	0.740**	0.201	−0.024								
Breast Chrm	−0.207	0.011	−0.153	−0.204							
Breast Hue	0.298	−0.161	−0.247	−0.154	0.145						
Song Rep	−0.600	0.426*	0.068	0.476	0.110	−0.079					
Sng Rte (NB)	0.246	−0.209	−0.234	0.154	−0.149	−0.397	NA				
Sng Rte (Inc)	−0.127	0.363	−0.507	−0.284	0.635*	0.655*	NA	−0.036			
Male Inc	NA	0.029	0.361	0.300	−0.015	−0.134	0.301	NA	NA		
Terr Size	0.848***	0.131	0.428	0.661	0.256	0.410	−0.143	0.505*	0.040	−0.195	
Hetero	−0.188	−0.020	−0.209	−0.092	0.218	−0.033	0.101	0.655**	0.029	0.088	0.137

Traits quantified are: throat patch area (Throat Patch), chin-stripe width (Chin Stripe), nape-band width (Nape Band), breast plumage brightness, chroma and hue (Breast Brght, Breast Chrm, and Breast Hue, respectively), song repertoire size (Song Rep), song rate during nest-building and incubation phases (Sng Rte (NB) and Sng Rte (INC), respectively), male egg incubation effort (Male Inc), territory size (Terr Size) and male genetic heterozygosity (Hetero). Values are Pearson correlation values (r) and *asterisks* denote significance at the 0.05 (*), 0.01 (**) and 0.001 (***) levels. "NA" signifies that two ornaments were not quantified during the same year and hence information regarding correlation is not available. The Bonferroni-corrected critical value for 61 correlations is $P = 0.002$ (with a relaxed alpha-level of 0.1—see Methods)

Table 2 Repeatability and interyear variability of male golden whistler traits

	n	Repeatability			Interyear variability			
		r	F	P	X ± SE (Year 1)	X ± SE (Year 2)	t	P
Breast brightness	8	−0.796	0.114	0.748	2774 ± 105	2898 ± 90	−0.971	0.364
Breast chroma	8	−1.000	0.160	0.703	0.89 ± 0.01	0.89 ± 0.01	0.103	0.921
Breast hue	8	−0.877	0.066	0.806	569.3 ± 5.0	567.6 ± 2.4	0.294	0.777
Song repertoire size	5	0.772	7.758	0.069	8.8 ± 4.4	14.2 ± 7.1	−2.527	0.065
Song rate	10	0.422	2.462	0.155	4.7 ± 0.8	3.5 ± 0.3	1.777	0.109
Chin-stripe width	9	0.046	1.099	0.329	5.5 ± 0.2	6.3 ± 0.2	−2.958	0.018
Nape-band width	9	0.345	2.055	0.195	7.5 ± 0.4	7.8 ± 0.4	−0.834	0.429
Territory size	12	0.541	3.356	0.097	2.2 ± 0.2	2.3 ± 0.2	−0.781	0.451

All traits expect song repertoire size were quantified over two successive years (2001 and 2002). Song repertoire sizes were quantified in 2001 and 2003. Throat-patch size was not included in the analysis because of the low sample of males whose throat patch size was known across two years. Note that repeatabilities are always negative and non-significant when the F ratio of the regression is less than unity (i.e. when $MS_A < MS_w$; see Methods for further explanation of how repeatability was calculated)

contained at least one extra-pair young. Of 65 genotyped broods, only seven contained nestlings of mixed paternity. Eight nests contained only extra-pair nestlings; the remaining 50 contained only nestlings sired by the social father. Of the eight nests that had more than one extra-pair nestling, only one contained nestlings sired by more than one extra-pair male. Eighty percent (16/20) of extra-pair nestlings with known fathers were sired by males defending territories immediately adjacent to that of the social father, 15% (3/20) by a male two territories away, and one nestling was sired by a male three territories away.

