

Original Article

Mate-feeding has evolved as a compensatory energetic strategy that affects breeding success in birds

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In many animals, females are fed by males during courtship or incubation (mate-feeding). According to the mate appraisal hypothesis, females may evaluate the parental capacity of males, whereas the pair bond hypothesis suggests that feeding may strengthen the pair bonds with them. Following the nutrition hypothesis, by contrast, females obtain direct nutritional benefits from being fed by males during periods of high-energy expenditure, such as egg formation and incubation. However, there is little support for these hypotheses at an interspecific level. We tested predictions from these hypotheses in a dataset of 170 species of passerine birds. As predicted by the nutrition hypothesis, we found that mate-feeding has evolved more often in species in which the female incubates and builds the nest alone and have noncarnivorous diets. This suggests that mate-feeding is a behavioral strategy that compensates for nutritional limitations of females during breeding, as both incubation and nest building are energetically costly processes, and noncarnivorous diets are deficient in proteins. We also found that incubation feeding has evolved more often in species that place nests at elevated sites, suggesting that these species face low predation risk that allows males to feed females. In the particular case of incubation feeding, we found that species that have evolved this behavior produce larger clutch size and have higher hatching success. Our results support the nutrition hypothesis from an interspecific perspective, suggesting that mate-feeding is a strategy to compensate for nutritional limitations of females during reproduction and that it has fitness consequences. *Key words:* courtship feeding, incubation feeding, nutrition hypothesis, phylogeny, predation risk. [*Behav Ecol* 22:1088–1095 (2011)]

INTRODUCTION

Many male animals feed females during courtship or incubation (mate-feeding hereafter). This is observed among both invertebrates (Eberhard 1994) and vertebrates (Lack 1940), but birds represent the group where this behavior has been reported most extensively (Lack 1940; Silver et al. 1985). Functional explanations for mate-feeding are diverse and currently debated. They can be divided in those that attempt to explain the occurrence of mate-feeding (particularly courtship feeding) in the context of sexual selection as a signal of parental quality, and those that attempt to explain the occurrence of either courtship or incubation feeding in the context of natural selection as a way of dealing with the female's energetic requirements during reproduction.

In the set of hypotheses related to sexual selection, Lack (1940) first proposed that males may feed their mates not to cover nutritional requirements of females but to signal their parental quality or to strengthen pair bonds because mate-feeding is not only observed in species where only the female incubates (the mate appraisal or pair bond hypothesis). Ricklefs (1974) reached a similar conclusion after noting that, although mate-feeding is observed in several species of birds,

these species belong to 3 main orders (Coraciiformes, Falconiformes, and Passeriformes), so it is probably not an extended energetic strategy among birds. Indeed, the pair bond hypothesis, albeit having a controversial theoretical justification (Wachtmeister 2001), seems to partly explain the observed frequency of mate-feeding in different species of birds (Donazar et al. 1992; Helfenstein et al. 2003). Related to this explanation, courtship feeding has been suggested to signal parental ability evaluated by females (e.g., Nisbet 1973; Simmons 1988; Korpimäki 1989). Indeed, males that make a large investment in mate-feeding also tend to invest in feeding offspring across species (Møller and Cuervo 2000). Other scientists have found that the occurrence of courtship feeding is related to copulation rates as a kind of exchange of copulations for food (González-Solís et al. 2001), which may represent a sperm competition strategy by increasing the certainty of paternity of males after obtaining repeated access to females (González-Solís and Becker 2002). This may not offer a general explanation for birds, however, as comparative studies have not found a relationship between occurrence of courtship feeding and certainty of paternity across species (Møller and Birkhead 1993; Møller and Cuervo 2000).

A second alternative, but nonexclusive hypothesis provides explanations for the occurrence of mate-feeding in the context of natural selection. Females could obtain direct benefits from their mates by being provided with the nutritional requirements during egg formation and incubation (nutrition hypothesis), periods during which the nutritional needs of

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females are high (Moreno 1989; Nager et al. 1997; Ramsay and Houston 1997; Reynolds 2001). Indeed, the fitness outcome can directly depend on the extent of nest attentiveness by parents, although this attentiveness is constrained by limited energy resources (Martin and Ghalambor 1999). Thus, males can reduce the frequency of incubation breaks to obtain food and increase nest attentiveness by providing females with supplemental food in species in which only the female incubates (Lyon and Montgomerie 1985; Martin and Ghalambor 1999), although mate-feeding is not only observed in these species (Lack 1940). Indeed, reproductive success in birds largely depends on female access to food during the periods of egg production and incubation (Martin 1987). As a consequence, laying date is advanced (Royama 1966; Tasker and Mills 1981; Daan et al. 1990), the duration of the incubation period and the frequency of incubation breaks are reduced (Nilsson and Smith 1988; Stein et al. 2010), and other life-history traits such as egg mass, clutch size, and hatching and fledging success increase with the frequency of mate-feeding (Nisbet 1973, 1977; Lyon and Montgomerie 1985; Lifjeld and Slagsvold 1986; Carlson 1989; Helfenstein et al. 2003). Therefore, mate-feeding represents a direct way of increasing the fitness of males and females.

