

Faithful females receive more help: the extent of male parental care during incubation in relation to extra-pair paternity in songbirds

B. MATYSIOKOVÁ*† & V. REMEŠ*

*Laboratory of Ornithology, Department of Zoology, Palacký University, Olomouc, Czech Republic

†Institute of Zoology, Poznań University of Life Sciences, Poznań, Poland

Keywords:

comparative analyses;
extra-pair fertilization;
male incubation;
nest attentiveness;
relative incubation effort.

Abstract

Parental care provided by males occurs in a diverse array of animals and there are large differences among species in its extent compared with female care. However, social and ecological factors responsible for interspecific differences in male's share of parental duties remain unclear. Genetic fidelity of females has been long considered important. Theory predicts that females should receive more help from their mates in raising the offspring in species with high genetic fidelity. Using avian incubation behaviour as a model system, we confirmed this prediction. The extent of male's help during incubation increased with decreasing rate of extra-pair paternity across species (22 species of socially monogamous songbirds from 13 families; male's share of incubation ranged from 6% to 58%), even after accounting for covariates, biases in species selection and intraspecific variability. Moreover, this result was not sensitive to two different phylogenies and branch length estimates. We suggest that our findings support the notion, backed by theory, that genetic fidelity is an important factor in the evolution of male parental care. We offer several behavioural scenarios for the coevolution between male's share of parental duties and the genetic mating system.

Introduction

Parental care is a critical component of the life history of many animal species (Clutton-Brock, 1991). Usually, only one sex is responsible for the care of the offspring with the exception of birds, in which at least 81% of species exhibit biparental care (Cockburn, 2006). Males take part in parental care either as sole caregivers (particularly common in fishes; Reynolds *et al.*, 2002) or alongside with females. Male participation in parental care can be found in a surprisingly diverse array of animal groups and there are marked differences among species in the extent of parental care provided by the male, including in insects (Gilbert & Manica, 2010), amphibians (Duellman & Trueb, 1986), fishes (Mank *et al.*, 2005), birds (Webb *et al.*, 2010) and mammals

(Adrian *et al.*, 2005). However, social and ecological factors responsible for these differences remain contentious (Ridley, 1978; Gross & Sargent, 1985; Ketterson & Nolan, 1994; Beck, 1998; Tallamy, 2000; Burley & Johnson, 2002; Székely *et al.*, 2006; Alonzo, 2009).

Social mating system was revealed to be an important correlate of male's contribution to parental care across species (Wright, 1998; Adrian *et al.*, 2005). For example, in polygynous species, it is mostly the female who provides parental care, whereas in monogamous species, parental care is usually shared by the breeding pair (Verner & Willson, 1969; Székely *et al.*, 2007). However, in addition to differences in the social mating system, there are often strong differences in the genetic mating system even within one social mating strategy. For example, genetic monogamy was found in only 10% of species of socially monogamous songbirds ($n = 60$; reviewed in Griffith *et al.*, 2002). Recent research revealed that genetic polyandry is probably driving the evolution of a number of traits such as sexual dichromatism (Møller & Birkhead, 1994; Bennett

Correspondence: Beata Matysioková, Laboratory of Ornithology, Department of Zoology, Palacký University, Tř. Svobody 26, 77146 Olomouc, Czech Republic.
Tel.: +00420585634221; fax: +00420585634002;
e-mail: betynec@centrum.cz

& Owens, 2002), sperm length (Lifjeld *et al.*, 2010) or development rates (Royle *et al.*, 1999; Lloyd & Martin, 2003). Given strong relationships between the social mating system and male's contribution to parental care, it is probable that the genetic mating system also plays a role in the evolution of male care.

Parental care is costly, and hence, there should be a positive relationship between the certainty of paternity and the amount of care provided by the male (Trivers, 1972; Queller, 1997; reviewed in Sheldon, 2002). This can occur on two levels. First, there may be an evolutionary response of parental investment to mean relatedness of offspring (Kokko & Jennions, 2008). Second, the linkage may be behavioural, whereby males adjust paternal investment facultatively in response to a hypothetical perception of their relatedness to offspring (Wright, 1998; Sheldon, 2002). However, both these mechanisms require parental care, or investment, to be costly in terms of future reproduction. Unlike post-hatching care, incubation was not originally considered to be costly for parents (King, 1973; Walsberg, 1983). However, now it is clear that incubation is highly energetically demanding and costly, sometimes rivalling post-hatching care, with negative consequences for future reproduction (Tatner & Bryant, 1993; Thomson *et al.*, 1998; Tinbergen & Williams, 2002). During incubation, overall intensity of care is influenced by environmental factors such as ambient temperature or nest predation (Conway & Martin, 2000; Fontaine & Martin, 2006; Matysioková *et al.*, 2011). However, male participation in incubating the eggs differs strongly across species even within individual orders (4.80–69.19%, $n = 107$ species of songbirds, B. Matysioková, unpublished). We might then ask whether this interspecific variation is related to the certainty of paternity, as predicted by both verbal and quantitative models (Houston & McNamara, 2002; Sheldon, 2002; Kokko & Jennions, 2008) and thus whether genetic polyandry can be responsible for the evolution of male participation in parental care during incubation.

