

Sexual selection on brain size in shorebirds (Charadriiformes)

G. E. GARCÍA-PEÑA*, D. SOL*†, A. N. IWANIUK‡§ & T. SZÉKELY¶

*CREAF, Cerdanyola del Vallès, Spain

†CSIC, Cerdanyola del Vallès, Spain

‡National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

§Department of Neuroscience, Canadian Centre for Behavioural Neuroscience, University of Lethbridge, Lethbridge, AB, Canada

¶Department of Biology and Biochemistry, University of Bath, Bath, UK

Keywords:

birds;
body size evolution;
Charadriidae;
life histories;
parental care;
trade-off.

Abstract

Natural selection is considered a major force shaping brain size evolution in vertebrates, whereas the influence of sexual selection remains controversial. On one hand, sexual selection could promote brain enlargement by enhancing cognitive skills needed to compete for mates. On the other hand, sexual selection could favour brain size reduction due to trade-offs between investing in brain tissue and in sexually selected traits. These opposed predictions are mirrored in contradictory relationships between sexual selection proxies and brain size relative to body size. Here, we report a phylogenetic comparative analysis that highlights potential flaws in interpreting relative brain size-mating system associations as effects of sexual selection on brain size in shorebirds (Charadriiformes), a taxonomic group with an outstanding diversity in breeding systems. Considering many ecological effects, relative brain size was not significantly correlated with testis size. In polyandrous species, however, relative brain sizes of males and females were smaller than in monogamous species, and females had smaller brain size than males. Although these findings are consistent with sexual selection reducing brain size, they could also be due to females deserting parental care, which is a common feature of polyandrous species. Furthermore, our analyses suggested that body size evolved faster than brain size, and thus the evolution of body size may be confounding the effect of the mating system on relative brain size. The brain size-mating system association in shorebirds is thus not only due to sexual selection on brain size but rather, to body size evolution and other multiple simultaneous effects.

Introduction

Most theories of vertebrate brain evolution consider natural selection as the main evolutionary force driving its diversification in size (Jerison, 1973; Bennett & Harvey, 1985a; Pagel & Harvey, 1988; Allman *et al.*, 1993; Aiello & Wheeler, 1995; Lefebvre *et al.*, 1997; Reader & Laland, 2002; Sol *et al.*, 2007). Although sexual selection is thought to shape brain size evolution, currently there is no theoretical consensus on how sexual selection may affect brain size (Jacobs, 1996; Lindenfors *et al.*, 2007). For some authors, sexual selection should

favour larger brains because it enhances cognitive skills needed to obtain mates (Miller, 2000; Madden, 2001). For example, Miller (2000) argued that sexual selection favouring creative males lead the evolution of unusually large brains in humans. Likewise, Garamszegi *et al.* (2005) argued that sexual selection favours larger brains in birds, but in this case because of the cognitive demands of female mate choice. These hypotheses are based on the assumption that a large brain enhances cognitive abilities that favour mating. In birds and mammals, this assumption is plausible as cognitive traits are under sexual selection (Boogert *et al.*, 2011) and brain size is correlated with cognition (Lefebvre & Sol, 2008). Alternatively, other authors propose that rather than favouring large brains, sexual selection should favour smaller brains on the grounds that suc-

Correspondence: Gabriel E. García-Peña, CREAF (UAB), Cerdanyola del Vallès, Barcelona, Spain. 08193.
Tel.: +34 93 5811312; fax: +34 93 5814151; e-mail: gegp01@gmail.com

cessfully competing for mates diverts energy available for the brain. The expensive sexual tissue hypothesis, for example, suggests a trade-off between allocating energy in brain tissue or in sexually selected traits (Pitnick *et al.*, 2006).

Tests of these two opposing views for the role of sexual selection on brain size evolution have yielded contradictory findings. Some studies support positive relationships between brain size and sexually selected traits (Madden, 2001; Garamszegi *et al.*, 2005), whereas others report negative relationships (Pitnick *et al.*, 2006) or no relationships at all (Schillaci, 2006; Guay & Iwaniuk, 2008; Lemaitre *et al.*, 2009). Perhaps, the only consistent pattern is that linking brain size and mating system. In birds and mammals, polygynous species – in which sexual selection favours males mating with multiple partners – have small brains compared with socially monogamous species (Bennett & Harvey, 1985b; Pitnick *et al.*, 2006; Dunbar & Shultz, 2007). However, in absence of evidence that selection acts differentially on female and male brains, it remains unclear whether the brain-mating system association is due to sexual selection or natural selection.

In addition, the controversial and sometimes bewildering evidence on the effects of sexual selection on brain size reflects our inability to readily manipulate brain size for experimentation, which forces us to draw conclusions based on comparative analyses (Healy & Krebs, 1992; Garamszegi & Eens, 2004; Pérez-Barbería *et al.*, 2007). Although the comparative approach is a powerful tool to investigate evolutionary patterns, its correlative nature makes it very sensitive to confounding factors (Harvey & Pagel, 1991; Martins, 2000; Bennett & Owens, 2002). For example, Pitnick *et al.* (2006) showed that echolocating bat species with large testes have smaller brains than bats with small testes. However, thorough studies showed that the correlation disappears when differences in the ecology of species are accounted for in the analyses (Jones & MacLarnon, 2004; Dechmann & Safi, 2009). This example illustrates that a number of factors may confound relationships between proxies of sexual selection and brain size because the whole brain is the target of multiple selection pressures (Healy & Rowe, 2007) and therefore species' life history deserves special attention (Sol, 2009). For example, a relationship between brain size and mating system may be confounded by the trade-off between an animal's decision to compete for mates or to provide parental care (Trivers, 1972; Clutton-Brock, 1991; Székely *et al.*, 2000; Olson *et al.*, 2008). Parental care opposes sexual selection and vice versa (Arnqvist & Rowe, 2005; Thomas & Székely, 2005; Gonzalez-Voyer *et al.*, 2008; Kokko & Jennions, 2008), and is associated with brain size enlargement via two mechanisms. First, the offspring of large-brained birds and mammals are born undeveloped and vulnerable (Bennett & Harvey, 1985a; Iwaniuk & Nelson, 2003; Shultz & Dunbar,

2010) and natural selection should favour parents that boost offspring survival by increasing parental care (Clutton-Brock, 1991; Garamszegi *et al.*, 2007). Thus, reductions in care associated with polygamy may constrain brain size enlargement. Second, parental care might select for a large brain in the caring parent with increased cognitive demands, particularly if parental care is essential for the offspring to survive. Indeed, studies in fish and mammals showed that the brain is larger in the sex that provides uniparental care (Gittleman, 1994; González-Voyer *et al.*, 2009).

Another difficulty when studying the role of sexual selection on brain size evolution is related to allometry. As larger animals have larger brains, to obtain biologically meaningful measures of brain size it is common practice to remove the allometric effect of body size (Jerison, 1973). Previous studies have shown that cognitive performance increases with the extent to which species have a larger or smaller brain than expected by their body size (relative brain size) rather than with absolute brain size (Lefebvre & Sol, 2008). However, because sexual selection often has strong effects on body size, a seldom tested but fundamental confound is that correlations between relative brain size and proxies of sexual selection could be due to differences in body size rather than in brain size (Deaner & Nunn, 1999; Lindenfors *et al.*, 2003; Fairbairn *et al.*, 2007; Fitzpatrick *et al.*, 2012).

