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LETTERS

Reproductive skew and selection on female ornamentation in social species

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Male animals are typically more elaborately ornamented than females[1]. Classic sexual selection theory notes that because sperm are cheaper to produce than eggs[2], and because males generally compete more intensely for reproductive opportunities and invest less in parental care than females[3], males can obtain greater fitness benefits from mating multiply[2,4]. Therefore, sexual selection typically results in male-biased sex differences in secondary sexual characters[1,4]. This generality has recently been questioned, because in cooperatively breeding vertebrates, the strength of selection on traits used in intrasexual competition for access to mates (sexual selection[1,4]) or other resources linked to reproduction (social selection[5,6]) is similar in males and females[7,8]. Because selection is acting with comparable intensity in both sexes in cooperatively breeding species, the degree of sexual dimorphism in traits used in intrasexual competition should be reduced in cooperative breeders[6]. Here we use the socially diverse African starlings (Sturnidae) to demonstrate that the degree of sexual dimorphism in plumage and body size is reduced in cooperatively breeding species as a result of increased selection on females for traits that increase access to reproductive opportunities, other resources, or higher social status. In cooperative breeders such as these, where there is unequal sharing of reproduction (reproductive skew) among females, and where female dominance rank influences access to mates and other resources, intrasexual competition among females may be intense[7] and ultimately select for female trait elaboration[9]. Selection is thereby acting with different intensities on males and females in cooperatively versus non-cooperatively breeding species, and female–female interactions in group-living vertebrates will have important consequences for the evolution of female morphological, physiological and behavioural traits.

Recent challenges to the utility[10] and ubiquity[10] of Darwin's classic concept of sexual selection[1]—which emphasizes selection on elaborate traits in males—have been based on the recognition that similar selection may act on females. Indeed, a growing awareness of the potential for social or intrasexual competition among females[5,6] has helped spur interest in sexual selection and trait elaboration in females[11,12]. Yet despite this renewed attention, we do not fully understand why females in some species are highly ornamented, whereas females in related species are drab or dull. Moreover, it is not clear if the same underlying principles and mechanisms that commonly operate in males act similarly in females.

The concept of sexual selection, which argues that elaborate traits may confer a fitness gain in the form of a mating advantage, is often invoked to explain ornamentation in animals. Although formulated upon the idea of differential investment in gamete production and parental care by the sexes[2,3], variation in reproductive success resulting from intrasexual competition for reproductive opportunities is also central to sexual selection theory[9]. In species with unequal sharing of reproduction among same-sex individuals—a pattern termed high reproductive skew—variance in lifetime reproductive success is a direct consequence of intrasexual competition for breeding and will be higher in the sex with the greatest potential rate of reproduction[13]. Since the intensity of sexual selection on traits that enhance breeding opportunities should be directly related to the variance in direct fitness among members of each sex[14], selection should thus act more strongly on the sex with the higher variance in reproductive success. In most species, males have higher variance in reproductive success than do females[15], and the traditional attention[1] given to elaborate, sexually selected male traits reflects this general trend. However, this pattern is often absent or reversed in cooperatively breeding vertebrates that live in family groups, where females frequently have a higher variance in reproductive success than males[8,16]. This female-biased reproductive variance in cooperative breeders has been observed in both high skew societies (singular breeders)[8] and lower skew societies (plural breeders)[16], as well as in both birds and mammals[8]. Although not all cooperatively breeding species show this relationship, the general pattern emerges because skew is high in both males and females in many cooperatively breeding species, whereas it tends to be high only in males in non-cooperatively breeding species. Indeed, skew is often higher in females than in males in cooperatively breeding species because non-pair-bonded males may have the option to reproduce via extrapair matings (which reduces male skew and variance in reproductive success), whereas non-paired females generally cannot reproduce at all[8].

Selection is likely to favour traits that improve a female's reproductive success directly via intrasexual competition for reproductive opportunities (sexual selection[4]), or indirectly via intrasexual competition for increased social status or access to resources other than mates (for example, food, nest sites, territories) linked to reproduction (social selection[5,6]). In cooperative breeders, sexual or social selection on traits used in intrasexual competition is expected to be relatively strong in both sexes[7], and should therefore result in a reduced degree of sexual dimorphism and females that are similar in ornamentation to males, as has been suggested for some gregarious and territorial species[6]. This hypothesis assumes that the same traits influence competitive success in both sexes. However, if males and females use different traits in intrasexual competition, the opposite might be expected and the sexes would be predicted to show divergent characters and an increased degree of sexual dimorphism in cooperatively breeding species[12].

