



# Does ecology and life history predict parental cooperation in birds? A comparative analysis

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## Abstract

In animals, species differ remarkably in parental care strategies. For instance, male-only care is prevalent in teleost fishes, while biparental care predominates in birds and female-only care is widespread in mammals. Understanding the origin and maintenance of diversified parental care systems is a key challenge in evolutionary ecology. It has been suggested that ecological factors and life-history traits play important roles in the evolution of parental care, but the generality of these predictions has not been investigated across a broad range of taxa. Using phylogenetic comparative analyses and detailed parental care data from 1101 avian species that represent 119 families of 26 orders, here we investigate whether parental strategies are associated with ecological variables (i.e., food type, nest structure, and coloniality) and life-history characteristics (i.e., chick development mode and body size). We show that parental care strategies are in relation to coloniality (solitary, semi-colonial, colonial) and chick development mode (altricial vs. precocial). Colonial and altricial species provide more biparental care than solitary and precocial species, respectively. In contrast, food type (plant, invertebrate, vertebrate), nest structure (open vs. closed), and body size do not covary systematically with parental care patterns in birds. Taken together, our results suggest that living in groups and/or having high-demand offspring are strongly associated with biparental care. Towards the end, we discuss future research directions for the study of parental care evolution.

## Significance statement

Animal species differ remarkably in the amount of care parents provide to their offspring and in the distribution of care tasks over the parents. In birds, for example, the young of some species are quite independent from the start, while the young of other species are helpless after hatching, requiring a lot of care. Moreover, either the female or the male does most of the caring in some species, while the parental tasks are shared equally in still other species. To understand the diversified parental care patterns, we applied advanced comparative methods to a large data set comprising over 1000 bird species. The analysis reveals that the parents tend to share their care duties equally when they live in groups and/or have offspring that are born helpless, and that parental care patterns are not associated with diet, nest type or body size. Hence, living in groups and having high-demand offspring seem to play important roles in the evolution of parental care.

**Keywords** Parental care · Food type · Nest structure · Coloniality · Chick development mode · Body size

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## Introduction

Biparental care, a form of cooperation between the male and female parent, is observed across many animal taxa including insects, fishes, amphibians, birds, and mammals (Balshine 2012; Trumbo 2012; Vági et al. 2019). When parents collaborate in caring, the offspring have a better chance of surviving, especially in situations where one parent cannot raise the young successfully (Brown et al. 2010; Pilakouta et al. 2018). However, conflicts over how much care each parent should provide are inescapable, because parents share the benefits of joint care while each parent pays its own costs of caring (e.g., time and energy); consequently, the sexes can typically not maximize their reproductive success simultaneously (Parker et al. 2002; Houston et al. 2005; Lessells 2012). Therefore, biparental care is an excellent system for investigating cooperation and conflict in animal societies (McNamara et al. 2000; van Dijk et al. 2012; Barta et al. 2014).

Recent work including experimental manipulations (Tumulty et al. 2014; Pilakouta et al. 2018), field-based studies (AlRashidi et al. 2011), and comparative analyses (Brown et al. 2010; Remeš et al. 2015) has furthered our understanding of the evolution of parental cooperation. Here, we define parental cooperation as a parental strategy that increases the reproductive success of caregivers' partner, ranging from egalitarian biparental care where the two parents equally share in the parental duties, to partial biparental care where one of the parents cares to a much higher extent than the other, and uniparental care where the parents do not share the care tasks and only one of the parents cares for the young (Cockburn 2006; Remeš et al. 2015). It has been suggested that ecological variables and life-history traits are associated with parental cooperation (Wilson 1975; Klug and Bonsall 2010), but little is known about the generality of these predictions.

That ecological factors predict parental care strategies has been the subject of considerable discussion (Cockburn 2006; Wong et al. 2013). One long-established hypothesis posits that a high level of parental cooperation can be expected in harsh and challenging conditions (Wilson 1975; Carey 2002). To investigate this hypothesis, we here look at the impact of three ecological factors on parental strategies: food type, nest structure, and coloniality. First, scarcity of food is supposed to be associated with biparental cooperation (Andersson 2005; Eldegard and Sonnerud 2009). It is argued that biparental care can be expected in species where parents have to catch large and dispersed prey (e.g., amphibians, fishes, and mammals) in order to provision their young (Crook 1964; Slagsvold and Sonnerud 2007). This could be because juveniles are not yet capable of finding and catching this type of prey (Newton 1979; Hunt et al. 2012), necessitating a higher level of care from their parents under such conditions. Therefore, parental

cooperation may be required to guarantee a consistent food supply and to protect the nest when one parent is absent. In contrast, species that feed on plant materials (e.g., fruits, seeds and nectar) might exhibit a greater prevalence of uniparental care, as such food resources tend to be seasonally abundant and one parent should suffice to efficiently provision the young (Lack 1968; Morton 1973; Barve and La Sorte 2016).

Second, nest structure is suggested to be correlated with the extent of parental cooperation, as it is crucial in determining breeding success (AlRashidi et al. 2011). Open nests such as scrapes and platforms are exposed to environment while closed nests such as cavities and burrows are covered by roofs and only accessible by a small entrance (Collias and Collias 1984; Hansell 2000). Previous studies have shown that open nests provide less protection from predators and lead to harsher microclimate than closed nests (Deeming 2011; Martin et al. 2017). Therefore, species that build open nests may exhibit higher levels of parental cooperation after nest construction than species that build closed nests.