Considering the above and building upon previous studies, we combined a robust phylogenetic hypothesis (Thomas *et al.*, 2004) with modern phylogeny-based statistical methods to analyse the associations between brain size and two widely used surrogates of sexual selection (mating system and testis size) in shorebirds (Charadriiformes: 380 species (Gill & Donsker, 2010) sandpipers, plovers, gulls and allies). Shorebirds are an excellent model system to test these relationships because they exhibit an unusual diversity in breeding systems, ecology and life histories (Székely & Reynolds, 1995; Reynolds & Székely, 1997; Figuerola, 1999; Bókonyi *et al.*, 2003; Thomas *et al.*, 2007). Since the intensity of sexual selection should be sex-specific, we measured both male and female brain sizes of 184 species and tested whether relative brain sizes of males and females are correlated with the two indicators of sexual selection, by using phylogenetic linear models (Pagel, 1997; Orme *et al.*, 2012). Relative brain sizes of males and females did not correlate with testis size, however, relative brains were smaller in polyandrous species than in monogamous ones. Second, using model selection methods (Burnham & Anderson, 2002) we corroborated that the brain size-mating system associations were robust over a set of confounding effects, such as offspring developmental mode and ecological effects (Garamszegi & Eens, 2004; Winkler *et al.*, 2004; Sol *et al.*, 2005; Dechmann & Safi, 2009). Our model selection procedure showed that correlations between

mating system and relative brain size were equally explained by reductions of female care. Third, we asked whether sexual size dimorphism in relative brain size was correlated with mating system, as predicted by the effect of sexual selection on brain size, and examined the extent to which males and females are different in body size and brain size. Multi-response phylogenetic generalized mixed linear models, MCMC_{GLMM} (Hadfield, 2010), showed that females had smaller relative brain sizes than males; however, both body size and brain size were larger in females than males. This was evidence that sexual size dimorphism in relative brain size was due to sexual dimorphism in body size rather than in brain size, and was further supported by verifying that body size evolved faster than brain size in polyandrous species (O'Meara *et al.*, 2006). Taken together, our results highlight the need to consider body size evolution when investigating whether sexual selection shaped brain size evolution, and suggest that sexual selection is not the only plausible explanation of the mating system-brain size association in shorebirds.

Materials and methods

Brain size

Two major criticisms of the comparative analyses on brain size are the use of brain measurements collected by different authors using different methodologies, and that brain size may vary within the life time of an individual (Healy & Rowe, 2007). To account for these potential problems in our study, one researcher (ANI) estimated adult brain volumes using a single technique, the endocast method, which estimates brain volumes by filling the skulls of museum specimens with lead shot. Although this is an indirect measure of brain size, endocranial measures yield unbiased and highly repeatable estimates of brain volumes and they bear the advantage that the endocranial cavity in birds does not change with age as long as the skull has completed development (Iwaniuk & Nelson, 2002). To account for the potential problem that brain size may vary within taxa, endocranial volumes were measured separately for males and females for 1346 specimens representing 184 shorebird species (median per species: 4 males (range = 1–9), and 4 females (range = 1–8)) (Appendix S1). We corroborated that there was no bias in the precision of the brain size estimates due to sample size, by establishing that standard errors in brain size estimates were not correlated with the sample sizes used (Males: $r_{\text{Pearson's}} = -0.093$, $P = 0.259$; Females: $r_{\text{Pearson's}} = -0.098$, $P = 0.227$).

Body size

Fresh body masses were rarely available for museum specimens, and individual body masses can be skewed

due to reproductive condition, migration and other seasonal effects. To account for body mass in an unbiased fashion, sex-specific averages of body masses were obtained from published sources (Appendix S1).

Sexual selection proxies

We analysed the associations between male and female brain sizes and two indicators of sexual selection: testis size and the social mating system (Reynolds & Székely, 1997; Bennett & Owens, 2002; Székely *et al.*, 2006; Thomas *et al.*, 2007). Extra-pair paternity is rare (4.3%, range = 0–15.4, $n = 9$ species) in socially monogamous shorebirds (Thomas *et al.*, 2007). Nevertheless, testis size is a proxy of sperm competition and it is an aspect of sexual selection that may be hidden from mating behaviour (Birkhead & Møller, 1998). The expensive sexual tissue hypothesis predicts a trade-off between male brain size and testis size, whereas brain size enlargement favoured by sexual selection predicts positive correlations between testis size and male brain size, and female brain size (Garamszegi *et al.*, 2005). For our study, measurements of testis mass (g) were obtained from the literature and transformed to natural logarithms for analyses (Dunn *et al.*, 2001).

The extent of male and female polygamy for each species was obtained from previous studies and scored in an ordinal scale (Liker & Székely, 2005; Thomas *et al.*, 2007; Olson *et al.*, 2008): 0 = no polygamy is reported in the species, 1 = polygamy is anecdotal (1%), 2 = polygamy is 1–5%, 3 = polygamy is 6–20%, or 4 = polygamy > 20%. However, the majority of species in our dataset have either monogamy or polygamy and very few species have intermediate scores. We therefore classified the social mating system as follows: (i) social monogamy, (ii) polyandry (monogamous males and polygamous females in the populations $\geq 1\%$), (iii) polygyny (polygamous males in the population $\geq 1\%$ and monogamous females) and (iv) promiscuous (polygamy $\geq 1\%$ in both males and females). Results did not change in quality when considering either the mating system as a factor or the ordinal scores of male and female polygamy (Appendices S2 and S3).

Confounding variables

To test the consistency of correlations between brain size and proxies of sexual selection, we considered all possible candidate models given by a set of confounding variables that are correlated with brain size: parental care system, offspring developmental mode and ecological effects. As explained previously, parental care is associated with both brain size and proxies of sexual selection, and may be a potentially confounding factor (Olson *et al.*, 2008). The duration of parental care by either or both sexes varies among shorebirds (Reynolds & Székely, 1997; García-Peña *et al.*, 2009). Although an

ordinal scale ranging from 0 to 7 was used by Székely & Reynolds (1995), very little variation in parental care was observed among the species in our data set; the majority of species exhibited either biparental care until the offspring hatches, or desertion by one of the parents before hatching. We therefore scored parental care as follows: (i) female care if the female alone cares for the offspring after eggs hatch; (ii) male care if the male alone cares for the offspring after eggs hatch; and (iii) biparental care if both parents care for the young after eggs hatch. The presented results did not change qualitatively when considering the original scores of male and female parental care as predictors of brain size (Appendices S2 and S3). The offspring's stage of development at hatching is also a significant explanatory variable of brain size (Starck & Ricklefs, 1998). Hence, we differentiate two types of development based on Thomas & Székely (2005). Each species was scored as '0' if the offspring is self-fed at hatching or '1' if the offspring is fed by the parents. These scores approximate precocial and semi-precocial developmental modes, respectively (Iwaniuk & Nelson, 2003), which are associated with the stage of development at hatching, growth rate (Tjørve *et al.*, 2009) and the amount and quality of parental care in shorebirds (Thomas & Székely, 2005).

