

The evolution of parental cooperation in birds

Vladimír Remes^{a,1}, Robert P. Freckleton^b, Jácint Tökölyi^c, András Liker^d, and Tamás Székely^{e,f}

^aDepartment of Zoology and Laboratory of Ornithology, Palacky University, 77146 Olomouc, Czech Republic; ^bDepartment of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; ^cMTA-DE “Lendület” Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, 4032 Debrecen, Hungary; ^dDepartment of Limnology, University of Pannonia, H-8201 Veszprém, Hungary; ^eDepartment of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom; and ^fState Key Laboratory of Biocontrol and College of Ecology and Evolution, Sun Yat-sen University, Guangzhou 5102275, China

Edited by Joan E. Strassmann, Washington University in St. Louis, St. Louis, MO, and approved September 23, 2015 (received for review June 26, 2015)

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.

Author contributions: V.R., R.P.F., A.L., and T.S. designed research; V.R. performed research; V.R., R.P.F., and J.T. contributed new reagents/analytic tools; V.R. analyzed data; and V.R., R.P.F., J.T., A.L., and T.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The data reported in this paper have been deposited in the Dryad Digital Repository, [dx.doi.org/10.5061/dryad.02jko](https://doi.org/10.5061/dryad.02jko).

¹To whom correspondence should be addressed. Email: vladimir.remes@upol.cz.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1512599112/-DCSupplemental.

Results and Discussion

The extent of parental cooperation is usually conserved within major clades (Fig. 1), which is consistent with high values of phylogenetic signal ($\lambda \sim 0.9$, Table 1; exact estimated λ values are available in *SI Appendix*, Table S1). At the same time, parental cooperation is highly variable between clades across birds. For example, grebes, woodpeckers, and sparrows are characterized by extensive parental cooperation, whereas others exhibit low cooperation (e.g., ducks, pheasants and grouse, and owls, Fig. 1). Several clades, however, exhibit high interspecific variation in parental cooperation; for example snipes, sandpipers and allies, and Old World warblers (Fig. 1).

Both sexual selection and social environment predict parental cooperation as shown by phylogenetic generalized least squares analyses (41) using the most recent complete avian phylogeny (42) (Table 1 and Figs. 2 and 3; for details of these relationships see *SI Appendix*, Table S1 and Fig. S2). First, intense sexual selection as indicated by extensive sexual size dimorphism (43) and high rates of extrapair paternity are consistently associated with low parental cooperation (Figs. 2 and 3). To confirm that our predictions also hold when testing the male involvement in care, we also analyzed relative male care, which is a proxy of parental care bias expressed on the scale from female-biased to male-biased care (frequency distribution of relative male care across 659 species of birds is available in *SI Appendix*, Fig. S1). Our

