High rates of infidelity in the Grey Fantail *Rhipidura albiscapa* suggest that testis size may be a better correlate of extra-pair paternity than sexual dimorphism

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The Grey Fantail *Rhipidura albiscapa* is a socially monogamous passerine endemic to Australia. Behavioural and morphological clues point to opposing conclusions as to its breeding system; sexual monomorphism and monochrome colorations suggest monogamy, whereas relatively large testes and a prominent cloacal protruberance are more indicative of multiple mating and sperm competition. We used five highly variable microsatellite loci to investigate the genetic breeding system of this species. Paternity was assigned to 49 of 69 (71%) offspring tested and the overall rate of partner infidelity was high, with 55% of offspring being sired by an extra-pair male and 64% of all clutches containing extra-pair young. This puts the Grey Fantail amongst the most promiscuous socially monogamous species yet studied. Where extra-pair fathers were identified, these were invariably in neighbouring territories, and although larger males did not gain more paternities overall, extra-pair offspring tended to be fathered by larger males than expected by chance. We interpret our findings in light of some of the potential costs and benefits associated with extra-pair paternity.

Keywords: mate choice, microsatellite, monogamy, passerine, testis size.

Despite Lack's famous assertion that 90% of bird species were monogamous (Lack 1968), true genetic monogamy occurs in < 25% of species studied (Griffith 2007). The benefits of extra-pair paternity (EPP) to a socially monogamous male bird are clear: he can produce additional offspring without the need for paternal care. In many cases, this benefit may outweigh potential costs such as sperm production, higher risk of contracting ectoparasites or sexually transmitted diseases (Hasselquist & Sherman 2001), or even desertion or divorce by the pair female (Cézilly & Nager 1995). However, males of many species are thought to be unlikely to be able to force a female to copulate (Birkhead & Møller 1992), raising the question of why females acquiesce to mate with extra-pair males.

As with males, female birds engaging in extra-pair copulations (EPCs) also risk contracting parasites or sexually transmitted diseases (Hasselquist & Sherman 2001). However, retaliation by their partners can be particularly costly, potentially including aggression (Valera *et al.* 2003), desertion (Cézilly & Nager 1995), reduced nest defence or brood provisioning (Dixon *et al.* 1994, Weatherhead *et al.* 1994), and even infanticide (Orsorio-Beristain & Drummond 2001). Much research has therefore focused on finding correspondingly large benefits accruing to the female that would counteract these costs and cause her to seek EPCs (reviewed by Jennions & Petrie 2000, Griffith *et al.* 2002, Westneat & Stewart 2003, Kempenaers 2007). These include direct benefits, such as access to food or paternal care (Wolf 1975, Burke *et al.* 1989), fertility assurance (Wetton & Parkin 1991), and indirect genetic benefits that serve to improve

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offspring health, attractiveness, survivorship and ultimately reproductive success (e.g. Kempenaers *et al.* 1999, Tregenza & Wedell 2000, Akçay & Roughgarden 2007).

The wide variation in rates of EPP among socially monogamous bird species (Griffith *et al.* 2002) is thought to reflect the contrasting costs and benefits that males and females experience. This generates an evolutionary conflict between the sexes over mating, the outcome of which can vary from species to species (Westneat & Stewart 2003, Arnqvist & Kirkpatrick 2005). The mating system of the Grey Fantail *Rhipidura albiscapa* provides an interesting case in point (Higgins *et al.* 2006, Munro 2007). It is a small (8–9 g), primarily socially monogamous passerine flycatcher, endemic to Australia, with conflicting indications as to its breeding behaviour. The species is monochromatic and sexually monomorphic, two traits that are generally found in species with lower levels of sexual selection (Owens & Hartley 1998). However, there are also clear morphological indications that infidelity and sperm competition may play a significant role in its breeding ecology. Thus, male Grey Fantails have exceptionally large testes for their size, with mean testis mass being almost twice that predicted from the allometric relationship between body and testes mass based on 248 passerine and non-passerine bird species (Munro 2007). Similarly, males also have pronounced cloacal protuberances (Rogers *et al.* 1986). Both of these traits are known to be associated with high levels of extra-pair mating (Birkhead *et al.* 1991).