Male traits and reproductive success

Within-pair success

Males that sired a high proportion of young in their own nest had large song repertoires and breast plumage with lower brightness and higher hue and chroma (Table 3). The repertoires of extra-pair mates were almost twice as large as those of the males they cuckolded, but this difference was not significant, perhaps because of our small sample size and concomitant low power (EP mate repertoire: 11.3 ± 0.5 song-types, cuckolded mate repertoire: 5.8 ± 1.5 song-types; paired t-test, $t = −2.55$, $n = 4$, $P = 0.084$). Extra-pair mates also tended to possess yellower plumage than the males they cuckolded (EP mate breast hue: 568 ± 2 nm, cuckolded mate breast hue: 560 ± 3 nm; paired t-test, $t = −2.98$, $n = 4$, $P = 0.059$).

Extra-pair success

Males displaying darker breast plumage with high hue and chroma attracted more extra-pair matings (Table 4).

Table 3 GLMM models for the effects of male golden whistler traits on proportion of extra-pair young in nest

	Effect	SE	W	P
Constant	−6.10	0.70		
Breast hue	−0.02	0.003	78.92	<0.001
Breast chroma	−10.51	2.73	14.70	<0.001
Breast brightness	0.0006	0.0002	10.64	0.001
Song-repertoire size	1.88	0.02	7743.14	<0.001
Territory size	−0.86	0.53	2.69	0.101
Chin-stripe width	−0.063	0.076	0.71	0.400
Throat-patch area	−0.010	0.012	0.59	0.444
Nape-band width	−0.274	0.345	0.63	0.428
Age	1.89	2.59	0.50	0.481
Heterozygosity	−2.18	3.17	0.47	0.491
Incubation effort	−3.13	6.06	0.27	0.606
Nest-building song rate	−0.059	0.255	0.05	0.817
Incubation song rate	0.01	1.31	0.00	0.993

Poisson model with logarithm link. Random effect: male ID/brood = 0.934 (SE = 0.311)

Total reproductive success

Males with larger song repertoires and "yellower" breast plumage had higher reproductive success (Table 5; Figs. 1a and 1b, respectively). Males possessing larger song repertoires and "yellower" breast plumage (i.e. higher hue values) were also more successful in producing fledglings (Table 6). Males that successfully raised offspring to fledging within a season possessed "yellower" plumage than unsuccessful males (male breast hue—successful: 568 ± 0.5 nm, unsuccessful: 560 ± 0.5 nm, Wald = 4.33, $n = 21$, $P = 0.037$), but did not have larger repertoires (male song repertoire—successful: 11.3 ± 0.1

Table 4 GLMM models for the effects of male golden whistler traits on number of extra-pair young sired

	Effect	SE	W	P
Constant	0.64	0.67		
Breast chroma	337.2	26.23	165.26	<0.001
Breast brightness	−0.026	0.004	41.29	<0.001
Breast hue	0.584	0.101	33.53	<0.001
Throat-patch area	−0.124	0.011	3.90	0.068
Song-repertoire size	0.182	0.119	2.31	0.129
Heterozygosity	3.78	4.00	0.89	0.344
Chin-stripe width	0.339	0.506	0.45	0.502
Territory size	−0.53	0.80	0.44	0.509
Age	0.633	1.17	0.29	0.589
Nape-band width	−0.058	0.357	0.03	0.871
Incubation song rate	−0.04	0.314	0.02	0.892
Incubation effort	−0.095	6.73	0.00	0.989

Poisson model with logarithm link. Note that nest-building song rate could not be analysed because of the low numbers of males with known song rates that also sired extra-pair young. Random effect: male ID/brood = 1.146 (SE = 1.295)

Table 5 GLMM models for the effects of male golden whistler traits on total number of offspring sired