The pattern of reversed reproductive variance in cooperatively breeding vertebrates[8] provides an unusual opportunity to test the relationship between reproductive skew and the traits that ultimately give rise to sexual dimorphism. To explore whether the degree of sexual dimorphism in traits used in intrasexual competition is reduced in cooperatively breeding species, we analysed patterns of morphological sexual dimorphism in a comparative framework

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using a complete species-level phylogeny of a socially variable lineage of birds, the 45 species of African starlings (Sturnidae). Nearly 40% of the starling species endemic to Africa are cooperative breeders, making them an appropriate group in which to examine the evolutionary causes and consequences of vertebrate sociality[17]. Although few of these starlings have been studied in detail, variance in reproductive success is higher in females than in males in cooperatively breeding superb starlings, *Lamprotornis superbus*[16], as has been found generally in cooperatively breeding vertebrates[8]. Additionally, reproductive skew is high in all cooperatively breeding starlings; although most species are singular breeders, even the few plural breeding species have relatively high skew among females[17–19].

Our phylogenetic hypothesis for the African Sturnidae was constructed using Bayesian likelihood methods applied to extensive mitochondrial and nuclear intron sequences, and its high topological resolution provides a robust framework for testing evolutionary hypotheses[17,20] (Fig. 1a). African starlings are a visually diverse and highly ornamented group that exhibits a range of plumage colours, feather structures and other ornaments ranging from iridescent plumage to crests[21]. We measured sexual dimorphism in two traits likely to be used in intrasexual competition: plumage and body size (wing length) dimorphism. These characters were mapped onto the tree and analysed using phylogenetically controlled comparative analyses.

We found that the degree of sexual dimorphism in both plumage and body size was lower in cooperatively breeding than in non-cooperatively breeding starling species. Cooperative breeders had sexually monomorphic plumage, whereas non-cooperative breeders had sexually dimorphic plumage ($\chi^2 = 14.7$, $n = 45$, $P = 0.0001$; phylogenetically controlled: likelihood ratio (LR) = 7.12, $P < 0.0001$; Fig. 1b). Additionally, females and males had more similar wing lengths in cooperatively breeding species than in non-cooperatively breeding species ($t = 2.13$, d.f. = 42, $P = 0.039$; phylogenetically independent contrasts (PICs): $F_{1,10} = 5.11$, $P = 0.029$; Fig. 1c). Although a variety of other demographic and ecological factors have been shown to influence sexual dimorphism in birds[22], these alternative explanations probably do not explain the patterns observed in African starlings, as the relationships we observed among body size, plumage dimorphism and social system were not related to any of a suite of alternative hypotheses (Supplementary Discussion), but instead are likely to reflect selection acting with different intensities on traits associated with intrasexual competition.

Cooperatively breeding starlings show reduced sexual dimorphism compared to non-cooperative breeders, but does this pattern in cooperative breeders stem from reduced selection on male traits, or increased selection on female traits used in intrasexual competition? Although there is no reason to predict that selection acts less intensely on males in cooperatively breeding species, there is reason to predict that the intensity of selection acting on female traits is increased in cooperatively breeding starlings, as it is in other group-living species[22,23]. For example, increased intrasexual competition for reproductive opportunities is particularly intense in cooperative breeders with high reproductive skew where one or a few females in a group monopolize the reproduction[7,8]. Similarly, since dominance rank and access to resources like food or breeding sites are important in many cooperative breeders, intrasexual competition for such resources probably explains the masculinized morphological and physiological adaptations in spotted hyenas and some other cooperatively breeding vertebrates[9,24].