We also considered a number of ecological variables that could potentially explain variation in brain size. First, we consider migratory distance and breeding latitude of each species. Bird species that breed at northern latitudes exhibit remarkably different life histories than species in the tropics (Moreau, 1944; Lack, 1968; Martin, 1996; Russell, 2000; García-Peña *et al.*, 2009), and relative brain size is negatively correlated with migratory distance (Winkler *et al.*, 2004; Sol *et al.*, 2005, 2010). For each species, breeding and nonbreeding latitudes were measured as the latitudes of its breeding and nonbreeding range centroids, respectively (del-Hoyo *et al.*, 1996; Riede, 2004), and the migratory distance was estimated as the distance between centroids measured over an earth model (WGS84 ellipsoid). Second, we considered the associations between foraging behaviour and brain size (Dechmann & Safi, 2009; González-Voyer *et al.*, 2009). We included male and female bill lengths (mm) transformed to natural logarithms in our analyses because bill length reflects foraging behaviour in shorebirds (Nebel *et al.*, 2005). Additionally, we considered the diversity of dietary habitats by adding four independent binary variables in our multivariate analyses. In fishes, species that feed on motile prey have smaller brains than species that feed on sessile prey (González-Voyer *et al.*, 2009). Therefore, we used the descriptions from del-Hoyo *et al.* (1996) to differentiate whether a species: (i) hunts fast prey such as fish, squid, terrestrial vertebrates (e.g. mice and birds) and flying insects; (ii) forages for slow prey such as insect larvae and intertidal invertebrates; (iii) it

forages for sessile prey such as seeds, carrion and/or zooplankton; and (iv) whether the species dives or not. Note that all these binary variables are independent such that species that eat zooplankton, intertidal invertebrates and fish but does not dive, will be scored as: fast prey = 1, slow prey = 1, sessile prey = 1, dives = 0 (Appendix S1). Finally, we differentiated between nest types: (0) species that nest on the ground and (1) species that nest on less accessible habitats such as trees, cliffs or floating vegetation. Bird species breeding in closed habitats have longer nestling periods than species breeding in open habitats (Martin & Li, 1992), and this may also confound the relationships between brain size and proxies of sexual selection.

Phylogeny

The phylogeny used in our analyses was the one proposed by Thomas *et al.* (2004), with branch lengths dated in million years and polytomies solved by randomly assigning branch lengths of 1000 years (Paradis *et al.*, 2004). Currently, it is the most complete phylogenetic hypothesis of shorebirds available.

Data analyses

We used phylogenetic generalized linear models (PGLM) (Grafen, 1989; Pagel, 1997; Freckleton *et al.*, 2002) to represent sex-specific brain size (ln-transformed) as a function of proxies of sexual selection (either mating system or testis size) while controlling for sex-specific body masses (ln-transformed) as covariates. PGLM parameters were estimated while accounting for the nonindependence of interspecific data by modifying the structure of the covariance matrix according to the phylogenetic distance between taxa (Harvey & Pagel, 1991; Martins, 2000). Phylogenetic distance was estimated from the shorebird super-tree (Thomas *et al.*, 2004); and we improved the fit of each PGLM to the data by estimating and fitting the maximum likelihood value of (λ) a parameter that scales the covariance matrix to maximize the fit of the data to a Brownian model of evolution (Pagel, 1999; Freckleton *et al.*, 2002). To test how robust the relationships were between brain size and surrogates of sexual selection, we used AIC (Akaike, 1974) to perform a model selection procedure (Burnham & Anderson, 2002). We examined the best PGLMs on ln brain size (response) among candidate models given by combinations of the variables: ln body size, parental care, offspring development, ecological variables and a sexual selection proxy (either testis size or mating system). Note that all candidate models included body size as a predictor of brain size because the interest of these analyses was on relative brain size. If a relationship between brain size and a sexual selection proxy is robust, models with an AIC difference $\Delta i \leq 2$ must

contain the sexual selection proxy ($\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$, for model i), otherwise evidence would suggest that there is an equivalent model that explains brain size without implying a sexual selection hypotheses. AIC is a useful criteria to compare the fit of these models because it accounts for the number of parameters in each model, and the fit of a model can be assessed in relation with the other candidate models by using the Akaike weight (Kullback & Leibler, 1951; Burnham & Anderson, 2002). Models must be fitted on the same data to be compared with the AIC, and thus, we only considered data for which we had information on all variables ($N = 87$).

Parental care and social mating system are correlated ($\chi^2 = 147.7$, d.f. = 6, $P < 0.001$) such that monogamous species tend to have biparental care, polyandrous species male care and polygynous species female care (Appendix S4). Thus, including both variables in the same model may generate multi-collinearity. In principle, however, models with multi-collinearity are expected to have higher AICs than simpler models with no multi-collinearity, and thus these should not be among the best candidate models ($\Delta_i \leq 2$).

Once we established that relative brain size in males and females was smaller in polyandrous species than in monogamous ones (see Results), we performed two tests: (i) whether sexual dimorphism in relative brain size is correlated with mating system, and (ii) whether sexual size dimorphism in relative brain size is due to brain size or to body size. To perform these tests, we used a Markov Chain Monte Carlo (MCMCGLMM) procedure that estimated the parameters of a generalized linear mixed model while accounting for the phylogenetic distance between taxa, as a random variable, and two predictors the mating system and sex. The latter was a factor describing whether the measurements were of a male or a female (Hadfield, 2010). For these analyses, we transformed brain size and body size to the same scale ($y = \ln y_i - \ln Y$), where i denotes a given observation of trait y and Y is the average of all observed values of y (males and females pooled). To test whether polyandrous species exhibit sexual size dimorphism in relative brain size, we tested the correlation between brain size (response variable) and the interaction between mating system and sex, with body size as a covariate. Then, we examined the extent to which males and females are different in body and brain size by analysing the relationships between mating system (predictor) and both body and brain sizes (multivariate response), while considering the covariation between brain size and body size (Appendix S5). MCMCGLMM used an inverse Wishart prior for the covariances, and for fixed effects we used diffuse normal priors centred around zero with very large (10^{10}) variance (Hadfield, 2010). Each linear predictor was allowed to have unique residuals, and we let the MCMC algorithm ran for 120 000 000

iterations, with a burn in period of 1 000 000 and sampling interval of 10 000 that generated 11 900 independent samples of the model parameters. Support for estimated parameters was assessed by the highest posterior density (HPD) intervals for the parameters in the in the Markov chain (Plummer *et al.*, 2006), and the independency of samples in the Markov chain was assessed by graphic diagnostics and testing for autocorrelation between samples (Appendix S6).