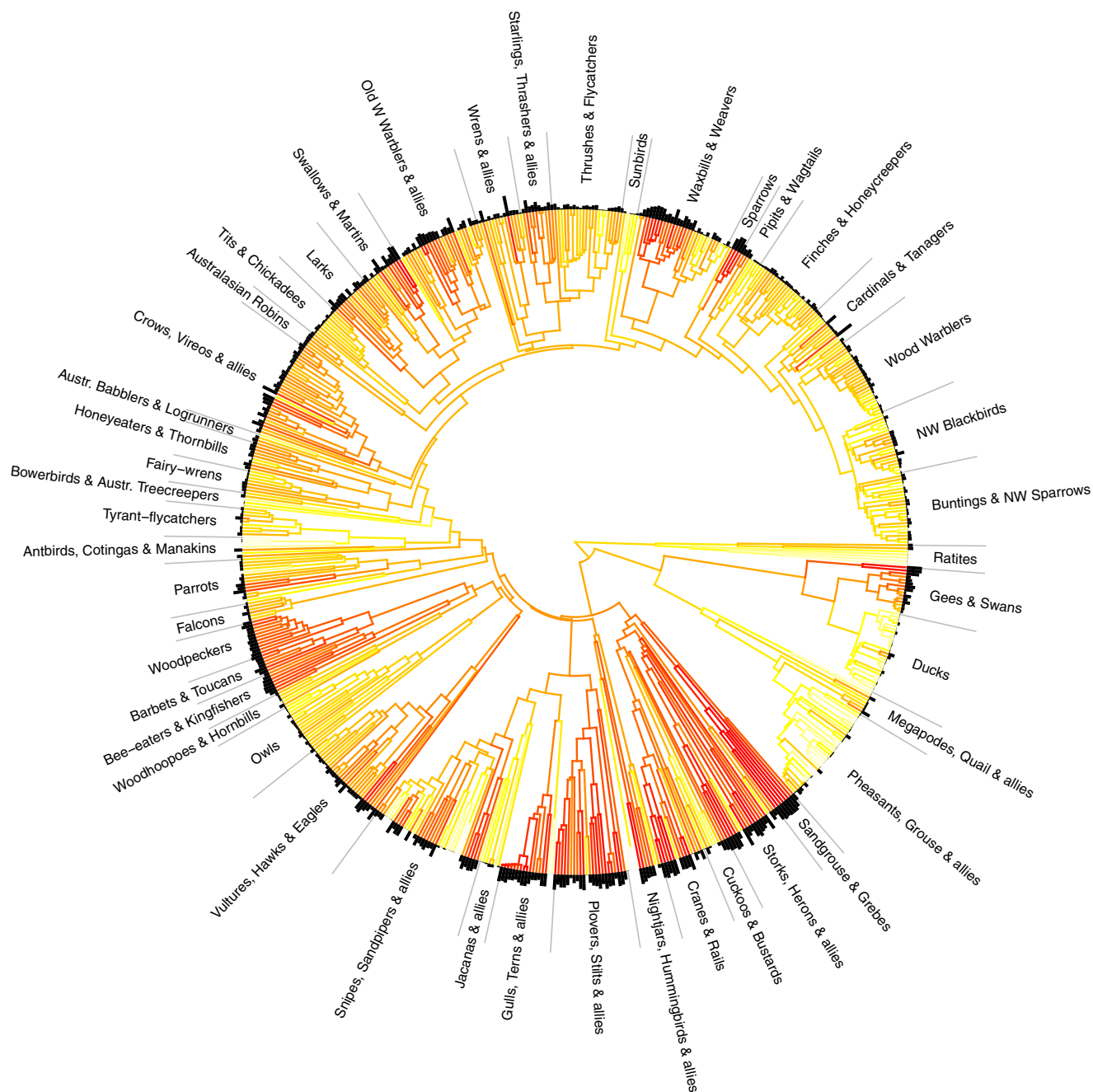


Fig. 1. Phylogenetic distribution of parental cooperation in 659 species of birds included in this study (Bayesian maximum credibility tree of 500 phylogenies). The figure shows parental cooperation for each species (black bars refer to parental cooperation; tall bars indicate high cooperation) and phylogenetic reconstruction along the branches (using plotBranchbyTrait [phytools] function of R software; red = high cooperation, yellow = low cooperation).

Table 1. Parental cooperation in relation to sexual selection, social environment, and climate in birds

Model and predictors	Estimate (SE)	F (P)
Sexual selection ($R^2 = 0.17$, $\lambda = 0.76$, $df = 4,221$)		
Sexual size dimorphism	-0.258 (0.057)	20.62 (<0.001)
Extrapair paternity	-0.264 (0.061)	18.55 (<0.001)
Body mass	0.299 (0.115)	6.83 (0.011)
Chick development	-0.157 (0.151)	1.12 (0.308)
Social environment ($R^2 = 0.07$, $\lambda = 0.91$, $df = 3,161$)		
Adult sex ratio	-0.186 (0.056)	11.05 (0.001)
Body mass	0.087 (0.135)	0.43 (0.524)
Chick development	-0.084 (0.261)	0.12 (0.750)
Climate ($R^2 = 0.01$, $\lambda = 0.90$, $df = 4,654$)		
Temperature	0.041 (0.033)	1.60 (0.214)
Rainfall	0.037 (0.031)	1.47 (0.233)
Body mass	-0.019 (0.074)	0.09 (0.795)
Chick development	-0.084 (0.145)	0.35 (0.564)
Full model ($R^2 = 0.29$, $\lambda = 0.82$, $df = 7,72$)		
Sexual size dimorphism	-0.168 (0.098)	2.93 (0.093)
Extrapair paternity	-0.230 (0.106)	4.70 (0.034)
Adult sex ratio	-0.234 (0.083)	7.88 (0.007)
Temperature	0.027 (0.105)	0.08 (0.796)
Rainfall	0.034 (0.087)	0.16 (0.696)
Body mass	0.334 (0.178)	3.54 (0.066)
Chick development	0.020 (0.223)	0.03 (0.900)

In all models, parental cooperation was the response variable and predictors included: sexual size dimorphism (log absolute size dimorphism index), extrapair paternity (sqrt EPP), adult sex ratio (sqrt ASR bias), temperature (first axis from PCA on climatic variables: higher values mean hot environments with low temperature variability; factor loadings available in *SI Appendix, Table S4*), rainfall (second axis from PCA on climatic variables: higher values mean dry environments with high rainfall variability; factor loadings available in *SI Appendix, Table S4*), body mass (log-transformed), and chick development (altricial vs. precocial). We use phylogenetic generalized least squares approach and present means from 500 analyses using different phylogenetic trees (see detailed results in *SI Appendix, Table S1*). Estimates are standardized regression coefficients and λ indicates the strength of the phylogenetic signal.

predictions are supported, because male care (relative to female care) is low in species with male-biased sexual size dimorphism and high in species with female-biased dimorphism. Moreover, males provide little care in species with high extrapair paternity (Fig. 3; summarized results are available in *SI Appendix, Table S2*, and detailed results are available in *SI Appendix, Table S3 and Fig. S3*).