Third, colonial breeding where individuals together occupy a territory which only consists of nesting sites might also be associated with biparental cooperation (Perrins and Birkhead 1983). Individuals living in colonies may benefit from the sharing of information (e.g., foraging sites) and increased anti-predator behavior (Brown and Brown 2001). However, leaving the young alone in a colony with high nest density might be dangerous, as the young can easily get lost (they have many stimuli attracting them away from the nest), and as they are vulnerable to attacks of neighbors and predators (Brown and Brown 2001; Ashbrook et al. 2008). Therefore, both parents may be required to raise the young successfully in colonies.

Life-history characteristics are also anticipated to be associated with parental care patterns (Stearns 1976; Kolm et al. 2006; Gilbert and Manica 2010; Klug and Bonsall 2010; Klug et al. 2013). One central concept of life-history theory is that parental strategies are constrained by the trade-off between current and future reproduction (Williams 1966). Here, we focus on two life-history variables that may influence the trade-off: chick development mode and body size. In empirical studies, both factors are often included as confounding variables (Liker and Székely 2005; Liker et al. 2015; Remeš et al. 2015); only a few small-scale studies tested directly whether body size or chick development mode has an impact on parental care behavior (Thomas and Székely 2005). Therefore, it is unclear whether life-history traits are associated with parental care in a broader range of taxa.

First, offspring demands differ between altricial and precocial species, corresponding to distinct care decisions (Vleck et al. 1979; Starck and Ricklefs 1998; Thomas et al. 2006). In altricial species, chicks are unable to obtain food

and regulate the body temperature on their own. Therefore, a deserting parent might pay a great cost in terms of growth and survival of the current brood (Vleck et al. 1979; Starck and Ricklefs 1998). Accordingly, a high level of biparental cooperation can be expected in altricial species. On the contrary, offspring of precocial species require relatively little care as hatchlings are adept at feeding themselves (Vleck et al. 1979; Starck and Ricklefs 1998), with the result that one parent might be able to raise the young efficiently (Lack 1968; Bennett and Owens 2002) and the deserting sex benefits more from seeking new mates (Olson et al. 2008).

Second, stable parental cooperation is probably much easier to achieve in species with large body size (Remeš et al. 2015; Vági et al. 2019). Species with large body size have relatively low metabolic rates, and thus take a long period to develop and become independent (West et al. 2001). Moreover, large-bodied species are long-lived, leading to prolonged pair bonding (Lindstedt and Calder 1976, 1981; Choudhury 1995; Jeschke and Kokko 2008); consequently, mating opportunities are probably limited after desertion. Taken together, providing care to current broods is more beneficial, and thus, biparental care may be selected in species with large body size. In contrast, species with small body size are short-lived, thus may tend to exhibit uniparental care more frequently.

Although previous studies offered insights into how some of the related factors (e.g., nesting density, developmental duration) might explain diversified care patterns (Owens 2002; Cooney et al. 2020), no study has yet investigated all of these hypotheses across a broad range of taxa and estimated their importance. To understand to what extent and in what way do ecological conditions (e.g., food type, nest structure and coloniality), and the life-history traits (e.g., chick development mode and body size) may explain parental cooperation, we here apply phylogenetic comparative methods to the most comprehensive dataset on parental cooperation, including 1101 avian species representing 26 orders and 119 families (Fig. 1). Birds are ideal organisms for investigating the evolution of parental cooperation on the grounds that avian taxa are characterized by an extraordinary diversity in the distribution of care tasks over the two parents (Remeš et al. 2015), and data on ecological factors, life-history traits, and parental behavior are available across a broad spectrum of species. In particular, parental care behaviors are studied at two breeding stages: pre-hatching stage (i.e., any parental behavior displayed before the chick hatches) and post-hatching stage (i.e., any parental behavior exhibited after the chick hatches). Previous research has discovered that parents tend to make different decisions between these two stages (Liker et al. 2015), suggesting that these two stages might be related to ecological and life-history traits in different ways. Moreover, some of the variables we are interested in might only be relevant in one of the stages.

For example, one may expect food type to be correlated with parental strategies during the post-hatching stage rather than the pre-hatching stage.

Specifically, the following predictions are investigated using phylogenetic comparative analyses. First, carnivorous species should show higher level of cooperation between parents than plant-eating species. Second, species which breed in open nests should provide biparental care more frequently than those that build closed nests. Third, colonially breeding species should exhibit a higher degree of biparental cooperation than solitary breeding species. Four, biparental care should be more common in altricial species than in precocial species. Last, parents are expected to cooperate to a greater extent in species with large body size.