Finally, we asked whether brain size sexual dimorphism in polyandrous species is the result of brain size evolving faster than body size. We performed 1000 reconstructions of the most likely transitions in mating systems during the evolutionary history of shorebirds (Appendix S7), by implementing stochastic character mapping, SIMMAP (Huelsenbeck *et al.*, 2003; Bollback, 2006), and then used a restricted maximum likelihood approach to fit Brownian rate variation (noncensored) models (O'Meara *et al.*, 2006) to female and male brain sizes and body sizes (each sex was analysed separately, and data were scaled as in MCMCGLMM analyses). The estimated rate of Brownian variation associated with the evolution of polyandry was used to assess the rate of evolutionary change in brain size and body size within polyandrous species. If sexual selection for polyandry affects female brain size, we would expect faster rates of evolution in female brain size than in female body size.

Phylogenetic and geographical analyses were performed in R 2.15.1 (R, 2011) using the packages: APE 2.8 (Paradis *et al.*, 2004), GEIGER 1.3-1 (Harmon *et al.*, 2009), OCE (Kelley, 2011), MCMCGLMM (Hadfield, 2010), CODA (Plummer *et al.*, 2006) CAPER (Orme *et al.*, 2012) and phytools (Revell, 2012). Geographical coordinates were estimated in ArcGIS and R when maps were available in literature (Riede, 2004; BirdLifeInternational & NatureServe, 2011).

Results

Controlling for sex-specific body masses in the models, testis size was not correlated with male brain size ($t = -1.56$, $P = 0.113$, $N = 68$; overall fit of PGLM: $R^2 = 0.91$) or female brain size ($t = -0.73$, $P = 0.462$, $N = 68$; overall fit of PGLM: $R^2 = 0.91$). Mating system, however, was correlated with relative brain size in both males ($F_{3,104} = 3.24$, $P = 0.025$; overall fit of PGLM: $R^2 = 0.93$) and females ($F_{3,106} = 4.60$, $P = 0.005$; overall fit of PGLM: $R^2 = 0.93$). After accounting for the effect of body mass, brain size was smaller in polyandrous species than in monogamous ones (males: $t = -2.43$, $P = 0.016$; females: $t = -2.9$, $P = 0.008$), whereas brain size of polygynous (male: $t = 1.6$, $P = 0.112$; female: $t = 1.9$, $P = 0.671$) and promiscuous species (male: $t = 0.55$, $P = 0.579$; female: $t = 0.91$, $P = 0.363$) were not different from that of monogamous species (Fig. 1). Remarkably,

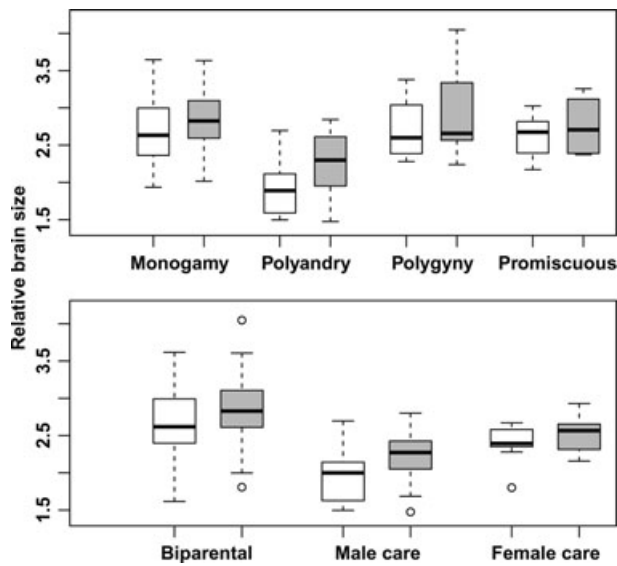


Fig. 1 Female brain size (white box) and male brain size (grey box) relative to female and male body masses (respectively), and their relationships with the social mating system (upper panel) and parental care system (lower panel). For visualization, relative brain sizes were calculated as $[y = \ln \text{brain size} * (\text{average } \ln \text{body mass across species} / \ln \text{species' specific body mass})^{0.6}]$. The mating and parental care systems were correlated ($\chi^2 = 147.7$, d.f. = 6, $P < 0.0001$). In polyandrous species usually the males care for the offspring after hatching, in polygynous species usually the females, and both parents tend to care for the offspring in monogamous species. A promiscuous mating system comprehends males and females exhibiting polygamy in which care after hatching can be provided by the male, the female or both.

absolute values of body size and brain size were not significantly different between mating systems (Fig. 2).

The relationships between testis size and relative brain sizes of males and females did not improve when considering other effects. Neither of the best candidate

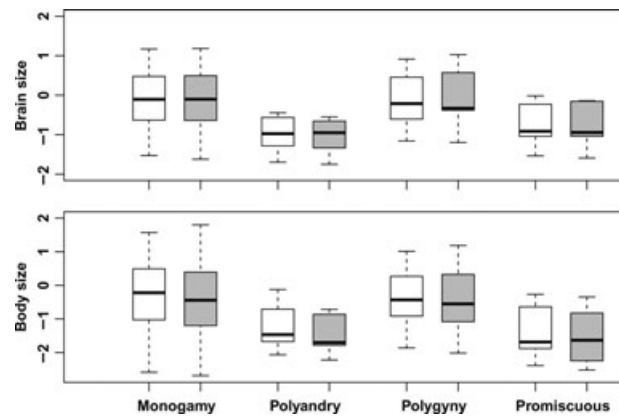


Fig. 2 Female (white boxes) and male (grey boxes) brain sizes and body masses in relation with the social mating system. Brain and body sizes were standardized. On average, brain size and body size are not different between mating systems. PGLMs: male brain ($F_{3,83} = 2.13$, $P = 0.103$); female brain ($F_{3,83} = 1.71$, $P = 0.171$); male body ($F_{3,83} = 0.94$, $P = 0.425$); female body ($F_{3,83} = 1.08$, $P = 0.364$).

models ($\Delta_i < 2$) included testis size as a significant predictor of male or female brain size. However, when we assessed how robust were the relationships between brain sizes and mating systems, each of the best candidate models ($\Delta_i < 2$) contained either mating system, parental care or both as predictors of brain size (Tables 1 and 2, Fig. 2). In males and females, there was no evidence that models including mating system fit the data better than those including parental care. Note that among the best models (Table 2), only one included mating system, parental care and female body mass as predictors of female brain size. In this particular model, the parameter for parental care was nonsignificant ($F_{2,80} = 1.87$, $P = 0.161$), whereas the mating system was still a significant predictor of female brain size ($F_{3,80} = 5.92$, $P = 0.001$). Models including parental

Table 1 Phylogenetic comparative models on \ln male brain size (response) with $\Delta_i < 2$, among 2047 candidate models. Models including mating system are presented in bold font. Residual sum of squares (RSSQ), number of parameters (k), Akaike's information index (AIC), $\Delta_i = (AIC - AIC_{\min})$ and weight (w_i).

