University of Groningen

How do ecological and social environments reflect parental roles in birds?

Long, Xiaoyan; Liu, Yang; Liker, András; Weissing, Franz J.; Komdeur, Jan; Székely, Tamás

Document Version
Early version, also known as pre-print

Publication date:
2020

1 **How do ecological and social environments reflect parental roles in birds?**

2 **A comparative analysis**

3 Xiaoyan Long[1,2], Yang Liu[1*], András Liker[3,4], Franz J. Weissing[2], Jan Komdeur[2], Tamás Székely[1,5,6*]

4

5 [1] State Key Laboratory of Biocontrol, School of Ecology/School of Life Sciences, Sun Yat-sen University,

6   Guangzhou, 5102275, China

7 [2] Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700CC, Groningen, The

8   Netherlands

9 [3] MTA-PE Evolutionary Ecology Research Group, University of Pannonia, H-8210 Veszprém, Pf. 1158,

10   Hungary

11 [4] Behavioural Ecology Research Group, Center for Natural Sciences, University of Pannonia, H-8210

12   Veszprém, Pf. 1158, Hungary

13 [5] Milner Centre for Evolution, Department of Biology and Biochemistry, University of Bath, Bath BA2

14   7AY, United Kingdom

15 [6] Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Egyetem

16   tér 1, 4032, Hungary

17

18 *email: liuy353@mail.sysu.edu.cn and bssts@bath.ac.uk

19

20

21

22

Abstract

24 Parental roles are highly diverse in animal taxa. Since caring is an important determinant of fitness,

25 understanding the origin and maintenance of various parental care strategies is a key question in

26 evolutionary biology. Here we investigate parental care patterns in birds, which exhibit a remarkable

27 diversity of parental sex roles. By means of phylogenetically informed comparative analyses we

28 investigate whether and how care provisioning is predicted by ecology and social environment. Making

29 use of the most comprehensive dataset including 1101 species that represent 126 avian families, we

30 show that sex differences in parental care are neither related to food type nor to nest type, two key

31 ecological factors. However, we found an effect of the social environment, as males tend to care

32 relatively more in in colonial species than in non-colonial species. Taken together, these results

33 highlight the importance of social effects for evolution of diverse parental sex roles.

34

Key words

36 food type, nest type, coloniality, parental roles, social behavior

37

38

39

INTRODUCTION

40

41 Parental care, which increases offspring survival at the cost of parents' viability and fecundity, varies
42 widely among animal taxa (Balshine 2012; Trumbo 2012). Birds are characterized by an extraordinary
43 diversity in parental roles, ranging from female-only care (e.g., hummingbirds, where only the females
44 build nests, incubate eggs and feed the young), to biparental care (e.g., woodpeckers, where the two
45 sexes share parental duties), and male-only care (e.g., some shorebirds, where the males incubate the
46 eggs and rear the young without any support by the females) (Cockburn 2006; Remeš et al. 2015).
47 Understanding this diversity is important as parental roles have repercussions on many other
48 characteristics, such as sex differences in morphology, demography and mating strategies (Emlen and
49 Oring 1977; Fairbairn et al. 2007; Royle et al. 2012; Klug 2018).

50 Various ecological and social variables have been proposed to influence parental sex roles (McGraw et
51 al. 2010; Klug et al. 2012). Firstly, it has been proposed that food type is related to sex differences in
52 parental care. It has been argued that uniparental care is to be expected in bird species feeding on
53 plant materials such as fruits and nectar; as such food sources tend to be seasonally abundant, one
54 parent should suffice to efficiently provision the young (Cockburn 2006; Barve and La Sorte 2016). In
55 contrast, biparental care might be expected in bird species feeding on insects or other animals; such
56 food is often dispersed and difficult to catch and both parents are required to satisfy the demands of
57 their offspring (Badyaev and Ghalambor 1998). However, this line of argumentation is not fully
58 convincing. Since plant food is nutritionally inferior to animal food, herbivorous chicks may need much
59 larger amounts of food to match their energetic demands; accordingly, both parents might be required
60 to collect or defend enough food. Conversely, a single parent might be sufficient to satisfy the demands
61 of carnivorous offspring if only few highly nutritious food items need to be collected per time unit.

62 Secondly, it has been proposed that nest type (open or closed) is an important determinant of parental
63 sex roles (Collias and Collias 1984; Hansell 2000). Open nests are exposed to the environment and
64 consequently face a high risk of predation (Collias 1964; Cody 1966; Martin 1995; Lima 2009). It has
65 been argued that this will select for biparental care, since the predation risk can be reduced
66 considerably if both parents are around (Montgomerie and Weatherhead 1988; Kleindorfer and Hoi
67 1997; Martin and Briskie 2009). In contrast, uniparental care might be expected to be common in
68 species with closed nests, which provide a good protection from predators. However, an argument
69 could also be made for the opposite pattern. For example, the presence of both parents (and, in
70 particular, the presence of a brightly coloured father) could make an open nest more conspicuous to
71 predators; hence predation risk might be enhanced rather than reduced if both parents are around
72 (Skutch 1949; Martin et al. 2000). Predation pressure is generally lower in species with closed nests,
73 but such species tend to have greater clutch sizes than those building open nests (Jetz et al. 2008).