These results are in line with theories of the evolution of parental cooperation (2, 17, 25, 44). Specifically, our results are consistent with the prediction that the larger sex (usually the male in birds), which is often under stronger sexual selection than the smaller sex, reduces its care provisioning (17, 19), translating into lower contribution to care on macroevolutionary time scales. Similarly, our results support the prediction that high rates of extrapair paternity will lead, on a macroevolutionary time scale, to a reduction in male care (22–25) and consequently to reduced parental cooperation. At the same time, this result is far from trivial, because some models predict variable relationships between male care and extrapair paternity depending on model assumptions (45) and results of previous empirical studies are also conflicting (e.g., refs. 22 and 46–48, reviewed in ref. 25). It is worth stressing that the relationship we document is the most comprehensive in any major taxon and makes a significant contribution to previous theoretical and empirical investigations of extrapair paternity and parental care. The macroevolutionary response of male care to extrapair paternity may not depend on the ability of males to perceive paternity loss in their contemporary broods and respond to it by facultative reduction of

paternal care (21, 22, 24, 46), although this ability seems to be widespread among animals (25). Reduction of male parental contribution due to female promiscuity might lead to lower overall parental effort (49), and eventual breakdown of biparental breeding systems (21).

Second, parental cooperation decreases with biased adult sex ratios (Table 1 and Figs. 2 and 3). This result is in line with theoretical prediction that biased sex ratios will promote divergent parental sex roles, because individuals of the rare sex reduce their care due to high mating success, whereas members of the more common sex get most reproductive success from caring for existing offspring (8, 23). This interpretation is supported by modeling of relative male care, which is low in species with female-biased sex ratio and high in species with male-biased sex ratio (Fig. 3; summarized results are available in *SI Appendix, Table S2*, and detailed results are available in *SI Appendix, Table S3 and Fig. S3*). Our results are also in line with previous findings in shorebirds, where ASR strongly predicted conventional and reversed parental sex roles (27). However, the directionality of the relationship between ASR and cooperation is unclear and the causality might be reversed. Unequal parental roles might lead to biased sex ratios because the sexes engage unequally in parental duties, have different time budgets, and consequently experience different mortality rates (50). Accordingly, sex-biased mortality rates are often correlated with biased ASR across populations and species (51–53). Moreover, some authors suggest positive feedbacks between changes in ASR and parental sex roles and thus the relationship may even be bidirectional (8, 23, 54).

The aforementioned results are not confounded by phylogeny because we use phylogeny-based comparative analyses, and remain robust to alternative phylogenetic hypotheses and incorporating potential confounds in the models (for phylogenetic robustness of our results, see *SI Appendix, Tables S1 and S3*). In addition to sexual selection and social environment, we find a positive relationship of parental cooperation to adult body mass, although this effect is less consistent between analyses (Table 1 and Fig. 3). Body mass is a typical allometric correlate of life history, including breeding cycle duration (for the relationship of breeding cycle duration to adult body mass in our dataset see *SI Appendix, Fig. S4*) and adult mortality rate (correlation in our dataset $r = -0.57$, $n = 323$ species), and of pair bond duration and divorce rate (55, 56). Consequently, it seems that long-lived species with prolonged pair bonds and low divorce rates would be expected to cooperate more, but more direct tests of this hypothesis are needed. We find that chick development (altricial vs. precocial) is not associated with the extent of cooperation or relative male care (Table 1 and Fig. 3), suggesting that chick demand does not affect parental cooperation strategies across birds. We highlight that sexual selection and social environment together with body mass explain a large proportion of variance in parental cooperation (~30–35%; summary in Table 1 and details in *SI Appendix, Table S1*), although these values are somewhat lower for relative male care (~12–26%; summary in *SI Appendix, Table S2* and details in *SI Appendix, Table S3*). We also emphasize that recent work suggests that ASR relates to sexual selection (57) and the precise relationship between ASR, demographic processes, and sexual selection are far from understood (53). Nevertheless, our results demonstrate large additive effects of major selective forces that were theoretically predicted to facilitate parental cooperation in animals.