As quantifying the absolute strength of selection is difficult in a comparative study, we assessed the relative intensities of selection acting on male and female phenotypic traits. We found that in cooperatively breeding starlings with reduced sexual dimorphism, selection is likely to be acting more strongly on female plumage elaboration and body size rather than more weakly on these traits in males. In many avian groups, plumage dimorphism with drab females and ornamented males is the ancestral condition, and transitions to monomorphism are associated with female trait elaboration[11,22,23]. We assessed plumage traits in male and female African starlings and found that females were less ornamented than males with dull or drab plumage in all 22 sexually dimorphic species, but equally ornamented as males with similarly bright or elaborate plumage in all 23 sexually monomorphic species. Therefore, females in cooperatively breeding species were more ornamented than those in

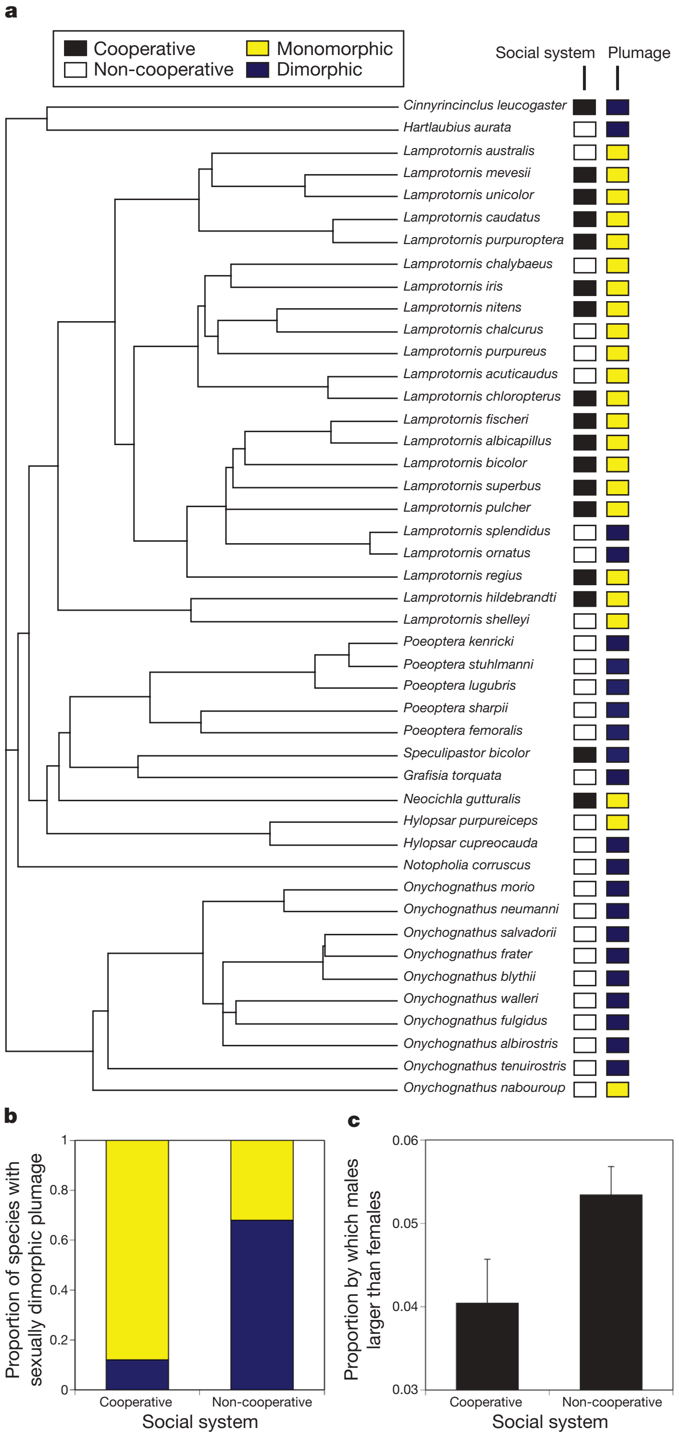

Figure 1 | Molecular phylogeny of African starlings with their associated behavioural and morphological traits. **a**, The tree is based on combined analysis of mitochondrial and nuclear intron sequences. Social and morphological characters are indicated at each terminal species; a key is given above. **b**, A greater proportion of a non-cooperative species had sexually dimorphic plumage than did cooperative species, suggesting a reduced degree of plumage dimorphism in cooperative species. **c**, Males and females in cooperative species had wings that were more similar in length than those in non-cooperative species (mean ± s.e.), suggesting a reduced degree of size dimorphism in cooperative species.