3

74 Accordingly, just in cavity breeders both parents may be needed to meet the energetic demands of
75 the offspring.

76 Thirdly, social environment is also predicted to affect parental care strategies. In colonial breeding
77 species, pairs live in groups and often in high density, which reduces the risk of predation and allows
78 for exchanging information about food resources (Alexander 1974; Perrins and Birkhead 1983; Krause
79 and Ruxton 2002; Evans et al. 2016). Accordingly, one might expect that uniparental care is more
80 prevalent in colonially breeding species than in solitarily breeding species. In addition, opportunities
81 for extra-pair copulations are typically high in colonial species as breeding density is high, lowering the
82 certainty of paternity (Westneat and Sherman, 1997; Mayer and Pasinelli 2013) and selecting for
83 reduced paternal care. But again, a case could also be made for a different prediction. Colonially
84 breeding species almost invariable face high intraspecific competition (interference competition and
85 competition for food and other resources, Perrins and Birkhead 1983; Krause and Ruxton 2002). Based
86 on this, one would expect biparental care, as both parents are needed to successfully raise the young.

87 In view of all this, it is not self-evident which parental care patterns are to be expected under different
88 ecological and social scenarios. It is therefore important to investigate what the data say. To what
89 extent and in what way do ecological conditions (like food quality or predation pressure) or the social
90 environment (like coloniality) reflect parental roles? To answer this question, we here apply
91 phylogenetic comparative analyses to a comprehensive dataset including 1101 avian species (26 orders
92 and 119 families). First, we examine whether parental roles are associated with food type. Specifically,
93 we investigate whether plant-eating species exhibit uniparental or sex-biased parental care while
94 carnivorous species exhibit more biparental care. Second, we explore whether parental care is
95 associated with nest type, where nest type is viewed as a proxy for the risk of predation. Specifically,
96 we test whether open nesters or closed nesters are more likely to provide biparental care. Third, we
97 study whether parental care patterns are associated with coloniality. Specifically, we test whether
98 colonial breeders tend to exhibit female-biased care while parental sex roles are less biased in solitarily
99 breeding bird species.

100

101 **METHODS**

102 **Data collection**

103 We collected data from reference works (e.g., The Birds of the Western Palearctic, The Birds of North
104 America, Handbook of Australian, New Zealand and Antarctic Birds), preexisting datasets (see below)

105   and primary literatures by using Web of Science and Google Scholar. We added more species with
106   available data on parental behavior to an existing dataset used by Liker et al. (2015). Then we
107   augmented the dataset with expanded information on parental roles by extracting ecological and
108   social traits (food type, nest type and coloniality). The final dataset included 1101 species (26 orders
109   and 119 families) representing a broad spectrum of avian taxa. All data are available in the
110   supplementary materials.

111   **Parental care variables**

112   Bird species exhibit diverse forms of parental care, ranging from the preparation of the nest to
113   nutrition provision. Here, we investigate eight types of avian parental behavior: nest building, nest
114   guarding, incubation, chick brooding, chick feeding, chick guarding, post-fledgling feeding and post-
115   fledgling guarding. Since quantitative data on parental contribution were not available for many
116   species, we scored each care type on a 5-point scale: -1: no male care; -0.5: 1–33% male care; 0: 34–
117   66% male care; 0.5: 67–99% male care; 1: 100% male care. When quantitative data were not measured,
118   we used the information from verbal descriptions. For instance, species with more male contribution
119   to nestling feeding would be scored 0.5 on chick feeding. By means of the scoring system, the estimates
120   of paternal contribution and maternal contribution were fully dependent, that is, male scores would
121   always be the additive inverse of female scores. Therefore, the scores directly reflected the sex
122   differences in parental roles. 0 indicated approximately equal parental investment by both parents,
123   0.5 and -0.5 represented male-biased and female-biased parental contribution, respectively, 1 and -1
124   suggested male-only care and female-only care, respectively.

125   We then divided parental activities into two breeding phases: (i) pre-hatching care, which involved
126   nest building, nest guarding and incubation and (ii) post-hatching care, which included chick brooding,
127   chick feeding, chick guarding, post-fledgling feeding and post-fledgling guarding. To score the relative
128   participation in pre-hatching care and post-hatching care by males, we calculated the mean scores of
129   different components of parental behavior for each state. The relative participation in pre-hatching
130   care by males strongly correlated with the relative participation in nest building, incubation and nest
131   guarding by males (r^2 = 0.508-0.644, P < 0.001, see details in Supplementary Figure S1 and Table S1).
132   Similarly, the relative participation in post-hatching care by males was significantly related to the
133   relative participation in chick brooding, chick feeding, chick guarding, post-fledgling feeding and post-
134   fledgling guarding by males (r^2 = 0.393-0.729, P < 0.001, see details in Supplementary Figure S1 and
135   Table S1). This suggested that pre- and post-hatching care can reliably represent a set of specific care
136   components.

Ecological and social variables

137   The diet of bird species was classified into two categories: (i) plant materials which included fruit, seed,

138

139   leaves and (ii) animals which included invertebrates and vertebrates. For omnivorous species, their

140   mainly eaten food category was allocated. Since parents and nestlings subsist on different food items

141   in some species (e.g., In willow ptarmigan (*Lagopus lagopus*) the adults forage for plant materials all

142   year round while their nestlings are usually fed on insects (Peters 1958)), we collected diet of parents

143   and nestlings separately.

144   Nest type was treated as binary variables (open or closed). Open nests, which are exposed to adverse

145   weather conditions and predators, included scrapes (e.g., nests of many shorebirds), cups (e.g., nests

146   of many passerines) and platforms (e.g., nests of raptors) (Hansell 2000). Closed nests are completely

147   covered by the walls or pliable materials, that is, they can only be accessed by the small entrance. For

148   instance, cavities (e.g., nests of woodpeckers), burrows (e.g., nests of many seabirds), domes and

149   globes (e.g., nests of weavers) are all enclosed structures (Hansell 2000). We only extracted data on

150   nest type from studies of natural nests (i.e., nest-box studies were excluded).