Finally, climatic conditions during the breeding season, thought to drive the evolution of cooperation (33, 34, 58), do not predict parental cooperation as none of the climatic factors is significantly associated with parental cooperation either in bivariate or multiple regression analyses (Table 1 and Fig. 3; for details of these relationships, see *SI Appendix, Table S1 and Fig. S2*). Our analyses thus suggest that climatic conditions prevailing during the breeding season are quite permissive in terms of cooccurring multiple parental cooperation strategies. This conclusion agrees with observations that species with extremely contrasting parental care systems (e.g., with reversed vs. conventional sex roles) may breed side-by-side sharing much of the environment (see ref. 27 for examples). Weak or inconsistent effects of climate have previously been identified in large-scale analyses of climatic correlates of cooperative breeding and

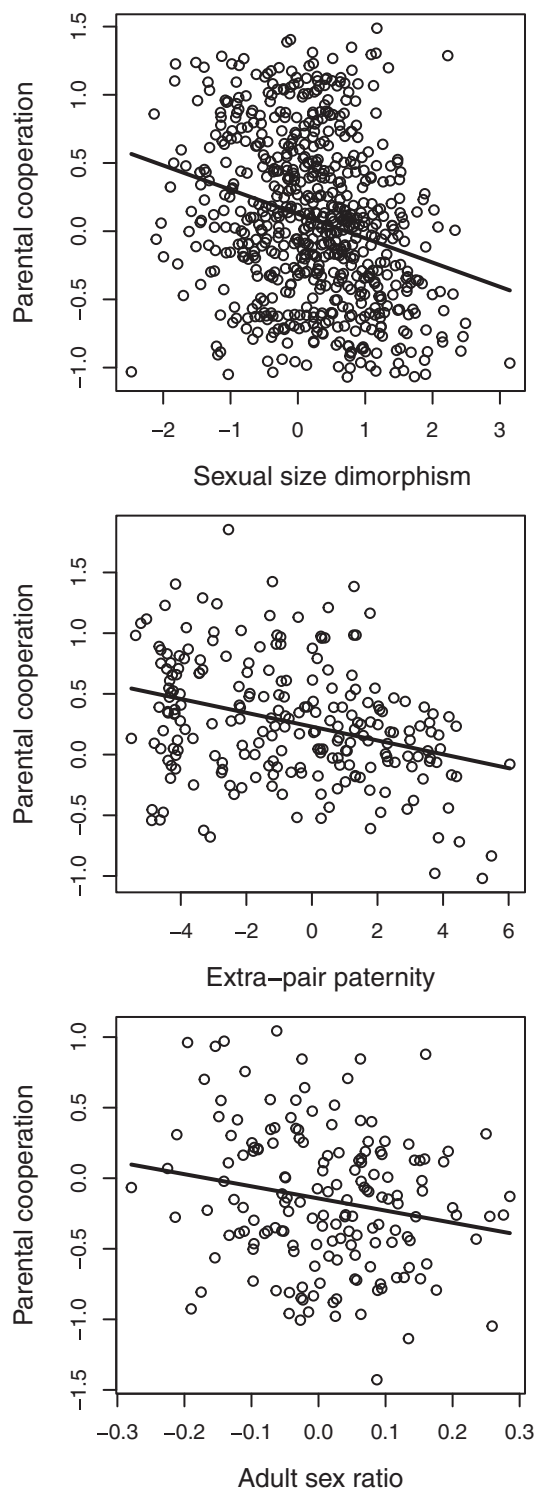


Fig. 2. Parental cooperation in relation to sexual size dimorphism (log absolute Size Dimorphism Index), extrapair paternity (sqrt EPP), and adult sex ratio (sqrt ASR bias) in birds. Variables in each panel were statistically adjusted for other predictors in a phylogenetic generalized least squares (PGLS) 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