Here we use microsatellites to describe the genetic mating system of the Grey Fantail, and interpret the observed rate of EPP in light of some of the potential costs and benefits to both males and females that may arise from mating with an extra-pair partner.

METHODS

Species and study area

The study was conducted during the austral summers of 2002–2005 in the Canberra Nature Park, Australian Capital Territory, Australia (35°27′S, 149°17′E). A population of between 25 and 30 pairs was monitored that inhabited approximately 157 ha of woodland comprising mostly Blakely's Red Box *Eucalyptus blakelyi* and Yellow Box *Eucalyptus melliodora*. The area included Camp-bell Park, a small area of woodland under the jurisdiction of the Australian Defence Force, and the Mount Ainslie area of the Canberra Nature Park.

The study population of Grey Fantails is described in detail by Munro (2007). The modal clutch size was three eggs, with smaller clutches of two eggs occasionally being laid towards the end of the breeding season. Of particular note was the high predation rate, with 68% of clutches laid during the study being predated prior to hatching. Eggs were sometimes damaged but not removed, but more often they were removed with no trace remaining in the nest. Predation events were not directly observed during the study, but known predators of Grey Fantails include domestic Cats *Felis catus*, Common Bushtail Possums *Trichosurus vulpecula* and Common Mynas *Acridotheres tristis* (Higgins *et al.* 2006).

Trapping, ringing and morphometric measurements

Pairs of Grey Fantails were located by systematically searching the study area and following individuals. Adult birds were caught using mist-nets and given a unique aluminium alloy size 01 Australian Bird and Bat Banding Scheme ring. In addition, a unique colour combination was given to each individual using A. C. Hughes's anodized aluminium rings. The sex of adults was determined by the size of the cloacal protuberance and confirmed later by behavioural observations and/or copulation observations. Male head-length (back of head to bill-tip) and the right tarsus were measured to the nearest 1 mm using plastic callipers and the right wing and tail were measured to the nearest 1 mm using a steel rule. As these measures were strongly intercorrelated, we conducted a principal component analysis (Rising & Somers 1989) using a correlation matrix within MINTAB version 15 to combine these morphological measures into a single variable.

The approximate centre of each male's territory for each year was calculated as the mean x and y Universal Transverse Mercator coordinate of all of his nests, as recorded using a hand-held global positioning device (Garmin GPS72). Nests were easily located as females call noisily whilst collecting and building. When the chicks were between 3 and 6 days old they were weighed to the nearest 1 g using a Pesola spring balance and their right

tarsus was measured to the nearest 1 mm using plastic callipers.

Blood sampling, DNA extraction and microsatellite genotyping

From each adult and chick a small blood sample (5–10 µL) was taken using a 26-gauge needle by brachial venipuncture and stored in 70% ethanol for later paternity analysis. In addition, wherever possible, deserted eggs were collected to recover the embryo, which was also stored in 70% ethanol. Total genomic DNA was extracted either from blood or from the entire embryo using an adapted Chelex 100 protocol (Walsh *et al.* 1991). All DNA samples were genotyped using a panel of five previously characterized dinucleotide microsatellite loci (Jin *et al.* 2006), following the procedure of Hoffman and Amos (2005). Samples that failed to amplify at two or more loci were excluded from the dataset (*n* = 10 tissue samples from eggs, one adult male and one chick). Each autoradiograph was independently scored by two different observers (J.H. and K.M.), and fragment sizes were determined relative to laboratory size standards. The genotyping error rate was assessed following Hoffman and Amos (2005) by independently re-genotyping 42 samples at all loci. GENEPOP version 3.1d (Raymond & Rousset 1995) was used to calculate observed and expected heterozygosity, and to test for deviations from Hardy–Weinberg equilibrium and linkage disequilibrium.