151   Coloniality was categorized into (i) solitary breeding, breeders never live in groups, (ii) semi-colonial

152   breeding, breeders are either solitary or colonial, and (iii) colonial breeding, individuals always breed

153   in groups and they defend a territory which only consists of the nest sites (Perrins and Birkhead, 1983,

154   Van Turnhout et al. 2010). We only extracted data on coloniality from studies of natural nests, since

155   the studies of nest-box artificially changed the spatial distribution of nests.

Phylogenetic analyses

157   To test whether pre-hatching care differs from post-hatching care, we conducted phylogenetic paired

158   t-tests (Lindenfors et al. 2010). We first estimated the corresponding phylogenetic mean value of pre-

159   hatching and post-hatching care of each species, then compared whether the mean difference was

160   different from zero (Lindenfors et al. 2010). The analyses were implemented in R (3.4.2) using the

161   'phytools' package (Revell 2012).

162   We analyzed the correlation between parental care variables and predictor variables by using

163   phylogenetic generalized least squares (PGLS) (Freckleton et al. 2002). This technique controls for the

164   dependence of species traits as a result of shared evolutionary history by estimating the expected

165   covariance structure, then modified slope and intercept estimates would be calculated. In all analyses,

166   Pagel's λ which varies between 0 and 1 was estimated to represent the phylogenetic signal (Freckleton

6

167   et al. 2002). A trait with strong phylogenetic signal is more similar among closely related species, while

168   data points are more independent if phylogenetic signal is weak.

169   Considering the uncertainty of phylogenetic estimation caused by the absence of empirical support on

170   the prediction of evolutionary relationships among species (Jetz et al. 2012), we randomly extracted

171   100 phylogenetic trees from the most comprehensive avian phylogenies (Jetz et al. 2012). Each PGLS

172   model was analyzed across all of the trees and the mean value of resulting 100 parameter estimates

173   were calculated.

174   For each dependent variable (i.e., the relative participation in pre-hatching care by males, the relative

175   participation in post-hatching care by males), we established separate PGLS models to investigate the

176   effect of each ecological and social traits. Here, we present (1) the results of bivariate models which

177   only included one of the main predictors, and (2) the results of multi-predictor models. Since nestling

178   diet was related to parental diet, two multi-predictor PGLS models were built in order to avoid the

179   problem of multicollinearity. These two multi-predictor models contained the following predictors i)

180   parental diet, nest type and coloniality; ii) nestling diet, nest type and coloniality. Moreover, two crucial

181   life-history traits were included in all multi-predictor models: body mass (log-transformed) and chick

182   development mode (precocial vs. altricial). This is due to the fact that body mass strongly correlated

183   with several life-history traits (e.g., longevity, Lindstedt and Calder 1976), and chick development was

184   suggested to affect parental roles (Thomas and Székely 2005; Olson et al. 2008). All PGLS analyses were

185   carried out in the R statistical computing environment as well, using the package "caper" (Orme 2013).

186

RESULTS

187

Pre-hatching care vs. post-hatching care

188

189   Birds exhibit diverse parental roles, consistently with expectations, including female-only care,

190   biparental care and male-only care (Figure 1). Even in the same clade, different parental care patterns

191   can be observed (Figure 1a-d), corresponding to the intermediate phylogenetic signal of each breeding

192   activities (λ = 0.187-0.755, see statistical estimates in Supplementary Table S1). For instance,

193   uniparental care by the male or the female, and biparental care coexist in Anseriformes,

194   Charadriiformes, Procellariiformes, Psittaciformes and Passeriformes. A remarkable diversity is

195   observed in shorebirds in that all care types (female-only care, female-biased care, biparental care,