Until now, only one comparative study analysed male incubation share in relation to extra-pair paternity in biparentally incubating species (i.e. male share is higher than zero; Schwagmeyer *et al.*, 1999) and found no relationship. However, the authors included species belonging to nine different orders and hence with very diverse life histories (Bennett & Owens, 2002), which might have confounded their analyses (Mauck *et al.*, 1999). In this article, we analysed the relationship between the certainty of paternity (estimated by the degree of extra-pair paternity) and male help during incubation in songbirds with biparental incubation. Taking into account how costly incubation is, we expected to find a positive relationship between male's incubation share and his certainty of paternity.

Materials and methods

Collection of data

We collected data for this study from the literature. To exclude confounding effects of diverse life histories and developmental types, we narrowed our search to songbirds (order Passeriformes). The occurrence vs. extent of male incubation might be the subject to different mechanisms (see Discussion) and thus we searched only songbird species in which both sexes incubate. For birds breeding in Europe, we started with The Complete Birds of Western Palearctic (BWP; Cramp, 1998). We used Web of Science (WoS) to find articles that were either published after BWP or were not included in BWP. We searched by the scientific name of every species of European songbirds in which the male participates in incubation. In every species, we search for all articles whose title or abstract included any of the following words: attentiveness, breeding biology, incubation, nest, nesting or parental care. We located additional sources from papers obtained in the above-mentioned way and from BWP. We did similar search for data on incubation behaviour of songbirds from North America and Australia (for more details, see Matysioková *et al.*, 2011). We excluded work conducted in captivity and articles without information on male share during incubation (i.e. only total nest attentiveness for the breeding pair was provided) or articles that provided male share without providing total nest attentiveness. To increase sample size, we included both socially monogamous and facultatively polygynous species in our data set. However, we included only monogamous pairs of the facultatively polygynous species to make those two groups comparable. Based on the articles obtained during our search, we calculated nest attentiveness as the percentage of daytime hours parents spent incubating the eggs. We excluded data on incubation during night and during the laying period. We calculated male relative incubation effort as the percentage of male incubation out of the total nest attentiveness. If there were more articles with this type of data in one species, we used averaged values.

To obtain data on extra-pair paternity, we searched by the scientific name of all species for which we obtained data on male relative incubation effort. We looked for articles whose title or abstract included any of the following words: extra-pair, paternity or fertilization. Based on the articles obtained in this way, we calculated extra-pair paternity as the percentage of the female's own offspring not sired by the social male. If those data were available from multiple populations, we used un-weighted averages. We included only estimates based on DNA methods (Griffith *et al.*, 2002). In the barn swallow (*Hirundo rustica*), we found data on male share for the North American subspecies and extra-pair paternity for two more subspecies (European and Asian). In this case,

we used only data belonging to the same subspecies we had data on male share from (i.e. *H. r. erythrogaster*). For every species in our data set, we obtained information on adult body mass (grams; Dunning, 2007).

Statistical analyses

Phylogenetic relationships among species might introduce nonindependence into data that violate assumptions of standard statistical tests (Harvey & Pagel, 1991). Thus, we adjusted for phylogeny using phylogenetic generalized least squares (PGLS), which adjust flexibly for the degree of phylogenetic signal present in data (Pagel, 1999). Moreover, intraspecific variability might introduce bias into analyses similar to that introduced by uncontrolled phylogenetic relationships (Garamszegi & Møller, 2010). Thus, besides running analyses on species-specific mean values, we randomly resampled our data 100 times so that every species was represented by one value of male relative incubation effort. For each of these 100 data sets, we fitted a PGLS analysis and summarized the results obtained from all 100 analyses.

We fitted models where male relative incubation effort was a dependent variable and adult body mass, total nest attentiveness and extra-pair paternity were independent variables, while simultaneously controlling for phylogenetic relationships among species. We used functions in caper package (Orme *et al.*, 2012) of R language (R Development Core Team, 2011). We also calculated the amount of phylogenetic signal in male relative incubation effort by estimating Pagel's (1999) λ in caper (Orme *et al.*, 2012), and K (Blomberg *et al.*, 2003) in picante (Kembel *et al.*, 2010). As there was no phylogenetic signal in our dependent variable (see below), we did not attempt to model other processes of trait evolution besides the Brownian motion, for example, the Ornstein-Uhlenbeck process (Martins & Hansen, 1997). Transformations of raw variables were applied as needed to meet the assumptions of additive linear relationships and multivariate normality.

To ensure that our results were not biased by a particular phylogenetic hypothesis used, we used two different phylogenies taken from literature: the phylogeny presented (by Barker *et al.*, 2004) supplemented by additional molecular phylogenies (Murray *et al.*, 1994; Leisler *et al.*, 1997; Carson & Spicer, 2003; Ericson & Johansson, 2003; Klicka *et al.*, 2003; Sheldon *et al.*, 2005; Spellman *et al.*, 2008; Gelang *et al.*, 2009; Päckert *et al.*, 2010) and the passerine supertree published by Jonsson & Fjeldsa (2006) supplemented by additional molecular phylogenies (Murray *et al.*, 1994; Nyári *et al.*, 2009; Yeung *et al.*, 2011). Due to the process of phylogeny assembly, we did not have consistent estimates of branch lengths. We thus used two arbitrary options widely used in comparative analyses: unit and Grafen's (1989) branch lengths. Both phylogenies are available in Supporting Information.