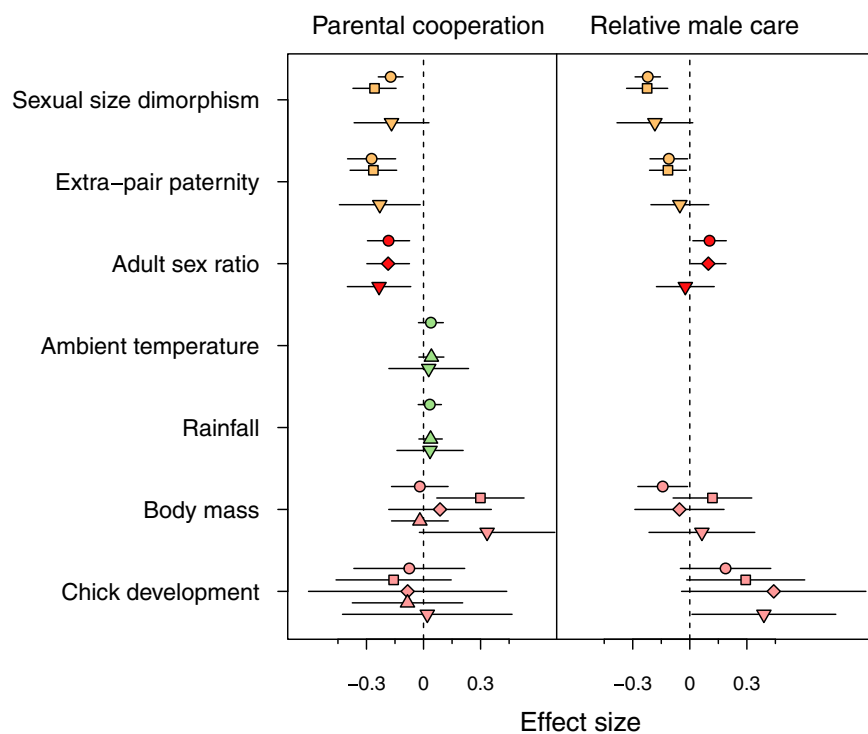


Fig. 3. Parental cooperation and relative male care (for their frequency distribution across 659 species of birds see *SI Appendix, Fig. S1*) in relation to sexual selection (orange), social environment (red), climate (green), and life-history traits (pink). The figure shows effect sizes (mean standardized regression coefficients ± 2 SE) from the phylogenetic generalized least squares analyses of parental cooperation and relative male care. Models were either bivariate (circles) or multiple regressions (other symbols). Multiple regression models parallel our hypotheses: sexual selection model (squares), social environment model (diamonds), climate model (upward facing triangles), and full model (downward facing triangles; see also Table 1). In analyses of parental cooperation, we used absolute SDI and ASR bias, whereas in analyses of relative male care, we used SDI and ASR (see *Materials and Methods* and *SI Appendix, Supplement S1*). Life-history covariates (body mass, chick development) were included in all models. Horizontal error bars not intercepting the vertical zero line indicate statistically significant effects. Note that climate was not fitted in models of relative male care.

parental cooperation (frequency distribution of parental cooperation across 659 species of birds is available in *SI Appendix, Fig. S1*) and varied across the phylogeny (Fig. 1). Here, minimum cooperation is when all activities are carried out by one sex (the male or the female, approximately around the value of -1.5), whereas the maximum cooperation is when all parental care activities are shared approximately equally between the male and the female (approximately around the value of 1.5). To test hypotheses that predict specific direction of effects on the scale from female-biased to male-biased care, we also calculated standardized relative male care based on the original scores. Relative male care ranged from -2 (strongly female-biased care) to 3 (strongly male-biased care; frequency distribution of relative male care across 659 species of birds is available in *SI Appendix, Fig. S1*). Data collection was designed to cover the broad phylogenetic diversity and full variability of breeding systems exhibited by birds. Our data set contained 659 species from 113 avian families.

We used two proxies of sexual selection that are widely available: sexual size dimorphism and extrapair paternity (63). We note that the relationship between the strength of sexual selection and EPP is complex. However, by using several indices of sexual selection (sexual size dimorphism, EPP) we hope to provide comprehensive analyses and characterize broad range of processes that underpin sexual selection, including male-male competition and female choice. We calculated size dimorphism index as $SDI = \text{body mass of the heavier sex} / \text{body mass of the lighter sex} - 1$ and made the values positive for male-biased dimorphism and negative for female-biased dimorphism. We then also calculated absolute SDI by taking absolute values of the original SDI. Greater values of absolute SDI thus mean greater difference in body masses between sexes, suggesting differential selection acting on males and females that may indicate sexual selection (15, 43). Extrapair paternity (EPP) was expressed as % of broods containing at least one extrapair offspring, in accordance with recent studies (64). However, to check the sensitivity of our analyses to this particular choice, we also repeated all analyses with % of extrapair offspring in the population (EPY). Although this variable strongly decreased sample size, results were largely robust to the choice of EPP vs. EPY (details of these sensitivity analyses are available in *SI Appendix, Tables S1 and S3*). Social environment was characterized by adult sex ratio (ASR), which was expressed as the proportion of males in the adult population (52, 65). We then calculated the absolute deviation from ASR of 0.5 to express the degree of bias in the frequency of males vs. females in the population. This value was always positive and increased with increasing deviation from ASR of 0.5 (ASR bias).

