

The colour of paternity: extra-pair paternity in the wild Gouldian finch does not appear to be driven by genetic incompatibility between morphs

P. E. BOLTON*, L. A. ROLLINS*†, J. BRAZILL-BOAST*¹, K-W. KIM‡, T. BURKE‡ & S. C. GRIFFITH*

*Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia

†Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, Vic., Australia

‡Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

Keywords:

colour polymorphism;
domestication;
Estrildidae;
mate choice;
polyandry;
post-zygotic isolation.

Abstract

In socially monogamous species, individuals can use extra-pair paternity and offspring sex allocation as adaptive strategies to ameliorate costs of genetic incompatibility with their partner. Previous studies on domesticated Gouldian finches (*Erythrura gouldiae*) demonstrated a genetic incompatibility between head colour morphs, the effects of which are more severe in female offspring. Domesticated females use differential sex allocation, and extra-pair paternity with males of compatible head colour, to reduce fitness costs associated with incompatibility in mixed-morph pairings. However, laboratory studies are an oversimplification of the complex ecological factors experienced in the wild and may only reflect the biology of a domesticated species. This study aimed to examine the patterns of parentage and sex ratio bias with respect to colour pairing combinations in a wild population of the Gouldian finch. We utilized a novel PCR assay that allowed us to genotype the morph of offspring before the morph phenotype develops and to explore bias in morph paternity and selection at the nest. Contrary to previous findings in the laboratory, we found no effect of pairing combinations on patterns of extra-pair paternity, offspring sex ratio or selection on morphs in nestlings. In the wild, the effect of morph incompatibility is likely much smaller, or absent, than was observed in the domesticated birds. Furthermore, the previously studied domesticated population is genetically differentiated from the wild population, consistent with the effects of domestication. It is possible that the domestication process fostered the emergence (or enhancement) of incompatibility between colour morphs previously demonstrated in the laboratory.

Introduction

Given that mating and raising offspring is costly, there is a trade-off between future and current reproductive events, and the two parents will be selected to

maximize their own fitness and modulate their investment in a reproductive event according to their own condition and the perceived reproductive value of their mate (Trivers & Willard, 1973; Burley, 1986, 1988). For example, mates that have low reproductive value could be closely related, therefore increasing the risk of inbreeding depression (Szulkin *et al.*, 2013). In socially monogamous species, the common goal of raising offspring together is tempered by constraints on optimal choice of partner (Griffith *et al.*, 2011), and individuals will use different strategies to maximize their fitness in these situations, including modifying parental effort,

Correspondence: Peri E. Bolton, Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia.
Tel.: +61298501304; fax: +61298509231; e-mail: peri.bolton@mq.edu.au

¹Present address: Ecosystems and Threatened Species Unit, Regional Operations Division, NSW Office of Environment and Heritage, Sydney South, NSW 1232, Australia

offspring sex ratio and through extra-pair paternity. For example, female zebra finches (*Taeniopygia guttata*) will modulate egg size and incubation effort in relation to partner quality (Rutstein *et al.*, 2004; Gorman *et al.*, 2005; Bolund *et al.*, 2009), and female collared flycatchers (*Ficedula albicollis*) will produce male-biased broods when paired with high-quality males (Bowers *et al.*, 2013). Partners may have low reproductive value because they are genetically incompatible, such that offspring are inviable or infertile (Tregenza & Wedell, 2000; Griffith, 2010; Presgraves, 2010). For example, female collared flycatchers (*F. albicollis*) paired with pied flycatchers (*F. hypoleuca*) use extra-pair paternity with conspecific males to reduce the number of infertile hybrid offspring produced in these heterospecific social pairings (Veen *et al.*, 2001).

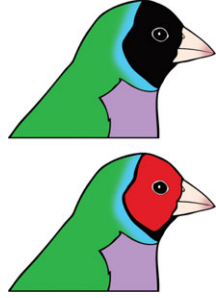
In colour polymorphic species, mate choice options are often discrete, and when colour is tightly correlated with a number of other traits, there can be fitness detriments to partnering with the wrong colour morph (McKinnon & Pierotti, 2010; Griffith *et al.*, 2011; Bolton *et al.*, 2015). For example, colour polymorphism in the white-throated sparrow (*Zonotrichia albicollis*) is controlled by an inversion polymorphism and pairings are almost always disassortative (Thornycroft, 1966; Houtman & Falls, 1994). Assortative white-throated sparrow pairs would lack necessary parental coordination to raise offspring successfully and risk production of inversion homozygotes that may suffer reduced fitness relative to inversion heterozygotes (Tuttle, 2003; Horton *et al.*, 2013). Moreover, if selection for colour morph differs between the sexes, then parents of a particular morph may bias their offspring sex ratio to match that selection. For example, large spotted barn owls (*Tyto alba*) produce female-biased brood sex ratios, whereas small-spotted parents have male-biased broods (Roulin *et al.*, 2010). Furthermore, because many colour polymorphic species are undergoing strong divergent correlational selection and mate assortatively, this may facilitate the evolution of genetic incompatibilities between sympatric colour morphs, although examples are rare (Sinervo & Svensson, 2002; Roulin & Bize, 2006; Seehausen *et al.*, 2014; Bolton *et al.*, 2015). In cases where colour morphs are genetically incompatible, there should be selection for strategies to avoid the costs of incompatibility.

The Gouldian finch (*Erythrura gouldiae*) is a colour polymorphic bird that has behavioural and physiological traits correlated with sex-linked Mendelian red and black head colour morphs, and exhibits a genetic incompatibility between morphs that strongly affects mortality of female offspring (Southern, 1945; Pryke & Griffith, 2006, 2009b; Pryke *et al.*, 2007) (Box 1). This is unusual, because until relatively recently genetic incompatibility is generally thought to be proportional to the degree of genetic divergence between allopatric populations (Presgraves, 2010). However, in the

Gouldian finch, head colour morphs are sympatric across the entire distribution at stable frequencies (Gilby *et al.*, 2009). In accordance with strong selection against offspring from mixed-morph parents, mate choice experiments on domestic Gouldian finches have demonstrated assortative mate preference for head colour (Fox *et al.*, 2002; Pryke & Griffith, 2007; Templeton *et al.*, 2012). To ameliorate some of the costs of incompatibility, females in mixed-morph pairs invest less in rearing offspring and offspring primary sex ratios favour the sex (males) less affected by incompatibilities (Pryke & Griffith, 2009a, 2010). Further, when experimentally given the opportunity for extra-pair copulations, a single copulation with a compatible male was able to sire a large proportion of the clutch, consistent with a post-copulatory cryptic female choice mechanism (Pryke *et al.*, 2010). All of the previous work (cited above) was conducted on domesticated Gouldian finches, and no previous work has examined the extent to which incompatibility and related selection occurs in the wild. Although controlled laboratory studies can tease apart possible factors guiding animal behaviour, they may not be completely relevant to the complex ecological contexts in the wild (Healey *et al.*, 2007), nor do they account for any behavioural and physiological differences that accrue as a result of the domestication process (Burns *et al.*, 2009; Christie *et al.*, 2012). Here, we have used the previous work on the domesticated Gouldian finch to guide predictions for patterns in incompatibility avoidance and morph selection in the wild.

Theoretical modelling (based on the parameters of incompatibility identified in domesticated populations) has demonstrated that incompatibility and morph interactions can be detrimental to population fitness and cause extinction of one or both morphs (Kokko *et al.*, 2014), and could be an additional threatening process for this threatened species (Environment Protection and Biodiversity Conservation Act 1999). In the wild, there are more red males than red females (and more black females than black males), because of uneven morph allele frequencies in the wild, and sex-linked inheritance (Box 1a) (Southern, 1945; Franklin & Dostine, 2000). This means that mates of the same head colour are limiting, and 15–20% of individuals are constrained to mate with an individual from a different morph to themselves (Pryke & Griffith, 2007; Griffith *et al.*, 2011). In such mixed pairs, any genetic incompatibilities would be exposed and this would reduce reproductive success. In contrast with findings on offspring survival in the domesticated birds (Pryke & Griffith, 2009b), previous work in the wild has shown that the survival of nestlings from mixed-morph pairs was not significantly lower in comparison with those from same-morph pairs (Brazill-Boast *et al.*, 2013a). The previous study in the wild (Brazill-Boast *et al.*, 2013a), however, did not account for strategic extra-pair

Box 1 (a) Explanation of the alleles and sex linkage of the red/black polymorphism in the Gouldian finch. (b) Explanation of the key predictions used in this paper that are derived from the laboratory studies on domesticated Gouldian finches.