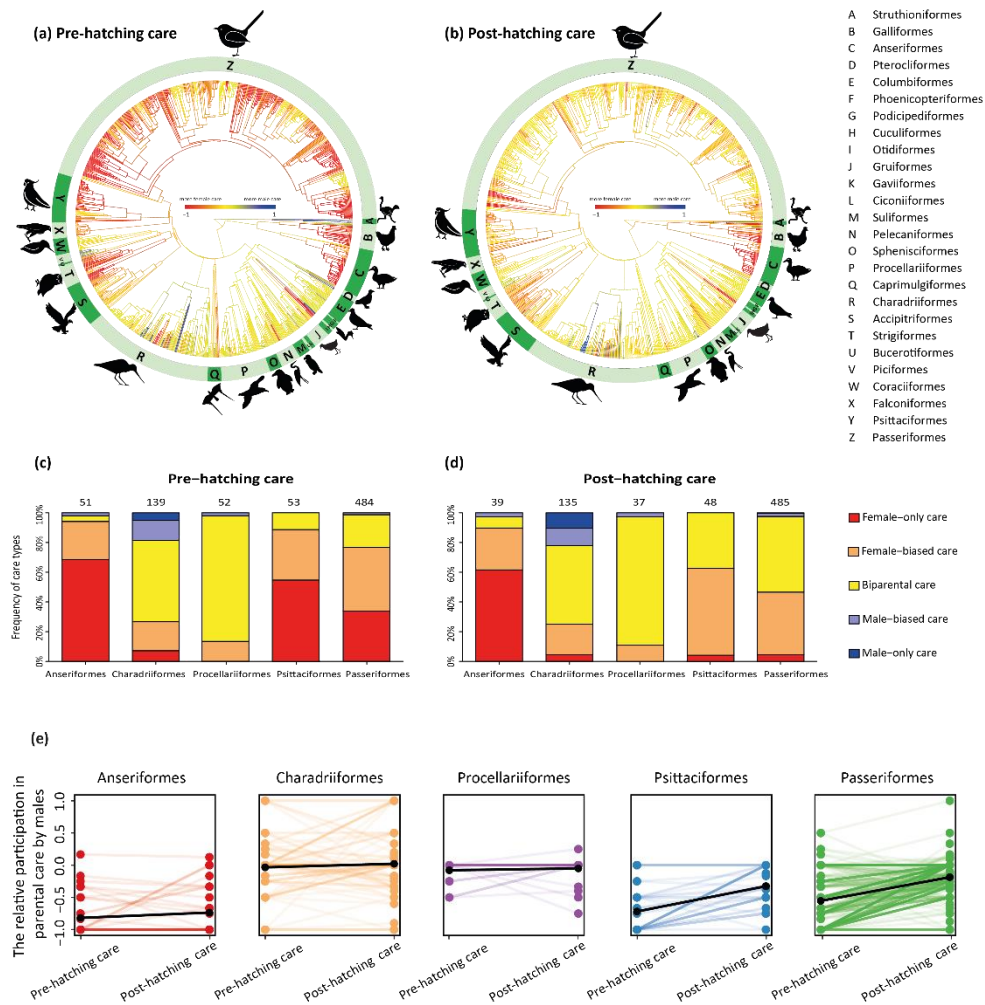196   male-biased care and male-only care) can be found (Figure 1c, d).

Figure 1. Distribution of parental roles in birds. (**a, b**) Phylogenetic distribution of pre-hatching care and post-hatching care (maximum clade credibility tree of 100 phylogenies using 1065 and 991 bird species, respectively). The figure shows the relative participation in parental care by males for each bird species. (Red = female-only care, yellow = biparental care, blue = male-only care, other colors = sex-biased care). (**c, d**) Frequencies of different parental care patterns in two breeding phases in five major clades. Care patterns are classified into 5 categories: female-only care: 0% male care (red); female-biased care: 1–33% male care (orange); biparental care 34–66% male care (yellow); male-biased care: 67–99% male care (purple); male-only care: 100% male care (blue). Sample size is shown at the top of each column. (**e**) Differences in parental roles between pre-hatching and post-hatching phases in five large clades of birds. Relative male pre-hatching care and post-hatching care are represented by scatterplots, the lines connect two breeding phases for each species and overplotted lines appear as darker lines. The means of pre-hatching care and post-hatching of each avian family are plotted in black.

197

8

198   Female-only care is more common in the pre-hatching phase (26.67% of 1065 species) than in the post-
199   hatching phase (7.87% of 991 species), while biparental care is more prevalent during post-hatching
200   (50.66%) than during pre-hatching (33.43%). In contrast, male-only care is rare in both breeding phases
201   (1.03% and 2.02% in the pre- and post-hatching phase, respectively) (Figure 1). This suggests biparental
202   care is predominant in both the pre-hatching and post-hatching phases, and the parental care offered
203   by the male does not differ from by the female in both breeding phases (PGLS fitted an intercept only
204   (with 100 phylogenies), pre-hatching care: *Slope ± SE* = -0.080 ± 0.188, *P* = 0.649, *n* = 1065 species;
205   post-hatching care: *Slope ± SE* = -0.187 ± 0.134 *P* = 0.170, *n* = 991 species). Furthermore, the relative
206   participation in parental care by males is not different between pre-hatching phase and post-hatching
207   phase (Figure 1 and Table 1). We only found that the relative contribution to post-hatching care by
208   males is marginally larger than in pre-hatching care by males in parrots (Psittaciformes, Figure 1e and
209   Table 1).

210

Table 1. Phylogenetic mean for the parental care differs between pre-hatching phase and post-hatching phase. The difference between the relative participation in pre- and post-hatching care by males is compared in all species and five large clades (Anseriformes, Charadriiformes, Procellariiformes, Psittaciformes and Passeriformes,). Estimates are phylogenetic mean difference with standard error (*Mean difference ± SE*), the corresponding *t* and *p*-values of 100 phylogenetic paired t-test repeated with different phylogenies. log-likelihood of the fitted model *log(L),* phylogenetic signal λ and the number of species *n* are also given for each model.

Phylogenetic paired t-test	Mean difference ± SE	t	p	Log(L)	λ	n
All species	0.052 ± 0.184	0.340	0.735	-401.4	0.626	955
Anseriformes	-0.080 ± 0.063	-1.405	0.181	-14.08	0.019	38
Charadriiformes	-0.024 ± 0.111	-0.221	0.826	-77.62	0.334	130
Procellariiformes	-0.084 ± 0.117	-0.798	0.437	0.198	0.502	35
Psittaciformes	**-0.299 ± 0.170**	**-1.921**	**0.079**	**-19.16**	**0.520**	**48**
Passeriformes	-0.257 ± 0.187	-1.684	0.102	-154.5	0.667	459

Table 2. Pre- and post-hatching care in relation to ecology and social environment in birds using phylogenetically generalized linear squares models (PGLS). In both bivariate and multi-predictor PGLS models, the relative participation in pre-hatching care and post-hatching care by males are the response variables, respectively. Predictors include parental diet (plant vs. animal food), nesting diet (plant vs. animal food), nest type (open vs. closed), coloniality (solitary, semi-colonial, colonial). Development mode (precocial vs. altricial) and body mass (log-transformed) are included in the full multi-predictor models. Estimates are means of regression coefficients with standard error (*Slope ± SE*), the corresponding *t* and *p-values* of 100 PGLS analyses repeated with different phylogenies, significant results are highlighted in bold. Sample size *n*, R-squared r^2 and phylogenetic signal *λ* are also given for each model.