Finally, other scientists have investigated the ecological factors that explain the observed variability in occurrence of mate-feeding in birds. In particular, the role of predation risk in determining the occurrence of incubation feeding in birds has been highlighted by Ghalambor and Martin (2002), who showed that predation risk reduces the frequency of male feeding to incubating females. Courtship feeding may also increase predation risk, as this is a conspicuous behavior in which females often adopt particular postures and produce calls, whereas males present food by means of ceremonial flights (Lack 1940; Andrew 1961). Thus, courtship feeding may be associated with increase predation risk like other conspicuous sexual displays (Boyko et al. 2004). In addition to predation risk, nest microclimate conditions can also have a role in the evolution of incubation feeding, as harsh conditions at certain nest sites limit the time that females can get off the nest and thus promote the feeding of females by males (Lyon and Montgomerie 1987).

Most studies of the evolution of mate-feeding in birds are intraspecific (see however Lyon and Montgomerie 1987; Møller and Birkhead 1993; Møller and Cuervo 2000; Ghalambor and Martin 2002), but to our knowledge, broad comparative studies on this issue are lacking. However, comparative studies of the evolution of mate-feeding are also necessary if general conclusions about the function of this behavior have to be reached. Our aim is to test the different hypotheses that have been suggested to explain the evolution of courtship and incubation feeding, as well as assess the importance of hypothetical ecological factors, in a large dataset of 170 species of passerine birds.

In a first set of predictions, we investigated the factors that can explain the prevalence (i.e., presence vs. absence) of mate-feeding in passerine birds. First, we predicted that 1) if the mate appraisal or pair bond hypothesis (Lack 1940; Green and Krebs 1995) is true, mate-feeding should have evolved more frequently among monogamous than polygamous species because there are more possibilities of evaluating the quality of mates or of strengthening pair bonds in monogamous than in polygamous species, as pair members spend more time together in the former species. The opposite prediction (i.e., that mate-feeding is more frequent in polygamous species) is also possible, however, as males may trade food resources for certainty of paternity, and females may determine which male will fertilize their eggs by evaluating the quality of males through this behavior. For the mate appraisal

hypothesis, we predicted that 2) the prevalence of mate-feeding should be negatively related to the number of broods in one breeding season, because multiple broods may increase the probability of finding fertile females during the nestling period (Møller and Birkhead 1993), which in turn may increase the probability of males obtaining extrapair copulations, and paternal investment (and mate-feeding can be considered a form of paternal investment; Møller and Cuervo 2000) is negatively related to degree of extrapair paternity (Dixon et al. 1994). However, the opposite prediction (i.e., that the prevalence of mate-feeding is positively related to the number of broods) is also possible because females may have more opportunities to evaluate future paternal quality, and thus, mate-feeding will provide more useful information for females on the quality of their mates in species with multiple broods. Lastly, we predicted that 3) the prevalence of mate-feeding should be more frequent in colonial than in noncolonial species because the probability that this behavior evolves as a signal of male quality should be higher in social contexts, where more signal receivers are present, and thus, there are more possibilities for the transfer of public information that may be used by neighboring females to choose their extrapair partners. In sum, we expected that the prevalence of mate-feeding should depend on mating system, coloniality, and/or number of broods in one breeding season.

Second, if the nutrition hypothesis (Nisbet 1973; Lyon and Montgomerie 1985) is true, mate-feeding should be more frequent in species with higher energetic demands during reproduction. Thus, we predicted that mate-feeding should be more frequent in 4) species in which only the female incubates as compared with species in which both sexes incubate (because incubation is an activity with high energy demand; Sanz 1996; Thomson et al. 1998; Reid et al. 2000; Ghalambor and Martin 2002); 5) species in which only the female builds the nest as compared with species in which both sexes or only the male build the nest (because nest building is an activity with high energy demand; Soler, Cuervo, et al. 1998; Soler, Møller, et al. 1998); and 6) species with larger clutch size as compared with species with smaller clutch size (because incubating large clutches demands more energy than incubating small clutches; Moreno and Sanz 1994; Thomson et al. 1998). Furthermore, in relation to the nutrition hypothesis, we predicted that 7) mate-feeding should be more frequent among strictly granivorous species than among species whose diet is entirely or partly composed by invertebrates because the low protein content of most seeds is a nutritional limitation that makes several granivorous species shift to an invertebrate diet during breeding (Newton 1967; Wiens and Johnston 1977). Thus, we expected that the prevalence of mate-feeding should depend on all or any of the following species characteristics: number of parents that incubate, number of parents that build the nest, clutch size, and diet.

