Mate guarding and territorial aggression vary with breeding synchrony in golden whistlers (*Pachycephala pectoralis*)

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Abstract Male paternity assurance behaviour during the female fertile period has been widely documented amongst birds. In contrast, how sex-specific behavioural strategies vary with local breeding synchrony levels remains largely unknown. This is important because, in many species, intra-population patterns of extra-pair fertilisation rates, and hence cuckoldry risk, are known to vary with the number of simultaneously fertile females. Each sex may therefore differ in how they behave towards male conspecifics during different degrees of breeding synchrony. Here I provide evidence of such sex-specific differences in the golden whistler (*Pachycephala pectoralis*), a species in which within-pair paternity assurance is negatively associated with breeding synchrony. Via simulated territorial intrusions using decoy males, I show that males, but not females, increase levels of aggression to male intruders during periods of low synchrony, possibly because cuckoldry risk is greatest during this period. In addition, males appear to invest more effort into mate guarding after, but not before, territorial intrusions during this period. These inter-sexual differences may reflect conflicts in interest between the sexes, with females consistently showing interest in males during the fertile period regardless of synchrony levels and males investing more resources into expelling intruders when the risk of paternity loss is greatest. This study thus provides evidence that males may be able to detect variation in breeding synchrony and cuckoldry risk and adjust their paternity assurance behaviour accordingly.

Keywords Breeding synchrony · Extra-pair matings · Golden whistler · Male–male aggression · Mate guarding

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Introduction

Extra-pair fertilisations (EPFs) are an important means by which males of many socially monogamous bird species augment their reproductive success (Westneat and Stewart 2003). However, successful EPFs also result in simultaneous within-pair paternity loss by other males within the population and individuals are therefore expected to adopt behavioural strategies that maximise their own EPF success while minimising cuckoldry. Paternity assurance behaviour during the female fertile period such as mate guarding and female fertility announcement is a common and effective strategy adopted by males of many species for increasing reproductive success (e.g. Møller 1991; Chuang-Dobbs et al. 2001a; Ballentine et al. 2003; Chelen et al. 2005; Marthinsen et al. 2005; Rios-Chelen and Garcia 2007).

Yet, the risk of paternity loss is not uniform across the fertility period of individual females. When few females within an area are simultaneously fertile, the ratio of extra-pair seeking males to fertile females is higher in that area compared to periods when females breed more synchronously (Emlen and Oring 1977; Westneat 1990). Therefore, assuming that the proportion of males seeking EPFs is directly related to the number that are successful, the probability of within-pair paternity loss via cuckoldry is expected to be greater during periods of low breeding synchrony (Westneat et al. 1990; Shuster and Wade 2003;

although see Stutchbury and Morton 1995; Stutchbury et al. 1997; Stutchbury 1998 for examples of how high breeding synchrony can promote within-pair paternity loss). Males are therefore expected to augment their paternity assurance behaviour during periods of low synchrony by increasing mate-guarding efforts and aggressiveness towards intruding males. In contrast, the strength of female responses to intruding males is not expected to covary with breeding synchrony. This is because the breeding activities of other females within the population are not expected to affect female abilities to assess the quality of individual male territorial intruders as extra-pair mates.

Despite these strong predictions, empirical support is rare. This is in part due to the relatively few species in which within-pair paternity actually varies with breeding synchrony levels (e.g. Saino et al. 1997; Conrad et al. 1998; Strohbach et al. 1998). For those few species in which EPF rates are known to vary with breeding synchrony, the behavioural strategies adopted by each sex during different degrees of synchrony remain largely unknown. In one of the few studies targeting male behaviour during different levels of local synchrony, Chuang-Dobbs et al. (2001a) reported that male black-throated blue warblers (Dendroica caerulescens) increase mate-guarding effort during periods of low breeding synchrony when cuckoldry risk was thought to be greatest. Yet, it remained unknown whether males also increase aggressiveness during this period towards potential cuckolding males or whether sex-specific strategies exist in response to intruding males during varying levels of local synchrony. Clearly, as both male and female behaviour can influence male extra-pair reproductive success (Westneat and Stewart 2003), information on the strategies adopted by both members of the pair is required to gain a comprehensive understanding on the mechanisms driving variation in extra-pair mating rates with local synchrony. Despite this important requirement, such data are severely lacking.