	Effect	SE	W	P
Constant	2.12	0.32		
Breast hue	0.09	0.03	8.18	0.004
Song-repertoire size	0.20	0.08	6.03	0.014
Age	1.135	0.615	3.40	0.065
Chin-stripe width	0.650	0.372	3.05	0.081
Nest-building song rate	−0.85	1.22	1.09	0.297
Territory size	0.545	0.568	0.92	0.337
Throat-patch area	0.007	0.007	0.89	0.344
Nape-band width	−0.165	0.206	0.64	0.425
Incubation song rate	0.036	0.514	0.43	0.514
Heterozygosity	1.548	2.658	0.34	0.560
Breast chroma	3.273	11.241	0.21	0.645
Incubation effort	−1.51	5.75	0.07	0.794
Breast brightness	−0.0001	0.0001	0.01	0.907

Normal distribution with identity link. Random effect: male ID/brood = 0.001 (SE = 1.674)

song-types, unsuccessful: 8.5 ± 0.3 song-types, Wald = 2.90, n = 21, P = 0.089).

Genetic diversity, relatedness and reproductive success

Males that gained extra-pair fertilisations were not more genetically heterozygous than the males they cuckolded (Heterozygosity: cuckolding male—0.96 ± 0.03, cuckolded male—0.88 ± 0.04; paired *t*-test, *t* = 1.51, *n* = 12,
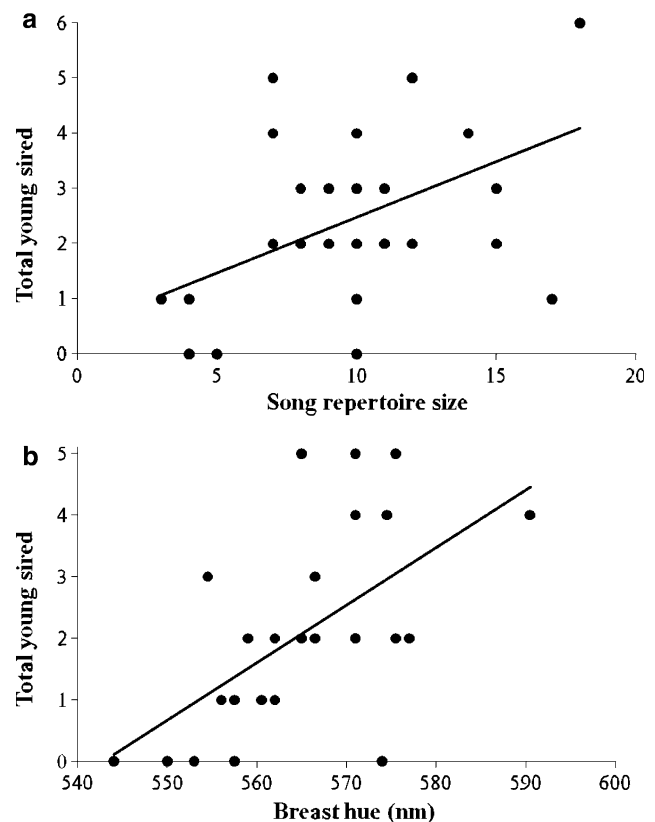
Fig. 1 Relationship between (**a**) song repertoire size and (**b**) breast plumage hue, and the total number of young sired by male golden whistlers within a season (within-pair young and extra-pair young combined)

Table 6 GLMM models for the effects of male golden whistler traits on the total number of offspring that fledged

	Effect	SE	W	P
Constant	−0.78	0.90		
Song-repertoire size	0.18	0.08	5.45	0.020
Breast hue	0.06	0.03	3.89	0.049
Heterozygosity	−2.716	2.790	0.95	0.330
Incubation effort	−5.243	5.750	0.83	0.362
Nape-band width	−0.123	0.135	0.82	0.365
Age	0.66	0.89	0.55	0.458
Nest-building song rate	−0.129	0.175	0.54	0.461
Incubation song rate	−0.120	0.165	0.53	0.468
Chin-stripe width	0.168	0.216	0.45	0.503
Throat-patch area	0.002	0.004	0.37	0.546
Breast brightness	0.0002	0.001	0.32	0.574
Breast chroma	−0.706	0.032	0.05	0.825
Territory size	0.0019	0.236	0.00	0.994