(a) Bivariate models	Relative participation in pre-hatching care by males						Relative participation in post-hatching care by males					
Predictors	*Slope ± SE*	*t*	*p*	r^2	*λ*	*n*	*Slope ± SE*	*t*	*p*	r^2	*λ*	*n*
Parental diet	0.032 ± 0.042	0.752	0.460	0.001	0.826	991	-0.015 ± 0.036	-0.417	0.679	<0.001	0.643	926
Nestling diet	-0.048 ± 0.058	-0.828	0.421	0.001	0.847	598	-0.035 ± 0.049	-0.707	0.484	0.001	0.624	573
Nest type	-0.026 ± 0.040	-0.656	0.518	<0.001	0.841	994	0.011 ± 0.036	0.313	0.756	<0.001	0.666	930
Coloniality	0.021 ± 0.017	1.248	0.217	0.002	0.843	835	**0.032 ± 0.016**	**1.927**	**0.055**	**0.005**	**0.551**	**782**

(b) Full model	Relative participation in pre-hatching care by males						Relative participation in post-hatching care by males					
Predictors	*Slope ± SE*	*t*	*p*	r^2	*λ*	*n*	*Slope ± SE*	*t*	*p*	r^2	*λ*	*n*
Parental diet	0.098 ± 0.055	1.791	0.079	0.011	0.853	637	0.029 ± 0.044	0.665	0.508	0.014	0.408	602
Nest type	-0.024 ± 0.048	-0.497	0.621	-	-	-	0.001 ± 0.039	0.028	0.942	-	-	-
Coloniality	0.022 ± 0.019	1.186	0.240	-	-	-	**0.044 ± 0.181**	**2.448**	**0.015**	-	-	-
Body mass	-0.008 ± 0.017	-0.487	0.630	-	-	-	-0.012 ± 0.014	-0.880	0.381	-	-	-
Development	-0.055 ± 0.049	-1.133	0.263	-	-	-	-0.036 ± 0.415	-0.877	0.385	-	-	-

(c) Full model	Relative participation in pre-hatching care by males						Relative participation in post-hatching care by males					
Predictors	*Slope ± SE*	*t*	*p*	r^2	*λ*	*n*	*Slope ± SE*	*t*	*p*	r^2	*λ*	*n*
Juvenile diet	0.092 ± 0.073	1.264	0.214	0.031	0.882	438	0.070 ± 0.061	1.142	0.256	0.046	0.542	420
Nest type	-0.024 ± 0.050	0.482	0.632	-	-	-	0.007 ± 0.042	0.155	0.876	-	-	-
Coloniality	**0.068 ± 0.022**	**3.105**	**0.002**	-	-	-	**0.068 ± 0.021**	**3.232**	**0.001**	-	-	-
Body mass	-0.024 ± 0.203	-1.208	0.232	-	-	-	-0.020 ± 0.017	-1.197	0.234	-	-	-
Development	-0.061 ± 0.059	-1.033	0.304	-	-	-	**-0.125 ± 0.051**	**-2.428**	**0.016**	-	-	-

Diet

Food type is not associated with parental roles: neither parental diet nor nestling diet is associated with sex differences in parental roles (Table 2). In the pre-hatching phase, females provide more care than males no matter what types of food they forage for. While the approximate identical care level is provided by the male and the female in both herbivorous and carnivorous bird species during the post-hatching phase (Figure 2a,b). The lack of relationship between food type and sex-specific parental roles is consistent between the bivariate (Table 2a) and multi-predictor models in which the effects of all potential variables are included (Table 2b,c).
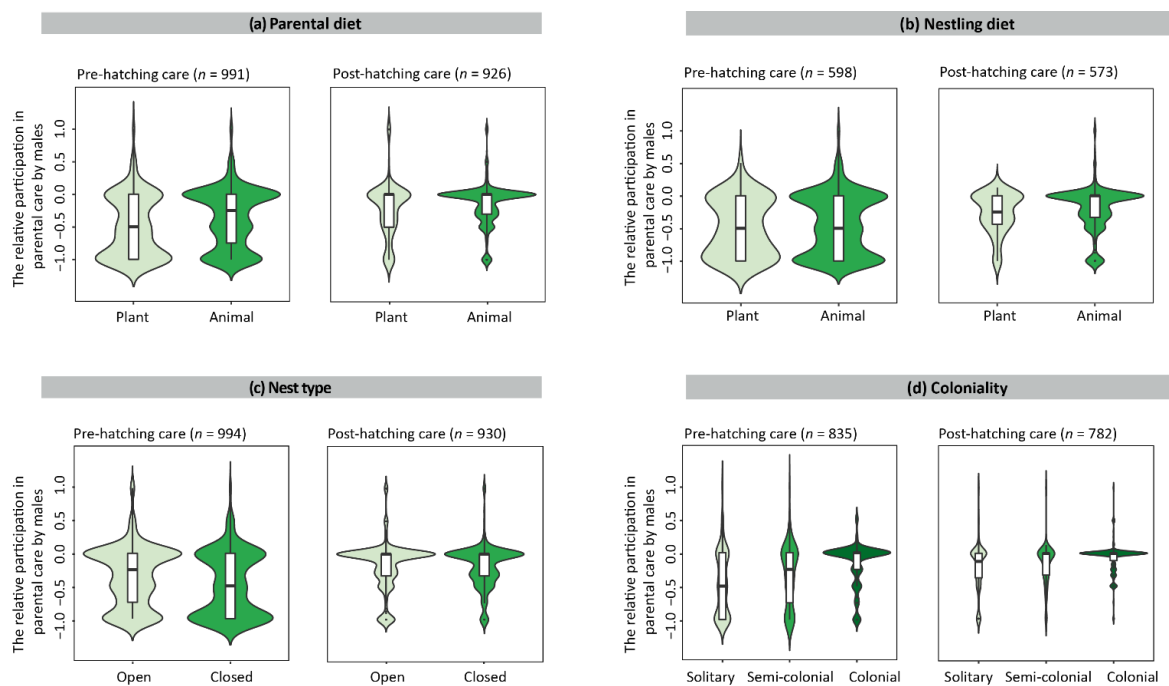

