

The evolution of parental cooperation in birds

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Parental care is one of the most variable social behaviors and it is an excellent model system to understand cooperation between unrelated individuals. Three major hypotheses have been proposed to explain the extent of parental cooperation: sexual selection, social environment, and environmental harshness. Using the most comprehensive dataset on parental care that includes 659 bird species from 113 families covering both uniparental and biparental taxa, we show that the degree of parental cooperation is associated with both sexual selection and social environment. Consistent with recent theoretical models parental cooperation decreases with the intensity of sexual selection and with skewed adult sex ratios. These effects are additive and robust to the influence of life-history variables. However, parental cooperation is unrelated to environmental factors (measured at the scale of whole species ranges) as indicated by a lack of consistent relationship with ambient temperature, rainfall or their fluctuations within and between years. These results highlight the significance of social effects for parental cooperation and suggest that several parental strategies may coexist in a given set of ambient environment.

parental care | sexual selection | behavior | sex ratio | climate

Parental cooperation, defined here as the extent of biparental care, varies along a continuum from approximately equal share by the male and female to obligate uniparental care, whereby one parent (the male or the female) provides all care for the young (1, 2). By cooperating with each other, the male and the female parent increase growth and survival of their young in various insects, fishes, amphibians, birds, and mammals (3–5). Thus, the extent of parental cooperation may influence reproductive success and population dynamics. Parental care is an excellent model system for investigating interactions between two unrelated individuals (6, 7), and it is one of the prime examples of game-theoretic analyses of conflict and cooperation both theoretically and empirically (8–11). Therefore, understanding the drivers of parental cooperation is one of the lynchpins of breeding system evolution and cooperative behavior.

Sexual selection, social environment, and ambient environment have been proposed to explain variation in the extent of cooperation between parents (7, 12–14). First, cooperation between parents should decrease with the intensity of sexual selection (10, 15, 16), and a reason for this reduction may be that sexual selection favors the sex with higher variance in mating success to reduce his (or her) care provisioning (17–19). Moreover, high mating effort might further decrease the ability of the sex under stronger sexual selection to contribute to parental care (20). Furthermore, high rates of extrapair paternity should lead to the evolution of reduced care provisioning by males (21–25). This evolutionary reduction of paternal care in species with high extrapair paternity would translate into reduced parental cooperation. Second, the sex that is in short supply in the population has an increased mating opportunity and is thus less likely to provide care than the more abundant sex (26–28). Therefore, social environment (i.e., sex ratio of adults in the population) is expected to influence parental behavior (8, 23, 29, 30). Third, environmental factors are known to influence complex social behavior in vertebrates (31–33). More specifically, demanding environmental conditions imposing higher costs of living, such as low food supply or harsh and unpredictable climates, should promote parental cooperation (34–36) and limit social

conflict (37), and this idea has been recently backed by extensive modeling (38, 39). Although previous tests of these hypotheses provided important insights into the potential drivers of parental cooperation, no study has yet tested all three hypotheses across a broad range of taxa and assessed their relative importance.

Here, we use data on parental cooperation in 659 bird species from 113 families to test these three major hypotheses. Birds are one of the most suitable organisms to test these propositions, because they exhibit the full range of parental cooperation from biparental care to uniparental care, and detailed data are available on parental behavior of a broad range of taxa from wild populations. Because parental care is a complex trait, we compiled data on eight components of care (40) and quantified parental cooperation based on sex-specific contribution to care in these parental activities spanning the whole parental care period (full materials and methods are available in *SI Appendix, Supplement S1*). We focused on care provisioning by the male and the female parent, and the extent of parental cooperation was estimated on a scale that varied between –1.5 when only one parent (the male or the female) provides all care and 1.5 when the male and the female parent share provisioning approximately equally (frequency distribution of parental cooperation across 659 species of birds is available in *SI Appendix, Fig. S1*).