Poisson model with logarithm link. Random effect: male ID/brood = 0.001 (SE = 0.220)

$P = 0.149$) and extra-pair young were not more heterozygous than within-pair offspring (Heterozygosity: extra-pair young—0.96 ± 0.03, within-pair young—0.96 ± 0.03; paired t-test, $t = -0.116$, $n = 7$, $P = 0.911$). Although females had extra-pair matings, this could not avoid the risk of inbreeding, as extra-pair mates were not more distantly related to the female in comparison to social mates (Relatedness: cuckolding male—0.009 ± 0.033, cuckolded male -0.052 ± 0.012; paired t-test, $t = 1.849$, $n = 12$, $P = 0.091$).

Breeding synchrony and reproductive success

We tested whether the paternity of nestlings in a nest was affected by the degree of local breeding synchrony (i.e. the number of neighbouring fertile females, controlling for the number of neighbouring territories). The degree of breeding synchrony did not seem to vary predictably with time of season, as we found no relationship between the date of first egg laying for each nest, and the number of neighbouring females that were fertile (GLMM, Poisson error, logarithm link; number of fertile females: Effect = -0.035, SE = 0.052, Wald = 0.46, $P = 0.496$, number of neighbouring territories: Effect = 0.034, SE = 0.021, Wald = 2.59, $P = 0.108$). Although males were not more likely to be cuckolded during periods of high synchrony (i.e. probability of being cuckolded: GLMM, binomial error, logit; constant = -1.057 ± 0.498; number of fertile females: Effect = -0.585, SE = 0.492, Wald = 1.41, $P = 0.235$, number of neighbouring territories: Effect = 0.099, SE = 0.185, Wald = 0.290, $P = 0.592$, laying date: Effect = 0.021, SE = 0.021, Wald = 0.960, $P = 0.327$), we found a negative relationship between breeding synchrony and number of extra-pair young in the nest. When a greater proportion of females were simultaneously fertile within three territories of the focal nest, males sired more young within their own nest (extra-pair young in own nest: GLMM, Poisson error, logarithm link; constant = -2.437 ± 0.721, number of fertile females: Effect = -1.145, SE = 0.401, Wald = 8.15, $P = 0.004$, number of neighbouring territories: Effect = 0.085, SE = 0.151, Wald = 0.320, $P = 0.573$, laying date: Effect = -0.007, SE = 0.011, Wald = 0.38, $P = 0.535$, total young in nest: Effect = 2.966, SE = 1.028, Wald = 8.33, $P = 0.004$).

Discussion

The most important factors affecting reproductive success in male golden whistlers seem to be the quality of male ornamentation and the degree of local breeding synchrony. Males with large song repertoires and high-quality breast plumage sired more extra-pair young and fledged more offspring. We also found a strong correlation between local breeding synchrony and reproductive success: when more females were simultaneously fertile within a given area, males within this area sired fewer extra-pair young. We found no evidence that other factors putatively affecting reproductive success including breeding density, male heterozygosity, and male incubation effort (e.g. Magrath and Elgar 1997; Foerster et al. 2003; Estep et al. 2005) had any effect on extra-pair mating success in this population.