<p>(a)</p> 	<p>Black morph, recessive allele</p> <p>Males: Z^rZ^r</p> <p>Females: Z^rW</p> <p>Red morph, dominant allele</p> <p>Males: Z^RZ^r, Z^RZ^R</p> <p>Females: Z^RW</p>												
<p>(b)</p> <table border="1"> <thead> <tr> <th>Results from domesticated birds</th><th>Prediction in the wild</th></tr> </thead> <tbody> <tr> <td>1. Females in mixed-morph pairs had a significantly higher fraction of offspring sired by a compatible extra-pair male, than females in same-morph pairs (Pryke <i>et al.</i>, 2010). This was an average of 56% of offspring per clutch, and 76.5% of all possible offspring</td><td>1. In the wild: a) Mixed-morph pairs will have a higher incidence of any extra-pair offspring than same-morph pairs b) Mixed-morph pairs will have a larger fraction of extra-pair offspring than same-morph pairs c) Extra-pair offspring will be sired by compatible males.</td></tr> <tr> <td>2. There is a significantly male biased sex-ratio in offspring of mixed-morph pairs (Pryke & Griffith, 2009a)</td><td>2. There will be a male bias in the offspring from mixed-morph pairs in the wild.</td></tr> <tr> <td>3. The offspring of red females paired with heterozygous red males did equally poorly as those from mixed-morph pairs (Pryke & Griffith, 2009b). These females also have male biased offspring, but not as strongly as in mixed pairs.</td><td>3. a) Red females paired with heterozygote red males will have similar compensation strategies as black females in mixed-morph pairs. b) Incompatibility effects are likely to be strongest in heterozygous red-headed young, therefore there will be a reduction in heterozygous red offspring.</td></tr> <tr> <td>4. Gouldian finches exhibit mutual mate choice preferences for individuals of the same morph (Fox <i>et al.</i>, 2002; Pryke & Griffith, 2007; Pryke, 2010).</td><td>4. There will be a pattern of assortative mating with respect to morph in the wild</td></tr> <tr> <td>5. Restriction of gene-flow not tested previously in captivity.</td><td>5. There will be genetic differentiation between morphs</td></tr> </tbody> </table>	Results from domesticated birds	Prediction in the wild	1. Females in mixed-morph pairs had a significantly higher fraction of offspring sired by a compatible extra-pair male, than females in same-morph pairs (Pryke <i>et al.</i> , 2010). This was an average of 56% of offspring per clutch, and 76.5% of all possible offspring	1. In the wild: a) Mixed-morph pairs will have a higher incidence of any extra-pair offspring than same-morph pairs b) Mixed-morph pairs will have a larger fraction of extra-pair offspring than same-morph pairs c) Extra-pair offspring will be sired by compatible males.	2. There is a significantly male biased sex-ratio in offspring of mixed-morph pairs (Pryke & Griffith, 2009a)	2. There will be a male bias in the offspring from mixed-morph pairs in the wild.	3. The offspring of red females paired with heterozygous red males did equally poorly as those from mixed-morph pairs (Pryke & Griffith, 2009b). These females also have male biased offspring, but not as strongly as in mixed pairs.	3. a) Red females paired with heterozygote red males will have similar compensation strategies as black females in mixed-morph pairs. b) Incompatibility effects are likely to be strongest in heterozygous red-headed young, therefore there will be a reduction in heterozygous red offspring.	4. Gouldian finches exhibit mutual mate choice preferences for individuals of the same morph (Fox <i>et al.</i> , 2002; Pryke & Griffith, 2007; Pryke, 2010).	4. There will be a pattern of assortative mating with respect to morph in the wild	5. Restriction of gene-flow not tested previously in captivity.	5. There will be genetic differentiation between morphs	
Results from domesticated birds	Prediction in the wild												
1. Females in mixed-morph pairs had a significantly higher fraction of offspring sired by a compatible extra-pair male, than females in same-morph pairs (Pryke <i>et al.</i> , 2010). This was an average of 56% of offspring per clutch, and 76.5% of all possible offspring	1. In the wild: a) Mixed-morph pairs will have a higher incidence of any extra-pair offspring than same-morph pairs b) Mixed-morph pairs will have a larger fraction of extra-pair offspring than same-morph pairs c) Extra-pair offspring will be sired by compatible males.												
2. There is a significantly male biased sex-ratio in offspring of mixed-morph pairs (Pryke & Griffith, 2009a)	2. There will be a male bias in the offspring from mixed-morph pairs in the wild.												
3. The offspring of red females paired with heterozygous red males did equally poorly as those from mixed-morph pairs (Pryke & Griffith, 2009b). These females also have male biased offspring, but not as strongly as in mixed pairs.	3. a) Red females paired with heterozygote red males will have similar compensation strategies as black females in mixed-morph pairs. b) Incompatibility effects are likely to be strongest in heterozygous red-headed young, therefore there will be a reduction in heterozygous red offspring.												
4. Gouldian finches exhibit mutual mate choice preferences for individuals of the same morph (Fox <i>et al.</i> , 2002; Pryke & Griffith, 2007; Pryke, 2010).	4. There will be a pattern of assortative mating with respect to morph in the wild												
5. Restriction of gene-flow not tested previously in captivity.	5. There will be genetic differentiation between morphs												

paternity or differential sex ratio allocation to ameliorate some of these costs, as shown in domesticated birds (Pryke & Griffith, 2009b; Pryke *et al.*, 2010).

Based on the collection of previous work on domesticated birds in the laboratory, we therefore predicted that compatibility selection will be the primary driver for patterns of extra-pair paternity and offspring sex ratio in the wild (Pryke & Griffith, 2009a,b; Pryke *et al.*, 2010). Like in the domesticated birds, we assumed that females of all morphs and pairing types are equally

likely to engage in extra-pair copulations (Pryke *et al.*, 2010) and that females in the wild are able to access at least one extra-pair copulation with a compatible male. This seems plausible as the species is nonterritorial and they forage in small flocks (J. Brazill-Boast & S.C. Griffith, Pers. Obs.), providing ample opportunity for females to find and copulate with an extra-pair partner. We therefore predicted that females in mixed-morph pairs should have a higher proportion of offspring sired by an extra-pair (compatible) male, than females in

same-morph pairs (Box 1b, Prediction 1). Further, offspring from mixed pairs are expected to have a male-biased sex ratio, due to the combined effects of sex allocation and female-biased mortality as demonstrated in the domesticated birds (Box 1b, Prediction 2; Pryke & Griffith, 2009a). The contribution of compatible males to extra-pair offspring is examined through the identification of extra-pair sires through genotyping and by inference from the head colour of extra-pair chicks using the novel PCR assay developed for the *red* head colour gene in Gouldian finches (Kim, 2011). This marker also allowed us to directly test whether there was any selection against heterozygote red males, as inferred from the work on domesticated birds (Box 1b, Prediction 3; Pryke & Griffith, 2009b). To explore mate limitation and adaptive mate choice, we measured the frequency of assortative and disassortative pairs in the population and predicted that there will be more assortative mate pairs than expected under random mating (Box 1b; Prediction 4). Further, if incompatibility is occurring, we predicted there to be a restriction of gene flow between red and black morphs (Box 1b; Prediction 5) and compared levels of genetic differentiation between head colour morphs both in the wild and in a sample of the domesticated population. We discuss how these findings relate to the evolution of genetic incompatibilities in this species and more broadly.

Materials and methods

Study site and nest monitoring

This study was conducted on a population of Gouldian finches, near Wyndham in the eastern Kimberly region, Western Australia (S15°340', 128°090'). This site comprises 109 Ha of suitable Gouldian finch breeding habitat (see Brazill-Boast *et al.*, 2011 for specific details). The study site was supplemented with nest boxes that resemble the natural cavities preferred by Gouldian finches to facilitate the study by providing access to the nest chamber (Brazill-Boast *et al.*, 2010, 2013b). The data were collected from February to August, which encompasses the breeding season of the Gouldian finch, in consecutive years (2008–2009). In the study area, all nest boxes and natural hollows were marked and checked for nest initiation every 7–10 days. After initiation, the nest was checked every 2–3 days to record brood size and hatching date. Once hatched, nestlings were monitored every 2–4 days, and if they were in nest boxes, nestlings were blood-sampled and banded between the age of 14 days and fledging, which occurred after day 18. On first capture, all adults were given a unique combination of plastic colour bands in addition to a metal band supplied by the Australian Bird and Bat Banding Scheme, and their head colour was recorded. Blood samples were taken from the brachial vein (< 50 µL) and stored in 95% ethanol.

Putative parentage (or social parentage, the pair that raises the offspring) was assigned by either: (1) capture of an adult entering an active nest using a hand net or (2) direct observations of a colour-banded adult visiting a nest to feed offspring. In addition, every 1–2 weeks, birds congregating around waterholes were mist-netted and blood-sampled, to gain a broader sample of the adult population, including individuals that were deemed to be nonbreeding (although it is possible that they were breeding in undetected nests either inside or outside the study area).

Only nestlings from nest boxes were bled, as offspring in natural hollows were inaccessible. In total, blood samples were collected from 51 putative families, including 257 offspring sampled at day 14. In total, we also had 252 adult blood samples from the population, which included parents sampled at nests and also adults caught in the local vicinity of the breeding areas. For more details on the total sample of natural hollows and nest boxes, see Appendix S1.

The above protocols were approved by the animal ethics committees at Macquarie University (AEC2007/037 & AEC 2007/038) and followed all Australian legislation.

Molecular methods and parentage assignment

Blood samples were extracted using a Qiagen PureGene Kit. We amplified 10 variable microsatellite loci described previously (Pryke *et al.*, 2010). In addition to these markers, we genotyped all adults and offspring in the sample for two consecutive SNPs that segregate almost perfectly with head colour phenotype (Kim, 2011). These SNPs (locus *Ego172*) were developed into a simple allele-specific PCR test, where alleles are differentiated by labelled dyes and a 3-bp size difference (Kim, 2011). This assay was included into the above microsatellite multiplexes. In our sample of 252 adults, only a single adult's genotype at this colour marker conflicted with the observed phenotype at the time of capture and blood sampling (see Appendix S1). All offspring were sex-typed at the *CHD* locus using primers 2550F and 2718R (Fridolfsson & Ellegren, 1999). The details for the protocols we used are in Appendix S2.

For each year in our data set, genetic data were used to assign parentage to offspring using a likelihood approach in CERVUS 3.0.6 (Marshall *et al.*, 1998; Lemons *et al.*, 2014). All families had at least one putative social parent identified at the nest through behavioural observations, and 47 of 51 families had both social parents identified. Allele frequencies were estimated using the default settings, and parentage was simulated using 100 000 offspring and assuming 80% of the adult population was sampled. We assigned mothers to all offspring in the data set, followed by fathers after the exclusion of maternal alleles. Parents were assigned on the basis of the highest log-likelihood

ratio score (LOD). The CERVUS assigned mother was compared with the field observation of the social mother to verify the results and to identify causes for mismatches (allelic dropout or different parents). Allelic dropout was inferred by a manual check when a chick mismatched its parents at a locus where either the respective parent or offspring was homozygous, but matched both parents at all other loci. We subsequently assigned paternity having accounted for the maternal alleles using the known mothers, based on the consensus mother derived from manual, automated and field observations of maternity. Rates of null alleles were calculated using CERVUS (Appendix S2).

Parents were assigned based on a conservative set of rules based on number of mismatches and allelic dropout. Parents were only assigned if they either matched at all loci, or mismatched at a maximum of two loci that could be readily explained by allelic dropout and backed up by a high LOD score. No more than two mismatches attributable to dropout were tolerated. Instances of extra-pair paternity were defined when offspring mismatched the social father at two or more loci (of ten). If an offspring mismatched both social parents at two or more loci (not attributable to dropout), then intraspecific brood parasitism (IBP) was inferred. For the identified extra-pair offspring, potential fathers from the population pool were only assigned when there were zero mismatches at all loci typed, or if there was just one mismatch readily attributable to allelic dropout. As can be seen in the results, the bimodal distribution of mismatches indicates that all offspring were assigned unambiguously.

Across genetically sampled nests, there were four families with only one social parent identified at the nest, and the missing parent was not identified with parentage analysis. The genotypes of the missing parents were reconstructed from the offspring genotypes, but to be conservative we excluded three (of four) families where reconstructed genotypes included more than three alleles because it was not possible to distinguish between multiple paternity and allelic dropout without the second parent as a reference.

The final genetic data set comprised 57 broods from 48 families (comprising 257 day 14 offspring), with a total of 92 sampled parents and an additional pool of 154 adults captured in the study area. Of the sampled families, six pairs were sampled over two breeding attempts, and two were sampled over three attempts.