Results

We collated data on both male relative incubation effort and extra-pair paternity for 22 species of songbirds belonging to 13 families. For several species, we obtained information on male relative incubation effort from more than one population (we had four and three populations for one species each, and two populations for four species; only one value was available for 16 remaining species). Repeatability of male relative incubation effort was 0.40 (calculated only for species with more than one population value available). Two of the species (*Emberiza schoeniclus* and *Sturnus vulgaris*) were facultatively polygynous, the remaining species were socially monogamous. Male relative incubation effort ranged from 5.93 to 57.95% across species (mean \pm SD = 38.58 \pm 13.82%, median = 40.27%, $n = 22$) and extra-pair paternity ranged from 0 to 55.10% across species (mean \pm SD = 14.54 \pm 14.74%, median = 11.94%, $n = 22$). Male relative incubation effort decreased with increasing degree of extra-pair paternity (Figs 1 and 2) and increased with increasing total nest attentiveness. It was not correlated with adult body mass (Table 1). The results were not sensitive to a particular phylogeny, branch lengths or population sampling (see Supporting Information) and did not change when we left only socially monogamous species in the analysis ($n = 20$; B. Matysioková & V. Remeš, unpublished). Phylogenetic signal in male relative incubation effort was higher when using unit branch lengths (mean $\lambda = 0.79$, mean Blomberg's $K = 0.91$; means across the two phylogenies) than in Grafen's branch lengths (mean $\lambda = 0.00$, mean $K = 0.23$; means across the two phylogenies; see also Supporting Information).

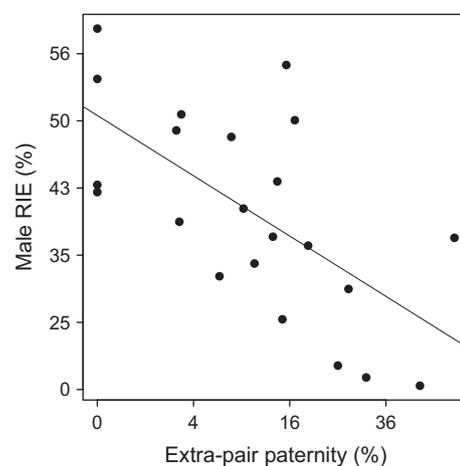


Fig. 1 Relationship between male's relative incubation effort (Male RIE, power-2 transformed) and extra-pair paternity (sqrt transformed). Ordinary linear regression line is depicted for illustration.

Table 1 Phylogenetic generalized least squares model of male's relative incubation effort (power-2 transformed) using phylogenetic tree based on Barker *et al.* (2004) and Grafen's (1989) branch lengths fitted in caper package; adjusted multiple $R^2 = 0.53$.

	Estimate (SE)	<i>t</i>	<i>P</i>
Intercept	389.83 (1254.57)	0.31	0.760
Body mass (\log_{10})	-334.38 (203.62)	-1.64	0.118
Attentiveness (power-2)	35.50 (13.75)	2.58	0.019
Extra-pair paternity (sqrt)	-243.03 (66.12)	-3.68	0.002

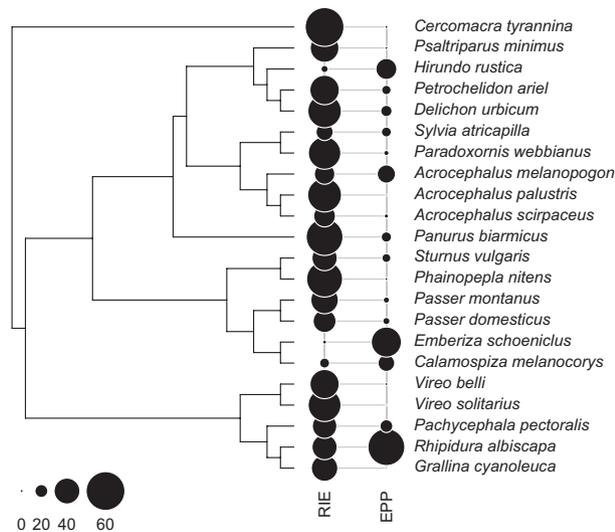


Fig. 2 Phylogeny based on Barker *et al.* (2004) with the values of male's relative incubation effort (RIE, %) and extra-pair paternity (EPP, %) depicted along the tips.

Discussion

As expected, males of species with lower certainty of paternity provided less help during incubation compared to those with more faithful mates. Previous comparative analyses did not find any relationship between male incubation effort and extra-pair paternity (Møller & Birkhead, 1993; Schwagmeyer *et al.*, 1999) or found only weak and inconsistent effects (Møller & Cuervo, 2000), which was attributed to the assumed low cost of incubation (Møller & Birkhead, 1993). This lack of relationship seemed to agree with models that predicted effects of extra-pair paternity only in costly parental care behaviours (Trivers, 1972; Sheldon, 2002). Nevertheless, it has been amply demonstrated that incubation is costly in terms of elevated metabolic rates and weight loss (Webb & King, 1983; Williams, 1996; Thomson *et al.*, 1998; Tinbergen & Williams, 2002). In addition to straining energy, incubation is extremely time-consuming and therefore the incubating parent has less time for foraging, self-maintenance, singing and/or defence of

breeding territory (White & Kinney, 1974; Hoi-Leitner *et al.*, 1993; Deeming, 2002; Chiver *et al.*, 2007). More importantly, incubation was demonstrated to bear long-term costs in terms of future survival and reproduction (e. g. Visser & Lessells, 2000; Reid *et al.*, 2001). In the light of these findings, it is not surprising that speaking in evolutionary terms, males are willing to invest more only if they are certain about own paternity.

