# Sperm competition and sexually size dimorphic brains in birds

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Natural selection may favour sexually similar brain size owing to similar selection pressures in males and females, while sexual selection may lead to sexually dimorphic brains. For example, sperm competition involves clear-cut sex differences in behaviour, as males display, mate guard and copulate with females, while females choose among males, and solicit or reject copulations. These behaviours may require fundamentally different neural government in the two sexes leading to sex-dependent brain evolution. Using two phylogenetic approaches in a comparative study, we tested for roles of both natural and sexual-selection pressures on brain size evolution of birds. In accordance with the natural-selection theory, relative brain size of males coevolved with that of females, which may be the result of adaptation to similar environmental constraints such as feeding innovation. However, the mode of brain size evolution differed between the sexes, and factors associated with sperm competition as reflected by extra-pair paternity may give rise to sexually size dimorphic brains. Specifically, species in which females have larger brains than males were found to have a higher degree of extra-pair paternity independently of potentially confounding factors, whereas species in which males have relatively larger brains than females appeared to have lower rates of extra-pair paternity. Hence, the evolution of sperm competition may select for complex behaviours together with the associated neural substrates in the sex that has a higher potential to control extra-pair copulations at the observed levels. Brain function may thus be affected differently in males and females by sexual selection.

**Keywords:** birds; brain size; extra-pair paternity; phylogenetic correlation; sexual dimorphism

## 1. INTRODUCTION

Brain space is assumed to be associated with information processing and interspecific variation in the size of specific brain regions corresponds to the complexity of the behaviour that they govern (Finlay & Darlington 1995; Barton & Harvey 2000; Clark *et al.* 2001; de Winter & Oxnard 2001). Among mammals and birds, relative brain size is known to reflect differences in ecology, life history, diet, parental care, behavioural flexibility, habitat and foraging technique (Jerison 1973; Clutton-Brock & Harvey 1980; Bennett & Harvey 1985; Lefebvre *et al.* 1997; Barton 1998; Pagel & Harvey 1998; Garamszegi *et al.* 2002; Garamszegi & Eens 2004). These factors are likely to shape the behaviour of males and females similarly, and natural selection should thus affect brain size in the two sexes in a similar fashion (Lande 1980). However, sexual selection may cause sexual dimorphism in behaviour, which can be expected to result in a different evolution of brains in males and females (Jacobs 1996). Sex-dependent patterns of overall brain size have been reported in carnivorous mammals in relation to maternal investment (Gittleman 1994).

During the course of reproduction, individuals perform several sex-dependent behaviours (Andersson 1994). In birds, males compete with each other, display elaborate traits, mount females and deposit sperm, while females select males, solicit copulations and produce eggs. The two sexes may also display different behaviours during parental care (Clutton-Brock 1991). These complex behavioural performances may require mental capacities that are necessary for the production and the perception of signals, entail the ability to recognize and remember encounters, and allow spatial navigation to find territories and receptive mates (Jacobs 1996). The neural bases of these cognitive functions may thus be under sexually divergent selection pressures. Sexual dimorphism in terms of size or structure of different brain nuclei that are associated with sex-dependent behaviour has been identified in many animal taxa (Gahr 1994; Jacobs 1996). Since cognitive enhancement allowing complex behavioural adaptation is associated with the evolution of neural tissues leading to the evolution of larger brains, selection shaping behaviour in the two sexes and corresponding cognitive performance may lead to sexual differences in overall brain size.

Sexual selection arising from sex-dependent behaviour occurs commonly at the level of sperm competition, as ultimately reflected by extra-pair paternity (Birkhead & Møller 1998). Hence, extra-pair paternity might be a good marker for an entire suite of sexually different, reproduction-related behaviours subject to sexual selection. Sperm competition not only predicts sexual differences in many behaviours such as mate guarding, territorial defence, courtship behaviour, solicitation displays and copulation and sperm ejection patterns, but also the behavioural consequences of paternity during parental care. In birds,

extra-pair paternity is known to be a major component of sexual selection, as it is interspecifically associated with the expression of sexually selected traits and paternal care (reviews in Bennett & Owens 2002; Griffith *et al.* 2002; but see Garamszegi & Møller 2004). If the evolution of the neural substrate of behaviours associated with sperm competition is sexually determined, there should be an interspecific relationship between sexual size dimorphism of brains and extra-pair paternity.

In a comparative analysis using generalized least-squares models and phylogenetically independent contrasts, we tested the hypothesis among avian species that natural selection favours sexually similar brain size evolution, while sexual selection favours sexual differences in behaviour that give rise to brain size differences between males and females.