Determinants of extra-pair paternity

Although the primary focus of this study was to explore morph- and incompatibility-related drivers of extra-pair paternity, other factors such as the opportunity for extra-pair copulations can be important in explaining variation in paternity (Griffith *et al.*, 2002). Breeding density and synchrony were explored in relation to

patterns of extra-pair paternity as described in Appendix S3. Additional insight into spatial constraints on extra-pair paternity was explored by characterizing the distances females travelled to attain extra-pair copulations, based on the nestlings that were confidently assigned to an individual extra-pair father. For these nestlings, we tabulated whether that father was observed nesting at the same time, and if so, how far his nest was from the focal female (the mother).

We focused on genetic incompatibility in mixed-morph pairs as a primary driver of extra-pair paternity patterns and compared our results directly with those from the previous captive experiments (Pryke *et al.*, 2010). We included only the first observed clutch in these analyses because (1) it was more directly comparable with the captive experiments and (2) to remove pseudoreplication, as there were not enough replicate clutches to run nested analyses. There was one nest included in the analysis where the social mother as not observed in the field and was not identified by the parentage analysis, but the head colour assay allowed us to reconstruct her head colour genotype based on the genotype of the social father and their offspring. We also repeated the analyses described below with respect to intraspecific brood parasitism and further explore our broader findings of intraspecific brood parasitism in relation to other Estrildid finches (Appendix S3).

We evaluated whether females in mixed-morph pairs were more likely to have any offspring from an extra-pair father (Prediction 1a). To do this, we coded whether any given family had at least one instance of extra-pair paternity. We compared the number of families with extra-pair paternity in mixed-morph (total families = 12; red female ($Z^R W$) \times black male ($Z^r Z^r$) = 4; black female ($Z^r W$) \times red male ($Z^R Z^r$) = 8) and same-morph pairs (total families = 36; black female \times black male = 34; red female \times red male = 2). Throughout this paper, females will be referred to first when describing pairing combinations. We tested the difference in number of families with any extra-pair offspring in mixed- and same-morph pairs using a Fisher's exact test.

To test whether the results in the wild conform to expectations from the captive females, we extracted the occurrence of extra-pair paternity across all families in the experimental data set from Fig. 1 in Pryke *et al.* (2010) and tested whether there was a difference in the occurrence of extra-pair paternity (see Appendix S3 for more details). From the previous study, we present only the level of extra-pair paternity in mixed pairs in the adaptive treatment ($n = 10$) and the pure pairs in the neutral treatment ($n = 10$). We use this subset of data throughout as a comparison with wild birds and it will hereafter be referred to as 'domesticated'.

In our wild sample, all red females in same-morph pairs were with heterozygous red males, and this

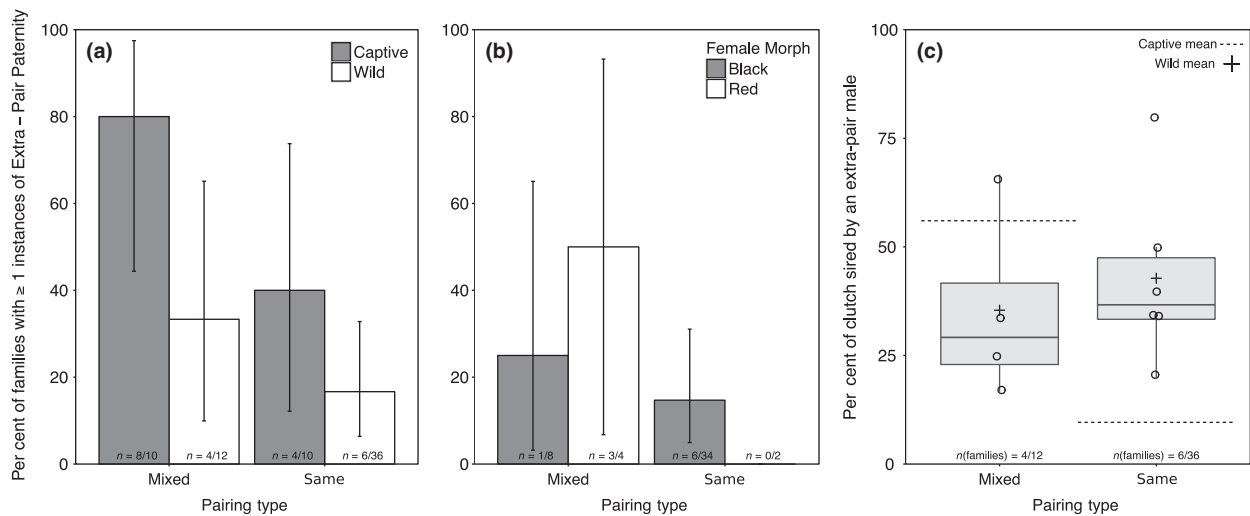


Fig. 1 (a) The per cent of all families that had at least 1 instance (extra-pair offspring ≥ 1) of extra-pair paternity by pairing type from the data set pooled across years (Fisher's exact test, one-sided P -value = 0.24). Number of families is above the category on the x-axis. Black bars represent results from experiments on domesticated birds where mixed pairs are in the adaptive context and same-morph pairs in the neutral context (Pryke *et al.*, 2010; Fig. 1); white bars are the results from wild birds. The error bars represent 95% binomial confidence intervals. (b) Per cent of wild families with ≥ 1 extra-pair offspring according to female head colour and pairing class. Black bars represent black females, and white bars are red females. There was no significant difference between the number of black-headed females engaging in extra-pair paternity across pairing contexts (Fisher's exact test, two-sided P -value = 0.17). Sample sizes for each category are above the x-axis. (c) The per cent of wild offspring that were sired by an extra-pair male, from those nests with extra-pair paternity (Mann-Whitney U -test: $W = 8$, $P = 0.45$). Dashed lines represent the average per cent of clutch in each context sired by an extra-pair male (in adaptive and neutral context for mixed- and same-morph pairs) from experiments on domesticated birds (Pryke *et al.*, 2010; Fig. S1), and the cross represents the mean per cent in the wild data set.

pairing type was previously found to be incompatible in the domesticated birds (Pryke & Griffith, 2009b). To test Prediction 3a, we tested for differences in the number of black females with any instance of extra-pair paternity using a Fisher's exact test (same morph, $n = 34$; mixed morph, $n = 8$).

We compared whether mixed-morph pairs had more extra-pair offspring (Prediction 1b). We tested this by comparing the proportion of extra-pair offspring in mixed pair broods with same-morph broods using a Mann-Whitney U -test. To control for differences in clutch size, we also compared mixed- and same-morph pairs using a binomial logistic regression with a logit link. From nests with any instance of extra-pair paternity, we tallied the total extra-pair offspring and compared pairing types with a Fisher's exact test and compared these values against the number of offspring observed in the Pryke *et al.* (2010) domesticated data set.

We also conducted power analyses on the Fisher's exact tests about whether we could reject a false null hypothesis of no difference between mixed- and same-morph pairs in the wild. We ran three different tests: (1) power when the effect size is as observed in the wild, (2) the sample size required to reject H_0 with the observed effect size and (3) power to reject H_0 from the effect size observed in the domesticated birds (subset

as above). All analyses were conducted in R using the 'pwr' package and considered 0.8 to be adequate power (Champely, 2015). All effect sizes reported are Cohen's h , as a measure of distance between two probabilities.

Offspring morph

Fathers of extra-pair offspring should be a compatible morph with the mother (Prediction 1c). When not all extra-pair offspring are assigned fathers, genotyping offspring with the head colour marker (*Ego172*) allows us to infer patterns of paternity by expectations from Mendelian inheritance and known allele frequencies in the parental generation. See Appendix S4 for details about how expected genotype proportions were calculated. For this, we pooled all extra-pair offspring across all broods (not just the first brood) by maternal morph. We then used a binomial exact test to compare whether extra-pair offspring genotype frequency deviated from expectation. We tested against two scenarios: whether offspring genotype frequency matched that expected under random paternity (no female preference or morph-specific fertilization) or under assortative morph preference. These were tested against expectations using a goodness-of-fit binomial exact test, or a multinomial exact ('XNomial' package) test in R (Engels, 2015).

In domesticated birds, red females paired with heterozygote red males showed evidence of incompatibility; therefore, heterozygote red offspring should be selected against (Prediction 3b). In our data from the wild, we tested selection through deviation from Mendelian expectations (based on their parents' genotypes) in each pairing type for all within-pair offspring of the first observed clutch ($n = 190$). Unfortunately, the PCR assay for head colour was not available when the original (captive) experiments were conducted, so we are not able to make quantitative predictions about the degree of deviation from Mendelian expectations from genotype-specific survival or allele-specific fertilization. For each pairing type, offspring genotype frequencies were compared to Mendelian expectations using a goodness-of-fit binomial exact test, or a multinomial exact ('*XNomial*' package) test in R (Engels, 2015).

Offspring sex ratio

If incompatibility is occurring in the wild as observed in domesticated birds (Pryke & Griffith, 2009b), along with adaptive sex ratio allocation (Pryke & Griffith, 2009a), then there should be a significantly male-biased sex ratio in the broods of mixed-morph pairs (Prediction 2). To account for variation in clutch size, we used a binomial logistic regression with a logit link, with offspring sex as the response and pairing type as the predictor. We tested pairing type as the two-factor mixed vs. same morph, and as four factors for each individual pairing type. The latter approach was used because, in captivity, red females in 'assortative' pairs with heterozygote males also showed (albeit weaker) male-biased sex ratios (Pryke & Griffith, 2009a) (Box 1b; Finding 3).

Assortative pairing

In the domesticated Gouldian finch, birds showed assortative mate preferences and therefore avoided the costs of incompatibility by pairing with same-morph partners, and we therefore predict an assortative social mating pattern in the Wyndham population (Prediction 4). We assessed the extent to which birds were pairing assortatively with respect to head colour in the Wyndham population. We compared unique breeding pairs Wyndham (pairs; $n = 59$), against two hypotheses: a) random mating, calculated by random union of morph genotypes, and b) 'perfect assortative mating'. Perfect assortment was defined as the situation where all individuals will always mate assortatively. As the frequency of head colours differs in males and females in the population, any strict assortative mate preference means that surplus red males are inevitably forced to breed with black females or forego reproduction (Southern, 1945; Griffith *et al.*, 2011). We compared the expected frequencies of mixed- and same-morph pairs in these scenarios against the observed social pairings in

Wyndham using a binomial exact test, where red males (regardless of underlying genotype) paired with red females were considered 'same morph'. We also assessed whether there was any difference in head colour frequency between the individuals that were observed to breed and the wider population using a Fisher's exact test by comparing breeders with non-breeders.