How can conflicting results of the previous studies and the present study be reconciled? Besides methodological issues concerning the study of Møller & Birkhead (1993) mentioned previously (Dale, 1995), there are two more possible problems we would like to mention. First, we believe that including species with uniparental incubation into comparative analyses of male share can bias the results. In species with female-only incubation, males may provide indirect incubation care by feeding the incubating female (behaviour typically not observed in biparental incubators) or guarding her during foraging, which enables her to spend more time on the nest (Fedy & Martin, 2009; Matysioková *et al.*, 2011). Zero rate of direct male incubation thus does not reflect real male effort during incubation unless indirect forms of male incubation care are taken into account. In previous comparative analyses, most of the species analysed had uniparental incubation (81.6%, 69.44% and 67.5% of species, respectively; Møller & Birkhead, 1993; Schwagmeyer *et al.*, 1999; Møller & Cuervo, 2000). Moreover, incubation feeding occurred in at least 32.4% (Møller & Birkhead, 1993), 47.6% (Schwagmeyer *et al.*, 1999) and 45.5% (Møller & Cuervo, 2000) of songbird species, which were treated as species with zero rates of male help during incubation (Cramp, 1998; Poole & Gill 1992–2002; Matysioková *et al.*, 2011).

Second, even though Schwagmeyer *et al.* (1999) repeated their analyses on a subset of 21 species with biparental incubation, they included both extremely long- and short-lived species belonging to nine different orders. Longevity is correlated with many traits such as age of first reproduction (Møller, 2006; Blumstein & Møller, 2008), clutch size and parental investment (Ghalambor & Martin, 2001; Martin, 2002) or divorce rate (Botero & Rubenstein, 2012). More importantly, it is predicted to be related to male's tolerance of extra-pair paternity (Mauck *et al.*, 1999). Thus, including species drastically differing in lifespan into one analysis without correcting for those variables could again lead to biased results. To avoid similar possible biases, we included only songbirds with biparental incubation (i.e. species with similar life history and male incubation share higher than zero). However, it is fair to acknowledge that although most of the life-history variation occurs among orders (Bennett & Owens, 2002), adult survival might differ strongly even within passerines. We were able to collect data on adult survival only for 16 of our species, too few to perform a rigorous

analysis. Even within this limited sample of species, adult survival varied from 26.5% (*Paradoxornis webbianus*) to 82% per year (*Cercomacra tyrannina*). Thus, although we focused on a group of birds with similar life history, our results still might have been at least partly confounded by variation in adult survival rate.

Several studies focused on a within-species relationship between certainty of paternity and male's parental investment during both incubation (Smith & Montgomerie, 1992; Whittingham & Lifjeld, 1995) and nesting stages (for example Dixon *et al.*, 1994; Bouwman *et al.*, 2005; Maguire & Safran, 2010), but the results were mixed. Some studies found that males adjusted their parental investment with respect to the perceived certainty of paternity (Dixon *et al.*, 1994; Weatherhead *et al.*, 1994; Møller & Tegelström, 1997; Sheldon *et al.*, 1997), whereas others did not (Smith & Montgomerie, 1992; Whittingham & Lifjeld, 1995; Wagner *et al.*, 1996; Bouwman *et al.*, 2005; Maguire & Safran, 2010). The reason why males of some species did not adjust their parental investment could be their inability to assess the extent or even pure presence of extra-pair paternity (Whittingham & Lifjeld, 1995; Briskie & Boag, 1998). Although some experiments with temporal male or female removal suggested that the male could be able to assess his certainty of paternity based on the time he could not guard the female (Sheldon *et al.*, 1997; Sheldon & Ellegren, 1998; but see Dickinson, 2003), the extent to which these experiments mimic reality is questionable (Sheldon & Ellegren, 1998) and they might be biased by previous individual history that is typically not accounted for (Hill *et al.*, 2011). However, it should be emphasized that evolutionary mechanism required to generate the relationship between paternal investment and certainty of paternity does not require any facultative change in parental behaviour on the part of males (Wright, 1998; Sheldon, 2002).