The golden whistler (Pachycephala pectoralis) is a socially monogamous passerine inhabiting forests throughout Australia. Mean extra-pair fertilisation rates are relatively high in this species (19% of all nestlings are sired by extra-pair males) but the actual rate is known to fluctuate with a range of factors including levels of local breeding synchrony (i.e. the synchrony of breeding between females within close proximity of each other, as opposed to population-wide synchrony; van Dongen and Mulder, submitted). During periods of low local synchrony, the proportion of extra-pair nestlings sired within the population increases. In addition, males increase singing rates during general territorial announcement during this period of low synchrony, possibly in an attempt to prevent intrusions from potentially cuckolding neighbouring males (van Dongen 2006). However, detailed knowledge on the

strategies adopted by each sex in relation to variation in breeding synchrony remains unknown. As a conflict of interest exists between the sexes (males attempt to mate with as many females as possible while assuring their own within-pair paternity while females benefit from mating with the highest quality males to ensure high offspring viability; Westneat and Stewart 2003), sex-specific behavioural responses to fluctuations in breeding synchrony are expected. Here I test this idea, focusing on the responses of each sex to intruding males during different levels of local breeding synchrony. By conducting simulated territorial intrusions with caged decoy males, I tested whether male and female responses to the intruder vary with the degree of local breeding synchrony and whether males increase mate-guarding attentiveness when the perceived risk of paternity loss is greater.

Materials and methods

Study site and species

The golden whistler is a socially monogamous, sexually dichromatic passerine. The simulated intrusions were carried out between November and December 2003 at Toolangi State Forest, Victoria, Australia (37°31′ S, 145°32′ E). The study area covered 106 ha consisting predominately of a mountain ash canopy (Eucalyptus regnans) and a variable understorey dependent on local topography (van Dongen and Yocom 2005).

I monitored 24 breeding pairs via daily censuses throughout the breeding season. All pairs defended contiguous territories which together occupied the majority of the study site. Average territory size is 2.4 ha (range 1.0–4.2 ha; van Dongen and Yocom 2005). The adult sex ratio at the study site was approximately 50:50, as only one male–female pair defended each territory and floaters were rare (van Dongen and Yocom 2005). Individuals were captured and individually marked with a unique combination of three colour bands. The breeding status of each pair was determined by locating the nest and subsequently monitoring its status every 2 or 3 days.

Quantification of female breeding synchrony

Studies of sperm usage in birds indicate that females can store sperm for subsequent egg fertilisation for more than 10 days before the first egg is laid (Birkhead and Møller 1992). Since no data on fertility in golden whistlers exist, I therefore defined the female fertile period for this species as the time extending from 10 days before the date of first egg laying until the penultimate egg was laid. However, on average, the time at which experiments were conducted was

within a much smaller timeframe of 5.8 ± 0.9 SE days ($N=22$) before first egg laying (range 2–10 days). This timeframe for female fertility is similar to those described in other species (e.g. Strohbach et al. 1998; Ballentine et al. 2003; van de Crommenacker et al. 2004; Lindstedt et al. 2007).

Extra-pair fertilisations in this species are common (van Dongen and Mulder, submitted). Successful extra-pair sires are typically immediate neighbours of the cuckolded male although, in some cases, males up to three territories away successfully sire extra-pair young. For the purposes of this study, I therefore quantified female breeding synchrony by determining the number of fertile females within a radius of three territories of the focal pair at the time of the experiment (mean number of neighbouring territories, 8.0 ± 1.0 SE territories; $N=10$, range=5–13). All focal pairs were neighbours of each other and therefore included in each other's three-territory radius. The identity of pairs within three territories of the focal pair could easily be quantified because I took global positioning system coordinates of all nesting attempts for each pair throughout the breeding season and superimposed these data onto a map of the study site.

Simulated territory intrusion trials

Although the focus of the current study was to document variation in male and female aggressive behaviour during different levels of breeding synchrony, individual aggression data were obtained from previous simulated territory intrusions (STIs) experiments that were conducted for a separate study on the effect of intruder male ornamentation on resident male aggression (van Dongen and Mulder, in press). Ninety-six trials were conducted for these ornament manipulation experiments in which both throat patch size and song rates of caged decoy males were manipulated in a 2×2 factorial design (throat patches were manipulated using black dye to reduce the size of the white throat patch, resulting in 'control' and 'reduced' throat patch treatments; singing rates were manipulated by varying song playback rates from speakers, resulting in 'high' and 'low' song rate treatments). Decoy males were then introduced onto the territories of focal pairs during 10-min simulated intrusion trials in which a range of aggression-related behaviours were quantified (see below for details). Treatments were assigned to focal pairs at random to control for order and sequence effects on individual behaviour. See van Dongen and Mulder (in press) for in-depth details of the experimental design.

