Genetic Incompatibility Drives Sex Allocation and Maternal Investment in a Polymorphic Finch

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Genetic compatibility may drive individual mate choice decisions because of predictable fitness effects associated with breeding with incompatible partners. In Gouldian finches (*Erythrura gouldiae*), females paired with genetically incompatible males of alternative color morphs overproduce sons, presumably to reduce investment in inviable daughters. We also observed a reduced overall investment in clutch size, egg size, and care to offspring resulting from incompatible matings. Within-female experimental pairings demonstrate that female birds have the ability to adaptively adjust the sex of their eggs and allocate resources on the basis of partner quality. Female Gouldian finches thus make cumulative strategic allocation decisions to minimize the costs of poor-quality pairings when faced with a genetically incompatible partner.

Life-history theory predicts that females may alter reproductive investment in a particular breeding attempt according to the quality of their partner (*1, 2*). When breeding with high-quality males is constrained, females may potentially accept incompatible mates but strategically alter their relative investment in sons and daughters to enhance the viability of their current offspring (*1*) or trade off maternal investment in lieu of future reproductive opportunities with higher quality partners (*3*). However, there is limited empirical support for adaptive maternal investment in relation to mate quality. Despite reports of sex ratio adjustment by female birds in relation to partner attractiveness (*3, 4*), differential sex allocation as an adaptive postcopulatory mechanism in birds remains controversial (*5–7*). Similarly, support for differential allocation of resources by females depending on whether they are paired with high- or low-quality mates is scarce (*8–11*). These studies have also typically demonstrated relatively weak effects related to a single maternal variable (*8–11*) rather than more cumulative allocations by females, which would be expected to have greater biological importance.

The inconsistent and limited empirical support for adaptive maternal investment in vertebrates may have resulted from analyses of individual allocation decisions in the absence of theoretical frameworks (*12, 13*) and in contexts or systems where parents are unable to precisely predict the net fitness gains from strategic adjustments. Most studies, for example, have focused on maternal allocation in the context of continuously variable male traits, such as color, environmental, or social factors, which may be quantitatively difficult for females to assess and from which the potential fitness benefits are often complex, unpredictable,

and relatively weak. Theoretically, it is perhaps unrealistic to expect females to make significant responses on the basis of such variables (*6*). Indeed, most avian studies of maternal investment (*4, 8, 10*) have been unable to convincingly demonstrate or even predict the adaptive value to females of differential investment (*12, 13*).

We investigated adaptive maternal investment in the Gouldian finch (*Erythrura gouldiae*), a color polymorphic bird in which we can make a priori predictions with respect to anticipated responses because of predictable sex-specific fitness effects associated with matings between genetically incompatible partners (*14*). Mate quality is signaled through head color, which is either black (70% of individuals) or red (30%)

and is determined by a Z-linked gene; red (Z^R) is dominant to black (Z^r) (*15*). Because of the sex determination system of birds, females are homozygous for this gene, and thus phenotype matches genotype (Z^r black, Z^R red), whereas male genotypes can be homozygous Z^rZ^r (black), Z^RZ^R (red) or heterozygous Z^RZ^r (red). Heterozygous and homozygous red males are phenotypically indistinguishable (*15*). Individuals discriminate between black and red mates and demonstrate precopulatory mate preferences for their own morph type (*16*). However, up to 30% of breeding pairs in wild populations are mixed (intermorph), perhaps because of constraints on preferred mate availability in this socially monogamous species (*16*). Precopulatory mate choice is probably adaptive because postzygotic genetic incompatibilities between red and black birds (i.e., different genotypes) forced to breed in captivity results in high offspring mortality (*14*). In particular, throughout offspring development (i.e., from egg to sexual maturity, 160 days), genetically incompatible pairs have 40.2% greater mortality of sons and 83.8% greater mortality of daughters than broods produced from genetically compatible pairs (*14*). Given that females can assess the phenotype of males and that mixed-morph pairing results in fitness costs, we predict that females unable to pair preferentially with genetically compatible mates should differentially adjust their relative breeding investment accordingly.