Two alternative proximate hypotheses were proposed to explain the relationship between male parental care and extra-pair paternity across species: physiological incompatibility and restricted schedule hypotheses (Ketterson & Nolan, 1994). First, incubation behaviour requires physiological changes inconsistent with sexual behaviour, such as a decline in testosterone at the onset of incubation (Schwagmeyer *et al.*, 2005; Smith *et al.*, 2005). Therefore, extra-pair paternity is predicted to be low in species with biparental incubation compared to those with female-only incubation (Schwagmeyer *et al.*, 1999). However, because we did not include species with female-only incubation, this hypothesis is unlikely to explain our findings, provided that there are clear cut differences in hormonal profiles in males of species with biparental vs. female-only incubation. Moreover, this argument also requires that there is no correlation between hormonal profiles and male incubation behaviour in species with biparental incubation, a notion for

which no empirical tests are available. Second, a temporal trade-off between extra-pair copulations and male incubation behaviour might be responsible. In species with high male share during incubation, males could simply have less time to seek for extra-pair copulations than in species in which males help less (Magrath & Komdeur, 2003). However, seeking for extra-pair copulations does not have to lower male parental care (Pitcher & Stutchbury, 2000), males might devote little time to it (Brodsky, 1988; Stutchbury, 1998), and extra-pair paternity is not necessarily correlated with the number of extra-pair copulations (Dunn & Lifjeld, 1994; Hsu *et al.*, 2006; but see Ewen *et al.*, 2004). Moreover, the logic of the restricted schedule hypothesis might be even inverted: incubating males cannot guard their females, similarly as they cannot guard their territories while incubating (Chiver *et al.*, 2007), at least in species where laying and incubation at least partially overlap. This could ultimately lead to higher rates of extra-pair paternity in eggs on which incubation has already started. Thus, although these two proximate hypotheses cannot be dismissed based on the evidence presented here, they seem unlikely to explain our results.

We suggest that the relationship between male share of incubation and extra-pair paternity we identified is the result of adaptive behavioural coevolution and not physiological or time constraints. However, what evolutionary scenarios can we propose? It is important to bear in mind that paternity is an outcome of the interactions between males and females. If paternity differs between species, then these interactions must differ (Houston & McNamara, 2002). If the female is decisive for the occurrence of extra-pair matings, her increased willingness to engage in extra-pair activities leads to higher frequency of extra-pair paternity. This in turn selects males to decrease their parental investment (Queller, 1997; Houston & McNamara, 2002) and increase their mating effort (Wright, 1998). Females might increase their willingness to engage in extra-pair copulations if potential indirect benefits of this activity are high (although their strength has been questioned; Arnqvist & Kirkpatrick, 2007). On the other hand, females might refrain from extra-pair copulations in species with high paternal contribution that is critical to breeding success to avoid losing male help (Møller, 2000; Arnold & Owens, 2002). On the other hand, if the male is decisive for the occurrence of extra-pair matings, such as in the model of sexually antagonistic 'seduction' (Arnqvist & Kirkpatrick, 2007), less time for his extra-pair mating seeking activity might lead to low rates of extra-pair paternity, thus generating the relationship we identified here. The interpretation of the evolutionary association we found thus ultimately rests on the view of which behavioural processes drive the frequency of extra-pair parentage in socially monogamous birds.

Acknowledgments

We are grateful to Gernot Segelbacher for providing unpublished data and to Miloš Krist and two anonymous reviewers for helpful comments on the manuscript.