However, for the purposes of the present study, I was only interested in how male and female aggression varies with local breeding synchrony and not with these manipulations. Yet, to investigate the effects of female breeding synchrony on male aggression during these trials, I required information on the breeding status of the focal pair and all neighbouring females within a three-territory radius of the focal pair. This information was not available for all 96 trials and the final analysis therefore only used 20 trials with males and 18 with females (i.e. the number of trials for each sex for which I had data on local breeding synchrony for the focal individual at the time of the trial). These trials were distributed relatively evenly across all manipulation treatments (number of trials within each treatment group: males—high/control=7, high/reduced=4, low/control=4, low/reduced=5; females—high/control=3, high/reduced=4, low/control=5, low/reduced=6). For this small subset of trials, there was some effect of the song and plumage manipulations on both male aggression (quantified via principal component analysis (PCA), see "Statistical analysis"; general linear mixed model (GLMM)—aggression PC1: throat patch reduction—Wald=0.00, $df=1$, $p=0.959$; song rate reduction—Wald=4.40, $df=1$, $p=0.036$; aggression PC2: throat patch reduction—Wald=0.01, $df=1$, $p=0.926$; song rate reduction—Wald=0.78, $df=1$, $p=0.377$) and female aggression (GLMM—aggression PC1: throat patch reduction—Wald=2.46, $df=1$, $p=0.117$; song rate reduction—Wald=17.78, $df=1$, $p<0.001$; aggression PC2: throat patch reduction—Wald=3.92, $df=1$, $p=0.048$; song rate reduction—Wald=0.43, $df=1$, $p=0.511$). However, the inclusion of song rate and throat patch treatment types as fixed factors in the analyses of breeding synchrony and individual aggression did not qualitatively change any results (van Dongen, personal observation). Therefore, as the plumage and song manipulations were not the focus of the current study, I omitted manipulation treatment types as fixed factors in all analyses of the STI data to increase the clarity of results and avoid unnecessary confusion. As these ornament manipulations are irrelevant to the current study question and had no significant effect on the results obtained for the current study, they are not discussed further.

STI trials were conducted by introducing caged males into the territories of resident pairs. Thirteen males were captured for use as decoy males that were captured within the same forest but outside the study area. Upon capture, males were placed in a wire cage (measuring $18\times18\times36$ cm) which was covered by a cloth to minimise stress and transported to housing aviaries measuring $120\times60\times60$ cm. Aviaries were located outdoors in a sheltered area and birds were provided with meal worms and water ad libitum. As 96 trials were conducted in the original ornament manipulation experiments, each decoy male was used in an average of 12.1 ± 1.4 SE trials ($N=13$, range 4–17 trials) and housed for a maximum of 11 days (average duration=4.9 ± 0.9 SE days; $N=13$, range 1–11 days) after which it was re-released at the site of capture. Release

weight of individuals was not different from capture weight (capture weight=28.6±1.4 SD g, release weight=27.0±0.9 SD g; paired t test, t_6=1.182; p=0.290).