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non-cooperatively breeding species ($\chi^2 = 23.3$, $n = 45$, $P < 0.0001$; phylogenetically controlled: LR = 7.12, $P < 0.0001$). We also examined the relationship between male and female wing length ($F_{1,42} = 3,579.06$, $P < 0.0001$, $R = 0.99$; Fig. 2a) and calculated the residuals to compare the relative intensity of selection on the sexes in cooperative and non-cooperative taxa. We found that males had longer wings than females in all species (Fig. 2a). However, in cooperatively breeding species females tended to have relatively longer wings (positive residuals), whereas in non-cooperatively breeding species, females tended to have relatively shorter wings (negative residuals) ($t = 1.87$, d.f. = 42, $P = 0.034$; PICs: $F_{1,10} = 3.82$, $P = 0.04$; Fig. 2b).

To further test the hypothesis that reduced sexual dimorphism in cooperatively breeding species reflects enhanced selection on female traits[22,23], we explored the relative magnitudes of variance in male and female body size. Simple tests of which sex has greater variance are not illuminating, as there are opposing predictions about the relationship between selection intensity and phenotypic trait variance. Because selection on a trait often leads to reduced phenotypic and genetic variance in that trait[25,26], the sex with the greater variance could be predicted to be under relatively weaker selection. Alternatively, because traits under strong selection might be expected to have high, not low, genetic variance under some conditions[27], the sex with greater phenotypic variance could be expected to be under relatively greater selection. Available evidence from other taxa provides support for both relationships: comparative studies of avian plumage suggest that phenotypic traits under greater sexual selection are often as variable as traits not under sexual selection[28], whereas experimental studies in insects suggest that genetic variance in sexually selected traits can be small[29] or large[30], depending upon the trait. Here, however, the key prediction is that under either scenario, males and females of cooperatively breeding species should have similar variances in body size, whereas these traits in males and females of non-cooperatively breeding species should have dissimilar variances because the relative intensity of selection is more similar between the sexes in the cooperatively breeding species.

Our results support this key prediction of dissimilar variances: we found no significant effect of sex or social system on the variance in wing length, but there was a significant interaction (sex: $F_{1,45.84} = 0.68$, $P = 0.42$, social system: $F_{1,40.03} = 2.89$, $P = 0.097$; interaction: $F_{1,41.08} = 7.84$, $P = 0.0078$) such that the variance in wing length did not differ between males and females in cooperative breeders ($F_{1,42.48} = 1.55$, $P = 0.22$) but, in non-cooperative breeders, females had greater variance in wing length than males ($F_{1,44.97} = 8.02$, $P = 0.0069$; Fig. 3a). The critical result is that phenotypic variance differs between males and females in non-cooperatively breeding species, but not in cooperatively breeding species. We confirmed this result in a phylogenetic framework by first calculating the residuals of the relationship between male and female variance in wing length and then using a comparative analysis to compare the residuals of this relationship in cooperative and non-cooperative species. We found a significant difference in the residuals of cooperative and non-cooperative breeders (PICS: $F_{1,10} = 6.14$, $P = 0.033$; Fig. 3b). To further control for within-species comparisons in a phylogenetic framework, we performed an additional series of analyses that yielded similar results to those presented here (Supplementary Data).

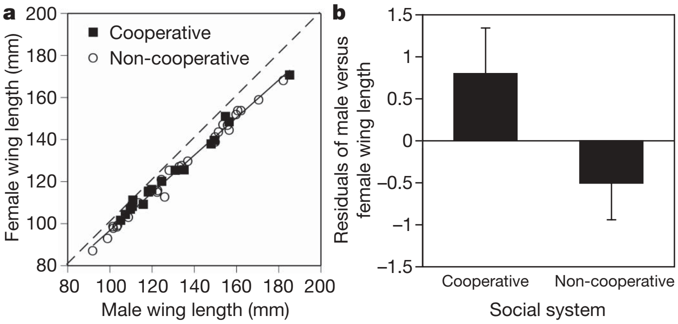

Figure 2 | Relationships between male and female wing lengths in cooperatively and non-cooperatively breeding African starlings. a, Male and female wing lengths were positively related, but males always had longer wings than females. Cooperative and non-cooperative starlings showed the same relationship (interaction: $F_{1,40} = 13.97$, $P = 0.10$); the dashed line indicates the line of equality. **b**, The residuals of the phylogenetically controlled relationship between male and female wing lengths were significantly greater in cooperative than in non-cooperative starlings (mean ± s.e.), suggesting that in cooperative species, females had relatively longer wings, whereas in non-cooperative species, females had relatively shorter wings.