Male ornamentation and reproductive success

Developing and maintaining elaborate display ornaments typically imposes high costs on the bearer (e.g. Evans 2004; Kilpimaa et al. 2004; Allen and Levinton 2007; Sullivan and Kwiatkowski 2007). Therefore, as only individuals of superior quality are able to bear the increased costs of elaborate signal expression, strong associations between ornament size and aspects of individual quality typically arise. For example, the carotenoid pigments typically necessary to produce red, orange, and yellow bird plumage must be extracted from the birds' diet, but are also required for efficient immune function (Lozano 1994; Hill 1999). Moreover, more complex carotenoids (i.e. oranges and reds) need to be metabolically derived from ingested yellow precursors, further increasing production costs (Davies 1985; Hill 1996; Andersson et al. 2007). The carotenoid content of a male's plumage may therefore reliably reflect male foraging abilities, access to high quality food resources (Hill 1990), or the ability to allocate this limiting resource to ornament pigmentation at the expense of other physiological processes (Blas et al. 2006; Fitze et al. 2007; Peters et al. 2007). Likewise, in many species, song repertoire sizes are strongly influenced by either genetic quality (Hasselquist et al. 1996) or stresses experienced by birds during early development (Nowicki et al. 1998; Spencer et al. 2003). Regardless of the specific costs associated with the elaboration of male display traits, both theoretical and empirical evidence predict that during mate choice decisions, females benefit from choosing males with more elaborate ornaments by gaining genetic or phenotypic benefits associated with these traits (Andersson 1994).

When females actively choose the most ornamented males, positive associations between male ornament size and reproductive success will arise. Therefore, documenting associations between male ornamentation and reproductive success has become a useful initial step in understanding which ornaments might be under strong female selection (e.g. Hasselquist et al. 1996; Pryke et al. 2001; Dowling and Mulder 2006; Kleven et al. 2006). In the golden whistler, both plumage breast colouration and repertoire size were positively related to within-pair, extra-pair, and total

reproductive success. In addition, the repertoire size and breast plumage hue of cuckolding males tended to be higher than that of cuckolded males. This suggests that these two ornaments may be assessed by females during extra-pair mate choice decisions and convey important information about male quality. In addition, the more elaborate ornaments displayed by genetic fathers compared with social fathers suggests that females may actively compare the ornaments of their social mate with those of neighbouring males before engaging in extra-pair matings.

It remains unknown what specific costs are associated with the development of carotenoid plumage and high song repertoires in this species, and what benefits females might gain. The primary carotenoid producing the yellow colouration in this species is lutein (high-performance liquid chromatography analysis; S. Andersson, personal communication), a pigment that is typically abundant in nature (Goodwin 1976). It therefore seems rather unlikely that significant production costs are associated with the yellow plumage. Instead, maintenance, social, or ecological costs may be more relevant. Likewise, song repertoire size was unrelated to any male traits that we quantified. Therefore, females may mate with these males solely for genetic "good genes" benefits, although it is possible that song repertoire size also advertises some other, as yet unmeasured, aspect of male phenotype. In addition, repertoire size seems to be, in part, related to male age. This pattern is common in many species and may arise if older males have a longer time frame in which to augment their repertoires (e.g. Hasselquist et al. 1996; Gil et al. 2001). Females may thus be selecting for older and more experienced males instead of genetically superior males. However, we controlled for male age in all our analyses (i.e. males in their first year of adult plumage vs. all other males), revealing that no measure of male reproductive success was related to age.

The question of why many species display multiple display signals, despite their apparent costs, has long puzzled behavioural ecologists. Theoretical and empirical studies suggest that individuals may simultaneously display multiple sexual displays either because they are highly intercorrelated and thus act as a reassurance mechanism to minimise mistakes associated with quality assessment based on a single and relatively unreliable signal ("back-up message signalling"; Møller and Pomiankowski 1993; Johnstone 1996) or because different signals are directed towards different receivers (e.g. Evans and Hatchwell 1992a; 1992b; Pryke et al. 2001), are used during different stages of the decision process (e.g. Collias 1979; Andersson 1989), or signal different aspects of male quality (e.g. Dale and Slagsvold 1996; Calkins and Burley 2003; Doucet and Montgomerie 2003; Jawor et al. 2004; all variants of "multiple message signalling"). Alternatively, multiple

signals may currently not be related to any aspect of male quality, having arisen because of Fisherian runaway selection or past selection pressures and are only maintained because of negligible development and maintenance costs ("unreliable message signalling"; Møller and Pomiankowski 1993; Pomiankowski and Iwasa 1993; Iwasa and Pomiankowski 1994).