All STI trials were conducted during the nest building stage (i.e. female fertile period) for each subject pair and between 0730 and 1130 Australian Eastern Standard Time (the peak singing period for this species; van Dongen, personal observation). A wire cage (18×18×36 cm) containing the live decoy male was placed on a stand (height 1.2 m) within 50 m of the focal individuals (mean distance from focal individual=26.3±2.4 SE m, N=22). Although I did not quantify the distance of the cage to the focal individuals' nest, cage proximity to the nest is unlikely to have a significant effect on the results as golden whistlers do not aggressively defend unfinished nests (van Dongen, personal observation). The playback track was broadcast from a Sony CDX-L460X portable car stereo with Realistic 30-W speakers placed adjacent to the cage. During the 5-min playback period, two observers were present, hidden from view. One observer described the subject's behaviour while the other transcribed this information. In order to avoid observer-related bias in the data, the same person described focal individual behaviour across all trials. We recorded the following response attributes: (a) latency (s, the time elapsed before the focal individual displayed an obvious response to the STI such as movement towards the cage), (b) number of songs sung, (c) distance of closest approach to the cage (m) and (d) the total duration of the response (s, the time elapsed between the first observed obvious response to the playback stimulus, as outlined above, and the point when the individual appeared to lose interest in the caged male by moving away from stimulus—this was easily quantified as I frequently dictated the individual's position relative to the cage onto a cassette recorder). Not all trials were conducted in the presence of both members of a whistler pair. In four trials, only the male was present; only the female was present in two trials while both members were present in the remaining 16 trials. However, due to the presence of only a small number of trials in which only one member of the sex was present, I could not test whether individual behaviour changed relative to partner presence/absence during the trial.

I also estimated the focal bird's distance from the cage during the trial using a three-dimensional zoning system. Nine different zones were identified (in a 3×3 design) from zone 1 (within 5 m from the cage, both horizontally and vertically) to zone 9 (further than 20 m from the cage horizontally and higher than 15 m above the cage; refer to van Dongen and Mulder, in press for details). Changes in the location of individuals within the zones throughout the trial were dictated onto a cassette recorder. Individual distance from cage was later estimated by calculating the length of the vector spanning the top of the cage to the

middle of each zone (i.e. distance from cage $=\sqrt{d^2 + h^2}$, where d=the zone's horizontal distance from cage and h= the zone's height above cage). I then estimated average distance of the individual from the cage throughout the trial by calculating the proportion of time spent within each zone.

Quantification of pair proximity during simulated intrusions

I explored patterns of mate guarding in relation to breeding synchrony and whether males guard their females more closely after an intrusion from a neighbouring male. This was done by conducting a detailed analysis of pair proximity during the simulated intrusions for trials when both members of a pair were sighted during the trial. At the commencement of the trial, I noted the actual distance (i.e. treating distance as a continuous variable rather than categorising distance within zones) and bearing (in degrees) of each individual from the caged decoy male. This was repeated upon the trial's completion. I was then able to use these data to calculate the distance separating the male and female members of the focal pair before and after the intrusion. To calculate this, I used the law of cosines: $c^2 = a^2 + b^2 - 2ab\cos C$, where a and b represent the distance between each individual and the caged decoy, c represents the distance separating the male from the female and C represents the angle created by the vectors spanning from the caged decoy to both the male and female.

Statistical analysis

Many of my measures of aggression during the simulated territorial intrusions were highly intercorrelated. To avoid the unnecessary use of a large number of tests and the subsequent risk of a type I error, I reduced the response data (five variables in total) to two estimators for each sex of aggression using PCA (Table 1). For each sex, two principal components with eigenvalues over 1 were extracted, the loading of each which were qualitatively the same for both sexes. PC1 scores were strongly related to

Table 1 Component loadings for the principal components analyses performed on responses of male and female golden whistlers to decoy males during simulated territorial intrusions

Component loadings	Males		Females	
	PC1	PC2	PC1	PC2
Latency	−0.854	0.289	−0.817	0.228
Duration	0.664	0.550	0.837	0.210
Average distance	−0.812	0.173	−0.777	0.302
Distance closest approach	−0.874	0.376	−0.882	0.035
Song rate	0.432	0.813	0.297	0.929
% variance explained	55.6	24.4	56.8	21.1

aggression, with more positive PC1 scores corresponding to a faster and longer response to the stimulus, a closer average distance to the threat throughout the trial and a nearer 'closest approach'. PC2 scores were positively related to singing rates throughout the trial. Together, the two components explained 80.0% of the variation recorded in the male responses and 77.9% of the variance in female responses.