First, we characterized the correlated evolution of male and female brain size. We expected that if behavioural adaptation owing to natural selection is associated with simultaneous brain enlargement in males and females, there should be a positive phylogenetic correlation between the relative brain sizes of the two sexes. To test whether similar selection pressures affect brain size evolution similarly in females and males, we related the frequency of opportunistic feeding innovations to relative brain size of the two sexes, as it may depend on selection independent of sex. In general, feeding innovations may allow animals to exploit different kinds of resources, or exploit resources in a novel way, compared to how resources were exploited before the feeding innovation appeared. Using descriptions of novel kinds of behaviour, feeding innovations have been quantified from the ornithological literature (Lefebvre *et al.* 1997). Previous studies have shown that the frequency of feeding innovations is correlated with forebrain size in birds (Lefebvre *et al.* 1997). This result has been extended to include the anatomical correlates of tool use and nesting innovation (Nicolakakis & Lefebvre 2000; Lefebvre *et al.* 2002). Feeding innovations may have ecological implications because introduction success of birds to New Zealand can be predicted by their frequency (Sol & Lefebvre 2000). Thus, a higher rate of innovation (or a correlate thereof) seems to be able to predict how individuals succeed in a novel environment, and, therefore, it has been suggested to reflect behavioural plasticity that involves cognitive and learning tasks. Since such behavioural plasticity may promote the success of individuals reaching novel environments independent of their sex, we assumed that feeding innovation is associated with ecological factors that act similarly in males and females thus involving similar selection pressures in the two sexes. Therefore, we expected a positive interspecific relationship between foraging innovation frequency and overall brain size, with similar exponents in females and males.

Second, to evaluate the importance of sperm competition as a potential determinant of different brain size evolution in the two sexes, we investigated the phylogenetic association between extra-pair paternity and the body size-independent ratio of female and male brain size reflecting brain size dimorphism. In this analysis, we controlled for potentially confounding effects caused by interspecific variation in paternal care and sexual dichromatism, as both have been found to relate to extra-pair paternity among species (e.g. Bennett & Owens 2002; Griffith *et al.* 2002).

We predicted that species with intense sperm competition, as reflected by a higher degree of extra-pair paternity, have sexually size dimorphic brains compared with species with relaxed competition, because of the differences in selection pressures acting on their behaviour. The outcome of extra-pair copulation may be controlled by both sexes (review in Westneat & Stewart 2003), which makes it difficult to formulate directional predictions. If females, by actively seeking extra-pair copulations, control extra-pair paternity in the majority of birds, species with intense sperm competition should have females with larger brains than males. By contrast, if males have much control, they should have larger brains than females in species with high rates of extra-pair paternity, because of the level of the intrasexual competition and the complexities of displaying and/or, mate guarding. In general, one may expect the sex that determines the patterns of extra-pair paternity to have relatively larger brains than the opposite sex when the rate of extra-pair paternity is high.

## 2. MATERIAL AND METHODS
### (a) *Dataset*
Relying on post-mortem examinations of dead birds that had been frozen, brain mass and body mass were measured by a taxidermist (J.E.) on a balance to the nearest 0.001 g, blindly with respect to the hypotheses under test. A detailed description of the standardized preparation procedure can be found on the Web site of J.E. (http://www.birdresearch.dk/). We assumed that effects of storage and preparation on measurements only caused random noise in the dataset. To test this assumption, by combining information on males and females for each species, we calculated mean body and brain sizes, and checked whether our measurements were significantly repeatable with respect to those reported in the literature (e.g. Crile & Quiring 1940; Portmann 1947; Armstrong & Bergeron 1985; Mlíkovsky 1990). For both traits we found large and highly significant repeatabilities ($\log_{10}$(body mass): $F_{84,206} = 296.668$, $p < 0.001$, $R = 0.992$; $\log_{10}$(brain mass): $F_{84,206} = 119.365$, $p < 0.001$, $R = 0.980$). Hence, potential differences in measurements among studies should not cause bias, and information from different sources may be combined.

We used data for 1489 individual adult birds of known sex belonging to 161 species for which we have data for both males and females. Data for nine species were from Crile & Quiring (1940). Variances in body and brain masses among species were larger than variances within species, as required for comparative analyses (females: $\log_{10}$(body mass), $F_{160,594} = 491.586$, $p < 0.001$; $\log_{10}$(brain mass), $F_{160,594} = 364.750$, $p < 0.001$; males: $\log_{10}$(body mass), $F_{160,900} = 870.756$, $p < 0.001$; $\log_{10}$(brain mass), $F_{160,900} = 504.832$, $p < 0.001$). Sex-specific brain and body sizes were significantly repeatable within species (females: $\log_{10}$(body mass), $R = 0.994$; $\log_{10}$(brain mass), $R = 0.992$; males: $\log_{10}$(body mass), $R = 0.996$; $\log_{10}$(brain mass), $R = 0.993$). These results indicate that intraspecific variation of these traits is negligible compared with interspecific variation, and that sex-specific body and brain sizes are species-specific attributes that can justifiably be represented by a single measurement (when we repeated our analyses with species for which we have at least two data points for females and males, the results were similar). We also tested for consistent bias owing to sample size differences between sexes. However, a repeatability analysis using $\log_{10}$-transformed sample sizes for sex-specific brain size measurements revealed that sample sizes for males