Parentage analysis

We used the program NEWPAT XL (Worthington-Wilmer *et al.* 1999) to check for mother–offspring mismatches and to assign paternities to chicks. This program searches for parent–offspring relationships according to user-defined criteria and then uses a randomization approach to assess the significance of any matches found (see Worthington-Wilmer *et al.* 1999 for details). For the paternity analysis, we allowed missing data at up to one locus, no mismatches and a null mismatch parameter of 0.05. Each male-offspring match was then assessed by randomization, with male-specific allele frequencies being used to draw random alleles, so creating a file of 'pseudomales'. The number of random genotypes created was set at 100 times the size of the male dataset, such that the number of matches found by randomization

equated to the percentage probability that the original dataset would yield at least one match by chance alone. A paternity was assigned to a male if: (i) it was the only male found to match a chick, or (ii) it was the male with the lowest randomization number among multiple candidates. As a guard against males being excluded through scoring errors, autoradiographs were rescored whenever a candidate male mismatched a chick at only one locus (*n* = 2).

Statistical analyses

All data were tested for normality before using parametric statistical tests or the appropriate non-parametric alternative. We assessed whether larger males were more likely to gain extra-pair fertilization success using a generalized linear model with a logit-link function and dispersion parameter fixed at 1, with the outcome of a male fathering extra-pair young (yes/no) as the dependent variable and male body size (i.e. PC1 score) as the independent variable. To control for the effect of sample size and incomplete spatial sampling, we also included as covariates the number of offspring genotyped and the median distance of the centre of the male's territory from nests genotyped while he was present on the study site. Data analyses were conducted using SPSS version 12.

RESULTS

Rates of EPP

A total of 143 individuals (adults, offspring and embryos) were genotyped for five microsatellite loci. Of these, 10 embryonic samples and one adult failed to amplify at all of the loci, and were thus excluded from the dataset. All of the loci were highly polymorphic, possessing between 13 and 20 alleles (Table 1).

Expected heterozygosity (H_E) ranged from 0.84 to 0.92. Following Bonferroni correction for multiple statistical tests (Hochberg 1988), only locus FT2.18 was found to deviate significantly from Hardy–Weinberg equilibrium. However, the results of the paternity analysis were unaltered when this locus was excluded. Similarly, no pairs of loci were found to be in linkage disequilibrium following Bonferroni correction. The genotyping error rate for the dataset was 0.04 per reaction or 0.03 per allele. As found by Hoffman and Amos (2005), the

Table 1. Summary of the microsatellite loci used in this study, including polymorphism characteristics for adult Grey Fantails sampled during 2002–2005 from the Canberra Nature Park, Australian Capital Territory, Australia. Hardy-Weinberg equilibrium (HWE) *P*-values are given following Bonferroni correction for multiple statistical tests.

Locus	No. of alleles	Size range (base pairs)	H_E	H_O	HWE *P*-value
FT1.10	19	209–247	0.92	0.85	0.270
FT1.6	20	162–202	0.90	0.91	0.891
FT2.18	13	140–154	0.84	0.70	0.005
FT2.32	19	194–238	0.90	0.91	0.214
FT2.5	18	197–233	0.89	0.92	0.999

majority of scoring errors were due to difficulty distinguishing homozygotes from heterozygotes with adjacent alleles. Consequently, we adjusted for this problem by allowing a single mismatch in

the paternity analysis and inspecting any resulting matches. No mother–offspring mismatches were detected, indicating Mendelian inheritance and suggesting an absence of conspecifc brood parasitism.

In total, over three seasons, 84 offspring from 40 clutches of 28 females were sampled. After excluding from the analysis samples that failed to amplify DNA successfully, together with offspring from polyandrous trios, 69 offspring remained. We were unable to identify 20 offspring as pair or extra-pair due to no genetic match for a sire being made, most probably a consequence of the pair male having not been caught. Of the 49 offspring for which paternity was successfully determined, paternity of chicks was assigned to the pair male in 22 cases (44.9%) and to an extra-pair male in 27 cases (55.1%, Table 2). Sixty-four per cent of all clutches contained at least one extra-pair young (16/25) and 75.0% of the females from which

Table 2. Summary of the Grey Fantail paternity analysis. Letter codes for individuals correspond to colour-rings. EPY denotes extra-pair young. UR refers to individuals that were not banded and therefore not sampled. The letters a and b suffixing a year indicate that two clutches were sampled during that year.