We randomly paired 200 females (100 black, 100 red) to either a black or red male (of known morph genotype) in a visually isolated cage (*17*). To control for genetic versus parentally derived environmental effects (*18*), we conducted cross-fostering experiments involving permanent recip-
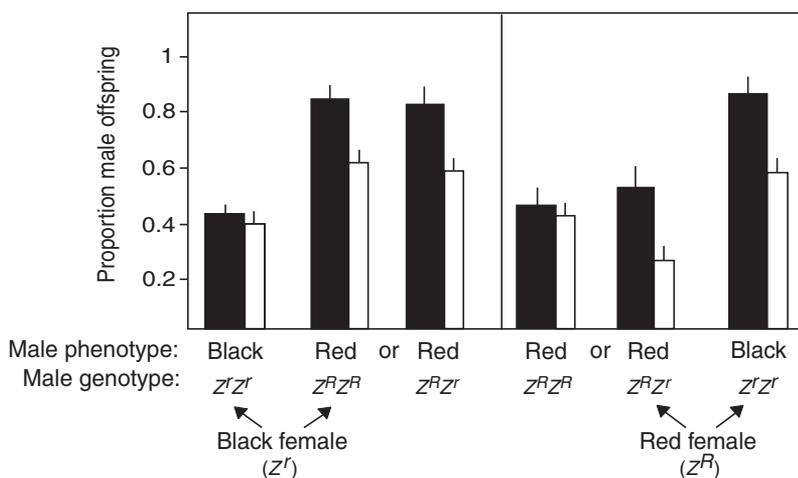
Fig. 1. Mean (±SEM) proportion of male offspring (laying to hatching) for each nest produced from within-female crosses between same (matched) and different (mixed) male morphs. Individual females given a male of a different genotype had offspring with a male-biased sex ratio (solid black bars). Even if we assume that all infertile eggs (of unknown sex) were female, a male-biased sex ratio remains (open bars). Although offspring from red females paired to heterozygous red males (i.e., genetically incompatible) suffered similar mortality rates as offspring from red-black pairings (*14*), in contrast to other incompatible mixed-morph pairs, red females in these matched pair crosses produced only a slight initial male bias (56%); if we assumed large differential female mortality in infertile eggs, these females would be predicted to produce very few male offspring.

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rocal translocation of whole broods (hatching day 1 to 2) within and between the different treatments. Once offspring reached independence (60 days), the male and offspring were removed, and 18 days later [to discount the possibility of stored sperm (19)] the female was paired with a random male of the alternate morph. Each female thus bred twice, once with a male of her own morph (matched pair) and once with a different morph (mixed pair); all reported results reflect this within-female breeding design.

Because daughters are particularly susceptible to genetic viability effects from an incompatible partner genome (14), as expected (20, 21), females in mixed pairs produced broods with male-biased primary sex ratios [82.1% males; generalized linear mixed model (GLMM), $\chi_1^2 = 14.26$, $P < 0.001$; $N = 324$ families, 1473 nestlings, and 27 dead embryos], whereas females in matched pairs produced an unbiased sex ratio (45.9%

males; GLMM, $\chi_1^2 = 1.64$, $P = 0.21$; $N = 324$ families, 1473 nestlings, and 27 dead embryos) (Fig. 1). In 369 eggs (20% of all eggs produced), there were no visible signs of embryonic development (despite normal incubation), and we were unable to sex these eggs. However, even if we assume that all infertile eggs were female, we would still have observed a male-biased sex ratio in mixed-morph pairs (60.3% males; GLMM, $\chi_1^2 = 3.87$, $P = 0.04$; $N = 324$ families, 1473 nestlings, and 369 infertile eggs) (Fig. 1).

To determine whether females in mixed-morph pairs overproduce sons, independent of any intrinsic mortality effects resulting from genetically incompatible mates, we next experimentally blackened the head colors of red males before pairing them to red and black females and allowing them to breed (17). We found that black females paired to red males who were experimentally blackened (i.e., to resemble black

males) produced a sex ratio that did not differ significantly from equality (55% males; GLMM, $\chi_1^2 = 1.06$, $P = 0.30$; $N = 18$ families, 94 chicks) despite the incompatible (red) genotype. Interestingly, this brood sex ratio was similar to the ratio of male offspring produced (56%) when red females were mated to heterozygous (genetically incompatible) red males (Fig. 1). Red females paired to experimentally blackened red males produced significantly more males (72%; GLMM, $\chi_1^2 = 13.54$, $P < 0.001$; $N = 22$ broods, 71 chicks), despite having fully compatible genotypes. These results indicate that maternal effects are most likely driven by female allocation rather than by interactions between incompatible genomes or through male coercion (22). These results also contrast with the prediction that females should overproduce sons when paired with attractive partners (3, 4, 13, 20). Instead, females gain greater fitness benefits from overproducing sons when paired with a nonpreferred male morph because of the severe mortality effects on daughters in mixed-morph pairs.