Finally, we made some predictions for the factors that may constrain the evolution of mate-feeding. If predation risk and nest microclimate constitute major selective pressures on mate-feeding (Lyon and Montgomerie 1987; Martin and Ghalambor 1999; Ghalambor and Martin 2002), we predicted that incubation feeding should be less frequent in 8) species that nest in sites exposed to high predation risk than in those that nest in sites with low predation risk (i.e., nests at low elevation and open nests vs. nests at high elevation and in holes; Martin 1988) or in species that nest in sites with mild microclimate conditions (i.e., open nests) than in those that nest in holes (Lyon and Montgomerie 1987; Martin and Ghalambor 1999); and 9) that both courtship and incubation feeding should be less frequent in species that inhabit open environments as compared with species that inhabit more vegetated habitats (because natural

selection exerts stronger pressure on open habitats due to higher predation risk; Götmark and Post 1996; Rodríguez et al. 2001). Thus, for this set of predictions, we expected that the prevalence of mate-feeding should depend on nest site, nest elevation, and/or habitat type.

We also made a second set of predictions to test the fitness consequences of the nutrition hypothesis in relation to several parameters of breeding success. Thus, we predicted that 10) the incubation period should be shorter (Nilsson and Smith 1988; Stein et al. 2010) and egg mass, clutch size, and hatching success should be larger (Nisbet 1973, 1977; Lyon and Montgomerie 1985; Lifjeld and Slagsvold 1986; Carlson 1989; Helfenstein et al. 2003) in species that have evolved mate-feeding than in species that have not evolved this behavior. Given the tight dependence of these life-history traits on body size (Blueweiss et al. 1978), the analyses were made controlling for female body mass. In sum, for this set of predictions, we expected that the duration of the incubation period, egg mass, clutch size, and hatching success (either alone or in combination) depend on the prevalence of mate-feeding, after controlling for the effects of female body mass.

METHODS

Collection of data

The dataset includes information on mate-feeding and life-history variables of 170 species of passerine birds. The information was extracted from Cramp and Simmons (1988–1992) and Cramp and Perrins (1993–1994). We extracted information on the following variables: 1) prevalence of courtship and incubation feeding, 2) mean body mass (g) of adult females during the breeding season, 3) mean egg mass (g), 4) mean clutch size, 5) mean duration of the incubation period (days), 6) mean hatching success (%), 7) mating system (with the following scores: 1, monogamous; 2, polygamous), 8) coloniality (with the following scores: 0, noncolonial; 1, colonial), 9) number of broods in one breeding season (on a continuous scale, but assigning values of 1.5 and 2.5 to species that normally have 1 and 2 broods, although 2 and 3 broods are sometimes observed, respectively), 10) number of parents that incubate (with the following scores: 1, female only; 2, female and male to some degree), 11) number of parents that build the nest (with the following scores: 1, male; 2, mainly male; 3, male and female at 50%; 4, mainly female; and 5, female), 12) diet (with the following scores: 1, seeds or plant material; 2, seeds or fruits supplemented with insects; and 3, invertebrates or omnivorous), 13) nest site (with the following scores: 1, open nest on ground or shrub; 2, open nest on tree or wall; and 3, hole nest), 14) nest elevation (with the following scores: 0, ground; 1, between 0 and 1 m above ground; 2, between 1 and 3 m above ground; 3, between 3 and 5 m above ground; and 4, more than 5 m above ground), and 15) habitat preferences (with the following scores: 1, treeless “open country”; 2, open woodland; and 3, dense forest). Information on these variables for the 170 species considered in the study is shown in Supplementary Material, Supplementary Appendix 1.

Data analyses

Bird species are evolutionarily related as reflected by phylogeny, and, therefore, they should not be treated as independent sample units (Felsenstein 1985; Harvey and Purvis 1991). Thus, the effect of common ancestry among taxa can lead to an overestimation of degrees of freedom if phylogenetic relationships are not taken into account. We used phylogenetic eigenvector regression (PVR; Diniz-Filho et al. 1998;

Desdevises et al. 2003) to quantify the amount of phylogenetic signal and to correct for it in the analyses. Diniz-Filho and Torres (2002) and Martins et al. (2002) have tested several comparative methods (Felsenstein's independent contrasts, autoregressive method, PVR, and phylogenetic generalized least squares) and have found that PVR yields good statistical performance regardless of the details of the evolutionary mode used to generate the data, and it provides similar results to other methods, with very good (i.e., low) error types I and II. Moreover, PVR does not assume any a priori evolutionary model (an advantage if the true evolutionary model is unknown or if it is too complex) and has similar statistical performance even under evolutionary processes distinct from Brownian motion. For these reasons, PVR is a comparative method that is widely used with a diversity of taxa and ecological questions (e.g., Giannini 2003; Krilloff et al. 2008; Montoya et al. 2008; Bisson et al. 2009).