Figure 2. The association between parental roles and ecological and social environment. (a) Parental diet, (b) nestling diet, (c) nest type and (d) coloniality are plotted against relative male pre-hatching care and relative male post-hatching care, respectively. The rectangle of small box plot in each violin plot shows the ends of the first and third quartiles and a vertical line indicates the median value of male care relative to female care. The kernel density plot of each violin plot shows the distribution of parental care and its probability density. The participation in parental care by males was scored on a 5-point scale, -1: 0% male care; -0.5: 1–33% male care; 0: 34–66% male care; 0.5: 67–99% male care; 1: 100% male care. Parental diet and nestling diet were scored on a 2-point scale, 0: plant food, 1: animal food. Nest type was scored on a 2-point scale, 0: open nest, 1: closed nest. Coloniality was scored on a 3-point scale, 0: solitary, 1: semi-colonial, 2: colonial. The number of species n is shown for each plot.

11

220 **Nest type**

221 Nest type does not predict parental sex roles, as the relative participation in parental care by males is
222 not significantly different between open and closed nests either in bivariate (Table 2a) or multiple
223 regression analyses (where parental diet and nestling diet are controlled for separately) (Table 2b,c):
224 female-biased pre-hatching care is associated with both open and closed nests, and more egalitarian
225 biparental post-hatching care is found in both nest types (Figure 2c), corresponding to the general care
226 pattern where female-biased care predominates in the pre-hatching phase while biparental care
227 predominates in the post-hatching phase (Figure 1).

228 **Coloniality**

229 Coloniality is associated with sex differences in parental care. First, coloniality predicts post-hatching
230 care: the relative participation in post-hatching care by males increases as coloniality increases (Table
231 2, Figure 2d). The relationship is marginally nonsignificant in the bivariate model (Table 2a), and is
232 significant in the full multi-predictor models where parental diet and nestling diet are controlled for
233 respectively (Table 2b,c). However, these fitted PGLS models account for a modest variability of post-
234 hatching care (r^2 = 4.6%). Second, relative male pre-hatching care is not related to coloniality (Table 2),
235 although we found a significant trend in the multi-predictor model in which nestling diet instead of
236 parental diet is statistically controlled for (Table 2c).

237

DISCUSSION

239 Our comprehensive phylogenetic comparative analyses confirm that parental roles are highly diverse
240 among avian species, and biparental care is the prevailing care pattern in both pre- and post-hatching
241 phases (Cockburn 2006). Moreover, female-only care is relatively common in the pre-hatching phase,
242 in line with the fact that in approximately 30% of passerine birds only females incubate the eggs (White
243 and Kinney 1974). In addition, the relative participation in parental care by each sex is not remarkably
244 differ between the pre- and post-hatching phases, indicating brood desertion after hatching by either
245 sex happens rarely, but in some precocial bird species such as shorebirds (see Clutton-Brock 1991,
246 Székely and Williams 1995).

247 The results consistently show that colonial breeding is associated with more equal share in parenting
248 duties than in solitary species, especially in post-hatching care. We think the interaction of two factors
249 could explain the outcome. First, intraspecific competition induces the cooperation between the male
250 and the female parent, since one of the parents has to protect the fragile broods which are completely

251   exposed to the environment, while the other parent competes for food which is used to feed the
252   offspring. Both chick feeding and chick guarding are involved in post-hatching state, therefore, the
253   association between colonial breeding and share in post-hatching care between two sexes is observed
254   in all models. Second, females in a colony synchronously produce the offspring (Gochfeld 1980, Nelson
255   1980, Coulson 2002), which remarkably reduces the mating opportunities of a deserting male and
256   consequently favors the emergence of biparental care. This outcome demonstrates that equal parental
257   roles are selected under resource and mating constraints in colonial species, whereas female-biased
258   care, mediated by other factors, is favored in solitary species.