Female	Year	Pair male	Clutch size	No. of chicks sampled in clutch	No. of pair young in sample	No. of extra-pair young in sample	Genetic father of EPY 1	Genetic father of EPY 2	Genetic father of EPY 3
YSM	2002/3	GBP	3	3	3	0			
	2003/4	UR	3	2	0	2	BSP	MBG	
	2004/5a	PBS	3	3	0	3	BMB	BMB	SPM
	2004/5b	PBS	3	1	1	0			
NMY	2002/3a	PBS	3	1	0	1	SPM		
	2002/3b	PBS	3	1	0	1	BMY		
PBY	2002/3	NNP	3	2	0	2	PBS	PPB	
YGN	2002/3	SPM*	2	1	0	1	PBS		
SBY	2002/3	NGM	3	3	2	1	BMG		
	2004/5	NGM	3	2	1	1	UR		
I6 UR	2002/3	PSB	3	1	1	0			
YPG	2002/3a	MYN	3	2	1	1	YGG		
	2002/3b	MYN	2	1	1	0			
W5 UR	2002/3	GPP	3	3	1	2	UR	UR	
YBP	2003/4a	MPM	3	1	1	0			
	2003/4b	MPM	3	1	1	0			
MSM	2003/4	BSP	3	2	2	0			
YMM	2003/4	UR	3	2	0	2	GBP	GBP	
OOO	2004/5	SPM*	2	2	1	1	PBS		
E21 UR	2004/5a	PPP	3	1	1	0			
	2004/5b	PPP	3	2	2	0			
C31 UR	2004/5	SYP	3	3	1	2	PBS	PBS	
W75 UR	2004/5	UR	3	3	0	3	BYN	BYN	SGM
P6 UR	2004/5a	SSM	3	3	1	2	UR	UR	
	2004/5b	SSM	3	3	1	2	UR	UR	
Total				72	49	22	27		

*Male SPM swapped females between years.

clutches were sampled produced at least one extra-pair young (12/16). The number of extra-pair offspring detected for each female correlated positively with the number of her offspring sampled (Pearson $\chi^2 = 0.732$, $n = 16$, $P = 0.001$).

Distribution of male fertilizations

If females consistently preferred one or a small number of high-quality males, one might expect these individuals to dominate the sample of extra-pair young. This did not appear to be the case, with the 31 adult males on the study site fathering between zero and five extra-pair young (Table 2, mean number of paternities per male = 0.58 ± 0.2 se). Furthermore, the distribution of paternities did not differ significantly from a Poisson distribution (one-sample Kolmogorov–Smirnov $Z = 0.656$, $n = 31$, $P = 0.782$), suggesting that individual males did not vary in their likelihood of producing extra-pair young. All of the extra-pair young for which the father was identified were sired by a male in the neighbouring territory or only separated by one intervening territory, whilst the four nests containing young with undetected extra-pair sires had at least one unringed neighbouring male, suggesting that the fathers may again have been neighbouring individuals. Interestingly, one male (PBS) swapped paternity with his neighbour (SPM) twice, with two of his clutches with different females containing young sired by SPM, and two of SPM's clutches with different females containing young sired by PBS.