and females within species were similar ($F_{160,321} = 5.099$, $p < 0.001$, $R = 0.672$). Hence, we used sex-specific traits in our subsequent investigation by calculating mean brain size and body size for each sex of each species. Larger animals have larger brains, and to control for allometric effects we calculated residuals from the phylogenetically corrected linear regression of $\log_{10}$-transformed brain size on $\log_{10}$-transformed body size for each sex (see § 2b). These residuals were used as estimates of sex-specific relative brain sizes. Sex-specific relative brain sizes were not confounded by variation due to sample size (females: $F_{1,160} = 0.015$, $p = 0.904$; males: $F_{1,160} = 0.814$, $p = 0.368$). As suggested by these analyses, we assumed that interspecific variation in relative brain mass in males and females holds biological information.

We expressed absolute brain size dimorphism as $\log_{10}$(absolute female brain size/absolute male brain size). We avoided calculating brain size dimorphism based on sex-specific relative brain sizes, because these variables are residuals from the relevant regression lines causing them to scale with the independent variable used (sex-specific body size). Therefore, combining residuals from two regression lines may introduce bias. Absolute brain size dimorphism measured as the $\log_{10}$-transformed ratio of absolute female and male brain size was normally distributed (Shapiro–Wilk $W$-test: $W = 0.985$, $p = 0.743$) with a mean of $-0.024$ (s.e. $= 0.005$). Since the numerator and the denominator of the absolute brain size ratio scale similarly, absolute brain size dimorphism larger than zero indicates that females have relatively larger brains than males, whereas values smaller than zero reflect the opposite trend. The mean absolute brain size dimorphism of 161 species was significantly smaller than an expectation of zero ($t_{160} = -5.257$, $p < 0.001$), implying that there are more species in which males have larger brains than females. However, owing to allometric effects absolute brain size dimorphism may result from absolute body size dimorphism. Thus, the $\log_{10}$-transformed ratio of absolute female and male brain size should be corrected for the similar ratio in body size. This correction was based on the phylogenetically independent regression of $\log_{10}$(absolute female brain size/absolute male brain size) on $\log_{10}$(absolute female body size/absolute male body size) (slope: 0.175, intercept $= -0.021$, the corresponding phylogenetic model: $\kappa = 0.316$, $\lambda = 0.215$, LR $= 7.922$, d.f. $= 1$, $p < 0.001$, $n = 161$). Note that absolute brain and body size dimorphism were not residuals by definition, allowing them to be combined in a single regression. Residuals from this regression were subsequently termed relative brain size dimorphism and used in the subsequent analyses. Positive values for relative brain size dimorphism thus indicate that females have relatively larger brains when allometric effects were held constant. When we calculated $\log_{10}$(brain size/body size) on the raw individual data (by comparing each individual with its own traits, using this variable we did not use a phylogenetic analysis at this stage), and using this measure of individual relative brain size, we tested for species and sex effects in a two-way analysis of variance. This analysis revealed significant effects for species and for species–sex interaction on relative brain size, which suggests that relative brain size difference is a species-specific attribute (species: $F_{160,1488} = 132.801$, $p < 0.001$; sex: $F_{1,1488} = 2.116$, $p = 0.146$; species$\times$ sex: $F_{160,1488} = 2.153$, $p < 0.001$).

Louis Lefebvre kindly provided us with the list of reported cases for innovative feeding styles in birds, which is the corresponding database for Lefebvre *et al.* (1997, 2001), Nicolakakis & Lefebvre (2000), Sol *et al.* (2002) and Nicolakakis *et al.* (2003). These data were gathered through an exhaustive survey lasting 30 years (1970–2000) in the short note sections of 65 generalist ornithol-