We first performed a principal coordinates analysis on the matrix of pairwise phylogenetic distances between the 170 bird species (after a double-center transformation). In a second step, we selected the first 10 eigenvectors obtained by the broken stick rule to account parsimoniously for the phylogenetic signal. Eigenvectors extracted from double-centered phylogenetic distance matrices are able to detect the main topological features of the cladogram under different sample sizes or number of taxa used in the analyses (Diniz-Filho et al. 1998). We found that the original matrix of phylogenetic distances between the 170 bird species and the reproduced matrix of distances estimated based on the first 10 eigenvectors were very similar (Mantel test with 999 randomized matrices to estimate significance: $r = 0.809$, $P < 0.0001$; test carried out using PopTools 3.2.3; Hood 2010). These eigenvectors were used as additional predictor variables in generalized and general linear models (see below) in order to control for similarity in phenotype due to common phylogenetic descent.

The phylogenetic hypothesis (see Supplementary Material, Supplementary Appendix 2) was taken from the species-level supertree constructed by Davis (2008), with additional information from other sources for some species not covered by Davis (2008): Wink et al. (2002), Lovette and Rubenstein (2007), Voelker et al. (2007), Alström et al. (2008), Nguembock et al. (2009), Outlaw et al. (2010), Zuccon and Ericson (2010), and the phylogeny compiled by Møller (2006). Although, to our knowledge, there is not a detailed phylogeny of *Corvus*, we considered the brown-necked raven (*Corvus ruficollis*) the sister group of the common raven (*C. corax*) because the former forms a superspecies with the pied crow (*C. albus*) (del Hoyo et al. 2009), which was reported by Davis (2008) to be phylogenetically closer to the common raven than the rest of the *Corvus* species considered in the present study. Although there are no molecular phylogenies analyzing the phylogenetic position of the pale rock finch (*Carpospiza brachydactyla*), we considered this species the sister group of the rock sparrow (*Petronia petronia*) as suggested by Bock (2004) on the basis of morphological characters. Because we used different phylogenies that employed different methods, we set all branch lengths equal to unity in our compiled phylogeny, thus assuming a speciation model of evolution. We mapped the prevalence of courtship and incubation feeding on the phylogeny, thereby providing a visual display of the distribution of both behavioral strategies (Supplementary Material, Supplementary Appendix 2).

By means of generalized linear models with a binomial response distribution and a logit link function, we investigated whether the prevalence of courtship and incubation feeding could be explained by mating system, coloniality, number of broods in one breeding season, incubating sex, sex that builds the nest, clutch size, diet, nest site, nest elevation, and habitat

type. Mating system (with the levels monogamous—0, polygamous—1), incubating sex (with the levels only female—0, female and male to some degree—1), and coloniality (with the levels noncolonial—0, colonial—1) were added to the models as dummy variables. The number of broods in one breeding season (\log_{10} -transformed), the sex that builds the nest (on a scale ranging from 1 to 5, see Collection of data), clutch size (the residuals of its regression against female body mass; see Blueweiss et al. 1978), and nest elevation (in a scale ranging from 0 to 4, see Collection of data) were added as covariates. For diet, nest site, and habitat preferences, we used linear contrast tables, ordering the 3 levels of these factors (see Collection of data) according to the following sequence: diet: seeds or other plant material (factor score -1), seeds or fruits supplemented with insects (0), and invertebrates or omnivorous ($+1$); nest site: open nest on ground or shrub (-1), open nest on tree or wall (0), and hole ($+1$); habitat preferences: treeless open country (-1), open woodlands (0), and dense forest ($+1$). Nest site and nest elevation were not considered in the model for courtship feeding. The first 10 phylogenetic eigenvectors (EV1–EV10 hereafter) were entered as covariates. Starting with the saturated models, nonsignificant terms were removed by a stepwise procedure, establishing a P level of 0.1 to abandon the model, excepting the phylogenetic eigenvectors that were never removed.