Relationship between EPP and male body size

Because one potential measure of male genetic quality in birds is body size (Griffith *et al.* 2002), we measured male tarsus-, wing-, tail- and head-length and reduced these to a single principal component (eigenvalues were 2.12, 0.98, 0.47 and 0.44, and character loadings were 0.31, 0.55, 0.53 and 0.57, respectively). The total variance explained by the first principal component (PC1) was 53.0% and all of the morphological measures were strongly positively correlated with PC1, such that high values of PC1 indicate larger birds. There was no significant relationship between the size of the male as represented by PC1 and the likelihood of his extra-pair young

being detected ($P > 0.05$). This held even after controlling for incomplete sampling by including both the number of nests genotyped while the male was present on the study site ($F_{1,28} = 5.29$, $P = 0.021$) and the median distance of the male from those genotyped nests ($F_{1,28} = 4.75$, $P = 0.029$). Similarly, no effect of male size was found in a direct comparison between extra-pair and within-pair males restricted to seven females for whom both males were known (Wilcoxon matched pairs test statistic = 9.00, $P = 0.438$), although with such a small sample size this test lacks power. As only one nest contained young sired by males further than 500 m away, we next compared the PC1 values of successful fathers with the average PC1 for all available males, defined as extra-pair males located within 500 m of the nest. In this analysis, successful extra-pair males were found to be significantly larger (paired *t*-test: $t = -2.64$, df = 9, $P = 0.027$).

DISCUSSION

Our study of Grey Fantails found a high rate of EPP, with 55% of all offspring sired by an extra-pair male, 64% of all clutches containing extra-pair young and 75% of all females producing at least one extra-pair young. Such a high rate of EPP puts the Grey Fantail amongst the most promiscuous socially monogamous species yet studied (e.g. Morton *et al.* 1998, Arnold & Owens 2002, Griffith *et al.* 2002) despite the fact that it is both sexually monomorphic and drably coloured (at least to human eyes), even though it does have unusually large testes. The rate of EPP in this species is undoubtedly high, but our results could potentially be biased by the necessity to exclude 20 young from our analysis because the pair male was not sampled and no genetic match was obtained among the other males. However, we assume that these young are broadly similar to the young for which we could assign paternity.

Female Fantails that engage in EPCs presumably do not gain direct benefits, but they may improve their fitness through indirect genetic benefits. Sexual monomorphism and drab plumage probably argue against a 'good genes' model, as this generally involves genes associated with elaborate male ornaments (Anderson 1994, Petrie 1994). Moreover, 'good genes' models tend to predict that one or a few males will be much more successful than all others, and this

does not seem to hold for Fantails. Instead, we can speculate that genetic compatibility could be important (e.g. Blomqvist *et al.* 2002, Foerster *et al.* 2003), females choosing males whose genotypes will tend to create fitter offspring, for example by the male being less related to the female. Another possibility, originally proposed by Wetton and Parkin (1991), is that females may engage in EPCs to guard against infertility in their social partners. Both hypotheses are difficult to test in most systems, and to address the former in Fantails would require a greatly enlarged dataset, both of individuals and of probably loci.

Most models in which females seek extra-pair fertilizations for indirect genetic benefits implicitly assume that extra-pair encounters are female-driven (Eliassen & Kokko 2008). However, although females of some species appear to make forays to seek EPCs (Smith 1988, Kempenaers *et al.* 1992, Sheldon 1994, Double & Cockburn 2000), forays by males into the home ranges of fertilizable females tend to predominate in species in which EPP is known to occur (Westneat & Stewart 2003). This is also the case for Grey Fantails, in which males make significantly greater number of intrusions than females and these intrusions are more often into the territories of nest-building than incubating females (Munro 2007). Similarly, where copulations have been observed, these involved males that intruded into a female's territory rather than the other way around (Munro 2007). Collectively, these observations suggest that if females do exert mate choice, the selection of available partners might be limited to males that are willing or able to intrude into their territories.

The drab coloration of male Grey Fantails raises the question of how females might discriminate among potential partners. Song plays an important role in courtship, with the two sexes duetting during the breeding season (Higgins *et al.* 2006). Thus females may assess male quality via song-repertoire size (e.g. Hasselquist *et al.* 1996). The Fantail's song has been described as consisting of a rapid series of short whistles descending in frequency, sounding somewhat like a trill, but beyond this little is known about intraspecific repertoire variation (Higgins *et al.* 2006). However, J. C. McLean (unpubl. data in Higgins *et al.* 2006) found that sonograms of male Fantail calls were more similar for two recordings taken from the same individual than for recordings taken from two different individuals, suggesting that songs may carry individual-specific information. This seems a promising avenue for further research.