To characterize ambient environment, first we recorded breeding season for each species from literature. Second, based on digitized ranges (66) and global climatic layers (CRU Dataset, www.cru.uea.ac.uk), we extracted climatic

conditions in the breeding range of every species during its breeding season. We extracted (*i*) the average monthly temperature ($^{\circ}\text{C}$) and rainfall (mm); (*ii*) within-year variation as SD of breeding season monthly averages for temperature and rainfall; and (*iii*) among-year variation as SD across 49 y (1961–2009) of monthly averages for temperature and rainfall during the species' breeding season. To control for potential life-history confounds, we included adult body mass (g) and chick development (altricial vs. precocial) in the models.

Phylogenetic Analyses. We used phylogenetic generalized least squares (PGLS) approach implemented in a fast likelihood algorithm (67) in the R language (68). In PGLS models, we estimated the phylogenetic signal by optimizing the λ parameter (41). We used 500 phylogenetic trees extracted from www.birdtree.org (Hackett constraint, ref. 42). We ran the PGLS analyses across all of the trees and then summarized the resulting 500 parameter estimates.

Parental cooperation and relative male care were the main response variables in our models. First, we fitted bivariate PGLS models between parental cooperation and the following predictors: sexual size dimorphism (log absolute SDI), extrapair paternity (sqrt EPP), adult sex ratio (sqrt ASR bias), climatic variables (means and among- and within-year variations in temperature and rainfall), adult body mass (log-transformed), and chick development (altricial vs. precocial). Predictors were the same for relative male care, except that we used SDI instead of absolute SDI, ASR instead of ASR bias, and we did not use climatic variables due to lacking predictions for relative male care. Second, we fitted PGLS models with several explanatory variables. To use the maximum number of species in each analysis, we fitted four models structured according to our three main hypotheses while controlling for life-history variables. For parental cooperation, these were: Sexual selection model: absolute SDI, EPP, adult body mass, chick development ($n = 226$ species); Social environment model: ASR bias, adult body mass, chick development ($n = 165$ species); Climate model: ambient temperature, rainfall, adult body mass, chick development ($n = 659$ species); Full model: absolute SDI, EPP, ASR bias, ambient temperature, rainfall, adult body mass, chick development ($n = 80$ species). For relative male care, these were: Sexual selection model: SDI, EPP, adult body mass, chick development ($n = 226$ species); Social environment model: ASR, adult body mass, chick development ($n = 165$ species); Full model: SDI, EPP, ASR, adult body mass, chick development ($n = 80$ species). We did not fit the climatic model due to lacking predictions for relative male care. Full details of materials and methods are available in *SI Appendix, Supplement S1*.

ACKNOWLEDGMENTS. We appreciate tremendous work of generations of field ornithologists. This work would not be possible without their effort. We thank the reviewers for very helpful comments. V.R. was supported by Palacky University (IGA PrF_2015_011). A.L. was supported by a Marie Curie Intra-European Fellowship, and by Grants OTKA K 112838 and TÁMOP-4.2.2. B-15/11/KONV-2015-0004. T.S. was a Mercator Visiting Professor at the

University of Bielefeld, and a Humboldt Award holder at the University of Göttingen while working on this paper, and was supported by an open project of State Key Laboratory of Biocontrol, Sun Yat-sen University, Guangzhou. J.T. was supported by TÁMOP-4.2.2.C-11/11/KONV-2012-0010 project, cofinanced by the European Social Fund and the European Regional Development Fund.