RSSQ	k	AIC	Δ_i	w_i	Model
0.02	6	-112.74	0.00	0.024	\ln male body mass + parental care + nest type
0.02	5	-111.80	0.94	0.015	\ln male body mass + parental care
0.02	7	-111.72	1.02	0.014	\ln male body mass + mating system + nest type
0.02	6	-111.50	1.24	0.013	\ln male body mass + mating system
0.02	7	-111.39	1.35	0.012	\ln male body mass + parental care + fast prey + nest type
0.02	7	-111.15	1.59	0.011	\ln male body mass + mating system + slow prey
0.02	6	-111.10	1.64	0.011	\ln male body mass + parental care + sessile prey + nest type
0.02	7	-110.94	1.80	0.010	\ln male body mass + mating system + offspring development
0.02	7	-110.92	1.82	0.010	\ln male body mass + parental care + slow prey + nest type
0.02	8	-110.90	1.84	0.010	\ln male body mass + mating system + offspring development + slow prey
0.02	8	-110.87	1.87	0.009	\ln male body mass + mating system + fast prey + nest type
0.02	6	-110.79	1.94	0.009	\ln male body mass + parental care + slow prey

Table 2 Phylogenetic comparative models on ln female brain size (response) with $\Delta_i < 2$, among 2047 candidate models. Models including mating system are presented in bold font. Residual sum of squares (RSSQ), number of parameters (k), Akaike's information index (AIC), $\Delta_i = (AIC - AIC_{\min})$ and weight (w_i).

RSSQ	k	AIC	Δ_i	w_i	Model
0.02	6	-127.32	0.00	0.032	In female body mass + mating system
0.02	7	-127.21	0.12	0.030	In female body mass + mating system + fast prey
0.02	7	-127.07	0.25	0.028	In female body mass + mating system + offspring development
0.02	8	-126.81	0.51	0.025	In female body mass + mating system + offspring development + fast prey
0.02	9	-126.36	0.97	0.020	In female body mass + mating system + parental care
0.02	5	-125.61	1.72	0.013	In female body mass + parental care
0.02	6	-125.33	1.99	0.012	In female body mass + parental care + offspring development

care and body mass as predictors of brain size indicated that in species where the female deserts and only the male provides care, males and females have smaller relative brains than in species with biparental care (male brain: $R^2 = 0.94$, $F_{4,83} = 419.01$, $t = -3.57$, $P < 0.001$; female brain: $R^2 = 0.94$, $F_{4,83} = 392.23$, $t = -3.53$, $P < 0.001$). In contrast, relative brain size was not significantly different between species with female-only care and species with biparental care (male brain: $t = -0.607$, $P = 0.545$, female brain: $t = -0.21$, $P = 0.832$, Fig. 1).

Finally, we examined whether sexual dimorphism in relative brain size was correlated with mating system. $MCMC_{GLMM}$ suggested that relative brain size was smaller in females than in males in polyandrous species (Table 3, Fig. 3), as would be expected if sexual selection promotes brain size reductions. However, we found no sexual dimorphism in polygynous species. Furthermore, a multivariate response $MCMC_{GLMM}$ (Materials and methods) showed that, in polyandrous species, females were larger in body size and had larger brains than males (Table 4, Fig. 3). Additionally, examining the evolutionary rates of brain and body sizes in polyandrous species, body size evolved faster than brain size in both males and females (Table 5).

Table 3 $MCMC_{GLMM}$ on sexual dimorphism in relative brain size, within mating systems. The model compares the female brain size against the male brain size, within each mating system, while accounting for sex specific body size as a covariate. We present posterior means of parameters (β), highest posterior density intervals at 95% (HPD), effective sample size (ESS) and bold fonts remarking support that $\beta \neq 0$. Brain and body sizes are standardized (Materials and methods).

	β	Lower HPD	Upper HPD	ESS
Body size	0.564	0.530	0.599	3967
Monogamy	-0.020	-0.035	-0.005	3967
Polyandry	-0.109	-0.147	-0.071	4329
Polygyny	-0.002	-0.043	0.040	3770
Promiscuous	-0.004	-0.054	0.053	4197

Discussion

Ours results yield little evidence for the expensive sexual tissue hypothesis because testis size was not correlated with male relative brain size in any of the analyses. Likewise, the lack of a significant correlation between testis size and female relative brain size does not support the idea that cognitive demands of female choice selects for larger brains (Garamszegi *et al.*, 2005). However, our results do suggest that relative brain size is associated with mating system. Although monogamous and polygynous species did not differ in relative brain size, as previous studies in mammals found (Bennett & Harvey, 1985b; Pitnick *et al.*, 2006; Dunbar & Shultz, 2007), polyandrous shorebirds have smaller relative brains than socially monogamous ones. As sexual selection is an important driver of polyandrous mating systems (Bennett & Owens, 2002), and because body size does not vary among mating systems, this result could be interpreted as sexual selection driving disproportional reductions of brain size in polyandrous species.

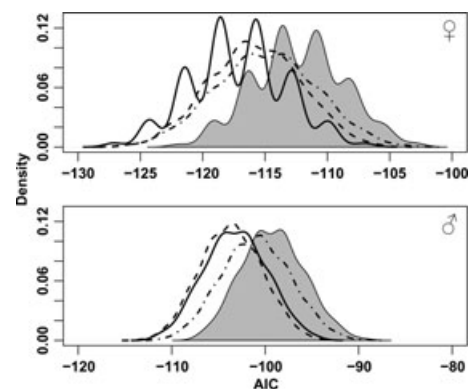


Fig. 3 Probability densities on the fit (AIC) of 2047 candidate phylogenetic linear models (PGLM) on female brain size (upper panel) and male brain size (lower panel) given by the mating system (solid line), parental care system (dashed line), both, mating and parental care systems (dot-dashed line) and null models (grey polygon). Null models include offspring development and ecological variables as predictors of brain size (see Materials and methods).

Table 4 MCMC_{GLMM} testing sexual size dimorphism within mating systems. The model compares the response variables (brain and body sizes) of the female against those of the male, within each mating system. We present posterior means of parameters (β), highest posterior density intervals at 95% (HPD), effective sample size (ESS) and bold fonts remarking support that $\beta \neq 0$. Brain and body sizes are standardized (Materials and methods).

	β	Lower HPD	Upper HPD	ESS
Brain:monogamy	-0.021	-0.036	-0.005	3967
Body:monogamy	-0.003	-0.034	0.032	3967
Brain:polyandry	0.055	0.018	0.092	3844
Body:polyandry	0.283	0.206	0.368	3967
Brain:polygyny	-0.039	-0.082	0.004	3967
Body:polygyny	-0.062	-0.146	0.031	3865
Brain:promiscuous	-0.004	-0.055	0.056	3967
Body:promiscuous	-0.009	-0.123	0.109	3967

Table 5 Evolutionary rates of scaled measurements of brain and body sizes in polyandrous species. The fit of Brownian rate variation models was performed over 1000 SIMMAP reconstructions of evolutionary transitions in mating systems. Median (rate) and confidence intervals (95% CI) are given. Estimated rates of all mating systems are available in Appendix S8.

	Rate	95% CI (lower, upper)	Convergence %
Female brain	0.0194	0.0193–0.0194	69.6
Female body	0.0455	0.0453–0.0456	91.2
Male brain	0.0264	0.0263–0.0265	73.3
Male body	0.0457	0.0455–0.0458	93.8

Nevertheless, before concluding that sexual selection is responsible for the relationship between polyandry and brain size in shorebirds, we first need to examine alternative mechanisms. First, the social brain hypothesis (Byrne & Whiten, 1988; Dunbar, 1998), interprets the larger brain of socially monogamous breeding species of mammals and birds as evidence that selection favouring pair bonding has triggered brain size enlargement (Dunbar & Shultz, 2007). This is a potential explanation for why polyandrous species have relatively smaller brains than monogamous species. However, the social brain hypothesis may not be the only explanation of the brain size-mating system association because relative brain size of monogamous species was not significantly larger than relative brain size of polygynous species.