259   Our results demonstrate that nest type does not predict sex-specific parental roles. In the pre-hatching
260   and post-hatching phases, both parents provide care in open nests and closed nests. In the open nests,
261   high predation rates might induce the same response by the male parent and the female parent. Both
262   the male and the female decrease their parental activities around the nests in order to reduce nest
263   visibility, or alternatively, both parents provide more protection against nest predation. In the closed
264   nests with large clutch size, the cooperation between parents is required as large amount of energy
265   and time are needed to raise the offspring. However, we neglected other factors which might be
266   important to explore the relationship between nest habitat and parental roles. For instance, nest sites
267   are essential for breeding success in that good nest sites might promote the development of the
268   offspring (e.g., open nests which are built on the water or in the trees can help to reduce the probability
269   of being predated (Martin 1993; Picman et al. 1993; Colombelli-Négrel and Kleindorfer 2009; Latif et
270   al. 2012)). Further studies investigating the effect of nest microhabitats on sex differences in parental
271   roles will be valuable.

272   Our results also illustrate that food type cannot explain the considerable variation in parental sex roles:
273   no matter plant or animal food the bird parents forage, the female and the male take care of the
274   offspring together. This suggests both plant-eating and animal-eating offspring might have high
275   demand for food: herbivores request large amount of food while carnivores require high quality but
276   secluded food, inducing biparental care in most of species. Nonetheless, our study did not directly
277   quantify the food availability which is crucial for breeding activities (Martin 1987; Low et al. 2012),
278   since just few empirical data are available. To dig into the impact of diet on parental roles, more
279   empirical studies on food availability are needed in the future. Besides, our study did not take into
280   account the situation where males feed the females during incubation in some avian species (Martin
281   and Ghalambor 1999, Matysioková et al. 2011). Male feeding should be considered as a type of
282   parental care as well, since it increases the survival probability of females and also the ability of females
283   to provide continuous incubation of the eggs, which consequently increases the survival probability of
284   the offspring. The food items which are fed to females might also play an important role in sex role
285   divergence.

286   In summary, our study provides the most comprehensive analyses of the effect of ecology and social
287   environment on sex differences in parental roles using birds as model organisms. We show that
288   ecological factors such as diet and nest type are not predictors of parental roles, although these factors
289   have strong impacts on some life-history traits. Besides, we found that social environment as
290   coloniality could predict parental care strategies. Further studies including empirical and comparative
291   analyses are needed to explore the relationship between food availability, nest habitats, breeding
292   density and parental sex roles.

293

294   REFERENCES

295   Alexander RD. 1974. The evolution of social behavior. *Annu Rev Ecol Evol Syst*. 5(1):325–383.

296   Badyaev AV and Ghalambor CK. 1998. Does a trade-off exist between sexual ornamentation and
297   ecological plasticity? Sexual dichromatism and occupied elevational range in finches. *Oikos*:319–324.

298   Balshine S. 2012. Patterns of parental care in vertebrates. In: Royle NJ, Smiseth PT, Kölliker M, editors.
299   *The Evolution of Parental Care*. Oxford: Oxford University Press. p. 62–80.

300   Barve S, La Sorte FA. 2016. Fruiting season length restricts global distribution of female-only parental
301   care in frugivorous passerine birds. *PLoS One*. 11(5):e0154871.

302   Clutton-Brock TH .1991. *The evolution of parental care*. Princeton: Princeton University Press.

303   Cockburn A. 2006. Prevalence of different modes of parental care in birds. *Proc R Soc B Biol Sci.*
304   273(1592):1375–1383.

305   Cody ML. 1966. A general theory of clutch size. *Evolution*. 174–184.

306   Collias NE. 1964. The evolution of nests and nest-building in birds. *Am Zool*. 175–190

307   Collias N, Collias E. 1984. *Nest building behavior in birds*. Princeton: Princeton University Press.

308   Colombelli-Négrel D, Kleindorfer S. 2009. Nest height, nest concealment, and predator type predict
309   nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecol Res*. 24(4):921–928.

310   Coulson JC. 2002. Colonial breeding in seabirds. In: Schreiber EA, Burger J, editors. *Biology of marine*
311   *birds*. Boca Raton: CRC Press. p. 87–113.

312   Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*.
313   197(4300):215–223.

314   Evans JC, Votier SC and Dall SR. 2016. Information use in colonial living. *Biol Rev*. 91(3):658–672.

315 Fairbairn DJ, Blanckenhorn WU, Székely T. 2007. *Sex, size, and gender roles: evolutionary studies of*
316 *sexual size dimorphism*. Oxford: Oxford University Press.

317 Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and
318 review of evidence. *Am Nat*. 160:712–726.

319 Gochfeld M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In:
320 J. Burger B, Olla L, editors. *Behavior of marine animals*. New York: Plenum Publishing Corporation. p.
321 207–270.

322 Hansell M, 2000. *Bird nests and construction behaviour*. Cambridge: Cambridge University Press.

323 Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008. The worldwide variation in avian clutch size across
324 species and space. *PLoS Biol*. 6(12):e303.

325 Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and
326 time. *Nature*. 491(7424):444–448.

327 Kleindorfer S and Hoi H. 1997. Nest predation avoidance: an alternative explanation for male
328 incubation in Acrocephalus melanopogon. *Ethology.* 103(8):619–631.

329 Klug H, Alonzo SH, Bonsall MB. 2012. Theoretical foundations of parental care. In: Royle NJ, Smiseth
330 PT, Kölliker M, editors. *The Evolution of Parental Care*. Oxford: Oxford University Press. p. 21–30.

331 Klug H. 2018. Why monogamy? A review of potential ultimate drivers. *Front Ecol Evol.* 6:30.

332 Krause J, Ruxton GD. 2002. *Living in groups*. Oxford: Oxford University Press.

333 Latif QS, Heath SK and Rotenberry JT. 2012. How avian nest site selection responds to predation risk:
334 testing an 'adaptive peak hypothesis'. *J Anim Ecol*. 81(1):127–138.