In golden whistlers, multiple ornaments are unlikely to have evolved via a backup mechanism, because the key traits of song repertoire size and breast quality were uncorrelated. Instead, the different costs associated with developing and maintaining the two ornaments may allow females to extract information on different aspects of male quality before engaging in extra-pair or social-pair matings. It is interesting to note that the two signals also differ in their assessment costs: whereas song repertoire size can be easily assessed at any time and at large distances, females can presumably only assess male breast colour at relatively short range during extra-pair forays. This suggests that assessment of potential extra-pair males may be a multistage process, involving initial assessment of neighbouring males based on song repertoire size from within a female's own territory, followed by visits to a subset of these males to assess breast plumage colouration. Finally, other ornaments displayed by male golden whistlers, such as the throat patch and singing rates, appear not to be under strong female selection but are more important during male-specific territorial encounters (van Dongen and Mulder 2007, 2008).

Female breeding synchrony and male reproductive success

Extra-pair mating success can vary greatly in frequency over the duration of a breeding season. One possible underlying factor affecting such variation is the degree of local breeding synchrony among neighbouring females, although the exact nature of this relationship remains controversial. First, when fewer females are simultaneously fertile the rate of extra-pair matings in the local area may rise (Birkhead and Biggins 1987; Westneat et al. 1990). This may occur when, during periods of low local breeding synchrony, relatively more males are freed from mate-guarding duties and the ratio of copulation-seeking males to fertile females subsequently increases. Therefore, during periods of low synchrony, the few nests that are active may bear a higher risk of cuckoldry, resulting in a negative association between local breeding synchrony and within-pair reproductive success. In sharp contrast, some authors have argued that positive associations between local breeding synchrony and extra-pair matings may arise. This may occur if the greater number of males simultaneously displaying to attract females during periods of high

breeding synchrony reduces search costs for females (Stutchbury and Morton 1995; Morton et al. 1998; Stutchbury 1998). The exact role of local breeding synchrony in controlling extra-pair activities thus remains a contentious and unresolved issue (Schwagmeyer and Ketterson 1999).

In this study, we have shown that, in golden whistlers, extra-pair mating success seems to be negatively related to local breeding synchrony. During periods in which a relatively high number of females were fertile, male within-nest paternity assurance increased. This pattern could arise for several reasons. First, this relationship may be a by-product of variation in breeding synchrony and extra-pair activities with date. For example, at the beginning of the breeding season, breeding synchrony may be high because individuals all arrive at the breeding site at approximately the same time (van Dongen and Yocom 2005). High rates of predation and re-nesting may then lead to more asynchronous and staggered breeding between neighbours as the breeding season progresses. If extra-pair fertilisation rates also increase during the season, for reasons unrelated to synchrony (e.g. Johnson et al. 2002; Stewart et al. 2006), any association between breeding synchrony and extra-pair success, will not be based on causality. However, this explanation seems improbable, as we have shown here that neither extra-pair paternity rates nor breeding synchrony undergoes predicable directional change during breeding season in this species.

An alternative, and more likely explanation, is that this pattern arises because of differences in male behaviour and cuckoldry risk between periods of high and low local breeding synchrony. To protect their within-pair paternity during the fertile period of their partners, males may mate guard more strongly and be less likely to stray from the territory to seek extra-pair fertilisations. This is supported by a previous study showing that males, but not females, increase aggression intensity towards intruding males during periods of low synchrony, when cuckoldry risk is, presumably, greatest (van Dongen 2008). In addition, males invest more effort into mate guarding after, but not before, territorial intrusions during this high-risk period (van Dongen 2008). Therefore, during periods of highly synchronised breeding, a greater proportion of males are engaged in intense mate guarding, resulting in a smaller pool of males available for extra-pair copulations. As males are also more aggressive towards intruders during this period, there may be fewer successful extra-pair matings by copulation-seeking males, thus resulting in a negative association between breeding synchrony and extra-pair reproductive success.