- Clutton-Brock TH (1991) *The Evolution of Parental Care* (Princeton University Press, Princeton).
- Royle NJ, Smiseth PT, Kölliker M, eds (2012) *The Evolution of Parental Care* (Oxford University Press, Oxford).
- McGraw L, Székely T, Young LJ (2010) *Pair bonds and parental behaviour. Social Behaviour: Genes, Ecology and Evolution*, eds Székely T, Moore AJ, Komdeur J (Cambridge University Press, Cambridge), pp 271–301.
- Balshine S (2012) Patterns of parental care in vertebrates. *The Evolution of Parental Care*, eds Royle NJ, Smiseth PT, Kölliker M (Oxford University Press, Oxford), pp 62–80.
- Trumbo ST (2012) Patterns of parental care in invertebrates. *The Evolution of Parental Care*, eds Royle NJ, Smiseth PT, Kölliker M (Oxford University Press, Oxford), pp 81–100.
- Lessells CM (2012) Sexual conflict. *The Evolution of Parental Care*, eds Royle NJ, Smiseth PT, Kölliker M (Oxford University Press, Oxford), pp 150–170.
- Klug H, Alonzo SH, Bonsall MB (2012) Theoretical foundations of parental care. *The Evolution of Parental Care*, eds Royle NJ, Smiseth PT, Kölliker M (Oxford University Press, Oxford), pp 21–39.
- McNamara JM, Székely T, Webb JN, Houston AI (2000) A dynamic game-theoretic model of parental care. *J Theor Biol* 205(4):605–623.
- Harrison F, Barta Z, Cuthill I, Székely T (2009) How is sexual conflict over parental care resolved? A meta-analysis. *J Evol Biol* 22(9):1800–1812.
- Barta Z, Székely T, Liker A, Harrison F (2014) Social role specialization promotes cooperation between parents. *Am Nat* 183(6):747–761.
- McNamara JM, Wolf M (2015) Sexual conflict over parental care promotes the evolution of sex differences in care and the ability to care. *Proc R Soc London B* 282(1803):20142752.
- Wilson EO (1975) *Sociobiology: The New Synthesis* (Harvard University Press, Cambridge).
- Olson VA, Liker A, Freckleton RP, Székely T (2008) Parental conflict in birds: Comparative analyses of offspring development, ecology and mating opportunities. *Proc Biol Sci* 275(1632):301–307.
- Webb TJ, Olson VA, Székely T, Freckleton RP (2010) Who cares? Quantifying the evolution of division of parental effort. *Methods Ecol Evol* 1(3):221–230.
- Andersson M (1994) *Sexual Selection* (Princeton University Press, Princeton).
- Adrian O, Brockmann I, Hohoff C, Sachser N (2005) Paternal behaviour in wild guinea pigs: A comparative study in three closely related species with different social and mating systems. *J Zool (Lond)* 265(1):97–105.
- Queller DC (1997) Why do females care more than males? *Proc Biol Sci* 264(1388):1555–1557.
- Gonzalez-Voyer A, Fitzpatrick JL, Kolm N (2008) Sexual selection determines parental care patterns in cichlid fishes. *Evolution* 62(8):2015–2026.
- Jennions MD, Kokko H (2010) Sexual selection. *Evolutionary Behavioral Ecology*, eds Westneat DF, Fox CW (Oxford University Press, Oxford), pp 343–364.
- Magrath MJL, Komdeur J (2003) Is male care compromised by additional mating opportunity? *Trends Ecol Evol* 18(8):424–430.
- Kokko H (1999) Cuckoldry and the stability of biparental care. *Ecol Lett* 2(4):247–255.
- Sheldon BC (2002) Relating paternity to paternal care. *Philos Trans R Soc Lond B Biol Sci* 357(1419):341–350.
- Kokko H, Jennions MD (2008) Parental investment, sexual selection and sex ratios. *J Evol Biol* 21(4):919–948.
- Alonzo SH, Klug H (2012) Paternity, maternity, and parental care. *The Evolution of Parental Care*, eds Royle NJ, Smiseth PT, Kölliker M (Oxford University Press, Oxford), pp 189–205.
- Griffin AS, Alonzo SH, Cornwallis CK (2013) Why do cuckolded males provide paternal care? *PLoS Biol* 11(3):e1001520.
- Forsgren E, Amundsen T, Borg AA, Bjelvenmark J (2004) Unusually dynamic sex roles in a fish. *Nature* 429(6991):551–554.
- Liker A, Freckleton RP, Székely T (2013) The evolution of sex roles in birds is related to adult sex ratio. *Nat Commun* 4:1587.
- Parra JE, Beltrán M, Zefania S, Dos Remedios N, Székely T (2014) Experimental assessment of mating opportunities in three shorebird species. *Anim Behav* 90(4):83–90.
- Székely T, Webb JN, Cuthill IC (2000) Mating patterns, sexual selection, and parental care: An integrative approach. *Vertebrate Mating Systems*, eds Apollonio M, Festa-Bianchet M, Mainardi M (World Scientific Publishing, Singapore), pp 159–185.
- Kokko H, Jennions MD (2012) Sex differences in parental care. *The Evolution of Parental Care*, eds Royle NJ, Smiseth PT, Kölliker M (Oxford University Press, Oxford), pp 101–118.
- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383.
- Jarman PJ (1974) Social organization of antelope in relation to their ecology. *Behaviour* 48(1):215–267.
- Rubenstein DR (2011) Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proc Natl Acad Sci USA* 108(Suppl 2):10816–10822.