Population genetics of morph phenotypes in domesticated and wild populations

If incompatibility is occurring, then we would expect to see associated genetic differentiation between red and black morphs (Prediction 5). We examined genetic differentiation in red and black wild birds and in a cohort of domesticated birds used in previous studies (Pryke *et al.*, 2010). We also examined genetic differentiation between domesticated and wild populations. These domesticated birds were selected as wild-type birds (those without avicultural colour mutations) from the broader population of domesticated Gouldian finches held by aviculturists in Australia and had been held by us for no more than four generations at the time that the key previous studies were conducted (Pryke & Griffith, 2009b; Pryke *et al.*, 2010). Little information is available on how many generations this domesticated population has been maintained in captivity, but it was difficult to breed Gouldian finches in captivity reliably prior to the 1980s (Evans & Fidler, 2005). Thus, we estimate the captive population to be around 30 years old (~ 30 generations). Although it has been illegal to trap wild Gouldian finches since 1987, there are still anecdotal reports of wild finches being taken into captivity, and thus the degree of isolation from the wild populations is difficult to ascertain.

To explore genetic changes since domestication, we genotyped 48 adult birds (16 red and 32 black) from the domesticated population that had been studied previously (Pryke *et al.*, 2010) and compared them with the wild birds. We genotyped these individuals at the same ten microsatellite loci using the laboratory protocols described above. We created a random sample of individuals from the wild population to match the data set of domesticated birds. We compared levels of genetic diversity between red and black morphs and between wild and domesticated populations, and calculated the rarefied allelic richness in FSTAT 2.9.3.2 (Goudet, 1995), and heterozygosity, deviation from Hardy–Weinberg equilibrium and inbreeding coefficients in ARLEQUIN v.3.5.2.2 (Excoffier & Lischer, 2010). Linkage disequilibrium between markers was assessed using GENEPOP v4.2 (Raymond & Rousset, 1995).

We examined population structure between red and black morphs in both wild and domesticated populations, and between wild and domesticated populations, using AMOVA implemented in ARLEQUIN (10 000

permutations) (Excoffier & Lischer, 2010). We also ran the AMOVA on the full data set of wild birds, comprising 47 red and 197 black birds. Groupings for the AMOVA were devised based on the provenance of the birds (wild or domesticated, $n = 48$ each), and the head colour morph observed of the individual bird (red ($n = 16$) or black ($n = 32$)), and analyses were run separately for each comparison (red vs. black, wild vs. domesticated).

To explore whether there was genetic structure that did not fall into our *a priori* population groups, we ran a genetic clustering analysis using STRUCTURE v2.3.4 with domesticated/wild or red/black in the captive population as *a priori* (LOCPRIOR) (Pritchard *et al.*, 2000; Hubisz *et al.*, 2009). The LOCPRIOR model sets sampling provenance as *a priori* in the analysis to be considered as potentially informative to population structure and will aid in the detection of weak population structure according to sampling provenance, but will not bias the result if there is not structure according to these localities (Hubisz *et al.*, 2009). We used the default admixture model and simulated genetic clusters (K) 1–10 with ten iterations per value of K . We chose a maximum K of ten to ensure that we captured any clusters additional to those in our *a priori* groups. For each value of k , the burn-in was 100 000 with a final MCMC length of 1×10^6 . A STRUCTURE analysis has previously been conducted on the red/black comparison in wild birds (Kim, 2011), so we do not present those results here. We compared the likelihoods ($\ln P(D)$) and ΔK of assignment for clusters in each comparison using the output in Structure Harvester v0.6.94 (Pritchard *et al.*, 2000; Evanno *et al.*, 2005; Earl & VonHoldt, 2012). Q -plots that graphically depict the probability an individual belongs to a particular genetic cluster were generated using CLUMPP v1.1.2 and DISSTRUCT v1.1 (Rosenberg, 2004; Jakobsson & Rosenberg, 2007). Because the Evanno method (2005) cannot distinguish between $k = 1$ and 2, a single genetic cluster was inferred when Q -plots were equally admixed and an $\ln P(D)_{\max} = 1$.

Results

Parentage analysis

Across years, CERVUS was able to correctly predict the social mother 94.5% of the time at 95% confidence levels. The combined nonexclusion probability for these data sets for the first parent in 2008 and 2009 was 0.0008 and 0.0009, and 0.00002 for the second parent (see Table S3 for characteristics of the individual loci used). Of 257 offspring, 212 were identified as the offspring of the social parents identified in the field. Of these, 67 offspring showed a mismatch with their putative parents, but in all cases CERVUS assigned parentage to the social parents observed in the field. All these mismatches could be readily attributed to allelic

dropout, as dropouts tended to run in families and matched the estimated rates of null alleles for each locus (Table S3). Of the nestlings that mismatched their putative father, 24 nestlings mismatched at one locus, and three nestlings mismatched at two; and 24 nestlings mismatched their putative mothers at one locus. Four nestlings mismatched both their parents at one locus, and twelve mismatched either maternal or paternal alleles at two loci.

There were 20 nestlings assigned as extra-pair offspring and these mismatched their social father at three or more loci (mean of 5.25 loci). Only one pair that re-nested was observed to have extra-pair paternity in both broods (Family 33). Five nests had multiple instances of extra-pair paternity within a clutch and, of these, three were from multiple extra-pair fathers (based on manually reconstructed genotypes). We were able to assign four (of 20) extra-pair offspring to fathers in our adult population pool, and three of these fathers matched the offspring at all loci (i.e. 10 of 10). One extra-pair father mismatched at one locus, but this could be attributed to allelic dropout. Of the observed first clutches with extra-pair paternity ($n = 10$) and IBP ($n = 9$), three of these contained both IBP and extra-pair offspring. Overall, the level of extra-pair paternity was found to be 22.8% of broods (13 of 57), representing 8.6% of offspring produced by the social mother (20 of 232).

There were eleven nestlings that mismatched both their social parents at more than one locus each, plus mismatched a mixture of maternal and paternal alleles at more than two other loci. These were considered to be the result of either intraspecific brood parasitism (IBP) or nest takeovers (where a new pair takeover a nest containing eggs laid by the female of the usurped pair) that were observed in the field (Brazill-Boast *et al.*, 2013a). IBP offspring mismatched the social mother at a mean of 4.5 loci and mismatched the social father at a mean of 6.1 loci. There was no evidence of pseudo-IBP or quasiparasitism, where the social father but not mother matches the offspring (Griffith *et al.*, 2004). Most observations of IBP were a single offspring per clutch, and no families had more than one clutch with any IBP offspring. Further, one family in each year had two IBP offspring; in each, less than four alleles were reconstructed and may represent offspring from the same parents. Two IBP offspring had both parents identified with no mismatches, and in one offspring the father was identified with no mismatches. Overall, the level of IBP was found to be 15.8% broods (9 of 57) representing 4.5% all offspring (11 of 243) (Table 1). See Appendix S3 for further exploration of the IBP data.

Determinants of extra-pair paternity

There was no evidence for any effect of either spatial constraints or breeding density on the incidence of

Table 1 Summary of the extra-pair paternity/offspring (EPP/O) and intraspecific brood parasitism (IBP) data in the Gouldian finch from 2008 to 2009 breeding season.

	Number families	Number Broods	Number WPO	Number EPO	EPO assigned fathers	Broods with EPP (%)	Offspring EP (%)	Average % Brood EP (\pm SE)*	Number IBPO	Broods with IBP (%)	Offspring IBP (%)
Overall	48	57	212	20	4	22.8	8.6	39.8 (\pm 6.4)	11	15.8	4.53
2008	26	27	108	7	0	18.5	6.1	30.3 (\pm 6.3)	7	22.2	5.74
2009	22	30	104	13	4	26.7	11.1	49.0 (\pm 10.0)	4	10.0	3.31
Mixed morph	12	17	51	7	1	35.3	12.1	35.4 (\pm 11.0)	4	23.5	6.45
Z ^R W \times Z ^R Z ^r	4	6	14	5	1	66.7	26.3	36.1 (\pm 15.5)	2	33.3	9.52
Z ^R W \times Z ^R Z ^r	8	11	37	2	0	18.2	5.1	33.3 (\pm 0)	2	18.2	4.88
Same morph	36	40	161	13	3	17.5	7.5	42.8 (\pm 8.5)	7	12.5	3.87
Z ^R W \times Z ^R Z ^r	34	38	153	13	3	18.4	7.8	42.8 (\pm 8.5)	7	13.2	4.05
Z ^R W \times Z ^R Z ^r	2	2	8	0	-	0	0	0	0	0.0	0.00

*Average calculated from only those broods with extra-pair paternity.

extra-pair paternity, and extra-pair sires were identified breeding themselves and nesting up to 4.28 km away from the nest in which they gained paternity (other males were 0.33 and 0.54 km away). There was no evidence that the number of pairs breeding or that time in the breeding season influenced patterns of extra-pair paternity. For more information, see Appendix S3.

Across pairing types, we compared the instances where females engaged in extra-pair paternity (≥ 1 extra-pair offspring). There was no difference between pairing types in the incidence of extra-pair paternity (4/12 vs. 6/36, Fisher's exact test, two-sided P -value = 0.24, Fig. 1a). However, the power to reject the null at the effect size observed in the wild was low ($h = 0.39$, power = 0.22), and we would have required a sample of 65 mixed pairs and 195 same-morph pairs to confidently conclude there was no difference. A sample size of 260 pairs represents about 20% of the estimated total adult population in the entire species (Garnett *et al.*, 2011). In the subset of birds from the domesticated study, there was no significant difference in whether a family had any instance of extra-pair paternity between mixed-morph pairs and same-morph pairs, although the effect size and power were much larger (8/10 vs. 4/10, Fisher's exact test $P = 0.17$, $h = 0.84$, power = 0.76, Appendix S3 (Pryke *et al.*, 2010a)). However, if the same biological effect size ($h = 0.84$) was present in the wild, we would have had much greater power to discriminate differences in extra-pair paternity between morphs (power = 0.72). Mixed pairs in the domesticated birds had a significantly higher incidence of extra-pair paternity than mixed pairs in the wild (two-tailed Fisher's exact test, $P = 0.043$, $h = 0.98$, power = 0.63).

We had insufficient power to determine whether black females in different pairing contexts had significant differences in extra-pair paternity to test Prediction 3a (1/8 vs. 6/34, Fisher's exact test, two-sided P -value = 1, $h = 0.14$, power = 0.066; Fig. 1b).