ogy journals covering six geographical areas in the world. We used data from the European and North American continents. We calculated the frequency of opportunistic feeding innovations separately for European and North American species, as the number of reported cases of novel feeding habits (European species: $n = 851$, North American species: $n = 613$). We only considered species for which at least one report was available, because the meaning of an innovation frequency of zero is obscure (Nicolakakis *et al.* 2003). For an interspecific analysis to be feasible, we intended to test whether the frequency of feeding innovation showed larger variation among than within species by using one-way analysis of variance. However, the distribution of feeding innovation frequency was strongly left skewed owing to the large number of species with relatively few reported cases. Indeed, $\log_{10}$-transformation did not achieve normality (Shapiro–Wilk $W$-test: $W = 0.927$, $p < 0.001$) violating a basic assumption of parametric tests. However, there was a significant positive correlation between feeding innovation frequencies of species for which records were available for both continents (Kendall $\tau = 0.474$, $n = 41$, $p < 0.001$), indicating that species on the European continent are ranked similarly to those on the North American continent based on feeding innovations of common species. When taking the liberty of performing parametric statistics, the repeatability was statistically significant ($R = 0.446$, $F_{19,39} = 2.611$, $p = 0.019$). Therefore, we used data for European birds in the subsequent analyses, under the assumption that feeding innovations measured in different continents are species-specific attributes. We have chosen European species because data availability in these species for organ size allowed statistical tests to be based on larger sample sizes (analyses relying on data for North American species provided similar results). As the phylogenetic approach based on generalized least-squares model (see § 2b) may be sensitive to the non-normal distribution of data (R. Freckleton, personal communication), we also applied non-parametric tests based on the raw species data. Notably, it has been shown that the relationship between relative brain size and feeding innovation is not confounded by phylogenetic effects (Lefebvre *et al.* 1997, 2001, 2002; Nicolakakis & Lefebvre 2000; Sol & Lefebvre 2000). The probability of finding a feeding innovation in a species may depend on the intensity of research and the abundance of this species. Here, we did not control for these potentially confounding effects on feeding innovation, because (i) previous studies reported that effects arising from research effort and population size do not confound the investigated associations in focus (Nicolakakis & Lefebvre 2000; Lefebvre *et al.* 2001), and (ii) these variables may not be expected to cause sex-dependent bias.

Data on extra-pair paternity ($n = 38$ species) were extracted from the literature and were square-root arcsine-transformed prior to analysis. See Griffith *et al.* (2002) and Møller & Cuervo (2000) for repeatability and reliability of this variable. We have used the relative frequency of extra-pair offspring for a particular species as a measure of extra-pair paternity, defined as the number of extra-pair offspring divided by the total number of offspring (when we used the relative frequency of broods containing extra-pair offspring the results and conclusions were very similar). Sex-dependent brain size did not differ significantly between species with and without information on extra-pair paternity indicating that our restricted sample for species with information on extra-pair paternity is not biased (female brain size: $t_{159} = 0.854$, $p = 0.395$; male brain size: $t_{159} = 0.904$, $p = 0.367$; brain size dimorphism: $t_{159} = -1.352$, $p = 0.178$). Based on partial phylogenetic correlations (see § 2b), we controlled for

confounding effects arising from interspecific differences in paternal care and sexual dichromatism, because both have been found to be associated with extra-pair paternity among species causing potential bias in the data (Møller & Cuervo 2000; Bennett & Owens 2002; Griffith *et al.* 2002; but see Schwagmeyer *et al.* 1999 and Dunn *et al.* 2001). We used information on paternal care defined as male proportional contribution to feeding of offspring from the literature, and scores for sexual dichromatism from Møller & Cuervo (2000) for 26 species.

The entire dataset is given in electronic Appendix A.

## (b) *Comparative methods*

Phylogenetic information for our comparative analyses originated from a number of sources, all using molecular techniques. The phylogenetic hypothesis was based on a composite phylogeny reported by Sibley & Ahlquist (1990), combined with information from other studies (Sheldon *et al.* 1992; Leisler *et al.* 1997; Cibois & Pasquet 1999; Grapputo *et al.* 2001). We applied branch lengths from the tapestry tree of Sibley & Ahlquist (1990) for higher taxonomic levels. Within families, the distance between different genera was set to 3.4 $\Delta T_{50}H$ units, and between species within genera to 1.1 $\Delta T_{50}H$ units (Sibley & Ahlquist 1990; Bennett & Owens 2002). The entire dataset and phylogeny are presented in the electronic Appendix A.