335 Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk
336 of predation. *Biol Rev*. 84(3):485–513.

337 Lindenfors P, Revell LJ, Nunn CL. 2010. Sexual dimorphism in primate aerobic capacity: a phylogenetic
338 test. *J Evol Biol*. 23(6):1183–1194.

339 Lindstedt SL, Calder WA. 1976. Body size and longevity in birds. *Condor*. 78(1):91–94.

340 Liker A, Freckleton RP, Remeš V, Székely T. 2015. Sex differences in parental care: Gametic investment,
341 sexual selection, and social environment. *Evolution*. 69(11):2862–2875.

342 Low M, Makan T, Castro I. 2012. Food availability and offspring demand influence sex-specific patterns
343 and repeatability of parental provisioning. *Behav Ecol*. 23(1):25–34.

344 Mayer C and Pasinelli G. 2013. New support for an old hypothesis: density affects extra‑pair paternity.
345 *Ecol Evol.* 3(3):694–705.

346 Martin TE. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu Rev Ecol Evol Syst*.
347 18(1):453–487.

348 Martin TE. 1993. Nest predation and nest sites. *Bio Science*. 43(8):523–532.

349 Martin TE. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecol*
350 *Monogr*. 65(1):101–127.

351 Martin TE, Ghalambor CK. 1999. Males feeding females during incubation. I. Required by microclimate
352 or constrained by nest predation? *Am Nat*. 153(1):131–139.

353 Martin TE, Scott J and Menge C. 2000. Nest predation increases with parental activity: separating nest
354 site and parental activity effects. *Proc Royal Soc B*. 267(1459):2287–2293.

355 Martin TE and Briskie JV. 2009. Predation on dependent offspring: a review of the consequences for
356 mean expression and phenotypic plasticity in avian life history traits. *Ann N Y Acad Sci*. 1168(1):201–
357 217.

358 Matysioková B, Cockburn A, Remeš V. 2011. Male incubation feeding in songbirds responds differently
359 to nest predation risk across hemispheres. *Anim Behav.* 82(6):1347–1356.

360 McGraw L, Székely T, Young LJ. 2010. Pair bonds and parental behaviour. In: Székely T, Moore A,
361 Komdeur J, editors. *Social behaviour: genes, ecology and evolution*. Cambridge: Cambridge University
362 Press. p. 271–301.

363 Montgomerie RD and Weatherhead PJ. 1988. Risks and rewards of nest defence by parent birds. *Q Rev*
364 *Biol.* 63(2):167–187.

365 Nelson B. 1980. *Seabirds: Their biology and ecology*. London: Hamlyn.

366 Olson VA, Liker A, Freckleton RP, Székely T. 2008. Parental conflict in birds: comparative analyses of
367 offspring development, ecology and mating opportunities. *Proc R Soc Lond B Biol Sci*. 275:301–307.

368 Orme CDL, Freckleton RP, Thomas GH, Petzoldt T, Fritz SA, Isaac NJB. 2012. Package 'caper', reference
369 manual. Available at http://cran.r-project.org/web/packages/caper/index.html.

370 Perrins CR, Birkhead TR. 1983. *Avian ecology*. Glasgow (UK): Blackie.

371 Peters SS. 1958. Food habits of the Newfoundland willow ptarmigan. *J Wildl Manage*. 22(4):384–394.

372 Picman J, Milks ML, Leptich M. 1993. Patterns of predation on passerine nests in marshes: effects of
373 water depth and distance from edge. *The Auk*. 110(1):89–94.

374 Remeš V, Freckleton RP, Tökölyi J, Liker A, Székely T. 2015. The evolution of parental cooperation in
375 birds. *Proc Natl Acad Sci USA*. 112(44):13603–13608.

376 Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things).
377 *Methods Ecol Evol*. 3(2):217–223.

378 Royle NJ, Smiseth PT, Kölliker M. 2012. *The Evolution of Parental Care*. Oxford: Oxford University Press.

379 Skutch AF. 1949. Do tropical birds rear as many young as they can nourish? *Ibis*. 91(3):430–455.

380 Székely T, Williams TD. 1995. Costs and benefits of brood desertion in female Kentish plovers,
381 Charadrius alexandrinus. *Behav Ecol Sociobiol*. 37(3):155–161.

382 Thomas GH, Székely T. 2005. Evolutionary pathways in shorebird breeding systems: sexual conflict,
383 parental care, and chick development. *Evolution*. 59(10):2222–2230.

384 Trumbo ST. 2012. Patterns of parental care in invertebrates. In: Royle NJ, Smiseth PT, Kölliker M,
385 editors. *The Evolution of Parental Care*. Oxford: Oxford University Press. p. 81–100.

386 Van Turnhout CA, Foppen RP, Leuven RS, Van Strien A, Siepel H. 2010. Life-history and ecological
387 correlates of population change in Dutch breeding birds. *Biol Conserv*. 143(1):173–181.

388 Westneat DF and Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative
389 analysis. *Behav Ecol Sociobiol*. 41(4):205–215.

390 White FN, Kinney JL. 1974. Avian incubation. *Science*, 186(4159):107–115.

391

392

393

394

395

396

397

398

Authors' contributions: All authors conceived the study. X.L. and A.L. collected the data, X.L. conducted the data analyses with inputs from A.L. All authors interpreted the results. X.L. wrote the manuscript and others contributed important edits.

DATA ACCEESBILITY

All relevant data within this paper and its electronic Supplementary material are available once the manuscript is accepted.