In the wild, there was no significant difference between mixed- and same-morph pairs in the proportion of the brood sired by an extra-pair male same morph (Mann–Whitney U -test: $W = 8$, $P = 0.45$), nor was there a difference when accounting for brood size (GLM: $\chi^2 = 0.073$, d.f. = 1 $P = 0.79$) (Fig. 1c; Prediction 1b). From those nests with extra-pair paternity, the number of extra-pair offspring in each pairing type did not differ (5/16 vs. 12/28 Fisher's exact test, two-sided P -value = 0.53, $h = 0.24$, power = 0.09). In mixed pairs, 31.3% of the offspring were sired by an extra-pair male, which is significantly less than the observed 75.0% of offspring observed in the domestic population (Fisher's exact test, two-sided $P = 0.002$, $h = 0.91$, power = 0.88). Further, total extra-pair offspring in same-morph pairs was higher (42.9%), but not significantly different from what was observed in the domesticated population (24.0%) (Fisher's exact test, two-sided $P = 0.245$, $h = 0.40$, power = 0.31) (Pryke *et al.*, 2010). In the domesticated birds, the biological effect size was four times greater (and in the opposite direction) than we observed in the wild, and for the total number of extra-pair offspring in pairing types, this effect size would have given ample power with our sample sizes ($h = 1.07$, power = 0.92).

Offspring morph

In the wild, we tested for an effect of morph on the paternity patterns of extra-pair offspring using the genotypes of the extra-pair offspring (Fig. 2; Prediction 1c). For the offspring of red females, goodness-of-fit tests were unable to reject that offspring were fertilized according to random mating, or according to a preference for red males, but our power was very low due to small sample size (extra-pair offspring from red female $n = 5$). From the genotypes of the extra-pair offspring we can conclude that none of their fathers were homozygote red males. There was no evidence of red

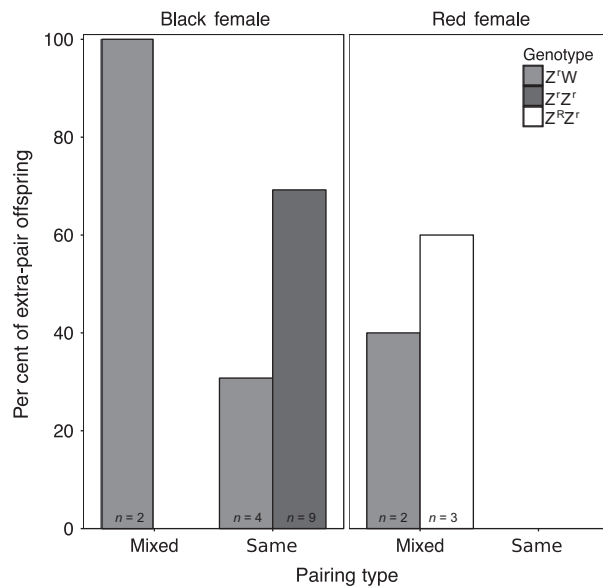


Fig. 2 The proportion of extra-pair offspring by morph genotype in each pairing type. Bar colours represent offspring morph genotype. The panes correspond to the maternal morph and bars correspond to offspring head colour genotype. Sample size of chicks is above the x-axis.

alleles in the extra-pair offspring of black morph mothers, and the three assigned extra-pair offspring from black morph mothers showed the father was also a black morph. Interestingly, the single remaining assigned offspring was from a red female in a mixed pair, but the father who was assigned was also a black morph male (matched 9/9 loci, LOD = 11.36, nest 4.28 km away).

We found little evidence that morph frequencies deviated from Mendelian expectations in WP offspring (Table 2; Prediction 3b), but power was low due to small sample sizes (sample sizes in Table 2). Contrary to our prediction, there was no significant reduction in heterozygote male offspring from red female and heterozygote red male parents (Table 2). There was

deviation from Mendelian expectations in offspring of same-morph black pairs ($Z^rW \times Z^rZ^r$), where black morph females were more numerous than expected by chance (binomial test, obs = 0.61, exp = 0.5, $P = 0.011$).

Offspring sex ratio

There was no effect of same-morph vs. mixed-morph pairing types on brood sex ratio (GLM: $\chi^2 = 1.52$, d.f. = 1, $P = 0.29$), nor when considering all four pairing types observed (GLM: $\chi^2 = 2.65$ d.f. = 3 $P = 0.45$) (Fig. 3), therefore brood sex ratios were not distinguishable from parity.

Assortative pairing

In Wyndham, observed social pairs did not differ significantly from the pattern expected by random mating with respect to head colour when the adult morph frequencies were accounted for (16 mixed, 43 same morph: binomial test: expected = 0.30, $P = 0.67$, $h = 0.07$, power = 0.081), but were significantly different from estimates of perfect assortment (binomial test: expected = 0.14, $P = 0.0076$, $h = 0.32$, power = 0.71). There was no difference in the head colour of females or males represented in the breeding vs. the wider population (Fisher's exact test: $P = 1.0$, $P = 0.844$ for females and males, respectively).

Population genetics of morph phenotypes in domesticated and wild populations

None of the markers used to explore population structure in the wild and captive populations were consistently out of Hardy–Weinberg equilibrium, and allelic richness and heterozygosity estimates for each locus are presented in Table S4. Two pairs of loci were in linkage disequilibrium in the domesticated population after Bonferroni correction (Table S5). One locus from each pair was excluded and the analyses were run on eight loci. The summary rarefied allelic richness and

Table 2 The observed and expected frequency of offspring genotypes in different pairing types. P -values are the outputs from binomial tests or multinomial tests (more than two cases), and w is the effect size.

Maternal genotype	Paternal genotype	Number families	Number offspring	Expected/ Observed	Offspring genotype					P	h	Power
					Z ^r W	Z ^R W	Z ^r Z ^r	Z ^R Z ^r	Z ^R Z ^R			
Z ^r W	Z ^r Z ^r	34	141	Expected	0.5	–	0.5	–	–	0.01	0.22	0.75
				Observed	86	–	55	–	–			
Z ^r W	Z ^R Z ^r	8	31	Expected	0.25	0.25	0.25	0.25	–	0.55	0.26	0.20
				Observed	6	8	6	11	–			
Z ^R W	Z ^r Z ^r	4	11	Expected	0.5	–	–	0.5	–	0.55	0.27	0.15
				Observed	7	–	–	4	–			
Z ^R W	Z ^R Z ^r	2	7	Expected	0.25	0.25	–	0.25	0.25	0.48	0.62	0.25
				Observed	3	3	–	0	2			

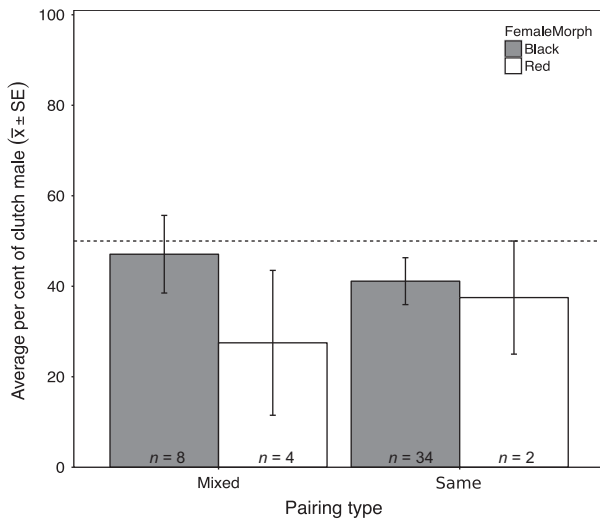


Fig. 3 Average sex ratio per clutch according to pairing type, where bar coloration represents the maternal morph. Number of clutches are above the x-axis.

heterozygosity estimates for reds and blacks in the domesticated and wild population are presented in Table 3. There was a significant reduction in allelic richness in the domesticated population compared with the wild population (paired two-tailed t -test, $t = -2.823$, d.f. = 9, $P = 0.02$), but no significant difference between expected heterozygosity (two-tailed paired t -test, $t = -1.95$, d.f. = 9, $P = 0.08$) and observed heterozygosity ($t = -1.81$, d.f. = 9, $P = 0.10$).

In the domesticated population, red and black were slightly, but significantly differentiated from each other (AMOVA $F_{ST} = 0.041$, $P = 0.00079$), but there was no evidence of differentiation between morphs in the wild in either the reduced data set (AMOVA $F_{ST} = -0.0038$, $P = 1$) or the full data set (AMOVA $F_{ST} = 0.0040$, $P = 0.31$). In the domesticated population, the clustering analysis indicated a $\Delta K_{max} = 2$, and LnP(D)_{max} was also $K = 2$ (Fig. 4a). There was slight but highly significant differentiation between the wild and domesticated populations ($F_{ST} = 0.016$, $P = 0.0015$). The clustering

analyses including the wild and domesticated populations indicated that $\Delta K_{max} = 2$ $\text{LnP(D)}_{max} = 4$. We compared the Q-plots for $K = 4$ (Fig. S5) and $K = 2$ (Fig. 4b), and it showed that the two additional clusters in $K = 4$ were restricted entirely to the domesticated population, which is consistent with hierarchical structure and with the result observed in Fig. 4a.

Discussion

The observed rate of extra-pair paternity in the Gouldian finch (22.8% of broods, 8.6% of offspring) is relatively low and less than the mean frequency found across socially monogamous bird species (11% of offspring; Griffith *et al.*, 2002). These estimates of extra-pair paternity are not different from those observed in another Australian Estrildid finch, the long-tailed finch (*Poephila acuticauda*) (12.8%) (Rooij *et al.*, 2016), but are different from the frequency observed in the zebra finch (*Taeniopygia guttata*) (2%) (Birkhead *et al.*, 1990; Griffith *et al.*, 2010). Intraspecific brood parasitism observed in the Gouldian finch is within the range observed in these same Estrildid finches (0.51–10% of offspring) (Appendix S3). In the wild population, females appeared not to be constrained by nesting synchrony or density in their ability to gain extra-pair paternity (Appendix S3), and some offspring were sired by extra-pair males breeding up to 4.2 km away which is within the normal daily movement previously observed in the Gouldian finch (Woinarski & Tidemann, 1992; K. Maute Pers Comm). This is in contrast to highly territorial bird species where distance to copulate and overall breeding synchrony can influence patterns of extra-pair paternity (e.g. Canal *et al.*, 2012; Garcia-Navas *et al.*, 2014).