We applied the general method of comparative analysis for continuous variables based on generalized least squares (GLS) models using the statistical software CONTINUOUS (Pagel 1997, 1999). First, we assessed the contribution of scaling parameters by estimating sequentially the maximum-likelihood values of the branch-length scaling parameters $\kappa$, and the phylogeny-scaling factor $\lambda$ (recent simulations showed that the estimation of $\delta$ (the overall path-length scaling factor) is biased (Freckleton *et al.* 2002), and thus we avoided estimating this parameter). If a significant effect was found ($p < 0.05$), the estimated values were used in the final model; otherwise, default ($= 1$) settings were used. Second, using the appropriate scaling parameters, the correlation between pairs of traits was tested by log-likelihood ratio statistics. These compare model $H_0$, fitting the data, while forcing the correlation to be zero, with the alternative $H_1$ model, permitting correlated evolution of the two characters. Third, using the model best fitting the data, we estimated the phylogenetic correlation between traits. The appropriate scaling parameters and the log-likelihood ratio statistics testing for correlated trait evolution are presented. When we controlled for potentially confounding factors, we entered these variables together with the variables of interest in the same model, and tested for correlated trait evolution. If the model offering the best fit with the data allowed correlation among traits, we calculated the partial phylogenetic correlation for the relationship in question. Some variables were clearly dependent on others owing to allometric effects (e.g. sex-specific brain size on body size, or absolute brain size dimorphism on absolute body size dimorphism). These effects were controlled by calculating the phylogenetically corrected regression of the dependent variable on the independent variable, using CONTINUOUS. Based on this equation, residuals were calculated for the raw species data (see Purvis & Rambaut 1995).

An anonymous referee noted that phylogenetic methods based on GLS models may be prone to Type I statistical errors. Therefore, when significant associations were found for the relationship in question, in a second series of analyses we controlled for similarity among species owing to common descent in linear regression analysis based on statistically independent linear contrasts (Felsenstein 1985; Harvey & Pagel 1991) using the software

CAIC (Purvis & Rambaut 1995). These regressions were forced through the origin (Garland *et al.* 1992). Before this analysis, we checked that values of contrasts were normally distributed and tested if values of contrasts were significantly correlated with the standard deviation of the contrast (Garland 1992; Garland *et al.* 1992; Purvis & Rambaut 1995). Since, the latter was found to be the case for the majority of the analyses, we calculated regressions based on the ranks of the contrasts for the independent variable. Using this approach, we obtained normality and we simultaneously reduced the importance of extreme data points (see also Møller & Birkhead 1994).

## 3. RESULTS

Our phylogenetic analysis revealed a strong correlation between male and female relative brain size (GLS approach: $\kappa = 0.560$, $\lambda = 0.813$, phylogenetic correlation $= 0.736$, LR $= 62.699$, d.f. $= 1$, $p < 0.001$, $n = 161$; phylogenetically independent contrasts: $F_{1,133} = 85.219$, $p < 0.001$, slope $= 2.88 \times 10^{-4}$ on ranked values; figure 1). This could result from similar selective forces acting on brain size in the two sexes. We found that feeding innovation was related to relative brain size to a similar extent in the two sexes (relative female brain size: GLS approach, $\kappa = 0.435$, $\lambda = 0.761$, phylogenetic correlation $= 0.239$, LR $= 2.173$, d.f. $= 1$, $p = 0.037$, $n = 74$; independent contrasts, $F_{1,69} = 4.667$, $p = 0.034$, slope $= 1.84 \times 10^{-4}$ on ranked values; relative male brain size: GLS approach, $\kappa = 0.577$, $\lambda = 0.768$, phylogenetic correlation $= 0.297$, LR $= 3.405$, d.f. $= 1$, $p = 0.009$, $n = 74$; independent contrasts, $F_{1,69} = 8.219$, $p = 0.006$, slope $= 2.68 \times 10^{-4}$ on ranked values; relative brain size dimorphism: GLS approach, $\kappa = 0.368$, $\lambda = 0.000$, phylogenetic correlation $= -0.056$, LR $= 0.117$, d.f. $= 1$, $p = 0.629$, $n = 74$; figure 2).

Careful inspection of covariation of relative brain size between the sexes (figure 1) suggests that some of the unexplained variance ($1 - r^2 = 0.458$, based on the phylogenetically corrected correlation coefficient for the relationship between male and female brain size given by the GLS approach) may be attributable to selection pressures acting differently on the two sexes. When we characterized the evolution of relative brain size in males and females separately, using the same phylogenetic tree, we found different patterns for the two sexes. In females, shorter branches in the phylogeny contributed more to trait evolution ($\kappa = 0.670$ versus $\kappa = 1.000$: LR $= 4.599$, d.f. $= 1$, $p = 0.002$, $n = 161$), and phylogenetic relationships had minor effects ($\lambda = 0.659$ versus $\lambda = 1.000$: LR $= 5.206$, d.f. $= 1$, $p = 0.001$, $n = 161$). By contrast, for males, there was no deviation from default gradualism ($\kappa = 0.917$ versus $\kappa = 1.000$: LR $= 0.248$, d.f. $= 1$, $p = 0.482$, $n = 161$), and the phylogeny correctly predicted the covariance of relative brain size among species ($\lambda = 0.993$ versus $\lambda = 1.000$: LR $= 0.281$, d.f. $= 1$, $p = 0.454$, $n = 161$).