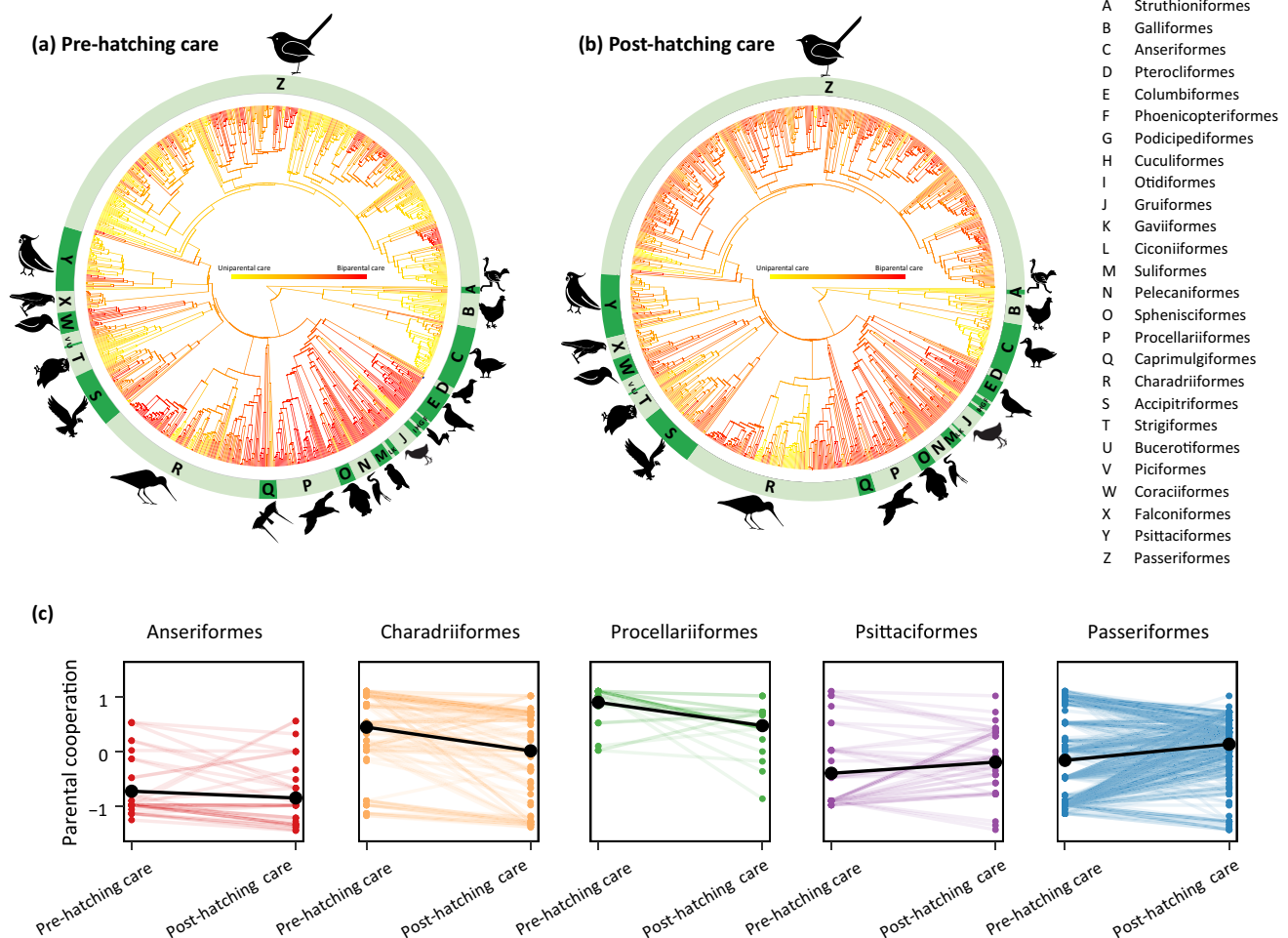
## Methods

### Data collection

We collected data from reference works (e.g., The Birds of the Western Palearctic, The Birds of North America, Handbook of Australian, New Zealand and Antarctic Birds), preexisting datasets (see below) and primary literatures by using Web of Science and Google Scholar. We added more species with available data on parental behavior to an existing dataset used by Liker et al. (2015). Then, we augmented the dataset with expanded information on parental roles by extracting data of ecological and life-history traits (food type, nest structure, coloniality, chick development mode, and body mass). The final dataset included 1101 species (26 orders and 119 families) representing a broad spectrum of avian diversity. For cooperatively breeding birds (132 of 1101 species; 1.2%), we collected the data on the parental behavior of the sexes only when parents raise the offspring without helpers. Detailed information on parental cooperation, ecology, and life history was collected for most of all species. Sample size varies for different traits as data on each trait were not available for all species. Sample size for each variable is shown in Supplementary Table S1.

### Parental care variables

Bird species exhibit diverse forms of parental care, ranging from the preparation for the nest to nutrition provision. Here, we investigate eight types of avian parental behavior: nest building, nest guarding, incubation, chick brooding, chick feeding, chick guarding, post-fledgling feeding, and post-fledgling guarding. For each type of parental behavior, we followed the most well-established and widely used protocol (see, for example, Liker et al. 2015; Remeš et al. 2015) to quantify the extent of parental cooperation. Hence, the results can be comparable to the greatest extent across