We have shown that genetic reproductive success in the golden whistler is determined by both the quality of male ornamental traits and synchrony of breeding. Despite the large range of traits measured, including phenotypic, ecological, and genetic factors, few had any effect in determining the number of young sired by males. Although, this may have partially been because of methodological issues, for example small sample sizes and a simplified estimate of paternal care, our data provide interesting clues into the complex factors effecting extra-pair reproductive success in birds. For example, unlike in many other species, extra-pair fertilisations do not increase the heterozygosity of offspring or eliminate the risk of inbreeding. Perhaps the migratory nature of this population and lack of natal philopatry (van Dongen and Yocom 2005) reduces the likelihood of females encountering related individuals, negating the need for avoidance of inbreeding. Similarly, inter-population variation in extra-pair paternity rates in the Australian magpie (*Gymnorhina tibicen*) vary with dispersal rates, possibly as a mechanism to avoid breeding with close kin (Durrant and Hughes 2005). Second, relatively high levels of extra-pair matings may be promoted in this population by the high levels of nest predation. Only 36% of nests successfully result in independent young, resulting in a large number of renesting attempts by most pairs within the population (van Dongen and Yocom 2005). This results in staggered timing of nesting between neighbouring pairs, low local breeding synchrony, and, hence, greater opportunity for males to seek extra-pair matings.

Zusammenfassung

Gefiederornamente, weibliche Brutsynchronität und Paarungserfolg außerhalb des Paarbundes beim Ockerbauch-Dickkopf (*Pachycephala pectoralis*)

Fremdvaterschaftsraten variieren beträchtlich sowohl zwischen Arten als auch zwischen und innerhalb von Populationen derselben Art. Erklärungen für diese Variation beinhalten ökologische (z.B. Brutsynchronität), morphologische (z.B. Gefiederornamente) und genetische (z.B. Verwandtschaft) Faktoren, aber nur selten untersuchen Studien all diese Faktoren gleichzeitig in einer einzigen Population. Dies trifft insbesondere auf aufwändig geschmückte Arten zu, bei denen auf Gefiederornamenten basierende Partnerwahl komplexer als bei weniger geschmückten Arten sein dürfte. Wir haben eine solche Studie in einer ziehenden Population des aufwändig geschmückten Ockerbauch-Dickkopfs durchgeführt. Wir haben genetischen Reproduktionserfolg der Männchen gemessen und zu einer Reihe von Faktoren in Beziehung gesetzt, die mutmaßlich an der Bestimmung des Paarungserfolgs außerhalb des Paarbundes beteiligt sind. Wir fanden weder Effekte genetischer Faktoren (männliche Heterozygosität

und Verwandtschaft), noch von Territoriumsgröße, Männchenalter oder Bebrütungsaufwand auf den Erfolg außerhalb des Paarbundes. Stattdessen genossen Männchen mit stärker gelbem Brustgefieder und großem Gesangsrepertoire höheren Fortpflanzungserfolg. Zusätzlich fanden wir eine negative Beziehung zwischen der lokalen Brutsynchronität und dem männlichen Paarungserfolg außerhalb des Paarbundes. Dies könnte eine Folge der Partnerbewachung während der fertilen Periode der Weibchen und der Unfähigkeit der Männchen, gleichzeitig ihr Weibchen zu bewachen und Kopulationen außerhalb des Paarbundes zu suchen, sein. Bei dieser Art scheint die Gelegenheit für Fremdverpaarungen zeitlich mit einer ökologischen Variable (lokale Brutsynchronität) zu variieren, während feine Unterschiede im Paarungserfolg zwischen Männchen durch individuelle Merkmale (Gefiederornamente der Männchen) beeinflusst sein könnten. Die Tatsache, dass es sich um eine Population von Zugvögeln handelt, sowie das Fehlen von Geburtsortstreue könnten bedeuten, dass Verwandtschaft und die Vermeidung von Inzucht weniger wichtige Faktoren bei der Partnerwahl sind.

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