By means of general linear models, we regressed egg mass (\log_{10} -transformed), clutch size (\log_{10} -transformed), duration of incubation period (\log_{10} -transformed), and hatching success (arcsine-squared-root transformed) on the prevalence of courtship or incubation feeding, which were added to the models as dummy variables with 2 levels (absence—0, presence—1), and EV1–EV10, which were added as covariates. The effect of female body mass on the response variables was controlled for by this variable (\log_{10} -transformed) as an additional covariate. Prevalence of courtship and incubation feeding were not included as predictor variables in the same models because these variables were strongly positively correlated (generalized linear model with a binomial response distribution and a logit link function, prevalence of incubation feeding as a fixed factor and EV1–EV10 as covariates; $\chi^2_1 = 57.80$, $P < 0.0001$). Thus, the models included prevalence of either courtship or incubation feeding to avoid multicollinearity between predictors. Prevalence of incubation feeding was not considered in the model for egg mass. In this case, nonsignificant terms were not removed from the models because, to control for the effects of body mass and phylogeny, these factors must be kept in the models, and the remaining factors (i.e., prevalence of courtship or incubation feeding) represent the effects of interest. The significance of the effect of phylogeny in these models was calculated by comparing the saturated models (M_1) with the models without EV1–EV10 (M_2), using the following formula (Zuur et al. 2009):

$$\frac{D_2 - D_1}{\phi(p_1 - p_2)} \sim F_{p_1 - p_2, n - p_1},$$

where ϕ is the overdispersion parameter, D_1 and D_2 are the deviances of the models, p_1 and p_2 are the number of parameters in the models, and n is sample size.

The phylogenetic signal (i.e., amount of deviance exclusively explained by phylogeny) in the prevalence of courtship and incubation feeding was calculated by regressing these variables on EV1–EV10, using a generalized linear model with a binomial response distribution and a logit link function. Generalized models were checked for deviations from canonical assumptions using the overdispersion coefficients. The assumption of normality in the general linear models was checked by exploring the distribution of residuals.

RESULTS

Phylogenetic signal in mate-feeding

The phylogenetic signal in prevalence of courtship feeding was significant ($\chi^2_{10} = 48.31$, $P < 0.0001$) and constituted 26.4% of deviance in this variable. The phylogenetic signal in prevalence of incubation feeding was also significant ($\chi^2_{10} = 60.93$, $P < 0.0001$) and constituted 30.8% of deviance.

Life-history and ecological traits as predictors of mate-feeding prevalence

In the model for prevalence of courtship feeding, neither diet ($\chi^2_1 = 0.07$, $P = 0.786$), mating system ($\chi^2_1 = 0.18$, $P = 0.672$), clutch size ($\chi^2_1 = 0.38$, $P = 0.538$), coloniality ($\chi^2_1 = 0.65$, $P = 0.420$), number of broods in one breeding season ($\chi^2_1 = 0.52$, $P = 0.472$), and the building sex ($\chi^2_1 = 1.32$, $P = 0.250$) nor habitat preferences ($\chi^2_1 = 1.18$, $P = 0.278$) significantly contributed to explain deviance in this variable. Therefore, these factors were removed from the model. The final model (Table 1) was significant ($\chi^2_{11} = 69.86$, $P < 0.0001$) and explained 38.2% of deviance in prevalence of courtship feeding across species. The incubating sex was an important predictor of prevalence of courtship feeding and indicated that this behavior has evolved more often in species in which the female incubates alone (Table 1). The effect of phylogeny was significant overall (Table 1; see Supplementary Material, Supplementary Table 1 for results for all phylogenetic eigenvectors).

In the model for prevalence of incubation feeding, neither the number of broods in one breeding season ($\chi^2_1 = 0.01$, $P = 0.919$), clutch size ($\chi^2_1 = 0.20$, $P = 0.651$), and habitat type ($\chi^2_1 = 1.60$, $P = 0.205$) nor coloniality ($\chi^2_1 = 2.24$, $P = 0.134$) had significant effects. The final model (Table 1) was significant ($\chi^2_{16} = 113.51$, $P < 0.0001$) and explained 57.3% of deviance in prevalence of incubation feeding. Again, the incubating sex was a strong predictor of prevalence of incubation feeding, indicating that this behavior has evolved more often in species in which the female incubates alone (Table 1). In this model, the nest building sex also had a significant effect (Table 1), indicating that incubation feeding was positively associated with female investment in nest building. Diet had a significant effect (Table 1), indicating that incubation feeding was positively associated with noncarnivorous diets. Incubation feeding was also positively associated with nest elevation and showed a nonsignificant trend for a positive association with hole nesting (Table 1), suggesting that predation risk constrains the evolution of incubation feeding. There was also a nonsignificant trend for an association between incubation feeding and monogamous mating systems (Table 1). The effect of phylogeny was significant overall (Table 1; see Supplementary Material, Supplementary Table 1 for results for all phylogenetic eigenvectors).