Because of the fitness costs of breeding in mixed-morph pairs (14), we also examined the relative investment by females into reproduction. We found that individual females in mixed pairs produced significantly fewer eggs (3.39 ± 1.07) than when breeding in matched pairs [5.67 ± 0.89 eggs; repeated measures analysis of variance (RM-ANOVA), $F_{1,160} = 16.26$, $P < 0.001$, $r^2 = 43.3$, $N = 324$ clutches] (Fig. 2A). Females in mixed pairs also laid significantly smaller eggs (198.23 ± 14.12 mm³) than when breeding with the same morph type (227.04 ± 12.35 mm³; RM-ANOVA, $F_{1,159} = 14.10$, $P < 0.001$, $r^2 = 62.8$, $N = 324$ clutches) (Fig. 2B). Egg volume was unrelated to the sex of the resulting offspring (RM-ANOVA, $F_{1,160} = 0.62$, $P = 0.80$, $r^2 = 0.18$), indicating that differential egg investment was not simply due to a differential investment into sons or daughters (23). Egg size influences fitness in birds (24); in Gouldian finches, egg size was positively correlated with chick mass (measured 2 days after hatching; Pearson's correlation, $r = 0.82$, $P < 0.001$, $N = 1473$). Furthermore, after controlling for the differences in egg and brood size between matched and mixed pairs, we found that when chicks (from both mixed and matched pairs) were fostered to nests of matched pairs they grew faster than foster chicks in mixed nests (RM-ANOVA, $F_{1,158} = 7.15$, $P = 0.007$, $r^2 = 7.82$), irrespective of their genetic origin ($F_{1,158} = 0.81$, $P = 0.34$). The difference in chick mass between nests reared by foster parents of mixed and matched pairs (9.1%) appeared to be due to a per capita increase in maternal (but not paternal) provisioning to chicks in matched pairs (RM-ANOVA, female visit rate: $F_{1,159} = 87.13$, $P < 0.001$, $r^2 = 44.8$; male visit rate: $F_{1,159} = 0.04$, $P = 0.83$, $r^2 = 6.4$, $N = 324$ broods) (Fig. 2C). These effects were also apparent when males were color-manipulated; black females paired to blackened red males (i.e., genetically incompatible) significantly increased their investment into their
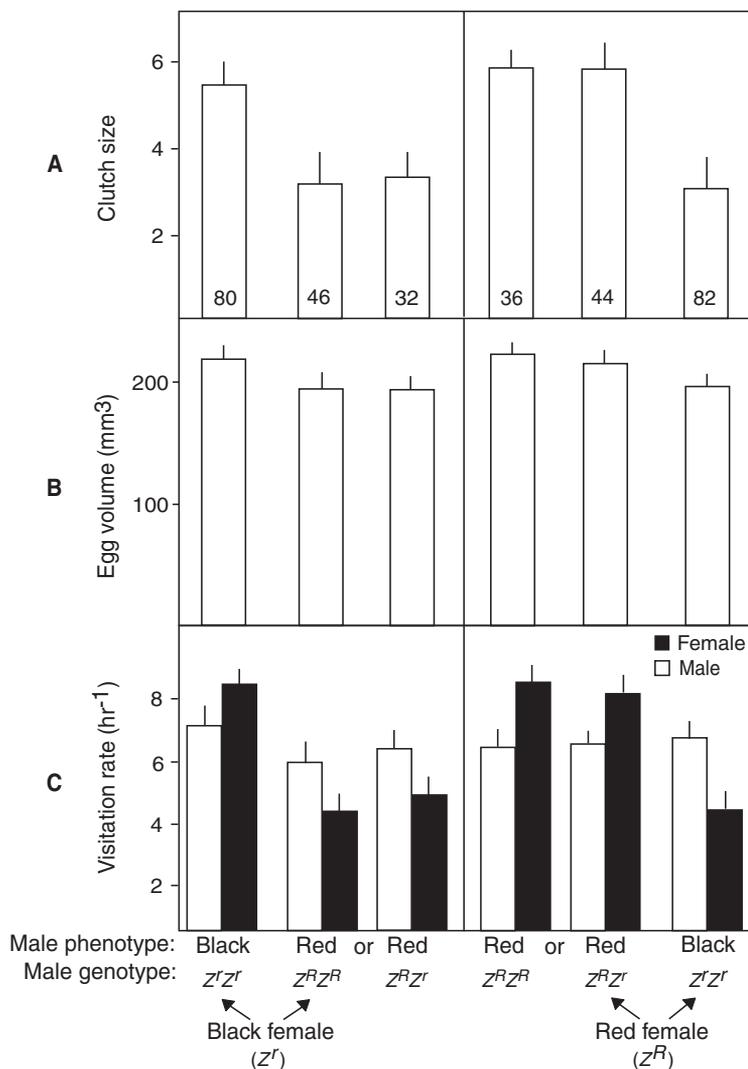
Fig. 2. Within-female differential investment when paired with the same (matched) and different (mixed) color morph. Females paired to a male of the same phenotype produced (**A**) 40.2% larger clutches, (**B**) 12.8% larger eggs, and (**C**) increased per capita provisioning of their offspring (46.1%) compared with when they were paired with a genetically incompatible male. The means ± SEM (error bars) are shown, and brood sample sizes are provided in the bars of (**A**).

brood relative to genetically incompatible mismatched (black-red) pairs (clutch: $t = 5.6$; egg size: $t = 6.8$; care: $t = 8.2$; df = 86, $P < 0.001$) and instead invested similarly to genetically compatible black pairs (clutch: $t = 1.2$; egg size: $t = 0.8$; care: $t = 0.5$; df = 94, $P > 0.15$). Similarly, red females paired to blackened red males (i.e., genetically compatible) significantly reduced their investment compared with matched red morph pairs (clutch: $t = 4.4$; egg size: $t = 5.7$; care: $t = 7.3$; df = 56, $P < 0.001$), in line with red females paired to genetically incompatible black males (clutch: $t = 0.9$; egg size: $t = 1.1$; care: $t = 0.7$; df = 102, $P > 0.18$).