We found little evidence to suggest that patterns of extra-pair paternity across Gouldian finch morph pairings were related to amelioration of genetic incompatibility, as predicted by work on domesticated birds (Pryke & Griffith, 2009b; Pryke *et al.*, 2010). Relatively small sample sizes, particularly of the key mixed-morph pairs, reduced the power of our tests. However, the biological effect size seen in earlier studies of

Table 3 Summary of genetic diversity indices using eight loci for red and black domesticated birds and a sample size-matched subset of the wild birds. N is the number of individuals in each category; N_{Ar} is the rarefied allelic richness; H_o is the observed heterozygosity \pm standard deviation; H_E is the expected heterozygosity \pm standard deviation; F_{IS} is the inbreeding coefficient, none of which were statistically significant.

Population	N	N_{Ar}	H_o	H_E	F_{IS}
Domesticated	48	9.75 (\pm 5.80)	0.72 (\pm 0.14)	0.75 (\pm 0.14)	0.04
Red	16	6.26 (\pm 3.78)	0.69 (\pm 0.15)	0.74 (\pm 0.13)	0.06
Black	32	7.50 (\pm 4.10)	0.73 (\pm 0.14)	0.73 (\pm 0.16)	-0.01
Wild	48	11.86 (\pm 7.66)	0.75 (\pm 0.16)	0.77 (\pm 0.15)	0.01
Red	16	8.76 (\pm 5.43)	0.74 (\pm 0.20)	0.74 (\pm 0.20)	0.01
Black	32	8.60 (\pm 4.91)	0.75 (\pm 0.14)	0.77 (\pm 0.16)	0.01

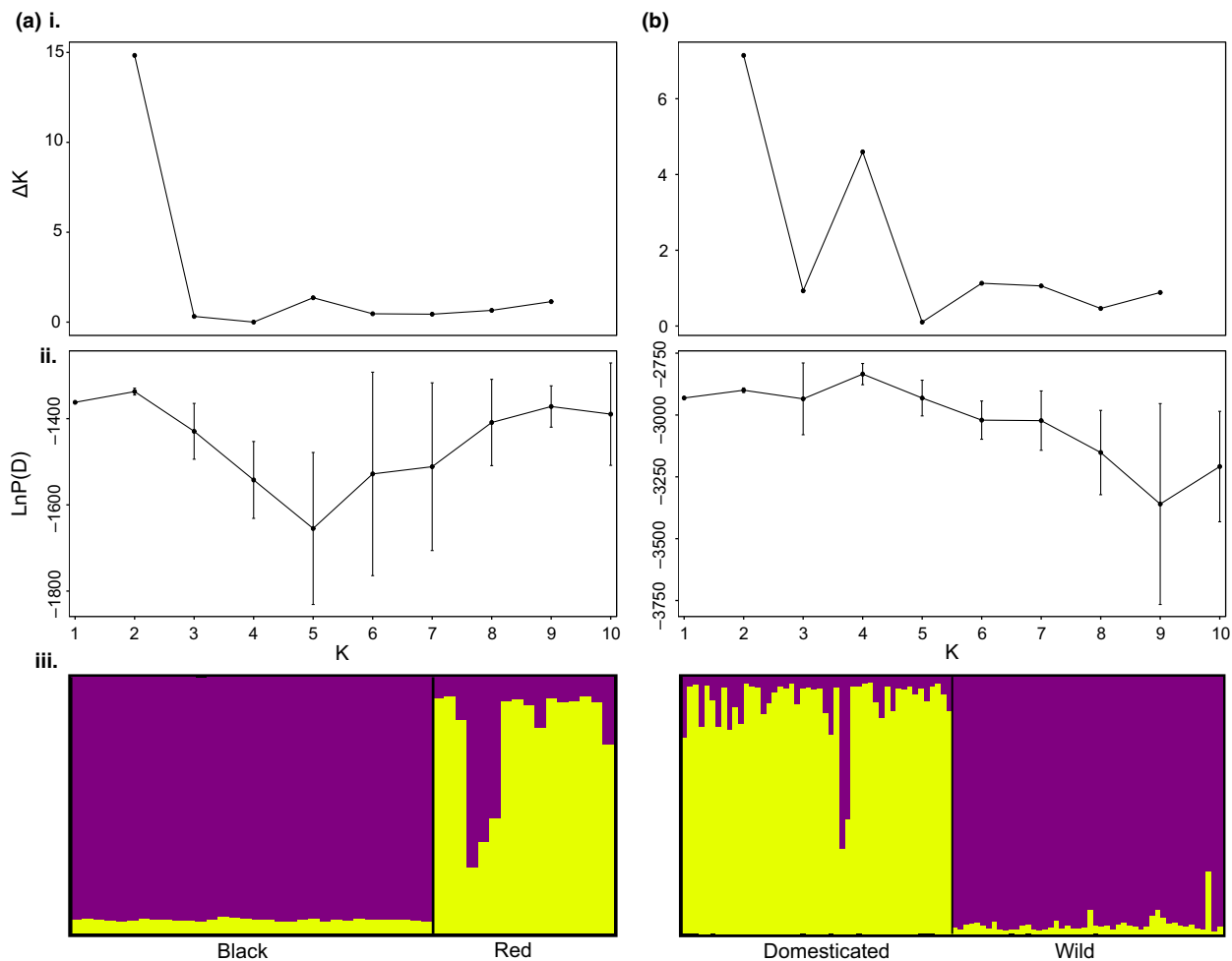


Fig. 4 Results of Bayesian genetic clustering analyses using STRUCTURE. (a) Analysis including domesticated red and black birds: (i) ΔK plot of the most likely number of genetic clusters in the sample where $\Delta K_{\max} = 2$, (ii) log posterior probabilities ($\ln P(D)$) for the number of clusters in the data set, where $K = 2$ is the most likely cluster; (iii) Q-plot for $K = 2$. (b) Analysis including domesticated and wild birds: (i) ΔK plot showing the most likely number of clusters is 2 (ΔK_{\max}), (ii) log posterior probabilities ($\ln P(D)$) for the number of clusters in the data set, where $K = 4$ is the most likely cluster; (iii) Q-plot for $K = 2$, showing distinct clusters for captive and wild populations. Q-plot for $K = 4$ is shown in Fig. S5.

domesticated birds was very strong and such a strong effect should have been apparent even with our sample size. Further, to achieve a sample size necessary to test the effect sizes observed in this study, we would have to sample approximately 20% of the adult population, which is estimated to be 2500 individuals (Garnett *et al.*, 2011). Across pairing types in the wild, we consistently observed fewer incidences of extra-pair paternity and an equivalent number of extra-pair offspring to domesticated females in pure pairs. Furthermore, there was no evidence of bias in the head colour of extra-pair or within-pair offspring despite the prediction that paternity would be biased towards compatible males and show a reduction in heterozygous red offspring. Another prediction for

incompatibility based on the domesticated population was that there would be a male bias in the brood sex ratio produced by females in mixed-morph pairs, given sex allocation and stronger female-specific mortality costs of genetic incompatibility (Pryke & Griffith, 2009a,b). However, we found there was no significant difference in day 14 offspring sex ratio between pairing types. Together with previous observations of no difference in offspring survival in the wild, we suggest that the genetic incompatibility previously observed in the domesticated population is weaker, or absent, in the wild (Pryke & Griffith, 2009b; Brazill-Boast *et al.*, 2013a).

In further contrast with findings in the domesticated birds, we found no evidence of assortative mating by

head colour morph. This contrasts with an earlier report of assortative mating in a population at Mornington, in the central Kimberley, WA (~ 300 km away) (Pryke & Griffith, 2007). However, in their study, Pryke & Griffith (2007) did not survey a wider sample of adults to sample the total pool of possible mates as we have done in this study. In addition, pairs in the earlier study were possibly pseudo-replicated (only 12 of 59 adults were uniquely identified by bands), as it was assumed that each water hole (where families were identified) had a unique complement of individuals (Pryke & Griffith, 2007). We know now from our subsequent work at Wyndham that the same individuals (identified uniquely by leg bands) will be sighted at different waterholes on different days (JBB, SCG Pers Obs), and the mobility of adults is also supported by the distance over which extra-pair paternity is gained. However, observed patterns of mating in the wild may not represent true mate preferences. For example, the choice of social partners may be constrained by inherent competitive interactions between head colour morphs, as seen in white-throated sparrows (Houtman & Falls, 1994). Competitive interactions are likely relevant to Gouldian finch mate choice, because Brazill-Boast *et al.* (2013a) found that red-headed males secured the best quality nesting cavities – an important and limited resource (Brazill-Boast *et al.*, 2010, 2011). Indeed, female pied flycatchers (*Ficedula hypoleuca*) choose partner according to resource quality (Alatalo *et al.*, 1986), so female Gouldian finches might choose partners on resource quality, or trade-off between head colour and resource quality. Even if there are constraints on the 'ideal' mate choice, these constraints should be alleviated or completely removed by selection if the cost of mating with a suboptimal partner is high enough (Brooks & Griffith, 2010). Our results suggest that mating with a partner of a different head colour in the wild may not be as costly to reproductive success as in the domesticated population (Pryke & Griffith, 2009b).

In the wild, the selection on head colour polymorphism and mate choice may be different from domesticated birds. This has been demonstrated in other systems, such as the colour polymorphic painted dragon (*Ctenophorus pictus*). Under experimental conditions, colour morphs exhibited alternative reproductive strategies, but these were not realized in the wild due to the constraints of habitat structure (Olsson *et al.*, 2007). In the zebra finch, the frequency of extra-pair paternity was significantly higher in multiple domesticated birds than in wild populations (Griffith *et al.*, 2010; Forstmeier *et al.*, 2011). Furthermore, wild female zebra finches show different mate choice preferences to their domesticated counterparts (Rutstein *et al.*, 2007). Therefore, these differences in polyandry and mating patterns in the Gouldian finch may be the result of the domestication process itself or may reflect the more complex factors faced in the wild that were removed from the

experiment, such as a constraint on extra-pair copulation through mate guarding (Komdeur *et al.*, 1999; Pryke *et al.*, 2010). We have presented results from the experiments on domesticated birds as a guide to the effect size expected between mixed- and same-morph pairs in the wild, but we fully appreciate that differences in experimental design make these studies difficult to compare directly. Therefore, although we cannot conclude unequivocally that there was no difference in incompatibility amelioration strategies between pairing types, we can conclude the effect was not as strong as observed in the domesticated birds.