Due to the relatively large number of trials conducted ($N=22$), individuals were inevitably subjected to multiple trials throughout the sampling period (mean number of trials per individual$=2.4\pm0.2$ SE trials, $N_{male}=9$, $N_{female}=7$, range 1–3). To allow for the non-independent nature of the data, I used GLMM incorporating individual identity as a random factor. This controlled for differences in responses between individuals. In all cases, the response variables followed a normal distribution and the models calculated using normal (with identity link) error variances. In all models, I included the following independent variables: number of neighbouring females within three territories of the focal pair that were fertile and the number of territories surrounding the focal territory (a maximum of three territories away). In addition, to control for the potentially confounding effect of date on both breeding synchrony and aggression, I also included date of trial as a fixed factor in all GLMM models. For the analysis of pair proximity, I used an additional but broader descriptor for breeding synchrony, quantifying the absence (no fertile neighbouring females) and presence (at least one fertile neighbouring female) of breeding synchrony. In this case, categorising breeding synchrony into absent or present allowed me to obtain additional distance estimates of how proximity

between members of a pair may differ between different stages of local synchrony and territorial intrusions.

All PCAs were conducted using Statistical Package for the Social Sciences 12.0 (SPSS Inc., Chicago, IL, USA) and all GLMMs using Genstat 7.0 (Lawes Agricultural Trust 2003). Data are reported as means and standard errors.

Results

Breeding synchrony and response to intruding males

Females did not change any aspect of their behaviour during the simulated intrusions in respect to levels of breeding synchrony. The number of neighbouring females was unrelated to both female PC1 scores and PC2 scores of aggression (Table 2, Fig. 1a and b). In contrast, males were less aggressive towards intruders during periods of high breeding synchrony. PC1 scores were negatively related to the number of simultaneously breeding females while PC2 scores were positively associated with synchrony (Table 2, Fig. 1a and b). Therefore, when a greater number of females were fertile, males spent less time in close proximity to the intruder and responded for a shorter period of time. However, during these periods, males were significantly more vocal than when fewer neighbouring females were simultaneously fertile. All interaction terms were non-significant (all $p>0.207$) and are therefore not shown here to increase clarity of the results. The small random effect values relative to their standard deviations revealed that there was no significant effect of the random

Table 2 GLMM models for the association between female breeding synchrony with the principal component scores of subject male and female responses during simulated territorial intrusions[a]

	Principal component 1					Principal component 2				
	Effect	SE	df	Wald	p	Effect	SE	df	Wald	p
Females										
Constant	−0.079	0.298				−0.245	0.161			
Date	−0.037	0.020	1	3.38	0.066	−0.0004	0.010	1	0.00	0.963
Number of territories	−0.025	0.101	1	0.06	0.807	0.003	0.055	1	0.00	0.961
Number of fertile females	−0.294	0.506	1	0.34	0.561	−0.184	0.262	1	0.49	0.484
Males										
Constant	0.045	0.215				−0.073	0.201			
Date	−0.007	0.017	1	0.18	0.669	0.023	0.016	1	2.10	0.147
Number of territories	0.185	0.087	1	4.50	0.034	−0.017	0.082	1	0.04	0.832
Number of fertile females	−0.593	0.272	1	4.74	0.029	0.766	0.257	1	8.88	0.003

In all analyses, $N_{male}=20$ and $N_{female}=18$

[a] Normal models with identity links. Random effects: male PC1—male ID$=0.019$ (SE$=0.311$); male PC2—male ID$=0.000$ (SE$=0.275$); female PC1—female ID$=0.308$ (SE$=0.472$); female PC2—female ID$=0.107$ (SE$=0.135$).
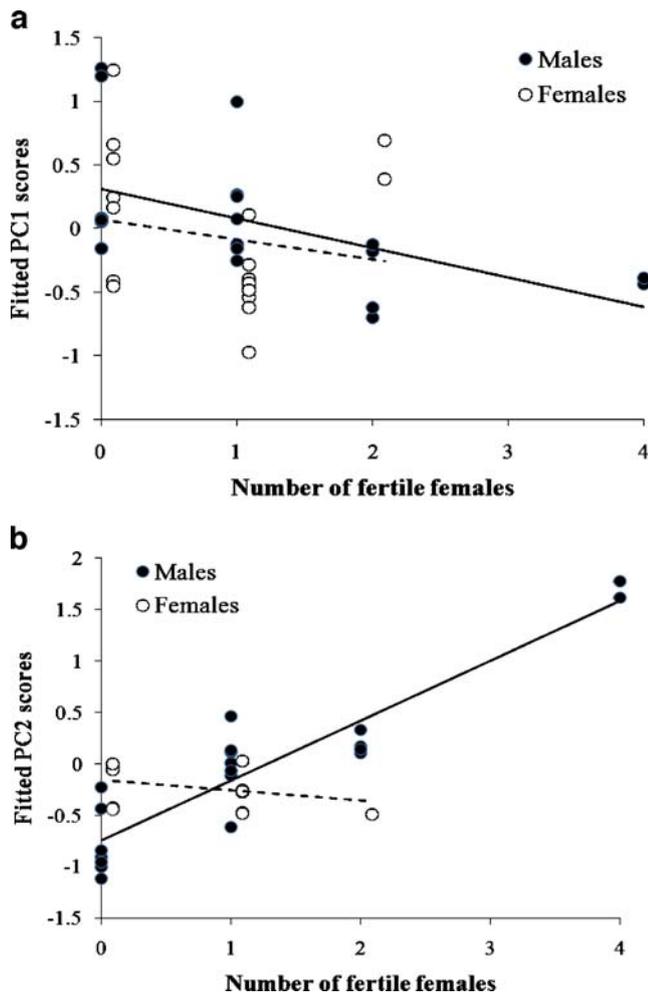
Fig. 1 Fitted principal component scores of golden whistler aggression during simulated territorial intrusions and degree of breeding synchrony (the number of fertile females within three territories of the focal territory). **a** Male and female PC1, **b** male and female PC2. For both sexes, higher values of PC1 correspond to a more intense response to the decoy male (i.e. response latency and duration, average distance to decoy male, closest approach to decoy) while higher values of PC2 reflect higher singing rates (refer to Table 1 for more details). In both cases, male but not female PC scores are significantly related to breeding synchrony levels