- Jetz W, Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr Biol* 21(1):72–78.
- Crook JH (1964) The evolution of social organisation and visual communication in the weaver birds (Ploceinae). *Behav* 10(Suppl):1–178.
- Leisler B, Winkler H, Wink M (2002) Evolution of breeding systems in acrocephaline warblers. *Auk* 119(2):379–390.
- Shen S-F, et al. (2012) Unfavourable environment limits social conflict in *Yuhina brunneiceps*. *Nat Commun* 3:885.
- Smaldino PE, Schank JC, McElreath R (2013) Increased costs of cooperation help cooperators in the long run. *Am Nat* 181(4):451–463.
- Smaldino PE, Newson L, Schank JC, Richerson PJ (2013) Simulating the evolution of the human family: Cooperative breeding increases in harsh environments. *PLoS One* 8(11):e80753.
- Székely T, Remeš V, Freckleton RP, Liker A (2013) Why care? Inferring the evolution of complex social behaviour. *J Evol Biol* 26(7):1381–1391.
- Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: A test and review of evidence. *Am Nat* 160(6):712–726.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. *Nature* 491(7424):444–448.
- Fairbairn D, Blanckenhorn W, Székely T (2007) *Sex, Size and Gender Roles* (Oxford University Press, Oxford).
- Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. *Science* 341(6145):526–530.
- Houston AI, McNamara JM (2002) A self-consistent approach to paternity and parental effort. *Philos Trans R Soc Lond B Biol Sci* 357(1419):351–362.
- Matysioková B, Remeš V (2013) Faithful females receive more help: The extent of male parental care during incubation in relation to extra-pair paternity in songbirds. *J Evol Biol* 26(1):155–162.
- Møller AP, Birkhead TR (1993) Certainty of paternity covaries with paternal care in birds. *Behav Ecol Sociobiol* 33(4):261–268.
- Schwagmeyer PL, et al. (1999) Species differences in male parental care in birds: A reexamination of correlates with paternity. *Auk* 116(2):487–503.
- Matysioková B, Remeš V (2014) The importance of having a partner: Male help releases females from time limitation during incubation in birds. *Front Zool* 11(1):24.
- Liker A, Székely T (2005) Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* 59(4):890–897.
- Arendt JD, Reznick DN, López-Sepulcre A (2014) Replicated origin of female-biased adult sex ratio in introduced populations of the trinidadian guppy (*Poecilia reticulata*). *Evolution* 68(8):2343–2356.
- Székely T, Liker A, Freckleton RP, Fichtel C, Kapperel PM (2014) Sex-biased survival predicts adult sex ratio variation in wild birds. *Proc R Soc London B* 281(1788):20140342.
- Székely T, Weissing FJ, Komdeur J (2014) Adult sex ratio variation: Implications for breeding system evolution. *J Evol Biol* 27(8):1500–1512.
- Lehtonen J, Kokko H (2012) Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. *Philos Trans R Soc Lond B Biol Sci* 367(1586):211–221.
- Jeschke JM, Kokko H (2008) Mortality and other determinants of bird divorce rate. *Behav Ecol Sociobiol* 63(1):1–9.
- Botero CA, Rubenstein DR (2012) Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PLoS One* 7(2):e32311.
- Liker A, Freckleton RP, Székely T (2014) Divorce and infidelity are associated with skewed adult sex ratios in birds. *Curr Biol* 24(8):880–884.
- Rubenstein DR, Lovette IJ (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr Biol* 17(16):1414–1419.
- Gonzalez J-CT, Sheldon BC, Tobias JA (2013) Environmental stability and the evolution of cooperative breeding in hornbills. *Proc R Soc London B* 280(1768):20131297.
- Friedman NR, Remeš V (2015) Global geographic patterns of sexual size dimorphism in birds: Support for a latitudinal trend? *Ecography*, 10.1111/ecog.01531.
- Alonzo SH (2010) Social and coevolutionary feedbacks between mating and parental investment. *Trends Ecol Evol* 25(2):99–108.
- Head ML, Hinde CA, Moore AJ, Royle NJ (2014) Correlated evolution in parental care in females but not males in response to selection on paternity assurance behaviour. *Ecol Lett* 17(7):803–810.
- Dunn PO, Whittingham LA, Pitcher TE (2001) Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55(1):161–175.
- Cornwallis CK, West SA, Davis KE, Griffin AS (2010) Promiscuity and the evolutionary transition to complex societies. *Nature* 466(7309):969–972.
- Donald PF (2007) Adult sex ratios in wild bird populations. *Ibis* 149(4):671–692.
- BirdLife International and NatureServe (2011) *Bird Species Distribution Maps of the World* (BirdLife International, Cambridge, UK and NatureServe, Arlington, VA).
- Freckleton RP (2012) Fast likelihood calculations for comparative analyses. *Methods Ecol Evol* 3(5):940–947.
- R-Core-Team (2013) R: A language and environment for statistical computing. Available at: www.r-project.org/.