There was no significant interspecific association between extra-pair paternity and relative brain size in either sex (females: $\kappa = 0.544$, $\lambda = 0.819$, phylogenetic correlation $= -0.072$, LR $= 0.099$, d.f. $= 1$, $p = 0.656$, $n = 38$; males: $\kappa = 0.488$, $\lambda = 0.787$, phylogenetic correlation $= -0.236$, LR $= 1.093$, d.f. $= 1$, $p = 0.139$, $n = 38$). However, we found a significant positive phylogenetic correlation between relative brain size dimorphism and
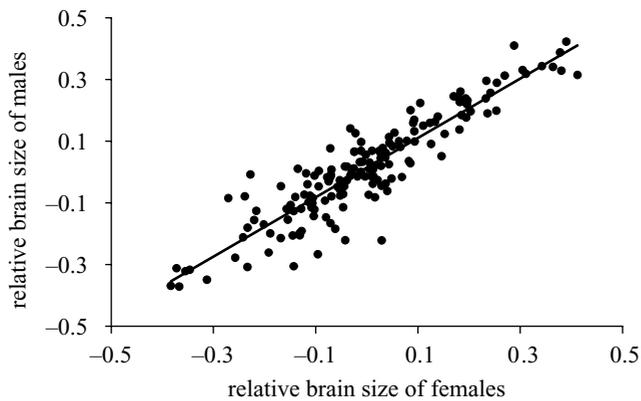
Figure 1. Relationship between relative brain size of female and male birds based on raw species data ($F_{1,160} = 813.684$, $p < 0.001$). The linear regression line is given (the corresponding equation: $Y = 0.962 \times X + 0.014$).



Figure 2. Interspecific relationship between frequencies of feeding innovation reported for European species and relative female brain size (filled circles) and male brain size (open triangles) based on raw species data. The solid line is for females, while the dashed line is for males, both representing linear regression lines. Corresponding statistics: relative female brain size: Kendall $\tau = 0.278$, $p < 0.001$, $n = 74$; relative male brain size: Kendall $\tau = 0.311$, $p < 0.001$, $n = 74$; relative brain size dimorphism: Kendall $\tau = -0.037$, $p = 0.652$, $n = 74$.

extra-pair paternity, indicating that in species with a higher degree of extra-pair paternity females have relatively larger brains than males (GLS approach, $\kappa = 0.019$, $\lambda = 0.000$, phylogenetic correlation $= 0.330$, LR $= 2.189$, d.f. $= 1$, $p = 0.036$, $n = 38$; independent contrasts, $F_{1,36} = 12.751$, $p = 0.001$, slope $= 4.83 \times 10^{-4}$ on ranked values; figure 3a). This pattern remained unchanged when we entered extra-pair paternity and relative brain size dimorphism together with the confounding variables (paternal care and sexual dichromatism) in the same phylogenetic model, and calculated partial phylogenetic correlations (GLS approach, LR test for correlated trait evolution: $\kappa = 0.000$, $\lambda = 0.000$, LR $= 10.572$, d.f. $= 6$, $p = 0.002$, $n = 26$; partial phylogenetic correlations with extra-pair paternity: relative brain size dimorphism: $r = 0.383$, $p = 0.032$; paternal care : $r = -0.519$, $p = 0.002$; sexual dichromatism: $r = 0.516$, $p = 0.002$; independent contrasts, extra-pair paternity and relative brain size dimorphism when controlling for sexual dichromatism and paternal care, $F_{1,24} = 6.008$, $p = 0.022$, slope $= 8.59 \times 10^{-4}$ on ranked values; figure 3b).

We checked whether the observed phylogenetic association between relative brain size dimorphism and extra-pair paternity was mediated by evolutionary increase in female relative brain size or by evolutionary decrease in male relative brain size relative to the opposite sex. We introduced relative brain sizes of the sexes in the same model and tested their effects on extra-pair paternity. When we controlled for covariation between sex-specific relative brain sizes, we found that male relative brain size was negatively related to extra-pair paternity, whereas female brain size was positively but not significantly related to extra-pair paternity (LR test for correlated trait evolution: $\kappa = 0.587$, $\lambda = 0.788$, LR $= 27.584$, d.f. $= 3$, $p < 0.001$, $n = 38$; partial phylogenetic correlations: female relative brain size: $r = 0.253$, $p = 0.091$; male relative brain size: $r = -0.333$, $p = 0.021$; figure 3c).

## 4. DISCUSSION

Our phylogenetic results revealed that among avian species, female and male relative brain size is positively correlated. This is in accordance with predictions based on natural selection, as behavioural adaptation to different

ecological conditions should act independently of sex, resulting in similar evolution of brain size in the two sexes. In an analysis of opportunistic feeding innovation, we found that selection may cause brain enlargement in both males and females in a similar way. By contrast, we found an association between relative sexual size dimorphism in brains and extra-pair paternity. This pattern was independent of the phylogenetic method used. Our results are in line with the hypothesis that sexual selection by favouring sex differences in behaviour may cause relative brain size differences between males and females.