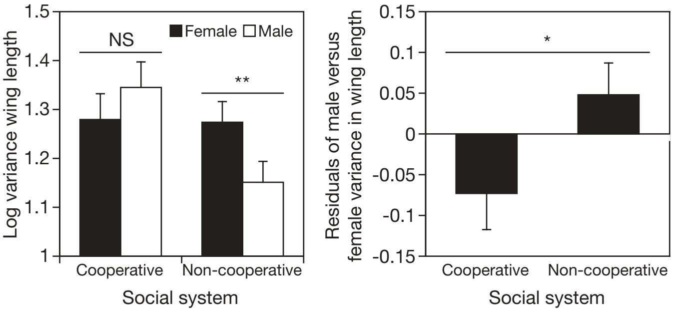

Figure 3 | Patterns of variance in male and female wing lengths in cooperatively and non-cooperatively breeding African starlings. a, In non-cooperative starlings, females had greater variance in wing length than males, but in cooperative starlings males and females had similar levels of variance in wing length (mean ± s.e.). The double asterisks indicate significance at $P < 0.01$. **b**, The residuals of the phylogenetically controlled relationship between male and female variance in wing length were significantly greater in non-cooperative starlings than in cooperative starlings (mean ± s.e.). The single asterisk indicates significance at $P < 0.05$.

Collectively, our results suggest that the patterns of sexual dimorphism related to social system in African starlings derive from intersexual differences in the relative intensity of selection acting on female traits used in intrasexual competition in societies with different levels of reproductive skew. Biologists have long recognized the link between mating systems and sexually selected traits[13]. Here, we describe a similar link between social systems, patterns of reproductive skew and secondary sexual characteristics. Sexual selection theory typically emphasizes intrasexual competition among males[1,9,12], yet female–female competition for reproductive opportunities and other resources related to breeding has important fitness consequences in many cooperatively breeding vertebrates[7], particularly those with high female reproductive skew where females compete for breeding status. When competition among females is intense, selection on traits that improve access to mates, other resources, or higher social status within the group will be strong. We have shown that this increased female–female competition in high skew societies results in more ornamented females and therefore less sexual dimorphism. Because high female reproductive skew is common in cooperatively breeding vertebrates[8], the patterns of reduced sexual dimorphism and increased selection on females in cooperatively breeding starlings are likely to be observed in other social vertebrates that live in groups with unequal sharing of reproduction. Although Darwin largely ignored the importance of female intrasexual competition as a selective force in the evolution of elaborate female traits[1], female–female interactions in group-living vertebrates will have important consequences for not only the evolution of female morphological traits like those reported here, but also for physiological and behavioural traits associated with intrasexual competition[9].

METHODS SUMMARY

A detailed description of phylogenetic reconstruction methods, samples and markers was published previously[20]. Briefly, we used Bayesian Markov chain Monte Carlo (MCMC) methods and maximum parsimony to reconstruct the

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phylogeny from a substantial nuclear and mitochondrial DNA sequence character matrix. We included all 45 Sturnidae species that are of African origin and endemic to mainland Africa and its satellite islands[17,20]. Species were classified as 'cooperative' or 'non-cooperative' using published species accounts and behavioural observations[17]. Plumage dimorphism was scored as 'dimorphic' or 'monomorphic' as determined from published descriptions and visual comparison of many specimens of all taxa. Body size dimorphism was calculated as the difference in male and female wing length relative to male wing length, as measured from museum specimens ($n = 1,614$). Phylogenetically controlled comparative analyses were conducted using Pagel's discrete algorithms in Mesquite v2.01 or using the BRUNCH algorithm in CAIC v2.6 (see Supplementary Methods for all program references).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions D.R.R. conceived the project and analysed the data. D.R.R. and I.J.L. jointly collected the data and prepared the manuscript.

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METHODS

Phylogeny reconstruction. We included all 45 Sturnidae species that are of African origin and endemic to mainland Africa and its satellite islands[17,20]. A detailed description of phylogenetic reconstruction methods, samples and markers was published previously[20]. Briefly, we used Bayesian Markov chain Monte Carlo (MCMC) methods and maximum parsimony to reconstruct the phylogeny from a substantial nuclear and mitochondrial DNA sequence character matrix.