factor (i.e. individual identity) and therefore all individuals of both sexes acted consistently across trials.

Pair proximity during territorial intrusions

At the commencement of the playback trial, the distance separating both individuals of the focal pair did not vary with levels of breeding synchrony. This was true both in terms of absolute number of neighbouring fertile females (GLMM, no. of territories—Wald=0.50, df=1, p=0.481; no. of fertile females—Wald=0.17, df=1, p=0.679) and in the presence/absence of any degree of breeding synchrony (i.e. there was no difference in pre-trial pair proximity between periods when local synchrony was absent or
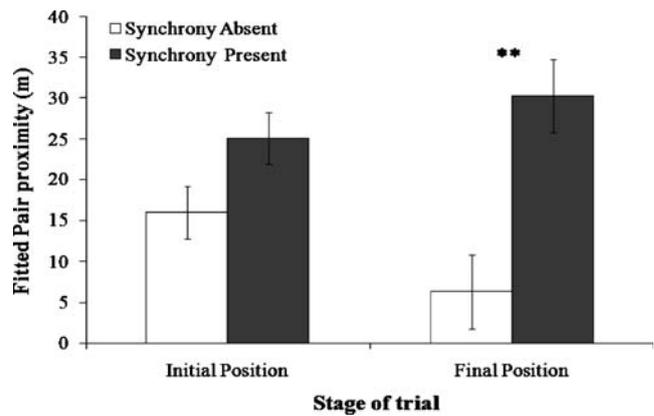
Fig. 2 Proximity of the male golden whistler to his partner before and after a simulated territorial intrusion during periods when breeding synchrony is absent (no fertile neighbouring females) and present (at least one fertile neighbouring female). The post-trial distance separating male and female pairs during periods of no synchrony is significantly closer than during periods when some level of synchrony is present. No such difference exists prior to trial commencement. The *double asterisks* signify a difference at the p<0.01 level

present—GLMM, Wald=0.48, df=1, p=0.487; Fig. 2). In sharp contrast, at the completion of the simulated intrusions, males were significantly closer to their partner during periods of low breeding synchrony than during periods of high synchrony (GLMM, absolute synchrony: no. of territories—Wald=0.57, df=1, p=0.448; no. of fertile females—Wald=9.43, df=1, p=0.002). Males were, on average, approximately 24 m closer to their partners in the absence of any degree of breeding synchrony compared to periods when breeding synchrony was present (GLMM, Wald=7.26, df=1, p=0.007; Fig. 2).

Discussion

I have shown here that male golden whistlers appear to be able to perceive fluctuations in local breeding synchrony and adjust their aggressiveness towards conspecifics relative to the risk of cuckoldry. Males may use different strategies during different degrees of synchrony—staying further away from intruding males but singing at high rates when breeding synchrony was high and singing less but physically pursuing the intruder when synchrony was low. The increased attentiveness of males to intruders during periods of low breeding synchrony was coupled with higher levels of mate guarding after, but not before, the intrusions. In contrast, females did not change any aspect of their behaviour towards intruding males in relation to the breeding patterns of neighbouring females.