Another possibility is that active precopulatory female choice may not be involved, with females operating a form of cryptic choice via a 'genetically loaded raffle'. Here, a female might mate with several males, with some trait in the sperm then influencing the outcome of sperm competition (reviewed by Griffith & Immler 2009). According to this hypothesis, close interactions between sperm and the female reproductive tract could favour the storage of the sperm of genetically compatible partners (Birkhead & Brillard 2007), allowing females to maximize offspring quality simply by mating with as many available partners as possible. Alternatively, Reyer *et al.* (1997) suggested that chance encounters arising from the temporal and spatial distribution of broods offer a better explanation for the occurrence of extra-pair activities than a female's search for genetic or phenotypic benefits. Our data, although limited, are broadly consistent with this second view, i.e. that females appear to show no consistency in their preference for extra-pair partners, with male body size failing to predict the incidence of extra-pair young. Rather, females appeared to mate with males holding territories nearby, with only a single brood containing extra-pair young sired by a male from more than 500 m away.

Despite the absence of an overall association between male body size and EPP, extra-pair sires were found to be significantly larger on average than other candidate extra-pair males residing within a 500-m radius of the female. One possible explanation for such a finding is that only the largest extra-pair males were able to make the successful territory intrusions necessary for gaining EPCs (Ketterson *et al.* 1992). However, large extra-pair males may also have been better able to coerce females into mating, either by forced copulation, repeated harassment or punishment for refusal (Clutton-Brock & Parker 1995). This is consistent with observations by Munro (2007) of intruder males harassing resident females, chasing them, pecking them and pinning them to the ground whilst attempting to copulate, and raises the possibility that female Fantails might mate with extra-pair males not for indirect genetic benefits, but instead as a means of avoiding the costs of

harassment from large intruder males, including forced copulations.

From the males' perspective, those which intrude risk being cuckolded themselves while they are away from their territory. Our data suggest that this cost may be outweighed by the benefits of mating with extra-pair females. Moreover, Grey Fantail nests are exceptionally vulnerable to attack by predators, with 83% of all active nests failing in this way (Munro 2007). Consequently, we believe that it is possible that males could seek EPCs as a bet-hedging strategy, spreading their progeny among different nests so that at least some avoid predation. Under high predation intensity, over and above any variation in clutch size due to inherent variation in parent quality, selection may act to reduce variance in nestling survival through dispersal of young among nests (Rubenstein 1982, Bulmer 1984). As Fantails produce small clutches of two to three eggs (Higgins *et al.* 2006), the loss of paternity they suffer in their own nest may be counter-balanced or even outweighed by paternities gained elsewhere, and the effort expended on misdirected paternal care could be relatively small (Munro 2006). However, the Zebra Finch *Taeniopygia guttata* shares similar ecological conditions and yet has a very low rate of EPP (2.4% of offspring tested, Birkhead *et al.* 1990). Consequently, further study is required to determine whether a life history shaped under high levels of nest predation could have produced a strong selective force for male-driven patterns of EPP.

REFERENCES

Akçay, E. & Roughgarden, J. 2007. Extra-pair paternity in birds: review of the genetic benefits. *Evol. Ecol. Res.* **9**: 855–868.

Anderson, M. 1994. *Sexual Selection.* Princeton, NJ: Princeton University Press.

Arnold, K. & Owens, I. 2002. Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. *Proc. R. Soc. Lond. B* **269**: 1263–1269.

Arnqvist, G. & Kirkpatrick, M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *Am. Nat.* **165**: S26–S37.

Birkhead, T.R. & Brillard, J.P. 2007. Reproductive isolation in birds: postcopulatory prezygotic barriers. *Trends Ecol. Evol.* **22**: 266–272.

Birkhead, T.R. & Møller, A.P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences.* London: Academic Press.