Association between mate-feeding and breeding success

The model for egg mass explained 91.8% of variance in this variable. Female body mass was strongly positively correlated with egg mass, but the prevalence of courtship feeding did not explain a significant proportion of variance (Table 2A). The contribution of phylogeny was marginally nonsignificant (Table 2A; see Supplementary Material, Supplementary Table 2A for results for all phylogenetic eigenvectors).

The model for clutch size explained 45.8% of variance when prevalence of courtship feeding was included as a predictor variable. Body mass had a negative effect. The effect of prevalence of courtship feeding was not significant, although a tendency of species with courtship feeding to have larger clutches was observed ($P = 0.065$; Table 2A). When prevalence of

Table 1

Results of the generalized linear models testing for effects of mating system, number of broods in one breeding season, number of parents that incubate, number of parents that build the nest, clutch size, diet, nest site, nest elevation, habitat preferences, and phylogenetic effects on the prevalence of courtship and incubation feeding in 170 species of passerine birds

Effect	Courtship feeding			Incubation feeding		
	<i>b</i>	χ^2	<i>P</i>	<i>b</i>	χ^2	<i>P</i>
Mating system	—	—	—	1.06	3.02	0.082
Coloniality	—	—	—	—	—	—
Number of broods in a breeding season	—	—	—	—	—	—
Incubating sex	-2.84	21.55	<0.0001	-4.56	33.48	<0.0001
Nest building sex	—	—	—	0.86	6.64	0.010
Size-corrected clutch size	—	—	—	—	—	—
Diet	—	—	—	-1.81	6.91	0.008
Nest site	—	—	—	0.76	2.76	0.096
Nest elevation	—	—	—	0.58	5.31	0.021
Habitat structural gradient	—	—	—	—	—	—
Phylogeny	—	32.33	<0.001	—	21.79	0.016

For each variable, we show the fitted regression coefficient (*b*) and its corresponding significance. Phylogenetic effects are computed from the first 10 eigenvectors (EV1–EV10) obtained from a principal coordinates analysis applied to the matrix of pairwise phylogenetic distances between the 170 species. Significant effects are shown in bold.

incubation feeding was included instead, the model explained 46.5% of variance in clutch size. Body mass again had a negative effect, but the effect of prevalence of incubation feeding was highly significant in this case (Table 2B), clearly indicating that clutch size was larger in species in which males feed their mates during incubation (Figure 1). In both models, the effect of phylogeny was highly significant (Table 2A,B; see Supplementary Material, Supplementary Table 2A,B for results for all phylogenetic eigenvectors).

The models for duration of incubation period explained 55.5% and 55.9% of variance when prevalence of courtship feeding or incubation feeding were included as predictor variables, respectively. However, neither prevalence of courtship feeding nor incubation feeding were associated with the duration of the incubation period (Table 2A,B). In both models, body mass had a positive but marginally nonsignificant effect (Table 2A,B). The effect of phylogeny was not significant in these models (Table 2A,B; see Supplementary Material, Supplementary Table 2A, for results for all phylogenetic eigenvectors).

Finally, the model for hatching success explained 11.1% of variance when prevalence of courtship feeding was included as a predictor variable. In this model, neither body mass, prevalence of courtship feeding nor phylogeny had significant effects (Table 2A). However, in the model including prevalence of incubation feeding, which explained 13.0% of variance, the effect of this variable was significant (Table 2B), indicating that hatching success was higher in species in which males feed their mates during incubation (Figure 1). The effect of phylogeny was not significant in these models (Table 2A,B; see Supplementary Material, Supplementary Table 2A,B for results for all phylogenetic eigenvectors).

DISCUSSION

We found support for the nutrition hypothesis of mate-feeding in passerine birds at an interspecific level. As predicted on the assumption that incubation and nest building are costly activities in terms of energy and time (Sanz 1996; Soler, Cuervo, et al. 1998; Soler, Møller, et al. 1998; Thomson et al. 1998;

Table 2

Results of the general linear models testing for effects of the prevalence of courtship (A) and incubation (B) feeding, female body mass and phylogenetic effects on egg mass, clutch size, duration of incubation period, and hatching success in 170 species of passerine birds

Effect	Egg mass			Clutch size			Incubation period			Hatching success		
	<i>b</i>	$F_{1,130}$	<i>P</i>	<i>b</i>	$F_{1,132}$	<i>P</i>	<i>b</i>	$F_{1,132}$	<i>P</i>	<i>b</i>	$F_{1,66}$	<i>P</i>
A												
Courtship feeding	-0.02	1.42	0.236	0.03	3.46	0.065	-0.01	0.69	0.409	-0.00	0.01	0.922
Female body mass	0.74	554.41	<0.0001	-0.13	20.34	<0.0001	0.02	3.22	0.075	-0.00	0.01	0.928
Phylogeny	—	1.71 ^a	0.085	—	5.43^a	<0.0001	—	1.14 ^a	0.337	—	0.65 ^a	0.766
B												
Incubation feeding	—	—	—	0.04	5.67	0.018	-0.00	0.47	0.492	0.05	4.41	0.039
Female body mass	—	—	—	-0.11	20.87	<0.0001	0.02	3.18	0.077	-0.02	0.26	0.610
Phylogeny	—	—	—	—	5.33^a	<0.0001	—	1.31 ^a	0.229	—	0.69*	0.731