As EPFs are common amongst golden whistlers (19% of offspring result from extra-pair matings; van Dongen and Mulder, submitted) they represent an important means by which males augment their reproductive success. Male

behaviour is therefore expected to vary to minimise the risk of cuckoldry by neighbouring males. Yet, the probability that a male will be cuckolded may be strongly related to breeding synchrony levels. For example, during periods of low synchrony, the ratio of copulation-seeking males to fertile females increases (Westneat et al. 1990). As a consequence, an increase in the number of extra-pair young in the active nests is observed, probably because the number of males seeking copulations is positively correlated with the number that eventually gains fertilisations. Thus, during periods of low synchrony, the few nests that are active bear a higher risk of cuckoldry.

In support of this, I have shown elsewhere that, during periods of low breeding synchrony, population-wide within-pair paternity rates are lower and male golden whistlers sing more during song bouts (van Dongen 2006; van Dongen and Mulder, submitted). This increase in singing rates during general territory announcement may be one means by which males increase mate-guarding efforts during periods of high cuckoldry risk. The current study provides further and novel insights into the strategies adopted by males relative to not only his partner's breeding activities but also of local-scale female fertility patterns. Firstly, during periods of low breeding synchrony and high risk of cuckoldry, males appear to undertake a more active and aggressive role towards intruders, investing more time in attempting to expel intruders and frequently coming in close proximity to the intruder. In contrast, during periods of lower apparent risk, males may adopt a different strategy by staying further away from the intruder but singing at higher rates. This suggests that males may adjust their territorial defensive strategies according to perceived risk of paternity loss and invest less effort into expelling intruders when there is a reduced risk of paternity loss. Interestingly, although males increase singing rates during general territorial announcement during periods of high risk, they actually sing less during such periods in response to intruding males, suggesting that males switch strategies depending on the immediate risk of cuckoldry.

The second important finding of the current study is that, during high risk periods, males increase their mate-guarding efforts by remaining close to their fertile female. Interestingly, before a territorial intrusion occurs, pair proximity is similar regardless of breeding synchrony levels. However, after an intrusion from a neighbouring male, males remain on average 24 m closer to their partner when risk of cuckoldry is greater. The fact that pair proximity is only related to breeding synchrony after (and probably also during) the intrusion and not before is very informative. This suggests that males may only invest more time into closely guarding their mate when there is a heightened risk of being cuckolded and that this increase in mate-guarding effort by males returns to normal levels before the next

intrusion. This pattern may possibly arise due to mate guarding conflicting temporally with other mutually exclusive activities such as feeding or pursuing extra-pair matings (e.g. Chuang-Dobbs et al. 2001a). However, it is also possible that selection favours this transitory nature of intense mate-guarding effort due to a relatively low frequency of territorial intrusions occurring during the female fertile period, which would in turn contradict the assumption that nests suffer a higher risk of cuckoldry during low synchrony due to an increase in male intrusions. However, no data currently exist on male intrusion frequencies or on the duration of heightened mate guarding after an intrusion, and thus the mechanisms promoting, and consequences of, this temporary mate-guarding behaviour remain unknown.

Although the data suggest that males perceive risk of cuckoldry via local breeding synchrony levels and adjust their mate-guarding strategies accordingly, alternate explanations exist. Firstly, the negative relationship between aggression and local breeding synchrony may be influenced by breeding date as a confounding factor. Under this scenario, male aggression towards conspecifics may decrease during the breeding season while local breeding synchrony concurrently increases. This, in turn, could drive an apparent, yet non-causal, relationship between the two variables. To avoid misinterpreting the data in this context, I controlled for breeding date in all analyses and so this alternate explanation is unlikely. Secondly, in addition to varying the risk of cuckoldry, breeding synchrony may also affect other factors that can influence male behaviour. For example, males may have fewer conflicting time demands when fewer females are receptive and possibly more difficult to locate. A more effective strategy during this time may be to remain within the territory and respond longer to intruders, regardless of risk of cuckoldry, rather than search the surrounding areas for receptive females. This alternate explanation is possible and, at this stage, it is unknown which mechanism is more likely to be driving male behaviour. It is possible that both mechanisms may be simultaneously operating to increase male aggressiveness and attentiveness during periods of low breeding synchrony.