**Fig. 1** Phylogenetic distribution of parental cooperation in (a) pre-hatching care and (b) post-hatching care (Bayesian maximum credibility tree of 100 phylogenies using 1065 and 991 bird species, respectively). Red=egalitarian biparental care, yellow=uniparental care. (c) The relationship between pre-hatching and post-hatching

parental cooperation in five speciose of birds. Each line connecting the degrees of pre- and post-hatching cooperation represents one species. For each avian family, the black points represent the mean levels of pre- and post-hatching parental cooperation. The phylogenetic tree was plotted in *R* (3.4.2) using the “phytools” package (Revell 2012)

studies, and the considerable diversity in parental care patterns in birds can be systematically investigated. According to the “standard” scoring system, here the extent of parental cooperation was scored on a 3-point scale, 0: uniparental care by females or males (no cooperation between parents: 0 or 100% male care); 1: partial biparental care (low and intermediate level of cooperation 1–33% or 67–99% male care); and 2: egalitarian biparental care (high level of cooperation 34–66% male care). Therefore, the lowest level of cooperation is uniparental care (score 0), while the highest level of cooperation is egalitarian biparental care (score 2). Scoring was necessary as quantitative data were not available for many species. For such quantitative data, it is necessary to establish arbitrary cutoff points, with the threshold being assumed prior to the data collection and analysis. When quantitative data were not available, we used the information from verbal descriptions. For instance, when a source

declared “only the female incubates eggs,” incubation was scored as zero.

We then divided the parental activities into (i) pre-hatching activities, which involved nest building, nest guarding, and incubation; and (ii) post-hatching activities, which included chick brooding, chick feeding, chick guarding, post-fledgling feeding, and post-fledgling guarding. We subsequently wanted to calculate average scores for pre- and post-hatching care. This could not be done immediately, as data for some of the eight parental activities were missing for most species (only 32 species had data on all care activities). Just averaging the scores of activities for which data were available would have generated a bias, as the distribution of scores differed markedly between different care forms, and the missing data were strongly related to the care forms. For instance, data on incubation were available for almost all species ( $n=1017$ ), with a mean score of 0.90, while data on nest guarding were only accessible for 196



species, with a mean score of 1.44. By averaging over scores, the score for incubation would therefore contribute much more to the final average. To make the scores more comparable, we therefore centralized them by subtracting the average score for this activity (for all species for which data were available on this activity) from the individual scores for each care activity. Subsequently, we determined mean scores for pre- and post-hatching care by averaging the centralized scores for the three pre-hatching activities and the five post-hatching activities (as far as data were available). After score centralization, mean pre-hatching and post-hatching scores ranged from  $-1.5$  (the minimum level of parental cooperation) to  $+1.5$  (the maximum level of parental cooperation).

### Ecological and life-history variables

Food type of bird species was classified into three categories: 0: plant materials which included fruits, seeds, and leaves; 1: invertebrates (e.g., crustaceans and insects); and 2: vertebrates (e.g., fishes and amphibians). For omnivorous species, their mainly eaten food category was allocated. For species in which parents and nestlings subsist on different food items, data on nestling diet was collected as it is more essential for parental care decisions, especially during chick feeding and post-fledgling feeding.

Nest structure was treated as binary variables (0: open and 1: closed). Open nests, which are exposed to adverse weather conditions and predators, included scrapes (e.g., nests of many shorebirds), cups (e.g., nests of many passerines), and platforms (e.g., nests of raptors) (Hansell 2000). Closed nests are completely covered by the walls or pliable materials, that is, they can only be accessed by the small entrance. For instance, cavities (e.g., nests of woodpeckers), burrows (e.g., nests of many seabirds), domes, and globes (e.g., nests of weavers) are all enclosed structures (Hansell 2000). We only extracted data on nest structure from studies of natural nests (i.e., nest-box studies were excluded).

Coloniality was categorized into 0: solitary breeding, individuals breed in isolation; 1: semi-colonial breeding, some individuals never breed in groups while others aggregate at specific sites; and 2: colonial breeding, individuals are always aggregated and breed in territories with densely distributed nests (Brown and Brown 2001; van Turnhout et al. 2010). We only extracted data on coloniality from studies of natural nests, since the studies of nest-box artificially changed the spatial distribution of nests.

Chick development mode was categorized as follows: 0: altricial species where newly hatched offspring require prolonged parental care as they cannot move or feed themselves, such as most passerines; and 1: precocial species where hatchlings are capable of moving and finding their own food, therefore they can leave the nest in a short period, such as many shorebirds. This classification is consistent

with other studies (Temrin and Tullberg 1995; Olson et al. 2008). Adult body mass (in gram) was collected as an index of body size across species in our study. When data on both males and females were available, we calculated the mean value of male and female body mass.

To check the robustness of our dataset, we compared it to previous research that included variables relevant in this study (see Supplementary Fig. S1). Parental care variables were compared to Cockburn (2006), who categorized care patterns into four groups: female-only care, biparental care, male-only care, and cooperative breeding. To make data comparable, we scored each care type on a 5-point scale: 0: no male care; 1: 1–33% male care; 2: 34–66% male care; 3: 67–96% male care; and 4: 100% male care. Moreover, because Cockburn (2006) did not explicitly present the care distribution between the male parent and the female parents in cooperatively breeding species, those species were excluded from consideration when we conducted the comparison. For ecological factors, food type was compared to Wilman et al. (2014), which has, to our knowledge, the largest dataset on diet categories in birds; nest type and coloniality were compared to Varela et al. (2007). In general, our data closely corresponds to previously published relevant datasets, implying that our data are very robust.