For each variable, we show the fitted regression coefficient (*b*) and its corresponding significance. Phylogenetic effects are computed from the first 10 eigenvectors (EV1–EV10) obtained from a principal coordinates analysis applied to the matrix of pairwise phylogenetic distances between the 170 species. Significant effects are shown in bold.

^a *F* ratio obtained with information on difference in deviance and number of parameters and on the overdispersion coefficient after comparing the saturated model with the model without EV1–EV10. Degrees of freedom for these *F* ratios thus differ from those for the other *F* ratios presented in the table.

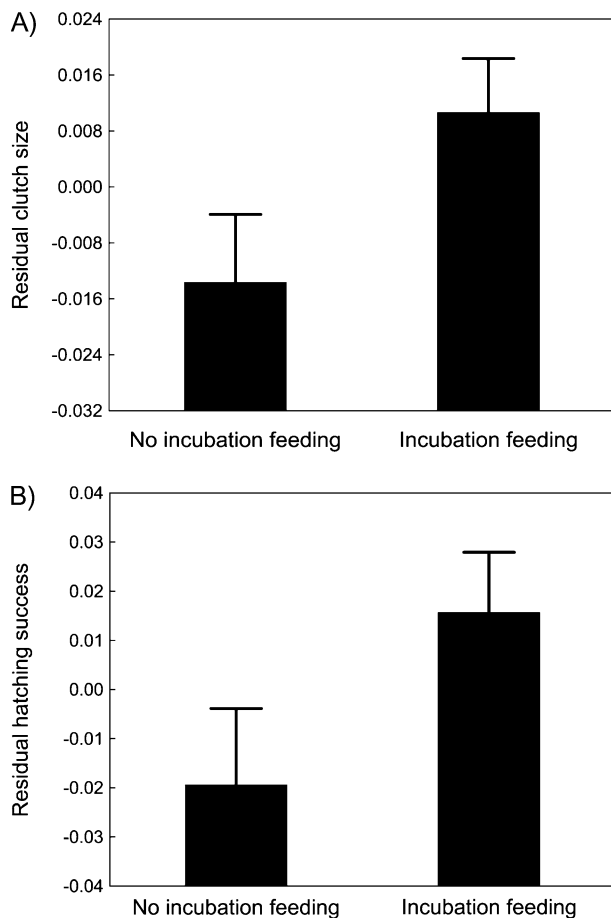


Figure 1
Clutch size (A) and hatching success (B) in passerine bird species in which males feed or do not feed their mates during the incubation period. The residual figures of the response variables are shown (i.e., partial effects after applying the full models in Table 2 without prevalence of incubation feeding). The bars are standard error.

Martin and Ghalambor 1999; Reid et al. 2000; Ghalambor and Martin 2002), mate-feeding has evolved more often in species in which females incubate and build the nest alone. Mate-feeding was also associated with noncarnivorous species with low dietary levels of protein (Robbins et al. 2005). This suggests that mate-feeding has evolved as a behavioral strategy to compensate for energetic limitations in females during reproduction, thus supporting previous intraspecific studies concluding that mate-feeding has nutritional value for females (Nisbet 1973, 1977; Lifjeld and Slagsvold 1986; Smith et al. 1989; Donazar et al. 1992; Halupka 1994; González-Solis et al. 2001; Helfenstein et al. 2003). By contrast, we found little support for the mate appraisal hypothesis (Lack 1940; Green and Krebs 1995), as prevalence of mate-feeding was not related to either the number of broods in one breeding season or to coloniality, and there was only a nonsignificant trend to an association between incubation feeding and monogamy.