A second alternative to the above hypotheses is that the brain size-mating system association is driven by the parental care system. The examination of a wide spectrum of candidate models, including potentially confounding effects, provides important insight into this possibility. Candidate models that included parental care instead of the social mating explained a similar amount of variation in male and female brain sizes than models considering the social mating system as a predictor. In fact, parental care system is strongly tied to the social

mating system such that the male alone cares for the offspring in polyandrous species, the female alone cares for the offspring in polygynous species, and biparental care is common in socially monogamous species (Lack, 1968; Thomas *et al.*, 2007). The models that included parental care suggest that relative brain size is smaller in species with male care than in species with either biparental care or female care. The fact that in polyandrous shorebirds the males care for the offspring and have larger relative brain size than females is consistent with other studies that suggested that the cognitive demands of post-zygotic parental care favour an increase in brain size in the sex that cares for the offspring alone (Gittleman, 1994; González-Voyer *et al.*, 2009). However, this interpretation is not consistent across mating systems because the female brain was not larger than the male brain in polygynous species. Furthermore, positive effects of post-zygotic care on male brain size cannot explain why brain size of polyandrous species is relatively small in both males and females, compared with monogamous species.

Finally, a third possibility is that the brain size-mating system association reflects life-history constraints on the evolution of large brains in polyandrous species. For example, growing a larger brain and learning the skills needed for survival require a longer developmental period (Bennett & Harvey, 1985a; Iwaniuk & Nelson, 2003; Shultz & Dunbar, 2010), which suggests that development of a large brain is constrained in precocial lineages. In shorebirds, a precocial offspring can leave the nest, feed by itself and reach independence faster than semi-precocial offspring, and the parents of precocial offspring can maximize reproduction by reducing parental care and pursuing new mating opportunities. In polyandrous species, precocial development and female desertion of care are common features and may constrain brain enlargement (Thomas & Székely, 2005). Moreover, there are other subtle ways by which the life history of the species may influence the brain size-mating system association. In polyandrous shorebirds, the females do not invest in costly sexually selected traits, but instead produce small eggs that facilitate producing multiple clutches (Liker *et al.*, 2001; Andersson, 2004, 2005). Reductions of prezygotic parental care may oppose the development of large brains that require longer embryonic periods (Iwaniuk & Nelson, 2003) and high quality eggs to offset the large energetic requirements of embryos (Garamszegi *et al.*, 2007; Martin, 2008).

In general, a strong test that sexual selection is acting on brain size evolution would be to detect correlations between sexual size dimorphism in brain size and surrogates of sexual selection. In polyandrous shorebirds, the females have a smaller relative brain size than males. However, in polyandrous species, the females are also larger than males, and thus the sexual size dimorphism in polyandrous species may be due to the evolution of body size rather than brain size. As suggested by Deaner & Nunn (1999), there are instances in which body size

enlargement evolves faster and brain size lags behind to catch up allometrically with body size. Our finding that body size evolved at a faster rate than brain size in polyandrous species supports the view that sex-specific differences in relative brain size in polyandrous species may be due to changes in body size rather than on brain size. Thus, in this case, the sexual size dimorphism in brain size cannot be interpreted as evidence of the effects of sexual selection on brain size only.

To sum up, we may not infer the importance of sexual selection on brain size evolution from a correlation between brain size and the social mating system. However, our study highlights that a scientific framework of brain size studies (Lefebvre, 2011) must consider the effects of body size evolution and other competing explanations. Given the complexity of the whole brain, pleiotropy and selection acting on different parts of it, may have slowed down the evolutionary rates of change of overall brain size (Wilson, 1975). Thus, it is not surprising that the effects of sexual selection on brain size are masked by the evolution of body size. Our study is consistent with other studies showing that using relative brain size as a measurement of behavioural complexity may entail problems of interpretation if, for example, the evolution of body size is not taken into account (Deaner & Nunn, 1999; Fitzpatrick *et al.*, 2012).

We should not neglect, however, that relative brain size is strongly correlated with complex behaviours (Lefebvre & Sol, 2008; Lefebvre, 2011). Thus, hypotheses predicting changes in relative brain size due to selection on some behaviour can be justified after other life history confounds and the evolution of body size are also considered. The methodological framework used here to test competing explanations also gave some insights into the many effects that can affect brain size-mating system relationships. Indeed, as an alternative to the sexual selection hypotheses, egg size reduction and female desertion in polyandrous species may explain why these species have smaller relative brain sizes than monogamous species, without any need to assume a trade-off between brain size and a sexually selected trait (Pitnick *et al.*, 2006) or that mating requires sophisticated cognitive abilities (Dunbar & Shultz, 2007). Hence, thorough and novel analyses that integrate and compare the different aspects that affect brain size (or parts of it) are needed to understand what factors drive the evolution of the brain.

Acknowledgments

GEGP was supported by Consejo Nacional de Ciencia y Tecnología (CONACyT-121695-161552). DS was supported by a Proyecto de Investigación (CGL2010-1838) grant and a Consolider Project from the Ministerio de Educación y Ciencia (Spain), ANI by a fellowship from the Smithsonian Office of Grants and Fellowships, and TS by NERC (NE/C004167/1). We thank the cura-

tors and technical staff of the Royal Alberta Museum (Edmonton, AB, Canada), Field Museum of Natural History (Chicago, IL, USA), National Museum of Natural History (Washington, DC, USA) and Melbourne Museum (Melbourne, Australia) for access to their collections. We thank Prof. Louis Lefebvre, Prof. Tadeusz Kawecki and an anonymous reviewer for their insightful comment on a previous version of the manuscript.