### Phylogenetic comparative analyses

To test whether the extent of parental cooperation in pre-hatching care differs from post-hatching care within each species across the birds in our study, we conducted phylogenetic paired *t* tests with maximum likelihood to find the best-fitting Pagel's  $\lambda$  as evolutionary history is shared among these species (Pagel 1999; Freckleton et al. 2002; Lindenfors et al. 2010).  $\lambda$  is estimated to represent the phylogenetic signal, and its value varies between 0 and 1. A trait with strong phylogenetic signal is more similar among closely related species, while data points are more independent if phylogenetic signal is weak (Freckleton et al. 2002). For a given  $\lambda$ , the corresponding phylogenetic mean of all of the differences between pre-hatching care and post-hatching care was estimated first, then we compared whether the mean difference was different from zero (Lindenfors et al. 2010). The analyses were implemented using the “phytools” package (Revell 2012) in R version 3.4.2 (R Development Core Team 2017).

We analyzed the correlation between parental care variables and predictor variables by using phylogenetic generalized least squares (PGLS) (Freckleton et al. 2002). This technique controls for the dependence among species traits by incorporating a variance–covariance matrix that expresses their shared evolutionary history. In all analyses, the phylogeny was incorporated by the maximum likelihood of  $\lambda$  ( $0 \leq \lambda \leq 1$ ) (Freckleton et al. 2002). Considering the uncertainty of phylogenetic estimation caused by the absence of empirical support on the prediction of evolutionary relationships among species (Jetz et al.

2012), we randomly extracted 100 phylogenetic trees from the most comprehensive avian phylogenies (Jetz et al. 2012). Each PGLS model was analyzed across all of these trees, and the mean value of resulting 100 parameter estimates were calculated. This approach only allows us to examine correlations, not causal relationships, among variables.

For each dependent variable (i.e., the extent of parental cooperation in pre-hatching care, the extent of parental cooperation in post-hatching care), we established separate PGLS models to investigate the effect of each ecological and life-history traits. Here, we present (1) the results of bivariate models which only included one of the main predictors and (2) the results of multi-predictor models. These multi-predictor models contained the following predictors: food type, nest structure, coloniality, chick development mode, and body mass (log-transformed). The reason for presenting bivariate models is that data availability across all species for all traits greatly reduced sample sizes when multi-predictor models were conducted, which can result in biased parameter estimates. As a result, multi-predictor models can be complemented by bivariate models, yielding relatively robust analytical results. Since food type, nest structure, coloniality, and chick development mode are categorical predictors, they were dummy coded in PGLS models by following previous studies (Olson et al. 2008; Remeš et al. 2015; Cooney et al. 2020). All PGLS analyses were carried out using the R package “caper” (Orme et al. 2012).

## Results

### Phylogenetic patterns in parental cooperation

The extent of parental cooperation varies in avian species ranging from uniparental care to egalitarian biparental care (Fig. 1). On the one hand, the level of parental cooperation differs between different clades (Fig. 1a, b). For instance, males and females contribute similarly to their offspring in

pigeons, penguins, and petrels, whereas one of the sexes invests more in parental care in Galliformes (gamebirds), Anseriformes (ducks, geese, and allies), and Strigiformes (owls). On the other hand, the extent of parental cooperation can be diverse even within clades (Fig. 1a, b). For example, in shorebirds, parrots, and passerine birds, both biparental care and uniparental care occur within the same clade. Moreover, the degree of cooperation is different between pre-hatching care and post-hatching care in shorebirds; a greater level of biparental cooperation is exhibited in pre- than in post-hatching care (Fig. 1c; Table 1). In addition, as indicated by the intermediate values of  $\lambda$  ( $\lambda$  ranges from 0.622 to 0.894), parental care strategies are phylogenetically correlated (Pagel 1999; Freckleton et al. 2002).

### Ecological factors

First, the extent of parental cooperation does not differ between plant-eating, invertebrate-eating, and vertebrate-eating species (Table 2). In other words, parental cooperation is not associated with food type. The lack of relationship between food type and parental cooperation is consistent between bivariate and multi-predictor models in which the effects of nest type, coloniality, chick development mode, and body mass were controlled for in the analysis.

Second, nest structure does not predict parental cooperation, as the extent of biparental cooperation is not different between species with open and closed nests. Lacking of correlation between nest structure and parental strategies remains in both bivariate model (Table 2) and multiple regression analyses where all potential confounding variables were included (Table 2).

Third, parental cooperation is associated with coloniality. In line with our prediction, colonial breeding species presents a higher level of parental cooperation than solitary breeding ones (Table 2; Fig. 2a). Coloniality is significantly related to post-hatching care in both bivariate and full models (Table 2). In contrast, no significant relationship between

**Table 1** Comparison of pre- and post-hatching parental cooperation. The difference in the levels of pre- and post-hatching parental cooperation was tested for significance using phylogenetic paired *t* tests. Tests were applied to all 955 bird species for which data were available and five large avian orders. A positive value indicates that the level of post-hatching biparental cooperation is higher than the level

of pre-hatching biparental cooperation. Estimates with standard error (mean difference  $\pm$  SE), the corresponding *t* and *p* values, log-likelihood of the fitted model *log(L)*, phylogenetic signal  $\lambda$ , and the number of species *n* are given for each model. Significant difference (*p* < 0.05) is highlighted in bold