References

- Adrian, O., Brockmann, I., Hohoff, C. & Sachser, N. 2005. Paternal behaviour in wild guinea pigs: a comparative study in three closely related species with different social and mating systems. *J. Zool.* **265**: 97–105.
- Alonzo, S.H. 2009. Social and coevolutionary feedbacks between mating and parental investment. *Trends Ecol. Evol.* **25**: 99–108.
- Arnold, K.E. & Owens, I.P.F. 2002. Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. *Proc. R. Soc. B Biol. Sci.* **269**: 1263–1269.
- Arnqvist, G. & Kirkpatrick, M. 2007. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *Am. Nat.* **169**: 282–283.
- Barker, F.K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004. Phylogeny and diversification of the largest avian radiation. *Proc. Natl Acad. Sci. USA* **101**: 11040–11045.
- Beck, C.W. 1998. Mode of fertilization and parental care in anurans. *Anim. Behav.* **55**: 439–449.
- Bennett, P.M. & Owens, I.P.F. 2002. *Evolutionary Ecology of Birds: Life History, Mating System and Extinction*. Oxford University Press, Oxford.
- Blomberg, S.R., Garland, T. & Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.
- Blumstein, D.T. & Møller, A.P. 2008. Is sociality associated with high longevity in North American birds? *Biol. Letters* **4**: 146–148.
- Botero, C.A. & Rubenstein, D.R. 2012. Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PLoS ONE* **7**: e32311.
- Bouwman, K., Lessells, C.M. & Komdeur, J. 2005. Male reed buntings do not adjust parental effort in relation to extrapair paternity. *Behav. Ecol.* **16**: 499–506.
- Briskie, J.V. & Boag, P.T. 1998. Paternity and paternal care in the polygynandrous Smith's longspur. *Behav. Ecol. Sociobiol.* **43**: 181–190.
- Brodsky, L.M. 1988. Mating tactics of male rock ptarmigan *Lagopus mutus*: a conditional strategy. *Anim. Behav.* **36**: 335–342.
- Burley, N.T. & Johnson, K. 2002. The evolution of avian parental care. *Phil. Trans. R. Soc. Lond. B* **357**: 241–250.
- Carson, R.J. & Spicer, G.S. 2003. A phylogenetic analysis of the emberizid sparrows based on three mitochondrial genes. *Mol. Phylogenet. Evol.* **29**: 43–57.
- Chiver, I., Morton, E.S. & Stutchbury, B.J.M. 2007. Incubation delays territory defence by male blue-headed vireos *Vireo solitarius*. *Anim. Behav.* **73**: 143–148.
- Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proc. R. Soc. B Biol. Sci.* **273**: 1375–1383.
- Conway, C.J. & Martin, T.E. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* **54**: 670–685.
- Cramp, S. 1998. *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press, Oxford.
- Dale, J. 1995. Problems with pair-wise comparisons: does certainty of paternity covary with paternal care? *Anim. Behav.* **49**: 519–521.
- Deeming, D.C. (ed). 2002. *Avian incubation: behaviour, environment, and evolution*. Oxford University Press, Oxford.
- Dickinson, J.L. 2003. Male share of provisioning is not influenced by actual or apparent loss of paternity in western bluebirds. *Behav. Ecol.* **14**: 360–366.
- Dixon, A., Ross, D., O'Malley, S.L.C. & Burke, T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* **371**: 698–700.
- Duellman, W.E. & Trueb, L. 1986. *Biology of Amphibians*. McGraw-Hill, New York.
- Dunn, P.O. & Lifjeld, J.T. 1994. Can extra-pair copulations be used to predict extra-pair paternity in birds? *Anim. Behav.* **47**: 983–985.
- Dunning, J.B. jr. (ed). 2007. *CRC Handbook of Avian Body Masses*. CRC Press/Taylor & Francis Group, Boca Raton.
- Ericson, P.G.P. & Johansson, U.S. 2003. Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. *Mol. Phylogenet. Evol.* **29**: 126–138.
- Ewen, J.G., Armstrong, D.P., Ebert, B. & Hansen, L.H. 2004. Extra-pair copulation and paternity defense in the hihi (or stitchbird) *Notiomystis cincta*. *New Zeal. J. Ecol.* **28**: 233–240.
- Fedy, B.C. & Martin, T.E. 2009. Male songbirds provide indirect parental care by guarding females during incubation. *Behav. Ecol.* **20**: 1034–1038.
- Fontaine, J.J. & Martin, T.E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**: 428–34.
- Garamszegi, L.Z. & Møller, A.P. 2010. Effects of sample size and intraspecific variation in phylogenetic comparative studies: a meta-analytic review. *Biol. Rev.* **85**: 797–805.
- Gelang, M., Cibois, A., Pasquet, E., Olsson, U., Alström, P. & Ericson, P.G.P. 2009. Phylogeny of babblers (Aves, Passeriformes): major lineages, family limits and classification. *Zool. Scr.* **38**: 225–236.
- Ghalambor, C.K. & Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**: 494–497.
- Gilbert, J.D.J. & Manica, A. 2010. Parental care trade-offs and life-history relationships in insects. *Am. Nat.* **176**: 212–226.
- Grafen, A. 1989. The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B* **326**: 119–157.
- Griffith, S.C., Owens, I.P.F. & Thuman, K.A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**: 2195–2212.
- Gross, M.R. & Sargent, R.C. 1985. The evolution of male and female parental care in fishes. *Am. Zool.* **25**: 807–822.
- Harvey, P.H. & Pagel, M. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.
- Hill, D.L., Lindström, J. & Nager, R.G. 2011. Carry-over effects of male extra-pair copulation opportunity on biparental effort in zebra finches. *Behav. Ecol. Sociobiol.* **65**: 2049–2059.
- Hoi-Leitner, M., Nechtelberger, H. & Dittami, J. 1993. The relationship between individual differences in male song frequency and parental care in blackcaps. *Behaviour* **126**: 1–12.