Birkhead, T.R., Burke, T., Zann, R., Hunter, F.M. & Krupa, A.P. 1990. Extra-pair paternity and intraspecific brood parasitism in wild Zebra Finches *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* **27**: 315–324.

Birkhead, T.R., Hatchwell, B.J. & Davies, N.B. 1991. Sperm competition and the reproduction organs of the male and female Dunnock (*Prunella modularis*). *Ibis* **133**: 306–311.

Blomqvist, D., Andersson, M., Kupper, C., Cuthill, I.C., Kis, J., Lanctot, R.B. & Sandercock, B.K. 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebirds. *Nature* **419**: 613–615.

Bulmer, M.G. 1984. Risk avoidance and nesting strategies. *J. Theor. Biol.* **106**: 529–535.

Burke, T., Davies, N.B., Bruford, M.W. & Hatchwell, B.J. 1989. Parental care and mating behaviour of polyandrous Dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* **338**: 249–251.

Cézilly, F. & Nager, R.G. 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. *Proc. R. Soc. Lond. B* **262**: 7–12.

Clutton-Brock, T.H. & Parker, G.A. 1995. Sexual coercion in animal societies. *Anim. Behav.* **49**: 1345–1365.

Dixon, A.D., Ross, D., O'Malley, S.L.C. & Burke, T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the Reed Bunting (*Emberiza schoeniclus*). *Nature* **371**: 698–700.

Double, M. & Cockburn, A. 2000. Pre-dawn infidelity: females control extra-pair mating in Superb Fairy Wrens. *Proc. R. Soc. Lond. B* **267**: 465–470.

Eliassen, S. & Kokko, H. 2008. Current analyses do not resolve whether extra-pair paternity is male or female driven. *Behav. Ecol. Sociobiol.* **62**: 1795–1804.

Foerster, K., Delhey, K., Johnson, A., Lifjeld, J.T. & Kempenaers, B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* **425**: 714–717.

Griffith, S.C. 2007. Intra- and extrapair paternity. In Jamieson, B.G.M. (ed.) *Reproductive Biology and Phylogeny of Birds, Vol. 6B: Sexual Selection, Behaviour, Conservation, Embryology and Genetics*: 271–294. Enfield, NH: Science Publishers.

Griffith, S.C. & Immler, S. 2009. Female infidelity and genetic compatibility in birds: the role of the genetically loaded raffle in understanding the function of extrapair paternity. *J. Avian Biol.* **40**: 97–101.

Griffith, S.C., Owens, I.P.F. & Thuman, K.A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**: 2195–2212.

Hasselquist, D. & Sherman, P.W. 2001. Social mating systems and extrapair fertilizations in passerine birds. *Behav. Ecol.* **12**: 457–466.

Hasselquist, D., Bensch, S. & von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the Great Reed Warbler. *Nature* **381**: 229–232.

Higgins, P.J., Peter, J.M. & Steele, W.K. 2006. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 7: Boatbill to Starlings*. Melbourne: Oxford University Press.

Hochberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of sign. *Biometrika* **75**: 800–802.

Hoffman, J.I. & Amos, W. 2005. Microsatellite genotyping errors: detection approaches, common sources and consequences for paternal exclusion. *Mol. Ecol.* **14**: 599–612.

Jennions, M.D. & Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* **75**: 21–64.

Jin, L., Munro, L., Tan, S., Hoffman, J.I. & Amos, W. 2006. Polymorphic microsatellite DNA markers for the Grey Fantail, *Rhipidura albiscapa*. *Mol. Ecol. Notes* **6**: 75–76.

Kempenaers, B. 2007. Mate choice and genetic quality: a review of the heterozygosity theory. *Adv. Study Behav.* **37**: 189–278.

Kempenaers, B., Verheyen, G.R., Van den Broeck, M., Burke, T., van Broekhoven, C. & Dhondt, A. 1992. Extra-pair paternity results for female preference for high-quality males in the Blue Tit. *Nature* **357**: 494–496.