By controlling for individual effects (i.e., within-female) and environmental effects (i.e., controlled cage environment), we demonstrated differences in maternal investment (offspring number, quality, and sex) in a system where the fitness benefits to females from skewed allocation are large (due to genetic incompatibility) and predictable (because head color is a reliable signal of genotype). By manipulating parameters pertinent to strategic maternal investment and by preventing active precopulatory mate choice (16) or the ability for females to engage in extra-pair copulations with a more compatible mate to counteract the costs of a genetically incompatible social mate (21), we exposed extreme postcopulatory strategies. This suggests that the extent to which females can control and manipulate important life-history components of fitness may have previously been underestimated.

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The Domestication Process and Domestication Rate in Rice: Spikelet Bases from the Lower Yangtze

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The process of rice domestication occurred in the Lower Yangtze region of Zhejiang, China, between 6900 and 6600 years ago. Archaeobotanical evidence from the site of Tianluoshan shows that the proportion of nonshattering domesticated rice (*Oryza sativa*) spikelet bases increased over this period from 27% to 39%. Over the same period, rice remains increased from 8% to 24% of all plant remains, which suggests an increased consumption relative to wild gathered foods. In addition, an assemblage of annual grasses, sedges, and other herbaceous plants indicates the presence of arable weeds, typical of cultivated rice, that also increased over this period.

The domestication of staple cereal crops represents the major economic and ecological transition that human societies made during the Holocene (1). A key change in domestication of cereals, resulting from cultivation, was the loss of natural seed dispersal, which led to domesticated cereals with dependence on humans (2, 3). Direct evidence for the evolution of this trait in wheat and barley in Southwest Asia suggests that this process was slower than earlier hypothesized (3–5). Rice has been less well documented, but archaeological finds of rice grains and phytoliths indicate that it was an early crop in the Lower and Middle Yangtze region of China (6, 7).

Tianluoshan is a Neolithic site of the local Hemudu Neolithic culture in Zhejiang Province, China (Fig. 1). Tianluoshan is 2 to 3 m above present-day sea level, with a high belowground water table that has preserved water-logged botanical remains in some contexts, along with charred remains throughout the site. Excavations between 2004 and 2007 revealed preserved wooden posts, boat paddles, wooden and bone tools, characteristic pottery and ground-stone axes, and animal and fish remains, as well as well-preserved plant remains (8). In total, 23,615 plant remains were identified from 24 systematically sieved samples, in addition to more than 12,000 hand-picked remains. More than 50 species were identified, mainly acorns (including *Lithocarpus* and *Cyclobalanopsis* types), *Trapa* water chestnuts, foxnuts (*Euryale ferox*), and rice. Probable storage pits retained acorns (*Quercus sensu lato* and *Lithocarpus*), water chestnuts (*Trapa natans sensu lato*), foxnuts, and several other edible fruit remains and seeds. One area of excavation (K3) had preserved distinct lenses of rice husks, acorn shells, *Trapa* shells, and persimmon seeds (*Diospyros* sp.).

Large quantities of rice spikelet bases, as well as a range of small seeds of wild species that may plausibly represent the arable weeds of rice cultivation, were recovered during the systematic sorting of sediment samples. Rice increased as a percentage of the total remains from sieved samples from 8% to 18% to 24% (Fig. 2). These phases were dated by direct accelerator mass spectrometry radiocarbon dates on nuts and rice grains (fig. S1) indicating a sequence for the plant samples between ~6900 and 6600 years ago, and divided into three periods (K3 midden, layers 8 and 7, and layers 6 and 5). These data suggest that rice increased in dietary importance through time. The increase in the proportion of rice supports the hypothesis that people became increasingly reliant on rice cultivation and gradually abandoned wild resources, such as acorns and *Trapa* water chestnuts.

Distinctions between wild and domestic rice are made through observations of the spikelet bases, which show key morphological differences (9–12), although in archaeological specimens this distinction can be complicated if immature specimens were harvested. We classified spikelet bases on the basis of a comparative study of spikelet bases in 140 modern populations (13). In domesticated rice, panicles are nonshattering, which allows most grains on the plant to reach maturity before being

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