The final key prediction is that incompatibility will be associated with a restriction of gene flow between the morphs. Accordingly, we find evidence of genetic differentiation between morphs in captivity, where the effects of incompatibility have been demonstrated (Pryke & Griffith, 2009b). In contrast, previous work found there was no evidence of genetic differentiation between morphs in the wild (Kim, 2011), which further strengthens the evidence for weak or absent incompatibility derived from the paternity and sex allocation data. Although we took steps to minimize the inclusion of highly related individuals, the presence of family groups may overestimate population structure (Rodríguez-Ramilo & Wang, 2012). Indeed, we found some evidence that there was substructuring beyond head colour morphs in our STRUCTURE analysis, which may represent family lineages from the original captive sources. Although the prediction is that incompatibility will be associated with genetic differentiation, the differentiation observed here is probably not caused by incompatibility, *per se*. It is more likely that the incompatibility arose due to differentiation between morphs, in small and isolated domesticated populations. Indeed, Gouldian finch breeders are often interested in establishing exaggerated traits for competitive avicultural shows, and their general management practices include the maintenance of same-morph red and black families to enhance plumage colour traits (Evans & Fidler, 2005; Hoffman *et al.*, 2014). If domesticated Gouldian finch morphs have consistently bred separately, then there is potential to exaggerate morph-specific traits and the associated agonistic interactions (Rice & Holland, 1997; Hesketh *et al.*, 2013; Pennell & Morrow, 2013). Experiments on *Drosophila* have shown that when females are not allowed to co-evolve with male sexual strategies, subsequent female generations will rapidly experience reduced fitness in response to matings (Rice, 1996). This, in combination with artificial selection, and perhaps bottlenecks, may generate the conditions necessary to establish incompatibilities between head colour morphs. Our analyses of microsatellite variation demonstrated some of the expected genetic differences between the populations of domesticated and wild Gouldian finches. We found that there was a significant reduction in allelic richness (but

not heterozygosity) in the domesticated population, which is expected to accompany a reduction in effective population size. Bottlenecks and artificial selection that accompany domestication can have profound effects on the genome (e.g. Montague *et al.*, 2014) and can alter genetic variation and the strength and direction of trait correlations (Bryant & Meffert, 1988; Haudry *et al.*, 2007). Therefore, we propose that the population history of the domesticated Gouldian finch may have driven the genetic incompatibility observed in the earlier studies (although this remains to be further examined in detail).

Our evidence from patterns of extra-pair paternity, sex ratio allocation, assortative mating and population structure in the wild is inconsistent with predictions about intermorph incompatibility that was observed in domesticated Gouldian finches. The effects seen in the domesticated birds could be a unique result of the domestication process and/or stochastic processes that have resulted from breeding small populations. If this is the case, the domesticated Gouldian finch provides an opportunity to investigate the emergence of genetic incompatibilities and sexual and intermorph conflict. The time is ripe to investigate these questions, as the rapid influx of genomic resources is allowing us to detect signatures of selection and genetic conflict in all manner of organisms (Parsch & Ellegren, 2013). Genomic comparison of the head colour polymorphism in both wild and captive birds will yield insights into the role of sex chromosomes in genetic conflict and speciation (Qvarnström & Bailey, 2009). Thus, comparisons between domesticated and wild Gouldian finches may provide an interesting future model into the evolution of colour polymorphism and genetic incompatibilities.

Acknowledgments

We thank Gareth Davies, Jo Dessmann, Christophe Dufresnes, Rowena Hamer, Jan Lewis, Dhanya Pearce, Sarah Pryke, Marjolein Schoe, Nina Svedin and Erica van Rooij, and Hanneke Wiggers for assistance in the field; Drew Allen, Duy Nguyen, Daisy Duursma and Camille Duval for computational and analytical help; and Lori Hurley for help in estimating male and female fertile periods. The work was supported by an Australian Research Council Grant to SCG and LAR (DP130100418); a Macquarie University Research Excellence Scholarship to JB-B; an Australian Postgraduate Award to PB; and logistic and financial support from the Save the Gouldian Fund.

References

Alatalo, R.V., Lundberg, A. & Glynn, C. 1986. Female pied flycatchers choose territory quality not male characteristics. *Nature* **323**: 152–153.
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.
Bolton, P.E., Rollins, L.A. & Griffith, S.C. 2015. The danger within: the role of genetic, behavioural, and ecological factors in population persistence of colour polymorphic species. *Mol. Ecol.* **24**: 2907–2915.
Bolund, E., Schielzeth, H. & Forstmeier, W. 2009. Compensatory investment in zebra finches: females lay larger eggs when paired to sexually unattractive males. *Proc. R. Soc. Lond. B Biol. Sci.* **276**: 707–715.
Bowers, E.K., Munclinger, P., Bureš, S., Kučerová, L., Nádvorník, P. & Krist, M. 2013. Cross-fostering eggs reveals that female collared flycatchers adjust clutch sex ratios according to parental ability to invest in offspring. *Mol. Ecol.* **22**: 215–228.
Brazill-Boast, J., Pryke, S.R. & Griffith, S.C. 2010. Nest-site utilisation and niche overlap in two sympatric, cavity-nesting finches. *Emu* **110**: 170–177.
Brazill-Boast, J., Dessmann, J.K., Davies, G.T.O., Pryke, S.R. & Griffith, S.C. 2011. Selection of breeding habitat by the endangered Gouldian Finch (*Erythrura gouldiae*) at two spatial scales. *Emu* **111**: 304–311.
Brazill-Boast, J., Griffith, S.C. & Pryke, S.R. 2013a. Morph-dependent resource acquisition and fitness in a polymorphic bird. *Evol. Ecol.* **27**: 1189–1198.
Brazill-Boast, J., Pryke, S.R. & Griffith, S.C. 2013b. Provisioning habitat with custom-designed nest-boxes increases reproductive success in an endangered finch. *Austral Ecol.* **38**: 405–412.
Brooks, R.C. & Griffith, S.C. 2010. Mate choice. In: *Evolutionary Behavioural Ecology* (D.F. Westneat & C. Fox, eds), pp. 416–433. Oxford University Press, Oxford.
Bryant, E.H. & Meffert, L.M. 1988. Effect of an experimental bottleneck on morphological integration in the housefly. *Evolution* **42**: 698–707.
Burley, N.T. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* **127**: 415–445.
Burley, N.T. 1988. The differential-allocation hypothesis: an experimental test. *Am. Nat.* **132**: 611–628.
Burns, J.G., Saravanan, A. & Helen Rodd, F. 2009. Rearing environment affects the brain size of guppies: lab-reared guppies have smaller brains than wild-caught guppies. *Ethology* **115**: 122–133.
Canal, D., Jovani, R. & Potti, J. 2012. Male decisions or female accessibility? Spatiotemporal patterns of extra pair paternity in a songbird. *Behav. Ecol.* **23**: 1146–1153.
Champely, S. 2015. pwr: Basic Functions for Power Analysis.
Christie, M.R., Marine, M.L., French, R.A. & Blouin, M.S. 2012. Genetic adaptation to captivity can occur in a single generation. *Proc. Natl. Acad. Sci. USA* **109**: 238–242.
Earl, D.A. & VonHoldt, B.M. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv. Genet. Resour.* **4**: 359–361.
Engels, B. 2015. XNomial: Exact Goodness-of-Fit Test for Multinomial Data with Fixed Probabilities.
Environment Protection and Biodiversity Conservation Act 1999 (Cth) s 13.
Evanno, G., Regnaut, S. & Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUC-TURE: a simulation study. *Mol. Ecol.* **14**: 2611–2620.
Evans, S. & Fidler, M. 2005. *The Gouldian Finch*. Indruss Productions, Brisbane, Qld, Australia.