The predictive capacity of these factors differed, however, between the components of mate-feeding considered here (i.e., courtship and incubation feeding). Although the identity of the sex that incubates was a strong predictor of prevalence of both courtship and incubation feeding, the identity of the sex that builds the nest was only a significant predictor of incubation feeding prevalence. This is somewhat surprising because nest building obviously takes place before incubation begins

and the eggs hatch. However, there is evidence that nest building is a costly activity in birds (Soler, Cuervo, et al. 1998; Soler, Møller, et al. 1998), so species in which females make a greater investment in nest building may face a trade-off between allocating energetic resources to nest building and to incubation later in the breeding season because incubation is indeed energetically costly (Sanz 1996; Thomson et al. 1998; Reid et al. 2000; Ghalambor and Martin 2002). This is likely, as the amount of energy allocated to a given reproductive phase limits the energy that can be allocated to other phases (Reid et al. 2000). Such a trade-off may thus explain why the identity of the sex that builds the nest is a better predictor of mate-feeding during incubation than during courtship. Noncarnivorous diets were also strongly associated with incubation feeding but not with courtship feeding. This difference may be related to the fact that courtship feeding occurs during egg development, when the nutritional needs of females are high (Helfenstein et al. 2003 and cited references), whereas during incubation, the activities of females may not only be constrained by energy but also by time limitation, as incubation requires high nest attentiveness (Martin and Ghalambor 1999). This suggests that mate-feeding may be of greater nutritional value for females during incubation than at the previous phase of egg formation (Martin 1987). This may explain why noncarnivorous passerine birds have evolved incubation feeding but do not have a particularly strong association with courtship feeding.

If mate-feeding is a behavioral strategy that provides direct nutritional benefits to females, it might be of adaptive value and should have consequences for breeding success. We found evidence for a relationship between mate-feeding and breeding performance, as 2 parameters of breeding success (clutch size and hatching success) were associated with the presence of incubation feeding among species. Thus, our study supports from an interspecific perspective previous intraspecific studies that reported benefits of courtship feeding on laying date (Royama 1966; Tasker and Mills 1981; Daan et al. 1990) and of courtship or incubation feeding on the duration of the incubation period, egg mass, clutch size, and hatching and fledging success in different species of birds (Nisbet 1973, 1977; Lyon and Montgomerie 1985; Lifjeld and Slagsvold 1986; Nilsson and Smith 1988; Carlson 1989; Helfenstein et al. 2003; Stein et al. 2010). In our case, only incubation feeding was associated with breeding success, suggesting again that the nutritional value for females of incubation feeding may be higher than that of courtship feeding. However, Helfenstein et al. (2003) found that courtship feeding reduced male arrival date (which is related to breeding success) between years and increased egg size in black-legged kittiwakes (*Rissa tridactyla*). Thus, the possibility that the fitness consequences of courtship feeding are more important and easier to detect in groups of birds different from those treated here (i.e., nonpasserines) should not be discarded. Alternatively, courtship feeding may compensate for energetic limitations of females during egg formation, making the breeding success of the species with these limitations similar to that of the other species. Incubation feeding may not only compensate for energetic limitations but even improve the reproductive performance of females in species that have evolved this behavior. Similar adaptive responses have been reported elsewhere (e.g., Dimova et al. 2008; Galván and Alonso-Alvarez 2009).

Ghalambor and Martin (2002) concluded that predation risk constitutes a major constraint for the occurrence of mate-feeding (in particular, incubation feeding) in birds because predation risk limits the frequency of nest attendance by males. Thus, we predicted that species that place the nest at higher elevation (i.e., exposed to lower predation risk) and in

holes should be more prone to evolve incubation feeding strategies. We found support for the former prediction, as incubation feeding was positively associated with nest elevation, whereas support for the second prediction was weak, as there was only a nonsignificant trend for an association between incubation feeding and hole nesting. Therefore, this gives some support to the hypothesis that the evolution of incubation feeding is constrained by predation risk. However, these results should be taken with caution, as we did not use direct indicators of predation risk, but proxies for this factor, such as nest site and nest elevation. Indeed, an alternative, nonexcluding explanation for the tendency of incubation feeding to be more frequent in hole nesting species is that nest microclimate conditions are harsher at holes than at open nests (Lyon and Montgomerie 1987; Martin and Ghalambor 1999), which would restrict the time that females can get off the nest, thus promoting the feeding of females by males (Lyon and Montgomerie 1987).

Finally, we found that the phylogenetic signal in prevalence of mate-feeding was relatively low, 28.3% and 26.1% in courtship and incubation feeding, respectively. This means that not all variation in occurrence of mate-feeding in extant birds can be attributed to the effects of selective pressures because part of this is constrained by phylogeny.

In conclusion, we found in 170 passerine birds that mate-feeding has evolved more often in species in which the female incubates and builds the nest alone, have noncarnivorous diets, and are exposed to low predation risk during breeding. The particular case of incubation feeding has fitness benefits, as species that have evolved this behavior produce larger clutches and have higher hatching success. Therefore, mate-feeding seems to have evolved in birds as a strategy to provide females with direct nutritional benefits, and it is constrained by predation risk. Because mate-feeding has also evolved in several groups of invertebrates (Eberhard 1994), our conclusions may not only be applicable to birds but to a wider phylogenetic spectrum.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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