Using phylogenetic analyses we test the following predictions: (i) Sexual selection: parental cooperation is higher in socially monogamous species and in species with low rates of extrapair paternity (EPP) than in polygamous and high EPP species. (ii) Social environment: species with balanced adult sex ratios (ASR, proportion of males in the adult population) exhibit more parental cooperation than species with biased ASR. (iii) Ambient environment: Species that live in environments with harsh and variable climates exhibit high parental cooperation.

Significance

Parents in many animal species care for their offspring. In some species, males care more; in other species, females care more; in still other species, the contribution of the sexes is equal. However, we do not know what explains these differences among species. Using the most comprehensive analyses of parental care to date, here we show that parents cooperate more when sexual selection is not intense and the adult sex ratio of males to females is not strongly skewed. However, the degree of parental cooperation is unrelated to harshness and predictability of the ambient environment during the breeding season. Our work therefore suggests that several types of parental care may coexist in a given set of ambient environment.

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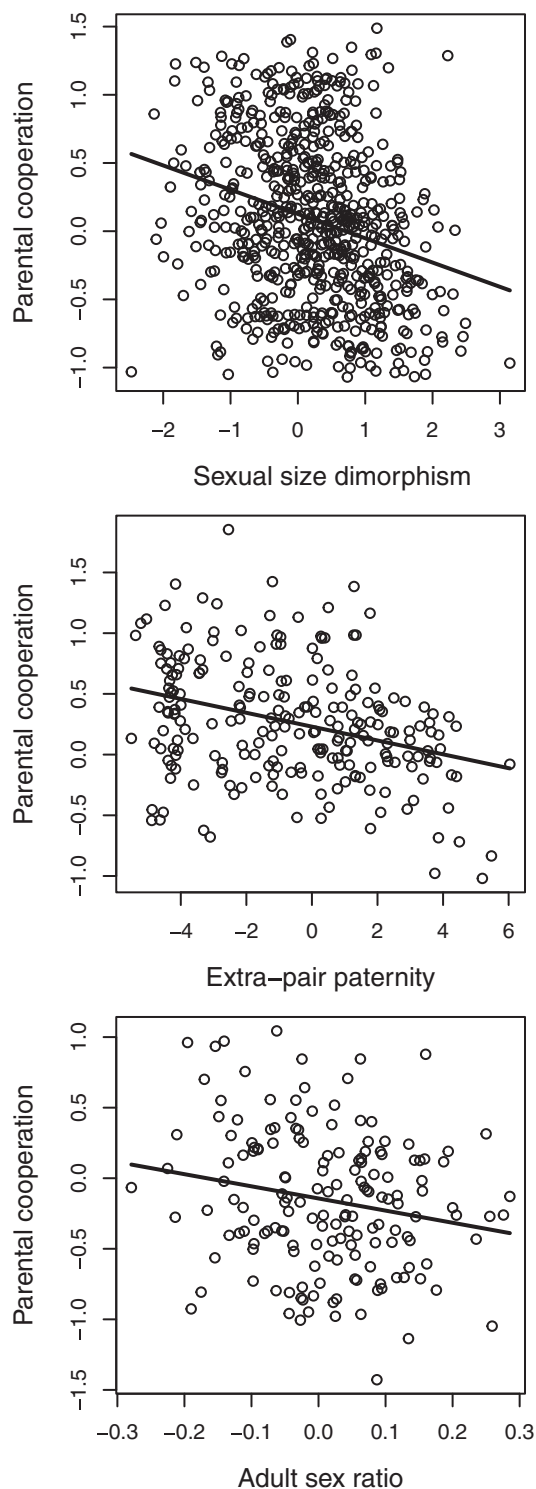


Fig. 2. Parental cooperation in relation to sexual size dimorphism (log absolute Size Dimorphism Index), extrapair paternity (sqrt EPP), and adult sex ratio (sqrt ASR bias) in birds. Variables in each panel were statistically adjusted for other predictors in a phylogenetic generalized least squares (PGLS) model and the residuals from statistical models are plotted (sexual selection model for sexual size dimorphism and extrapair paternity, and social environment model for ASR, see Table 1). Ordinary least squares regression lines are included.