Specifically, the observed relationship indicates that the evolution of extra-pair paternity towards higher rates appeared to be accompanied by both a reduction of male brain size relative to female brain size, and an increase of female brain size relative to male brain size. This dual effect may have simultaneously led to sexually size dimorphic brains with females having relatively larger brains than males in species with intense sperm competition. By contrast, males have relatively larger brains than females in species with a lower degree of extra-pair paternity. Based on our findings it is difficult to make a judgement about the causal mechanism, namely whether the evolution of extra-pair paternity promotes sexual differences in brain size, or whether sexual differences in brain size allow intense sperm competition. In addition, the small sample size that was available for this study requires cautious interpretations.

The decrease in relative male brain size with increasing extra-pair paternity may appear to be owing to a causal mechanism in which the efficient behavioural control of extra-pair paternity by males results in reduced levels of cuckoldry. For example, males having larger brains may be more successful in coping with the neurological demands of active mate guarding by rapidly following the females by adopting superior manoeuvring techniques. By contrast, in species with intense sperm competition, females may benefit from evolving large brains, because of the increased cognitive capacities required to compare potential copulation
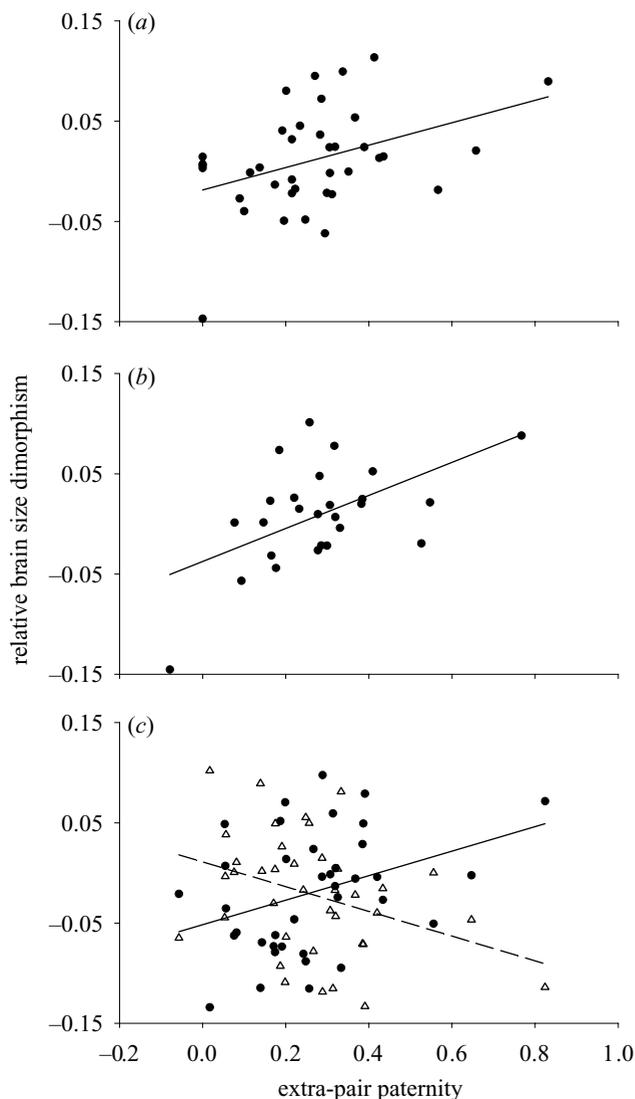
Figure 3. Interspecific relationship between relative brain size dimorphism and extra-pair paternity in birds. (*a*) Raw species data with extra-pair paternity being square-root arcsine-transformed ($F_{1,37} = 6.641$, $p = 0.014$). (*b*) The relationship between relative brain size dimorphism and extra-pair paternity when the potentially confounding effects of sexual dichromatism and paternal care on extra-pair paternity were controlled in a multiple regression (dependent variable: brain size dimorphism, independent variables: extra-pair paternity square-root arcsine transformed, paternal care square-root arcsine-transformed, sexual dichromatism; overall $F_{3,25} = 3.031$, $p = 0.051$; extra-pair paternity, $F_{1,25} = 8.919$, $p = 0.007$; paternal care, $F_{1,25} = 0.784$, $p = 0.385$; sexual dichromatism, $F_{1,25} = 2.508$, $p = 0.128$). Values are residuals from this regression. (*c*) The relationship between extra-pair paternity and sex-specific, relative brain sizes when covariation between male and female brain size was held constant in a multiple regression (dependent variable: extra-pair paternity, independent variables: relative brain size of females, relative brain size of males; overall $F_{2,37} = 3.733$, $p = 0.034$; relative brain size of females, $F_{1,37} = 4.438$, $p = 0.042$; relative brain size of males, $F_{1,37} = 7.000$, $p = 0.012$). Values are residuals from this regression. The interaction term represents the association between brain size dimorphism and extra-pair paternity (see statistics above). We assessed the importance of extreme data points by calculating non-parametric correlations, thus based on ranked values, between relative brain size dimorphism and extra-pair paternity. This approach revealed similar results compared with the results based on parametric statistics ((*a*) Kendall $\tau = 0.218$, $p = 0.056$, $n = 38$; (*b*) Kendall $\tau = 0.311$, $p = 0.026$, $n = 26$; (*c*) females, Kendall $\tau = 0.181$, $p = 0.110$, $n = 38$; males, Kendall $\tau = -0.289$, $p = 0.011$, $n = 38$). The linear regression lines are given. Filled circles and solid line are for females, whereas open triangles and dashed line are for males.