References

- Aiello, L. & Wheeler, P. 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**: 199–221.
- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Trans. Autom. Control* **19**: 716–723.
- Allman, J.M., McLaughlin, T. & Hakeem, A. 1993. Brain-weight and life-span in primate species. *Proc. Natl Acad. Sci. USA* **90**: 3559–3563.
- Andersson, M. 2004. Social polyandry, parental investment, sexual selection and evolution of reduced female gamete size. *Evolution* **58**: 24–34.
- Andersson, M. 2005. Evolution of classical polyandry: three steps to female emancipation. *Ethology* **111**: 1–23.
- Arnqvist, G. & Rowe, L. 2005. *Sexual Conflict*. Princeton University Press, Woodstock, UK.
- Bennett, P.M. & Harvey, P.H. 1985a. Brain size, development and metabolism in birds and mammals. *J. Zool.* **207**: 491–509.
- Bennett, P.M. & Harvey, P.H. 1985b. Relative brain size and ecology in birds. *J. Zool.* **213**: 327–363.
- Bennett, P.M. & Owens, I.P.F. 2002. *Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction*. Oxford University Press, Oxford, UK.
- BirdLifeInternational & NatureServe. 2011. *Bird Species Distribution Maps of the World*. BirdLife International, Cambridge, UK and NatureServe, Arlington, VA.
- Birkhead, T.R. & Møller, A.P. 1998. *Sperm Competition and Sexual Selection*. Academic Press, London, UK.
- Bókony, V., Liker, A., Székely, T. & Kis, J. 2003. Melanin-based plumage coloration and flight displays in plovers and allies. *Proc. Biol. Sci.* **270**: 2491–2497.
- Bollback, J.P. 2006. Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics* **7**: 88.
- Boogert, N.J., Fawcett, T.W. & Lefebvre, L. 2011. Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behav. Ecol.* **22**: 447–459.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multi-Model Inference. A practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.
- Byrne, R.W. & Whiten, A. 1988. *Machiavellian Intelligence*. Oxford University Press, Oxford, UK.
- Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton, NJ.
- Deaner, R.O. & Nunn, C.L. 1999. How quickly do brains catch up with bodies? A comparative method for detecting evolutionary lag. *Proc. Biol. Sci.* **266**: 687–694.
- Dechmann, D.K.N. & Safi, K. 2009. Comparative studies on brain evolution: a critical insight from the Chiroptera. *Biol. Rev.* **84**: 161–172.
- Dunbar, R.I.M. 1998. The social brain hypothesis. *Evol. Anthropol.* **6**: 178–190.

- Dunbar, R.I.M. & Shultz, S. 2007. Evolution in the social brain. *Science* **317**: 1344–1347.
- Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**: 161–175.
- Fairbairn, D.J., Blanckenhorn, W.U. & Székely, T. 2007. *Sex, Size, and Gender Roles*. Oxford University Press, Oxford, New York.
- Figuerola, J. 1999. A comparative study on the evolution of reversed size dimorphism in monogamous waders. *Biol. J. Linn. Soc.* **67**: 1–18.
- Fitzpatrick, J.L., Almbro, M., Gonzalez-Voyer, A., Hamada, S., Pennington, C., Scalan, J. *et al.* 2012. Sexual selection uncouples the evolution of brain and body size in pinnipeds. *J. Evol. Biol.* **25**: 1321–1330.
- Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**: 712–726.
- Garamszegi, L.Z. & Eens, M. 2004. The evolution of hippocampus volume and brain size in relation to food hoarding in birds. *Ecol. Lett.* **7**: 1216–1224.
- Garamszegi, L.Z., Eens, M., Erritzøe, J. & Møller, A.P. 2005. Sperm competition and sexually size dimorphic brains in birds. *Proc. Biol. Sci.* **272**: 159–166.
- Garamszegi, L.Z., Biard, C., Eens, M., Møller, A.P., Saino, N. & Surai, P. 2007. Maternal effects and the evolution of brain size in birds: overlooked developmental constraints. *Neurosci. Biobehav. Rev.* **31**: 498–515.
- García-Peña, G.E., Thomas, G.H., Reynolds, J.D. & Székely, T. 2009. Breeding systems, climate, and the evolution of migration in shorebirds. *Behav. Ecol.* **20**: 1026–1033.
- Gill, F. & Donsker, D. 2010. *IOC World Bird Names*. (v 3.2). URL <http://www.worldbirdnames.org> [accessed on 21 December 2012].
- Gittleman, J.L. 1994. Female brain size and parental care in carnivores. *Proc. Natl Acad. Sci. USA* **91**: 5495–5497.
- Gonzalez-Voyer, A., Fitzpatrick, J.L. & Kolm, N. 2008. Sexual selection determines parental care patterns in cichlid fishes. *Evolution* **62**: 2015–2026.
- González-Voyer, A., Wingberg, S. & Kolm, N. 2009. Social fishes and single mothers: brain evolution in African cichlids. *Proc. Biol. Sci.* **276**: 161–167.
- Grafen, A. 1989. The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **326**: 119–157.
- Guay, P.J. & Iwaniuk, A.N. 2008. Interspecific variation in relative brain size is not correlated with intensity of sexual selection in waterfowl (Anseriformes). *Aust. J. Zool.* **56**: 311–321.
- Hadfield, J.D. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R Package. *J. Stat. Softw.* **33**: 1–22.
- Harmon, L., Weir, J., Brock, C., Glor, R., Challenger, W. & Hunt, G. 2009. *geiger: Analysis of evolutionary diversification*. (v 1.3–1). URL <http://cran.r-project.org/web/packages/geiger/index.html> [accessed on 02 September 2009].
- Harvey, P.H. & Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, UK.
- Healy, S. & Krebs, J.R. 1992. Food storing and the hippocampus in corvids—amount and volume are correlated. *Proc. R. Soc. Lond. B Biol. Sci.* **248**: 241–245.
- Healy, S.D. & Rowe, C. 2007. A critique of comparative studies in brain size. *Proc. Biol. Sci.* **274**: 453–464.
- del-Hoyo, J., Elliott, A. & Sargatal, J. 1996. *Handbook of the Birds of the World*. Lynx Edicions, Spain.
- Huelsensbeck, J.P., Neilsen, R. & Bollback, J.P. 2003. Stochastic mapping of morphological characters. *Syst. Biol.* **52**: 131–138.
- Iwaniuk, A.N. & Nelson, J.E. 2002. Can endocranial volume be used as an estimate of brain size in birds? *Can. J. Zool.* **80**: 16–23.
- Iwaniuk, A.N. & Nelson, J.E. 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Can. J. Zool.* **81**: 1913–1928.
- Jacobs, L. 1996. Sexual selection and the brain. *Trends Ecol. Evol.* **11**: 82–86.
- Jerison, H.J. 1973. *Evolution of the Brain and Intelligence*. Academic Press, London, UK.
- Jones, K.E. & MacLarnon, A.M. 2004. Affording larger brains: testing hypotheses of mammalian brain evolution on bats. *Am. Nat.* **164**: 20–31.
- Kelley, D. 2011. *oce: Analysis of Oceanographic Data*. (v 0.9–6). URL <http://cran.rproject.org/web/packages/oce/> [accessed on 16 December 2012].
- Kokko, H. & Jennions, M.D. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**: 919–948.
- Kullback, S. & Leibler, R.A. 1951. On information and sufficiency. *Ann. Math. Stat.* **22**: 79–86.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Lefebvre, L. 2011. Taxonomic counts of cognition in the wild. *Biol. Lett.* **7**: 631–633.
- Lefebvre, L. & Sol, D. 2008. Brains, lifestyles and cognition: are there general trends? *Brain Behav. Evol.* **72**: 135–144.
- Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997. Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**: 549–560.
- Lemaitre, J.F., Ramm, S.A., Barton, R.A. & Stockley, P. 2009. Sperm competition and brain size evolution in mammals. *J. Evol. Biol.* **22**: 2215–2221.
- Liker, A. & Székely, T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* **59**: 890–897.
- Liker, A., Reynolds, J.D. & Székely, T. 2001. The evolution of egg size in socially polyandrous shorebirds. *Oikos* **95**: 3–14.
- Lindfors, P., Székely, T. & Reynolds, J.D. 2003. Directional changes in sexual size dimorphism in shorebirds, gulls and alcids. *J. Evol. Biol.* **16**: 930–938.
- Lindfors, P., Nunn, C.L. & Barton, R.A. 2007. Primate brain architecture and selection in relation to sex. *BMC Biol.* **5**: 20.
- Madden, J. 2001. Sex, bowers and brains. *Proc. Biol. Sci.* **268**: 833–838.
- Martin, T.E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? *J. Avian Biol.* **27**: 263–272.
- Martin, T.E. 2008. Egg size variation among tropical and temperate songbirds: an embryonic temperature hypothesis. *Proc. Natl Acad. Sci. USA* **105**: 9268–9271.
- Martin, T.E. & Li, P. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* **73**: 579–592.
- Martins, E.P. 2000. Adaptation and the comparative method. *Trends Ecol. Evol.* **15**: 296–299.
- Miller, G. 2000. *The Mating Mind*. Vintage, London, UK.
- Moreau, R.E. 1944. Clutch size: a comparative study, with reference to African birds. *Ibis* **86**: 286–347.
- Nebel, S., Jackson, D.L. & Elner, R.W. 2005. Functional association of bill morphology and foraging behaviour in calidrid sandpipers. *Anim. Biol.* **55**: 235–243.