sexual size dimorphism in birds (34, 58–60). Taken together with our results presented here, this body of work suggests that sexual, social, and parenting strategies in birds are largely independent of climatic

effects on the scale of whole breeding ranges of species and instead might be driven by eco-evolutionary feedbacks between social behavior, life history, and demography (29, 61). It is also possible that parental cooperation may covary with environmental factors at finer spatial scales not captured by our analyses of breeding range-wide environment, for example as seems to be the case of mating systems and sexual selection (31, 32, 35, 60). We suggest that detailed analyses of the plasticity of parental cooperation within species in relation to environmental conditions on smaller spatial scales (e.g., food supply, ambient temperature) will shed critical light on this important question.

In conclusion, we show that the evolution of parental cooperation is predicted by sexual selection and social environment at least in birds, whereas climatic conditions at the scale of the whole species' breeding ranges do not predict parental cooperation. Thus, several parental cooperation strategies may be adaptive in a given set of climatic conditions, depending on the species' social and genetic mating systems and demographic structure. These patterns are valid across a broad range of bird species and clades that breed in diverse settings. They highlight the significance of feedbacks between sexual selection, social environment, and parental care, because all of these have mortality consequences and are thus linked in ecoevolutionary feedback loops (61).

Further works are needed to advance parental cooperation research. First, drivers of the effects we identify are sometimes unclear. For example, it is not clear whether evolutionary changes in parental cooperation are driven by sexual selection acting on male behavior (24, 46), on female behavior (62), or on both sexes simultaneously. Second, further studies should explore which sex is more responsive and whether sex-specific parenting abilities can bias responses to intense sexual selection (10, 11). Third, new phylogenetic comparative analyses are needed to test whether sexual selection and social environment may influence parental cooperation in nonavian taxa, for instance in fishes, frogs, and mammals. Although the details of care differ between these major clades, our results here establish the working hypotheses that can be followed up in a diverse range of taxa. Fourth, environmental factors other than climate can have important effects on parental cooperation. For example, food availability predicts cooperation during nestling feeding in several avian groups (35, 36), and the generality of this relationship should be tested using large-scale data sets. Moreover, our range-wide analyses might have missed the importance of ecological factors operating on smaller spatial scales. We encourage researchers to evaluate potential effects of small-scale ecological factors on parental cooperation. Finally, insights gained by our comparative study should be further tested in the natural habitat of animals. These field-based observations and experimental manipulations combined with comparisons across populations and long-term population monitoring data will be immensely useful to tease apart various social and ecological effects and allow evolutionary ecologists to test the positive and negative feedbacks that underpin mating systems and parental care.

Materials and Methods

Data Collection. We quantified sex-specific contribution to care on an ordinal scale from 0 to 4 as follows: 0, no male contribution; 1, male contribution 1–33%; 2, male contribution 34–66%; 3, male contribution 67–99%; 4, male contribution 100%. Thus, this score varied from female-only care (0) to approximately equal care by male and female (2) to male-only care (4). Scores were gathered separately for nest building, incubation, nest guarding (i.e., guarding and defending the nest during incubation), chick brooding, chick feeding, chick guarding (i.e., guarding and defending the brood after hatching), postfledging feeding of chicks, and postfledging guarding of chicks (i.e., guarding and defending the brood after fledging, for details see ref. 40). To represent the extent of biparental care, the eight parental activities were recoded on a 3-level scale so that 0 represented exclusive uniparental care by the male or female (original scores 0 or 4), 1 represented biparental care biased toward either the male or the female (original scores 1 or 3), and 2 represented approximately equal contribution by the male and female (original score 2). Finally, we calculated parental cooperation by averaging the statistically centered extent of biparental care across the eight activities. The resulting parental cooperation ranged from minimum parental cooperation to maximum

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