Characters. Species were classified as 'cooperative' or 'non-cooperative' using published species accounts and behavioural observations[17]. Plumage in African starlings is highly ornamented, but the type and biochemical structure of the ornaments varies among clades[21]. Because it is unlikely that a single type of ornament is used for inter- or intrasexual communication across species, plumage dimorphism was scored conservatively and categorically as 'dimorphic' or 'monomorphic' as determined from published descriptions and visual comparison of many specimens of all taxa. We then determined whether females had reduced ornamentation compared to males (that is, more drab or dull in colour), or if they were as ornamented as males using published species accounts[17]; there were no cases in starlings where females were more ornamented than males.

We calculated body size dimorphism as the difference in male and female wing length relative to male wing length, as measured from museum specimens ($n = 1{,}614$). Although selection can operate more strongly on plumage dichromatism than body size dimorphism in some avian species, these two measures of sexual dimorphism were significantly related in African starlings, as species with plumage dimorphism also had greater body size dimorphism ($t = 2.05$, d.f. $= 42$, $P = 0.047$). Wing lengths were measured by the same researcher (I.J.L.) to the nearest 0.5 mm. Variance in wing length was log-transformed to meet the assumptions of normality. The median number of males and females measured for each species was 20 individuals of each sex (females: mean $= 17.4$; range $= 0$–23 individuals; males: mean $= 18.8$ males; range $= 1$–23). Because of the rarity of specimen material, we were able to measure only one female *Pholia femoralis* and one *Onychognathus neumanni*, and hence we did not include these two species in our analyses of continuous traits. For all other species, we measured at least five individuals of each sex.

Statistical analyses. To examine the relationship between plumage dimorphism and sociality, we used a chi-squared test (non-phylogenetically controlled) and Pagel's discrete algorithms in the program Mesquite v2.01 (phylogenetically controlled) (see Supplementary Methods for all program references). This latter analysis uses a continuous-time Markov model and allows for tests of correlated evolution as well as for the order and direction of evolution for binary traits. Models of evolution are fitted to the data and phylogeny using maximum likelihood, and described by the log-likelihood of the model. Correlated evolution is detected by comparing a model where two traits are allowed to evolve independently with one in which they are constrained to co-evolve. The transition rates for the traits were treated as identical, in a one-parameter model where the forward transition (α) was equal to the backwards transition (β). This test compares the log-likelihoods of the model of independent evolution (H_0) to that of the mode of dependent evolution where the traits are linked (H_1). Monte Carlo simulations of the independent and dependent models were run 10,000 times, and the likelihood ratio (LR) and P-value were reported.

To examine the relationship between body size dimorphism and social system, we used a t-test (non-phylogenetically controlled) and CAIC v2.6 to conduct comparative analyses on phylogenetically independent contrasts. We used the BRUNCH algorithm with the binary discrete characters for social system (cooperative versus non-cooperative). CAIC performs a regression on the contrasts and reports an F-ratio with the appropriate degrees of freedom for the number of phylogenetically independent contrasts (PICs) calculated from the phylogeny.

To test the prediction that the reduced degree of sexual dimorphism in cooperatively breeding starlings results from increased selection on females, we used a chi-squared test (non-phylogenetically controlled) and Pagel's discrete algorithms in the program Mesquite v2.01 (phylogenetically controlled) to examine the relationship between female ornamentation and social system. We used a correlation analysis to examine the relationship between male and female wing length, followed by a t-test of the residuals (non-phylogenetically controlled) and a phylogenetically controlled analysis using the BRUNCH algorithm in CAIC to examine whether males or females differed more in cooperative and non-cooperative species. Because we made an a priori prediction that the reduced sexual dimorphism resulted from increased selection on females, we used one-tailed tests for these analyses.

Generalized linear mixed models were used to examine the relationship between social system, sex and variance in wing length. Sex, social system and their interaction were included in the model as fixed effects, species was included as a random effect to control for comparisons within a species, and wing length was included to control for differences in body size among species. Contrasts were used to examine least square means in post-hoc analyses. Results were confirmed in a phylogenetic framework by comparing the residuals of the relationship between female and male variance in wing length in cooperative and non-cooperative species using the BRUNCH algorithm in CAIC.

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