The strategies adopted by females are predicted to differ from those of males. Fertile females are always expected to pay attention to intruding males as potential extra-pair mates regardless of temporal and spatial breeding patterns throughout the rest of the population. Therefore, no relationship between response to intruders and breeding synchrony is expected or was detected in the current study. However, additional experiments would need to be carried out that specifically investigate female evaluation of intruders as potential extra-pair partners to gain an in-depth understanding of variation in female behaviour with local breeding synchrony. It would additionally be interesting to

test whether female responses to intruders vary depending on whether or not they are fertile and therefore receptive to extra-pair copulations with neighbouring males.

To date, many studies have shown that male behaviour can change in response to cuckoldry risk associated with the onset of their partner's fertility (e.g. Møller 1991; Chuang-Dobbs et al. 2001a; Ballentine et al. 2003; Chelen et al. 2005; Marthinsen et al. 2005; Rios-Chelen and Garcia 2007) and that this increased investment in mate guarding can lead to greater within-pair paternity assurance (e.g. Kempenaers et al. 1995; Chuang-Dobbs et al. 2001a; Brylawski and Whittingham 2004; Marthinsen et al. 2005). However, such studies tend to only consider variation in partner fertility as a potential driver of male mate-guarding behaviour. In contrast, little information exists on how male behaviour varies with changes in local breeding synchrony. Local synchrony can also have a strong influence on the risk of paternity loss by males and is therefore expected to influence male mate-guarding behaviour (Westneat and Gray 1998; Schwagmeyer and Ketterson 1999; Chuang-Dobbs et al. 2001a). In addition, although extra-pair mating strategies can represent a conflict of interest between males and females (Westneat and Stewart 2003), little is known on how the behaviour towards potential cuckolding males of both members of the pair varies with perceived cuckoldry risk and availability of extra-pair mates. Such research is important because convincing evidence that local breeding synchrony is related to extra-pair reproductive success is rare and the mechanisms remain poorly understood. For example, in some species, extra-pair fertilisations appear to increase with synchrony (e.g. Stutchbury and Morton 1995; Stutchbury et al. 1997; Stutchbury et al. 1998) and decrease in others (e.g. Saino et al. 1997; Conrad et al. 1998; Strohbach et al. 1998), while the vast majority of studies report no association between the synchrony of breeding activities and extra-pair reproductive success (e.g. Chuang-Dobbs et al. 2001b; Johnsen and Lifjeld 2003; Arlt et al. 2004; Kraaijeveld et al. 2004; Westneat and Mays 2005; Stewart et al. 2006). How the behavioural strategies adopted by each sex towards male conspecifics influence these links between extra-pair mating rates and local synchrony remain largely unknown.

In one of the few studies that quantified variation in male behaviour with breeding synchrony, Chuang-Dobbs et al. (2001a) reported that in black-throated blue warblers (*D. caerulescens*), males increase mate-guarding effort during periods of low breeding synchrony. However, it was not clear what strategies each sex adopted towards intruders during different levels of breeding synchrony. Therefore, the current study provides much-needed insights into the behavioural strategies adopted by each sex that maximise their reproductive success during different degrees of local synchrony and the consequences of these strategies on intra-population associations between synchrony and extra-pair fertilisation rates.

I have demonstrated here that male golden whistlers appear to increase their aggression towards intruding males and guard their female more closely after territorial intrusions during periods of local asynchronous breeding, possibly as a response to an increase in perceived risk of paternity loss. However, it remains unknown what cues males use to assess breeding synchrony levels, how males mated to non-receptive females respond behaviourally to variation in breeding synchrony and what strategies females adopt when assessing potential extra-pair mates during different levels of breeding synchrony when the costs of mate assessment drastically vary (Fishman and Stone 2005, 2006). In addition, it remains unknown how male behaviour during the STI trials relates to realised paternity success or female extra-pair mating behaviour. Unfortunately, insufficient genetic data exist for the focal individuals of this study to resolve this issue. Finally, this study highlights an extra source of variation that can account for the high variability in inter-individual responses typically observed during simulated territorial intrusion experiments, which future studies would thus benefit from taking into account.

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