Phylogenetic paired <i>t</i> -test	Mean difference $\pm$ SE	<i>t</i>	<i>p</i>	<i>Log(L)</i>	$\lambda$	<i>n</i>
All species	$-0.248 \pm 0.329$	-0.991	0.326	-898.17	0.616	955
Anseriformes	$-0.181 \pm 0.280$	-0.758	0.479	29.368	0.383	38
Charadriiformes	<b><math>-0.422 \pm 0.124</math></b>	<b>-3.431</b>	<b>0.001</b>	<b>-114.72</b>	<b>0.224</b>	<b>130</b>
Procellariiformes	$-0.328 \pm 0.220$	-1.585	0.147	-25.986	0.519	35
Psittaciformes	$0.043 \pm 0.326$	0.140	0.885	-44.049	0.610	48
Passeriformes	$0.066 \pm 0.362$	0.232	0.818	-444.77	0.642	459

**Table 2** Parental cooperation in relation to ecology and life history in birds using phylogenetically generalized linear square models (PGLS). In both bivariate and multi-predictor PGLS models, the extent of parental cooperation in pre-hatching and post-hatching care is the response variable, respectively. Predictors include food type (plants, invertebrates, vertebrates), nest structure (open vs. closed), coloniality (solitary, semi-colonial, colonial), chick development

Predictors	Parental cooperation in pre-hatching care						Parental cooperation in post-hatching care					
	<i>Slope</i> ± <i>SE</i>	<i>t</i>	<i>p</i>	<i>r</i> <sup>2</sup>	$\lambda$	<i>n</i>	<i>Slope</i> ± <i>SE</i>	<i>t</i>	<i>p</i>	<i>r</i> <sup>2</sup>	$\lambda$	<i>n</i>
(a) Bivariate models												
Food type	−0.072 ± 0.048	0.406	−1.490	0.002	0.857	1057	−0.046 ± 0.045	−1.016	0.313	0.001	0.741	985
Nest type	−0.018 ± 0.069	−0.261	0.785	<0.001	0.862	994	−0.023 ± 0.063	−0.367	0.716	<0.001	0.742	930
Coloniality	0.043 ± 0.028	1.542	0.131	0.003	0.870	835	<b>0.080 ± 0.028</b>	<b>2.845</b>	<b>0.005</b>	<b>0.010</b>	<b>0.671</b>	<b>782</b>
Development	<b>−0.333 ± 0.106</b>	<b>−3.133</b>	<b>0.002</b>	<b>0.011</b>	<b>0.881</b>	<b>881</b>	<b>−0.456 ± 0.106</b>	<b>−4.301</b>	<b>&lt;0.001</b>	<b>0.022</b>	<b>0.738</b>	<b>828</b>
Body mass	−0.020 ± 0.023	−0.855	0.399	0.001	0.854	1060	−0.024 ± 0.021	−1.135	0.263	0.001	0.743	986
(b) Full model												
Food type	−0.004 ± 0.054	−0.068	0.894	0.024	0.894	685	−0.049 ± 0.056	−0.880	0.381	0.053	0.622	645
Nest type	0.036 ± 0.075	0.480	0.635				−0.019 ± 0.070	−0.276	0.784			
Coloniality	0.054 ± 0.029	1.843	0.070				<b>0.104 ± 0.031</b>	<b>3.388</b>	<b>&lt;0.001</b>			
Development	<b>−0.404 ± 0.111</b>	<b>−3.627</b>	<b>&lt;0.001</b>				<b>−0.540 ± 0.112</b>	<b>−4.819</b>	<b>&lt;0.001</b>			
Body mass	−0.001 ± 0.026	−0.018	0.900				−0.012 ± 0.024	−0.508	0.614			

coloniality and pre-hatching is found in neither bivariate nor multi-predictor models (Table 2).

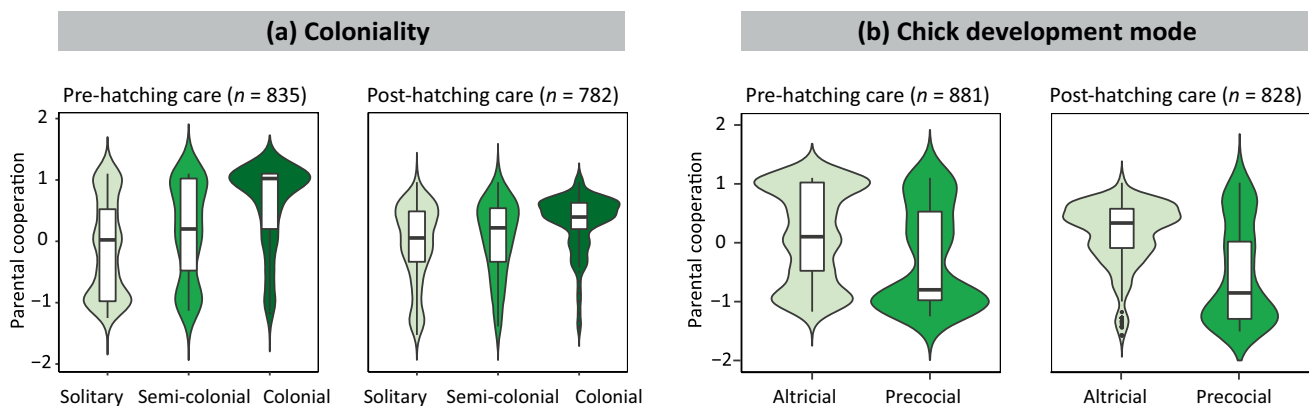
### Life-history traits

Corresponding to our predictions, parental cooperation is significantly associated with chick development mode (Table 2): a higher level of parental cooperation occurs in altricial species than in precocial species, and this relationship is found in both pre- and post-hatching care (Table 2; Fig. 2b). In addition, the effect of chick