- Excoffier, L.G. & Lischer, H.E.L. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetic analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**: 564–567.
- Forstmeier, W., Martin, K., Bolund, E., Schielzeth, H. & Kempenaers, B. 2011. Female extrapair mating behavior can evolve via indirect selection on males. *Proc. Natl. Acad. Sci. USA* **108**: 10608–10613.
- Fox, S., Brooks, R., Lewis, M.J. & Johnson, C.N. 2002. Polymorphism, mate choice and sexual selection in the Gouldian Finch (*Erythrura gouldiae*). *Aust. J. Zool.* **50**: 125–135.
- Franklin, D.C. & Dostine, P.L. 2000. A note on the frequency and genetics of head colour morphs in the Gouldian finch. *Emu* **100**: 236–239.
- Fridolfsson, A.-K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **20**: 116–121.
- García-Navas, V., Ferrer, E.S., Bueno-Enciso, J., Barrientos, R., Sanz, J.J. & Ortego, J. 2014. Extrapair paternity in Mediterranean blue tits: socioecological factors and the opportunity for sexual selection. *Behav. Ecol.* **25**: 228–238.
- Garnett, S.T., Szabo, J.K. & Dutton, G. 2011. *The Action Plan for Australian Birds 2010*. CSIRO Publishing, Collingwood, Vic.
- Gilby, A.J., Pryke, S.R. & Griffith, S.C. 2009. The historical frequency of head-colour morphs in the Gouldian Finch (*Erythrura gouldiae*). *Emu* **109**: 222–229.
- Gorman, H.E., Arnold, K.E. & Nager, R.G. 2005. Incubation effort in relation to male attractiveness in zebra finches *Taeniopygia guttata*. *J. Avian Biol.* **36**: 413–420.
- Goudet, J. 1995. FSTAT: a computer program to calculate F-statistics. *J. Hered.* **86**: 485–486.
- Griffith, S.C. 2010. The role of multiple mating and extra-pair paternity in creating and reinforcing boundaries between species in birds. *Emu* **110**: 1–9.
- Griffith, S.C., Owens, I.P. & Thuman, K.A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**: 2195–2212.
- Griffith, S.C., Lyon, B.E. & Montgomerie, R. 2004. Quasi-parasitism in birds. *Behav. Ecol. Sociobiol.* **56**: 191–200.
- Griffith, S.C., Holleley, C.E., Mariette, M.M., Pryke, S.R. & Svedin, N. 2010. Low level of extrapair parentage in wild zebra finches. *Anim. Behav.* **79**: 261–264.
- Griffith, S.C., Pryke, S.R. & Buttemer, W.A. 2011. Constrained mate choice in social monogamy and the stress of having an unattractive partner. *Proc. R. Soc. Lond. B Biol. Sci.* **278**: 2798–2805.
- Haudry, A., Cenci, A., Ravel, C., Bataillon, T., Brunel, D., Poncet, C. *et al.* 2007. Grinding up wheat: a massive loss of nucleotide diversity since domestication. *Mol. Biol. Evol.* **24**: 1506–1517.
- Healey, M., Uller, T. & Olsson, M. 2007. Seeing red: morph-specific contest success and survival rates in a colour-polymorphic agamid lizard. *Anim. Behav.* **74**: 337–341.
- Hesketh, J., Fowler, K. & Reuter, M. 2013. Genetic drift in antagonistic genes leads to divergence in sex-specific fitness between experimental populations of *Drosophila melanogaster*. *Evolution* **67**: 1503–1510.
- Hoffman, J.I., Krause, E.T., Lehmann, K. & Krüger, O. 2014. MC1R genotype and plumage colouration in the zebra finch (*Taeniopygia guttata*): population structure generates artefactual associations. *PLoS ONE* **9**: e86519.
- Horton, B.M., Hu, Y., Martin, C.L., Bunke, B.P., Matthews, B.S., Moore, I.T. *et al.* 2013. Behavioral characterization of a white-throated sparrow homozygous for the ZAL2(m) chromosomal rearrangement. *Behav. Genet.* **43**: 60–70.
- Houtman, A.M. & Falls, J.B. 1994. Negative assortative mating in the white-throated sparrow, *Zonotrichia albicollis*: the role of mate choice and intra-sexual competition. *Anim. Behav.* **48**: 377–383.
- Hubisz, M.J., Falush, D., Stephens, M. & Pritchard, J.K. 2009. Inferring weak population structure with the assistance of sample group information. *Mol. Ecol. Resour.* **9**: 1322–1332.
- Jakobsson, M. & Rosenberg, N.A. 2007. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics* **23**: 1801–1806.
- Kim, K. 2011. The molecular genetic basis of a plumage colour polymorphism in the Gouldian finch (*Erythrura gouldiae*). University of Sheffield: PhD Thesis.
- Kokko, H., Griffith, S.C. & Pryke, S.R. 2014. The hawk – dove game in a sexually reproducing species explains a colourful polymorphism of an endangered bird. *Proc. R. Soc. Lond. B Biol. Sci.* **281**: 20141794.
- Komdeur, J., Kraaijeveld-Smit, F., Kraaijeveld, K. & Edelaar, P. 1999. Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. *Proc. R. Soc. Lond. B Biol. Sci.* **266**: 2075.
- Lemons, P.R., Marshall, T.C., McCloskey, S.E., Sethi, S.A., Schmutz, J.A. & Sedinger, J.S. 2014. A likelihood-based approach for assessment of extra-pair paternity and conspecific brood parasitism in natural populations. *Mol. Ecol. Resour.* **15**: 107–116.
- Marshall, T.C., Slate, J., Kruuk, L.E.B. & Pemberton, J.M. 1998. Statistical confidence for likelihood-based paternity. *Mol. Ecol.* **7**: 639–655.
- McKinnon, J.S. & Pierotti, M.E.R. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Mol. Ecol.* **19**: 5101–5125.
- Montague, M.J., Li, G., Gandolfi, B., Khan, R., Aken, B.L., Searle, S.M.J. *et al.* 2014. Comparative analysis of the domestic cat genome reveals genetic signatures underlying feline biology and domestication. *Proc. Natl. Acad. Sci. USA* **111**: 17230–17235.
- Olsson, M., Healey, M., Wapstra, E., Schwartz, T., Lebas, N. & Uller, T. 2007. Mating system variation and morph fluctuations in a polymorphic lizard. *Mol. Ecol.* **16**: 5307–5315.
- Parsch, J. & Ellegren, H. 2013. The evolutionary causes and consequences of sex-biased gene expression. *Nat. Rev. Genet.* **14**: 83–87.
- Pennell, T.M. & Morrow, E.H. 2013. Two sexes, one genome: the evolutionary dynamics of intralocus sexual conflict. *Ecol. Evol.* **3**: 1819–1834.
- Presgraves, D.C. 2010. Darwin and the origin of interspecific genetic incompatibilities. *Am. Nat.* **176**(Suppl): S45–S60.
- Pritchard, J.K., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**: 945–959.
- Pryke, S.R. 2010. Sex chromosome linkage of mate preference and color signal maintains assortative mating between interbreeding finch morphs. *Evolution* **64**: 1301–1310.
- Pryke, S.R. & Griffith, S.C. 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc. R. Soc. Lond. B Biol. Sci.* **273**: 949–957.

- Pryke, S.R. & Griffith, S.C. 2007. The relative role of male vs. female mate choice in maintaining assortative pairing among discrete colour morphs. *J. Evol. Biol.* **20**: 1512–1521.
- Pryke, S.R. & Griffith, S.C. 2009a. Genetic incompatibility drives sex allocation and maternal investment in a polymorphic finch. *Science* **323**: 1605–1607.
- Pryke, S.R. & Griffith, S.C. 2009b. Postzygotic genetic incompatibility between sympatric color morphs. *Evolution* **63**: 793–798.
- Pryke, S.R. & Griffith, S.C. 2010. Maternal adjustment of parental effort in relation to mate compatibility affects offspring development. *Behav. Ecol.* **21**: 226–232.
- Pryke, S.R., Astheimer, L.B., Buttemer, W.A. & Griffith, S.C. 2007. Frequency-dependent physiological trade-offs between competing colour morphs. *Biol. Lett.* **3**: 494–497.
- Pryke, S.R., Rollins, L.A. & Griffith, S.C. 2010. Females use multiple mating and genetically loaded sperm competition to target compatible genes. *Science* **329**: 964–967.
- Qvarnström, A. & Bailey, R.I. 2009. Speciation through evolution of sex-linked genes. *Heredity* **102**: 4–15.
- Raymond, M. & Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J. Hered.* **86**: 248–249.
- Rice, W.R. 1996. Sexually antagonistic adaptation triggered by experimental arrest of female evolution. *Nature* **381**: 232–234.
- Rice, W.R. & Holland, B. 1997. The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behav. Ecol. Sociobiol.* **41**: 1–10.
- Rodríguez-Ramilo, S.T. & Wang, J. 2012. The effect of close relatives on unsupervised Bayesian clustering algorithms in population genetic structure analysis. *Mol. Ecol. Resour.* **12**: 873–884.
- Rooij, E.P.Van., Rollins, L.A., Holleley, C.E. & Griffith, S.C. 2016. Extra-pair paternity in the long-tailed finch *Poephila acuticauda*. *PeerJ* **4**: e1550.
- Rosenberg, N.A. 2004. DISTRUCT: a program for the graphical display of population structure. *Mol. Ecol. Notes* **4**: 137–138.
- Roulin, A. & Bize, P. 2006. Sexual selection in genetic colour-polymorphic species: a review of experimental studies and perspectives. *J. Ethol.* **25**: 99–105.
- Roulin, A., Altwegg, R., Jensen, H., Steinsland, I. & Schaub, M. 2010. Sex-dependent selection on an autosomal melanistic female ornament promotes the evolution of sex ratio bias. *Ecol. Lett.* **13**: 616–626.
- Rutstein, A.N., Gilbert, L., Slater, P.J.B. & Graves, J.A. 2004. Mate attractiveness and primary resource allocation in the zebra finch. *Anim. Behav.* **68**: 1087–1094.
- Rutstein, A.N., Brazill-Boast, J. & Griffith, S.C. 2007. Evaluating mate choice in the zebra finch. *Anim. Behav.* **74**: 1277–1284.
- Seehausen, O., Butlin, R.K., Keller, I., Wagner, C.E., Boughman, J.W., Hohenlohe, P.A. et al. 2014. Genomics and the origin of species. *Nat. Rev. Genet.* **15**: 176–192.
- Sinervo, B. & Svensson, E. 2002. Correlational selection and the evolution of genomic architecture. *Heredity* **89**: 329–338.
- Southern, H.N. 1945. Polymorphism in *Poephila gouldiae* Gould. *J. Genet.* **47**: 51–57.
- Szulkin, M., Stopher, K.V., Pemberton, J.M. & Reid, J.M. 2013. Inbreeding avoidance, tolerance, or preference in animals? *Trends Ecol. Evol.* **28**: 205–211.
- Templeton, J.J., Mountjoy, D.J., Pryke, S.R. & Griffith, S.C. 2012. In the eye of the beholder: visual mate choice lateralization in a polymorphic songbird. *Biol. Lett.* **8**: 924–927.
- Thornycroft, H. 1966. Chromosomal polymorphism in the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). *Science* **154**: 1571–1572.
- Tregenza, T. & Wedell, N. 2000. Genetic compatibility, mate choice and patterns of parentage. *Mol. Ecol.* **9**: 1013–1027.
- Trivers, R. & Willard, D. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**: 90–92.
- Tuttle, E.M. 2003. Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behav. Ecol.* **14**: 425–432.
- Veen, T., Borge, T., Griffith, S.C., Sætre, G., Bures, S., Gustafsson, L. et al. 2001. Hybridization and adaptive mate choice in flycatchers. *Nature* **411**: 45–50.
- Woinarski, J.C.Z. & Tidemann, S. 1992. Survivorship and some population parameters for the endangered Gouldian Finch *Erythrura gouldiae* and two other finch species at two Sites in tropical northern Australia. *Emu* **92**: 33–38.

Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Sampling of families at Wyndham

Table S1 Sample sizes for breeding used in this study, where a) describes the overall breeding dataset, and b) describes the sample of nests for which parents and 14 day old offspring were sampled

Appendix S2 Laboratory methods and genetic analyses

Table S2 Primers and multiplexes used in this study

Table S3 Characteristics for each locus used in this study, as calculated for all adults and nestlings in those years

Table S4 Diversity of microsatellite loci used for population genetic analysis in the 48 samples in domesticated and 245 wild samples: (a) red and black morphs in the domesticated sample (b), and red and black morphs in the wild sample (c)

Table S5 Results from linkage disequilibrium analysis conducted in GenePop, for 244 wild (a) and 48 domesticated sample (b)

Appendix S3 Determinants of Extra-Pair Paternity & Intra-specific brood parasitism

Table S6 Results from generalized linear models exploring the relationship between measures of nesting synchrony and density on the rates of extra-pair paternity

Figure S1 Plot showing the observed proportion of extra-pair offspring per nest according to the day initiated in the season

Figure S2 Percent of families with at least one instance of intra-specific brood parasitism according to pairing type, where bar colours represent male morph

Figure S3 Boxplot showing the median and mean percent of clutch that is the result of intra-specific brood parasitism in mixed and pure pairing types

Figure S4 Frequency of genotypes resulting from intra-specific brood parasitism (IBP), where panes represent the morph of the social father of the parasitised nest

Appendix S4 Offspring morph

Appendix S5 Supplementary results for Population

Genetics and Incompatibility

Figure S5 Q-Plot from STRUCTURE analysis for domesticated and wild comparison at $K = 4$

Data deposited at Dryad: doi: 10.5061/dryad.2m2r2

Received 13 July 2016; accepted 16 October 2016