- Olson, V.A., Liker, A., Freckleton, R.P. & Székely, T. 2008. Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. *Proc. Biol. Sci.* **175**: 301–307.
- O'Meara, B.C., Ané, C., Sanderson, M.J. & Wainwright, P.C. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution* **60**: 922–933.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. *et al.* 2012. *Comparative Analyses of Phylogenetics and Evolution in R, R-Project: Functions for Performing Phylogenetic Comparative Analyses*. (v 0.5). URL <http://cran.r-project.org/web/packages/caper/index.html> [accessed on 21 February 2012].
- Pagel, M.D. 1997. Inferring evolutionary processes from phylogenies. *Zoolog. Scr.* **26**: 331–348.
- Pagel, M.D. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.
- Pagel, M.D. & Harvey, P.H. 1988. How mammals produce large-brained offspring. *Evolution* **42**: 948–957.
- Paradis, E., Claude, J. & Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language (v 3.0–6). *Bioinformatics* **20**: 289–290.
- Pérez-Barbería, F., Schultz, S. & Dunbar, R.I.M. 2007. Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution* **61**: 2811–2821.
- Pitnick, S., Jones, K.E. & Wilkinson, G.S. 2006. Mating system and brain size in bats. *Proc. Biol. Sci.* **273**: 719–724.
- Plummer, M., Best, N., Cowles, K. & Vines, K. 2006. CODA: convergence diagnosis and output analysis for MCMC. *R News* **6**: 7–11.
- R. 2011. *The R Project for Statistical Computing, Institute for Statistics and Mathematics*. WU, Wien.
- Reader, S.M. & Laland, K.N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**: 4436–4441.
- Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.
- Reynolds, J.D. & Székely, T. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behav. Ecol.* **8**: 126–134.
- Riede, K. 2004. *Global Register of Migratory Species-from Global to Regional Scales*. Federal Agency for Nature Conservation, Bonn, Germany.
- Russell, E. 2000. Avian life histories: is extended parental care the southern secret? *Emu* **100**: 377–399.
- Schillaci, M.A. 2006. Sexual selection and the evolution of brain size in primates. *PLoS ONE* **1**: e62.
- Shultz, S. & Dunbar, R.I.M. 2010. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol. J. Linn. Soc.* **100**: 111–123.
- Sol, D. 2009 The cognitive-buffer hypothesis for the evolution of large brains. In: *Cognitive Ecology II* (R. Dukas, J.M. Ratcliffe, eds), pp. 111–134. The University of Chicago Press, Chicago, IL.
- Sol, D., Lefebvre, L. & Rodriguez-Teijeiro, J.D. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palearctic birds. *Proc. Biol. Sci.* **272**: 1471–2954.
- Sol, D., Székely, T., Liker, A. & Lefebvre, L. 2007. Big-brained birds survive better in nature. *Proc. Biol. Sci.* **274**: 755–761.
- Sol, D., García, N., Iwaniuk, A., Davis, K., MEade, A., Boyle, A.W. *et al.* 2010. Evolutionary divergence in brain size between migratory and resident birds. *PLoS ONE* **5**: e9617.
- Starck, J.M. & Ricklefs, R.E. 1998. *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*. Oxford University Press, Oxford.
- Székely, T. & Reynolds, J.D. 1995. Evolutionary transitions in parental care in shorebirds. *Proc. Biol. Sci.* **262**: 57–64.
- Székely, T., Webb, J.N. & Cuthill, I.C. 2000. Mating patterns, sexual selection and parental care: an integrative approach. In: *Vertebrate Mating Systems* (M. Apollonio, M Festa-Bianchet & D. Mainardi, eds.), pp. 194–223. World Science Press, London, UK.
- Székely, T., Thomas, G.H. & Cuthill, I.C. 2006. Sexual conflict, ecology, and breeding systems in shorebirds. *Bioscience* **56**: 801–808.
- Thomas, G.H. & Székely, T. 2005. Evolutionary pathways in shorebird breeding systems: sexual conflict, parental care, and chick development. *Evolution* **59**: 2222–2230.
- Thomas, G.H., Wills, M.A. & Székely, T. 2004. A supertree approach to shorebirds phylogeny. *BMC Evol. Biol.* **4**: 28.
- Thomas, G.H., Székely, T. & Reynolds, J.D. 2007. Sexual conflict and the evolution of breeding systems in shorebirds. *Adv. Study Behav.* **37**: 279–342.
- Tjørve, K.M.C., García-Peña, G.E. & Székely, T. 2009. Chick growth rates in Charadriids: comparative analyses of breeding climate, development mode and parental care. *J. Avian Biol.* **40**: 553–558.
- Trivers, R.L. 1972. *Sexual Selection and the Descent of Man*. Heinemann, London.
- Wilson, E.O. 1975. *Sociobiology. The New Synthesis*. Harvard University Press, Cambridge.
- Winkler, H., Leisler, B. & Bernroider, G. 2004. Ecological constraints on the evolution of avian brains. *J. Ornithol.* **145**: 238–244.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Units and references.

Appendix S2 Best candidate models on the relationship between ln male brain size (response) and predictors: ln male body mass, male polygamy scores, parental care (scores of male care and female care), offspring development and ecological effects (see Materials and methods).

Appendix S3 Best candidate models on the relationship between ln female brain size (response) and predictors: female polygamy scores, parental care (scores of male care and female care), offspring development and ecological effects (see Materials and methods).

Appendix S4 Contingency table on mating system and parental care system.

Appendix S5 MCMCGLMM. Model structure and priors.

Appendix S6 Diagnostics of MCMCGLMM.

Appendix S7 Online file, readable in R, with 1000 reconstructions of the most likely transitions in mating systems during the evolutionary history of shorebirds.

Appendix S8 Evolutionary rates of scaled measurements of brain and body sizes in shorebird mating systems.

Received 23 July 2012; revised 21 October 2012; accepted 10 December 2012