mode (altricial, vs. precocial), and body mass (log-transformed). Parameter estimates with standard error (*slope* ± *SE*), the corresponding *t* and *p* values, *R*-squared *r*<sup>2</sup>, phylogenetic signal  $\lambda$ , and sample size *n* are given for each model. All estimates are means of 100 PGLS analyses using different phylogenies. Significant predictors (*p* < 0.05) are highlighted in bold

development mode is consistent between bivariate and multi-predictor analyses (Table 2). Note that coloniality together with chick development mode only explains a modest proportion of variance in parental cooperation (*R*<sup>2</sup> in the PGLS model: 0.01–0.03).

However, we found that the degree of parental cooperation in pre-hatching care and post-hatching care does not correlate with adult body mass (Table 2), which means body size cannot predict parental cooperation. There is no correlation between parental cooperation and body size in either bivariate model or full model (Table 2).



**Fig. 2** Association of parental cooperation before and after hatching with (a) coloniality and (b) chick development mode. The rectangle of the small box plots inside the violin plots represents the two central quartiles; the horizontal line indicates the median level of parental cooperation, and the far ends of the upper and lower whiskers show

the highest and lowest levels of parental cooperation, respectively. The kernel density plot of each violin plot shows the distribution of parental care and its probability density. The extent of parental cooperation is centered at the mean (see Methods), and the number of species *n* is shown for each plot

To ensure that the general findings were not an artifact of the methodology used, we conducted the same analysis with the original data on parental care variables (i.e., without centralization). Supplementary Table S2 shows that our findings are still valid when the original data are applied: colonial breeding species are associated with a high degree of parental cooperation in post-hatching care, although this correlation is not found in the bivariate model; altricial species exhibit a higher level of biparental cooperation than precocial species in both pre- and post-hatching care; care patterns are not explained by factors such as food type, nest type, or body size.

## Discussion

To our knowledge, this is the first study that explicitly investigates whether coloniality predicts parental strategies across a wide range of taxa. Although previous studies explored the correlation between breeding density and care patterns (Owens 2002; van Dijk et al. 2010), coloniality of species has not been considered specifically in these studies.

In line with the prediction, our study consistently shows that coloniality is related to parental cooperation in birds: Colonial breeding species exhibits a higher level of parental cooperation than solitary breeding species in post-hatching care, although this correlation is not found in pre-hatching care. This variation in the correlation between parental strategies and coloniality can be explained by different benefits and costs of various care components. In colonially breeding species, post-hatching care is essential for offspring survival and growth. After hatching, chicks might experience a higher frequency of conspecific attacks (Ashbrook et al. 2008) and predation risks (Varela et al. 2007), especially in the circumstance where only one parent rears the young, leaving chicks completely exposed to the environment when the single parent is away foraging. Moreover, opportunity of obtaining an additional mate is low for deserting males, since females synchronously produce offspring in colonial species (Gochfeld 1980; Nelson 1980; Coulson 2002). As a consequence, biparental cooperation in post-hatching care may evolve in colonial breeding. On the other hand, biparental cooperation might be the cause rather than the consequence of colonial breeding. By cooperating together, the two parents might reduce potential costs of colonial breeding, such as intense infanticide and mate competition (Kiestler and Slatkin 1974; Danchin and Wagner 1997), making colonial breeding more likely to arise. Further research is required to investigate the causal relationship between parental care patterns and coloniality. Moreover, it is not clear whether colonial breeding is associated with parental cooperation as a result of division of parental labor (e.g., one parent protects the broods from predators and conspecifics while the other parent feeds and

nurtures the young) or equally dividing care duties (e.g., both parents invest in chick feeding at a similar level). Further studies are needed to explore whether or not males and females specialize in different care tasks in colonial species. In addition, it might be valuable to explore whether coloniality (and/or breeding density) is correlated with parental cooperation in other animal taxa, such as in insects, frogs, and fishes.

In contrast to our predictions, we found that the extent of parental cooperation is neither related to food type nor to nest structure, two key ecological factors. We assumed that the parents of animal-eating species would cooperate more than the parents of plant-eating species. However, our results suggest that food type cannot explain the considerable variation in parental care patterns. This conclusion is in line with the observations that frugivorous and insectivorous birds exhibit a broad spectrum of parental care patterns (Barve and La Sorte 2016; Cockle and Bodrati 2017), and large-scale analyses which indicate diet of species has no effect on care duration that might influence cooperative behavior among breeders (Langen 2000; Russell et al. 2004). However, it is noteworthy that we used food type as a proxy to reflect food availability which are only available from few species (Morton 1973). This proxy might only capture part of the information in food accessibility and abundance. In further studies, a more direct estimate, such as vegetation growth in the breeding site and the distribution of animal food during the breeding season, will be valuable to justify our conclusions. Furthermore, a recent experimental study on the burying beetle (*Nicrophorus vespilloide*) demonstrates that high abundance of food promotes instead of reducing cooperation between parents (Ratz et al. 2021). It would be worthwhile to test the generality of this finding using large-scale databases on insects.