partners, and the improved spatial memory used to return to the chosen male after initial assessment. Sperm competition may be under the behavioural and physiological control of both males and females, and female choice and male–male competition may play partial roles in determining extra-pair paternity in birds (Westneat & Stewart 2003). Our analyses imply that male-driven sperm competition requiring behavioural and neural adaptation may be more important in species with reduced extra-pair paternity, as males have larger brains relative to females in species with little extra-pair paternity. By contrast, female control of paternity by complex behaviours may be more pronounced when sperm competition is intense, as females have relatively larger brains than males in species with a high rate of extra-pair paternity.

Extra-pair paternity is negatively related to paternal care among species of birds (e.g. Griffith *et al.* 2002), and this may generate an indirect relationship between brain size dimorphism and extra-pair paternity. Uncertainty in paternity decreases male parental care, and in species with a high level of extra-pair paternity females provide relatively more care for nestlings than males. In such cases, intense maternal care could be associated with enhanced neural functions in females, also leading to sex-biased brain

enlargement (see also Gittleman 1994). However, when we controlled for this potentially confounding factor, together with sexual dichromatism that is also related to extra-pair paternity (Møller & Birkhead 1994; Owens & Hartley 1998; Bennett & Owens 2002; Griffith *et al.* 2002), the relationship between extra-pair paternity and brain size dimorphism remained significant. Therefore, it seems that extra-pair paternity is related to brain size dimorphism independent of its association with paternal care. Therefore, it remains unlikely that reduced male parental care would lead to brain enlargement in females through increased parental duties in species with a high level of extra-pair paternity. The phylogenetic analysis with the potentially confounding variables showed that there was a significant and positive partial correlation between sexual dichromatism and extra-pair paternity, which strengthens previous evidence (Griffith *et al.* 2002). Our results imply that sperm competition enhances sexual dimorphism in plumage coloration and brain size independently of each other. Thus, selection pressures resulting from increased extra-pair paternity select for males with elaborate sexual characters, and for females with cognitive capacities, perhaps facilitating behavioural control over extra-pair copulations. By contrast, in species with low rates of extra-pair paternity males evolve larger brains than females, but they display less elaborate sexual signals. Our results show that these mechanisms may be independent of each other,

since the relationship between extra-pair paternity and brain size dimorphism was not confounded by the relationship between extra-pair paternity and sexual dichromatism.

The evolution of reproductive mechanisms is determined by both natural and sexual selection to optimize reproductive success under given environmental conditions. Hence, factors associated with natural selection may also be linked to reproduction, which may potentially favour similar brain size evolution in the two sexes, as driven by similar selection pressures causing female brain size to evolve alongside male brain size due to pleiotropy (Lande 1980; Lindenfors & Sillén-Tullberg 1998). Data on bowerbirds suggested that interspecific variation in bower complexity, a sexually selected trait, was associated with variation in relative brain size in both males and females (Madden 2001). However, natural selection seems to not mediate a similar link for extra-pair paternity in birds, since we did not find a relationship between brain size and extra-pair paternity in either of the sexes when analysed separately. Only sexual dimorphism in brain size appeared to be associated with sperm competition, which emphasizes the role of sexual selection.

In conclusion, we have shown among birds for the first time that brain size evolution may be independent in the two sexes. Deviations from the intersexual relationship in brain size were explained by factors associated with extra-pair paternity, which suggests a selective role for sex-specific behavioural patterns in sperm competition. The relationship between brain size dimorphism and extra-pair paternity is likely to arise from selection due to sex-dependent control of paternity affecting the evolution of sexually dimorphic, complex behaviour and associated neural tissues. Brain capacity in relation to sex-specific behaviour can thus be shaped differently in the two sexes by sexual selection.

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