- Houston, A.I. & McNamara, J.M. 2002. A self-consistent approach to paternity and parental effort. *Phil. Trans. R. Soc. Lond. B* **357**: 351–362.
- Hsu, Y.-C., Li, S.-H., Lin, Y.-S., Philippart, M.T. & Severinghaus, L.L. 2006. High frequency of extra-pair copulation with low level of extra-pair fertilization in the Lanyu scops owl *Otus elegans botelensis*. *J. Avian Biol.* **37**: 36–40.
- Jonsson, K.A. & Fjeldsa, J. 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). *Zool. Scr.* **35**: 149–186.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. *et al.* 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**: 1463–1464.
- Ketterson, E.D. & Nolan, V. 1994. Male parental behavior in birds. *Annu. Rev. Ecol. Syst.* **25**: 601–628.
- King, J.R. 1973. Energetics of reproduction in birds. In: *Breeding Biology of Birds* (D.S. Farner, ed.), pp. 78–107. National Academy of Sciences, Washington D.C.
- Klicka, J., Zink, R.M. & Winker, K. 2003. Longspurs and snow buntings: phylogeny and biogeography of a high-latitude clade (Calcarius). *Mol. Phylogenet. Evol.* **26**: 165–175.
- Kokko, H. & Jennions, M.D. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**: 919–948.
- Leisler, B., Heidrich, P., Schulze-Hagen, K. & Wink, M. 1997. Taxonomy and phylogeny of reed warblers (genus *Acrocephalus*) based on mtDNA sequences and morphology. *J. Ornithol.* **138**: 469–496.
- Lifjeld, J.T., Laskemoen, T., Kleven, O., Albrecht, T. & Robertson, R.J. 2010. Sperm length variation as a predictor of extrapair paternity in passerine birds. *PLoS ONE* **5**: e13456.
- Lloyd, J.D. & Martin, T.E. 2003. Sibling competition and the evolution of prenatal development rates. *Proc. R. Soc. B Biol. Sci.* **270**: 735–740.
- Magrath, M.J.L. & Komdeur, J. 2003. Is male care compromised by additional mating opportunity?. *Trends Ecol. Evol.* **18**: 424–430.
- Maguire, S.E. & Safran, R.J. 2010. Morphological and genetic predictors of parental care in the North American barn swallow *Hirundo rustica erythrogaster*. *J. Avian Biol.* **41**: 74–82.
- Mank, J.E., Promislow, D.E.L. & Avise, J.C. 2005. Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. *Evolution* **59**: 1570–1578.
- Martin, T.E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proc. R. Soc. B Biol. Sci.* **269**: 309–316.
- Martins, E.P. & Hansen, T.F. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* **149**: 646–667.
- Matysioková, B., Cockburn, A. & Remeš, V. 2011. Male incubation feeding in songbirds responds differently to nest predation risk across hemispheres. *Anim. Behav.* **82**: 1347–1356.
- Mauack, R.A., Marschall, E.A. & Parker, P.G. 1999. Adult survival and imperfect assessment of parentage: effects on male parenting decisions. *Am. Nat.* **154**: 99–109.
- Møller, A.P. 2000. Male parental care, female reproductive success, and extrapair paternity. *Behav. Ecol.* **11**: 161–168.
- Møller, A.P. 2006. Sociality, age at first reproduction and senescence: comparative analyses of birds. *J. Evol. Biol.* **19**: 682–689.
- Møller, A.P. & Birkhead, T.R. 1993. Certainty of paternity covaries with paternal care in birds. *Behav. Ecol. Sociobiol.* **33**: 261–268.
- Møller, A.P. & Birkhead, T.R. 1994. The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution* **48**: 1089–1100.
- Møller, A.P. & Cuervo, J.J. 2000. The evolution of paternity and paternal care in birds. *Behav. Ecol.* **11**: 472–485.
- Møller, A.P. & Tegelström, H. 1997. Extra-pair paternity and tail ornamentation in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* **41**: 353–360.
- Murray, B.W., McGillivray, W.B., Barlow, J.C., Beech, R.N. & Strobeck, C. 1994. The use of cytochrome B sequence variation in estimation of phylogeny in the vireonidae. *Condor* **96**: 1037–1054.
- Nyári, Á.S., Benz, B.W., Jönsson, K.A., Fjeldså, J. & Moyle, R. G. 2009. Phylogenetic relationships of fantails (Aves: Rhipiduridae). *Zool. Scr.* **38**: 553–561.
- Orme, D., Freckleton, R.P., Thomas, G.H., Petzoldt, T., Fritz, S., Isaac, N. *et al.* 2012. *Capre: Comparative Analyses of Phylogenetics and Evolution in R. R package version 0.5*. Available at: <http://cran.r-project.org/web/packages/caper/>.
- Päckert, M., Martens, J. & Sun, Y.-H. 2010. Phylogeny of long-tailed tits and allies inferred from mitochondrial and nuclear markers (Aves: Passeriformes, Aegithalidae). *Mol. Phylogenet. Evol.* **55**: 952–967.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.
- Pitcher, T.E. & Stutchbury, B.J.M. 2000. Extraterritorial forays and male parental care in hooded warblers. *Anim. Behav.* **59**: 1261–1269.
- Poole, A. & Gill, F. 1992–2002. *The Birds of North America*. The Birds of North America, Philadelphia.
- Queller, D.C. 1997. Why do females care more than males? *Proc. R. Soc. B Biol. Sci.* **264**: 1555–1557.
- R Development Core Team. 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reid, J.M., Monaghan, P. & Ruxton, G.D. 2001. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proc. R. Soc. B Biol. Sci.* **267**: 37–41.
- Reynolds, J.D., Goodwin, N.B. & Freckleton, R.P. 2002. Evolutionary transitions in parental care and live bearing in vertebrates. *Phil. Trans. R. Soc. Lond. B* **357**: 269–281.
- Ridley, M. 1978. Paternal care. *Anim. Behav.* **26**: 904–932.
- Royle, N.J., Hartley, I.R., Owens, I.P.F. & Parker, G.A. 1999. Sibling competition and the evolution of growth rates in birds. *Proc. R. Soc. B Biol. Sci.* **266**: 923–932.
- Schwagmeyer, P.L., St. Clair, R.C., Moodie, J.D., Lamey, T.C., Schnell, G.D. & Moodie, M. N. 1999. Species differences in male parental care in birds: a reexamination of correlates with paternity. *Auk* **116**: 487–503.
- Schwagmeyer, P.L., Schwabl, H. & Mock, D. 2005. Dynamics of biparental care in house sparrows: hormonal manipulations of paternal contributions. *Anim. Behav.* **69**: 481–488.
- Sheldon, B.C. 2002. Relating paternity to paternal care. *Proc. R. Soc. B Biol. Sci.* **357**: 341–350.
- Sheldon, B.C. & Ellegren, H. 1998. Paternal effort related to experimentally manipulated paternity of male collared flycatcher. *Proc. R. Soc. B Biol. Sci.* **265**: 1737–1742.