Kempenaers, B., Congdon, B., Boag, P. & Robertson, R.J. 1999. Extrapair paternity and egg hatchability in Tree Swallows: evidence for the genetic compatibility hypothesis? *Behav. Ecol.* **10**: 304–311.

Ketterson, E.D., Nolan, V. Jr, Wolf, L. & Ziegenfus, C. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behaviour and correlates of fitness in the Dark-eyed Junco (*Junco hyemalis*). *Am. Nat.* **140**: 980–999.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen Ltd.

Morton, E.S., Stutchbury, B.J.M., Howlett, J.S. & Piper, W.H. 1998. Genetic monogamy in Blue-headed Vireos and a comparison with a sympatric vireo with extrapair paternity. *Behav. Ecol.* **9**: 515–524.

Munro, K. 2006. *Reproductive strategies in the Grey Fantail* Rhipidura albiscapa. PhD Thesis, University of Cambridge.

Munro, K. 2007. Breeding behaviour and ecology of the Grey Fantail *Rhipidura albiscapa*. *Aust. J. Zool.* **55**: 1–9.

Orsorio-Beristain, M. & Drummond, H. 2001. Male boobies expel eggs when paternity is in doubt. *Behav. Ecol.* **12**: 16–21.

Owens, I.P.F. & Hartley, I.R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond. B* **265**: 397–407.

Petrie, M. 1994. Improved growth and survival of offspring of Peacocks with more elaborate trains. *Nature* **371**: 598–599.

Raymond, M. & Rousset, F. 1995. Genepop (version 1.2): population genetics software for exact tests and ecumenicism. *J. Hered.* **86**: 248–249.

Reyer, H.-U., Bollmann, K., Schlapfer, A.R., Schymainda, A. & Klecack, G. 1997. Ecological determinants of extra-pair fertilizations and egg dumping in Alpine Water Pipits (*Anthus spinoletta*). *Behav. Ecol.* **8**: 534–543.

Rising, J.D. & Somers, K.M. 1989. The measurement of overall body size in birds. *Auk* **106**: 666–674.

Rogers, K.G., Rogers, A., Rogers, D., Lane, B. & Male, B. 1986. *Banders Aid: A Guide to Aging and Sexing Bush Birds*. St. Andrews: Victoria.

Rubenstein, D.I. 1982. Risk, uncertainty and evolutionary strategies. *Current Problems in Sociobiology*. Cambridge: Cambridge University Press.

Sheldon, B.C. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proc. R. Soc. Lond. B* **257**: 25–30.

Smith, S.M. 1988. Extra-pair copulations in Black-capped Chickadees: the role of the female. *Behaviour* **107**: 15–23.

Tregenza, T. & Wedell, N. 2000. Genetic compatibility, mate choice and patterns of parentage: an invited review. *Mol. Ecol.* **9**: 1013–1027.

Valera, F., Hoi, H. & Kritín, A. 2003. Male Shrikes punish unfaithful females. *Behav. Ecol.* **14**: 403–408.

Walsh, P.S., Metzger, D.A. & Higuchi, R. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques* **10**: 506–513.

Weatherhead, P.J., Montgomerie, R., Gibbs, L. & Boag, P.T. 1994. The cost of extra-pair fertilizations to female Red-winged Blackbirds. *Proc. R. Soc. Lond. B* **258**: 315–320.

Westneat, D.F. & Stewart, I.R.K. 2003. Extra-pair paternity in birds: causes, correlates and conflict. *Ann. Rev. Ecol. Evol. Syst.* **34**: 365–396.

Wetton, J.H. & Parkin, D.T. 1991. An association between fertility and cuckoldry in the House Sparrow (*Passer domesticus*). *Proc. R. Soc. Lond. B* **260**: 91–98.

Wolf, L.L. 1975. 'Prostitution' behaviour in a tropical hummingbird. *Condor* **77**: 140–144.

Worthington-Wilmer, J.A., Allen, P.J., Pomeroy, P.P., Twiss, S.D. & Amos, W. 1999. Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Mol. Ecol.* **8**: 1417–1429.