Moreover, we expected that species with open nests show a greater level of biparental care than those with closed nests. However, this hypothesis is not confirmed by our results. The reason for this might be that the presence of both parents (and, in particular, the presence of a brightly colored father) could make an open nest more conspicuous to predators; hence, predation risk may be enhanced rather than reduced if both parents are around (Skutch 1949; Martin et al. 2000). As a result, species building open nests might take different strategies, with some exhibiting great nest protection by both parents and others displaying low frequency of nest visiting by the brighter parent. It is also possible that nest structure only captures parts of the complexity of nest characters. A recent study showed that nest structure interacts strongly with other nest characteristics in avian species, such as nest site and nest attachment, and that nest environment is determined by all aspects of the nests (Fang et al. 2018). Thus, birds may make parenting decisions based on multidimensional array of nest characteristics. It will be valid for future



studies to take nest structure, nest site, and nest attachment all into account when investigating the relationship between parental strategies and nest characteristics. Furthermore, it is possible that our range-wide analyses overlooked the importance of those two ecological factors operating at smaller scales, i.e., within specific clades. We might reach different conclusions if we conduct the phylogenetical comparative analysis at such scale. Therefore, investigating the effects of ecological factors on small-scale datasets with more explicit assumptions and collecting high-quality data hold potential solutions in the future.

Our study also confirms the prediction that chick development mode is associated with parental cooperation: Parents provide more biparental care in altricial than in precocial species. Our analysis complements earlier studies, which have found that chick development mode plays a crucial role in parental care and mating system in shorebirds (Thomas and Székely 2005; Thomas et al. 2006), implying that the relationship between parental care patterns and chick development mode is general across bird species. These findings suggests that chick demand can be an important determinant of parental care strategies. However, this relationship between offspring demands and parental care patterns can go the other way around: The willingness of both parents to care for their offspring might increase the care demand of offspring (Kölliker et al. 2005), shifting precocial life-history strategy towards altricial life-history strategy. It will be profoundly valuable to investigate the causal links between parental strategies and chick development in the future.

Our analyses reveal that the hypothetical correlation between large body size and high levels of parental cooperation does not exist in birds. This suggests that allometric constraints are unlikely to explain variation in parental care patterns. The correlation between body size and parental behavior was indirectly analyzed by some studies, but the outcomes are not consistent between studies (Liker et al. 2013, 2015; Remeš et al. 2015). It is possible that various studies are conducted at different spatial scales, or using different methodology, more detailed studies are needed to verify our outcome.

Furthermore, our analyses confirm that the extent of parental cooperation is diverse in avian species, with prevalence of egalitarian and partial biparental care in both pre- and post-hatching care (Cockburn 2006). Intriguingly, we found that in one avian order Charadriiformes (e.g., plovers, sandpipers, and allies), the extent of biparental cooperation decreased tremendously after incubation, whereas this pattern was not consistent across birds. Corresponding to our findings, this might be because many shorebirds are precocial (Székely and Reynolds 1995); the young require little parental care after being hatched (Thomas and Székely 2005). Therefore, one parent is probably sufficient to raise hatchlings to be independent. Nevertheless, both parents have the chance to desert and search for new mating

opportunities. Other factors such as adult sex ratio, sexual selection, and certainty of paternity may determine which sex should continually contribute to care (Kokko and Jennions 2008). The remarkably diversified care patterns correspond to unusual variations in mating system in shorebirds (Reynolds and Székely 1997; Eberhart-Phillips et al. 2018), suggesting that shorebirds are an ideal group for testing the theoretical predictions of the evolution of breeding system.

In conclusion, our study provides the most comprehensive analysis to date investigating the effect of ecology and life history on parental cooperation in birds. We show that parental cooperation is not, as often thought, related to food type, nest structure, or body size but rather to coloniality and chick development mode. However, the two recognized factors, coloniality and chick development mode, account for only around 5% of variation in parental care patterns, suggesting that these two factors play a minor role in predicting parental strategies. Experimental studies and field-based observations are needed to unravel the causal relationships between coloniality, chick development mode, and parental sex roles in the future. And detailed data from species are needed to advance phylogenetic comparative analyses. For instance, variations in parental strategies among populations and within a single population have been observed in various species (van Dijk et al. 2010; Bulla et al. 2017; Eberhart-Phillips et al. 2018). Quantifying between- and within-population variations and including these variations might be valuable in future studies.

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**Author contribution** All authors conceived the study. XL and AL collected the data. XL conducted the data analyses with inputs from AL. All authors interpreted the results. XL wrote the manuscript, and others contributed important edits.

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**Data availability** All data analyzed in this study are included in the supplementary information files.

## Declarations

**Ethics approval** Not applicable.

**Consent for publication** The authors consent to the publication of this manuscript in Behavioral Ecology and Sociobiology.

**Conflict of interest** The authors declare no competing interests.

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