- Sheldon, B.C., Rasanen, K. & Dias, P.C. 1997. Certainty of paternity and paternal effort in the collared flycatcher. *Behav. Ecol.* **8**: 421–428.
- Sheldon, F.H., Whittingham, L.A., Moyle, R.G., Slikas, B. & Winkler, D.W. 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* **35**: 254–270.
- Smith, H.G. & Montgomerie, R. 1992. Male incubation in Barn Swallows: the influence of nest temperature and sexual selection. *Condor* **94**: 750–759.
- Smith, L.C., Raouf, S.A., Brown, M.B., Wingfield, J.C. & Brown, C.R. 2005. Testosterone and group size in cliff swallows: testing the “challenge hypothesis” in a colonial bird. *Horm. Behav.* **47**: 76–82.
- Spellman, G.M., Cibois, A., Moyle, R.G., Winker, K. & Barker, F.K. 2008. Clarifying the systematics of an enigmatic avian lineage: what is a bombycillid? *Mol. Phylogenet. Evol.* **49**: 1036–1040.
- Stutchbury, B.J.M. 1998. Extra-pair mating effort of male hooded warblers, *Wilsonia citrina*. *Anim. Behav.* **55**: 553–561.
- Székely, T., Thomas, G.H. & Cuthill, I.C. 2006. Sexual conflict, ecology, and breeding systems in shorebirds. *Bioscience* **56**: 801–808.
- Székely, T., Kosztolányi, A., Küpper, C. & Thomas, G.H. 2007. Sexual conflict over parental care: a case study of shorebirds. *J. Ornithol.* **148**: 211–217.
- Tallamy, D.W. 2000. Sexual selection and the evolution of exclusive paternal care in arthropods. *Anim. Behav.* **60**: 559–567.
- Tatner, P. & Bryant, D.M. 1993. Interspecific variation in daily energy expenditure during avian incubation. *J. Zool.* **231**: 215–232.
- Thomson, D.L., Monaghan, P. & Furness, R.W. 1998. The demands of incubation and avian clutch size. *Biol. Rev.* **73**: 293–304.
- Tinbergen, J.M. & Williams, J.B. 2002. Energetics of incubation. In: *Avian Incubation: Behaviour, Environment and Evolution* (D.C. Deeming, ed.), pp. 298–313. Oxford University Press, Oxford.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (B. Campbell, ed.), pp. 136–179. Heinemann, London.
- Verner, J. & Willson, M.F. 1969. Mating systems, sexual dimorphism, and the role of male north american passerine birds in the nesting cycle. *Ornithol. Monogr.* **9**: 1–76.
- Visser, M.E. & Lessells, C.M. 2000. The costs of egg production and incubation in great tits (*Parus major*). *Proc. R. Soc. B Biol. Sci.* **268**: 1271–1277.
- Wagner, R.H., Schug, M.D. & Morton, E.S. 1996. Confidence of paternity, actual paternity and parental effort by purple martins. *Anim. Behav.* **52**: 123–132.
- Walsberg, G.E. 1983. Avian ecological energetics. In: *Avian Biology*, **7** (D.S. Farner, J.R. King & K.C. Parkes, eds), pp. 161–220. Academic Press, London and New York.
- Weatherhead, P.J., Montgomerie, R., Gibbs, H.L. & Boag, P.T. 1994. The cost of extra-pair fertilizations to female Red-winged Blackbirds. *Proc. R. Soc. B Biol. Sci.* **258**: 315–320.
- Webb, T.J., Olson, V.A., Székely, T. & Freckleton, R.P. 2010. Who cares? Quantifying the evolution of division of parental effort. *Methods Ecol. Evol.* **1**: 221–230.
- White, F.N. & Kinney, J.L. 1974. Avian incubation. *Science* **186**: 107–115.
- Whittingham, L.A. & Lijfeld, J.T. 1995. High parental investment in unrelated young: extra-pair paternity and male parental care in house martins. *Behav. Ecol. Sociobiol.* **37**: 103–108.
- Williams, J.B. 1996. Energetics of avian incubation. In: *Avian Energetics and Nutritional Ecology* (C. Carey, ed.), pp. 375–415. Chapman and Hall, London.
- Wright, J. 1998. Paternity and paternal care. In: *Sperm Competition and Sexual Selection* (T.R. Birkhead & A.P. Møller, eds), pp. 117–145. Academic Press, London.
- Yeung, C.K.L., Lin, R.-C., Lei, F., Robson, C., Hung, L.M., Liang, W. *et al.* 2011. Beyond a morphological paradox: complicated phylogenetic relationships of the parrotbills (Paradoxornithidae, Aves). *Mol. Phylogenet. Evol.* **61**: 192–202.

Supporting information

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

Figure S1 Phylogeny based on Barker *et al.* (2004) with Grafen’s (1989) branch lengths.

Figure S2 Phylogeny based on Jönsson & Fjeldså (2006) with Grafen’s (1989) branch lengths.

Tables S1–S3 Results of PGLS models using different phylogenies and branch lengths run on species averages of male’s relative incubation effort (power-2 transformed) fitted in caper package.

Tables S4–S7 Results of PGLS models using different phylogenies and branch lengths run on population-level values of male’s relative incubation effort (power-2 transformed) fitted in caper package.

Data deposited at Dryad: doi:10.5061/dryad.3b869

Received 28 August 2012; revised 28 August 2012; accepted 8 October 2012