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The evolution of parental cooperation in birds

Short title

Parental cooperation in birds

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Abstract

Parental care is one of the most variable social behaviors and it is and 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 co-exist in a given set of ambient environment.

Significance Statement

Parents in many animal species care for their offspring. In some species males care more, in other species females care more, whereas in still other species the contribution of the sexes is equal. Yet, 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 co-exist in a given set of ambient environment.

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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 extra-pair paternity should lead to the evolution of reduced care provisioning by males (21–25). This evolutionary reduction of paternal care in species with high extra-pair 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, since 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. Since parental care is a complex trait, we compiled data on 8 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 extra-pair paternity (EPP), than in polygamous and high EPP species, respectively; 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; and iii) ambient environment: species that live in environments with harsh and variable climates exhibit high parental cooperation.

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 ($\lambda \approx 0.9$, 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 inter-specific 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, Figs. 2, 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 extra-pair paternity are consistently associated with low parental cooperation (Figs. 2, 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 predictions are supported, since 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 extra-pair paternity (Fig. 3; summarized results are available in SI Appendix, Table S2 while 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 timescales. Similarly, our results support the prediction that high rates of extra-pair paternity will lead, on a macroevolutionary timescale, 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 extra-pair paternity depending on model assumptions (45) and results of previous empirical studies are also conflicting (e.g. 22, 46–48, reviewed in 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 extra-pair paternity and parental care. The macroevolutionary response of male care to extra-pair 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, Figs. 2, 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, while 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 while 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 since 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, 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, 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 (approx. 30-35%; summary in Table 1 and details in SI Appendix, Table S1), although these values are somewhat lower for relative male care (approx. 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, 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 co-occurring 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 sexual size dimorphism in birds (34, 58–60). Taken together with our new 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, since all of these have mortality consequences and are thus linked in eco-evolutionary 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 non-avian taxa, for instance in fishes, frogs, and mammals. Whilst 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), post-fledging feeding of chicks, and post-fledging 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 re-coded 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 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, ca. 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 (ca. 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 extra-pair 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 = body mass of the heavier sex divided by body mass of the lighter sex minus one 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). Extra-pair paternity (EPP) was expressed as % of broods containing at least one extra-pair 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 extra-pair 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, http://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 (°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 years (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 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), extra-pair 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.

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Figure legends

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).

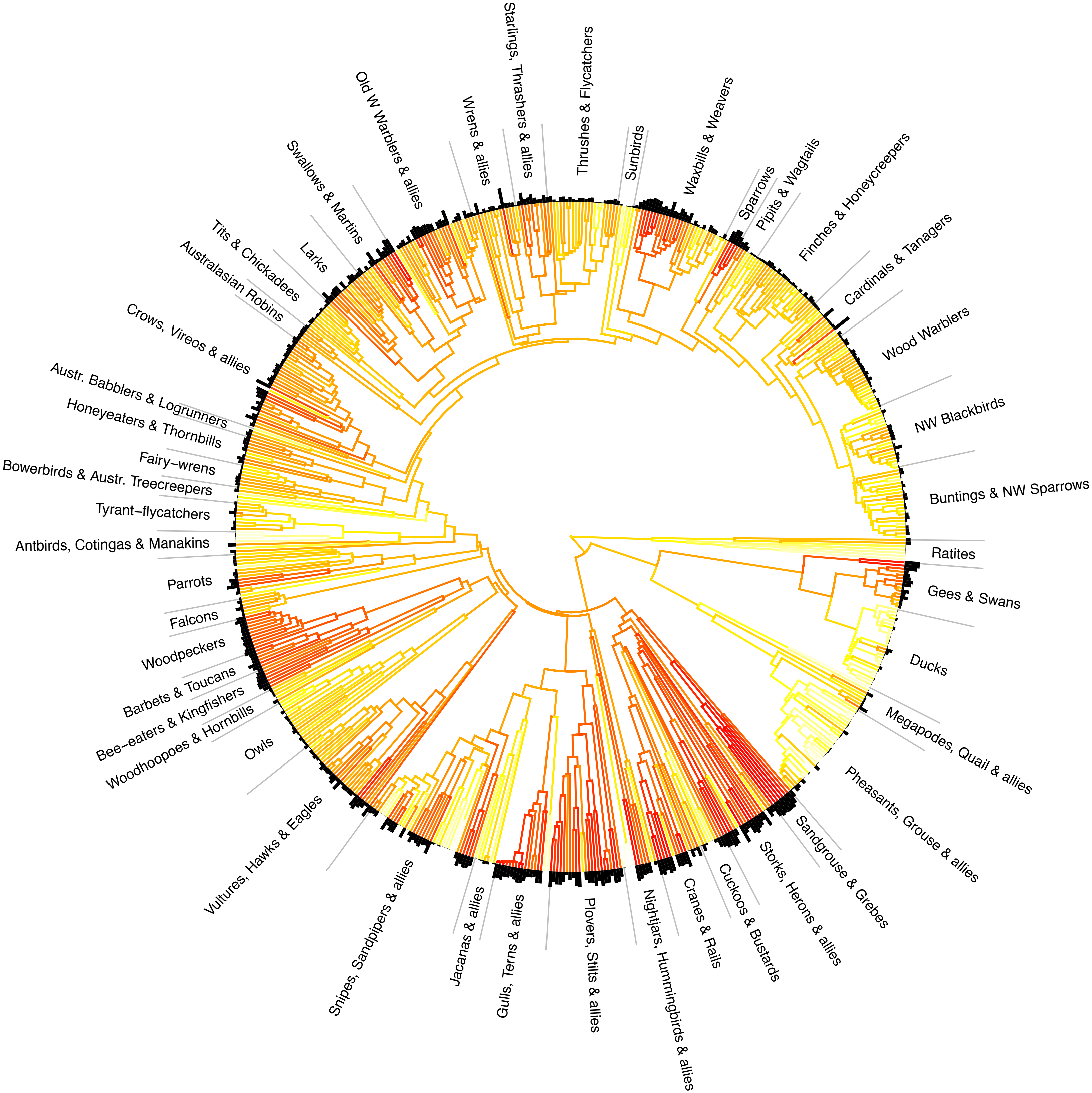
Fig. 2. Parental cooperation in relation to sexual size dimorphism (log absolute Sexual Dimorphism Index), extra-pair paternity (sqrt EPP), and adult sex ratio (sqrt ASR bias) in birds. Variables in each panel were statistically adjusted for other predictors in a phylogenetic generalized least squares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

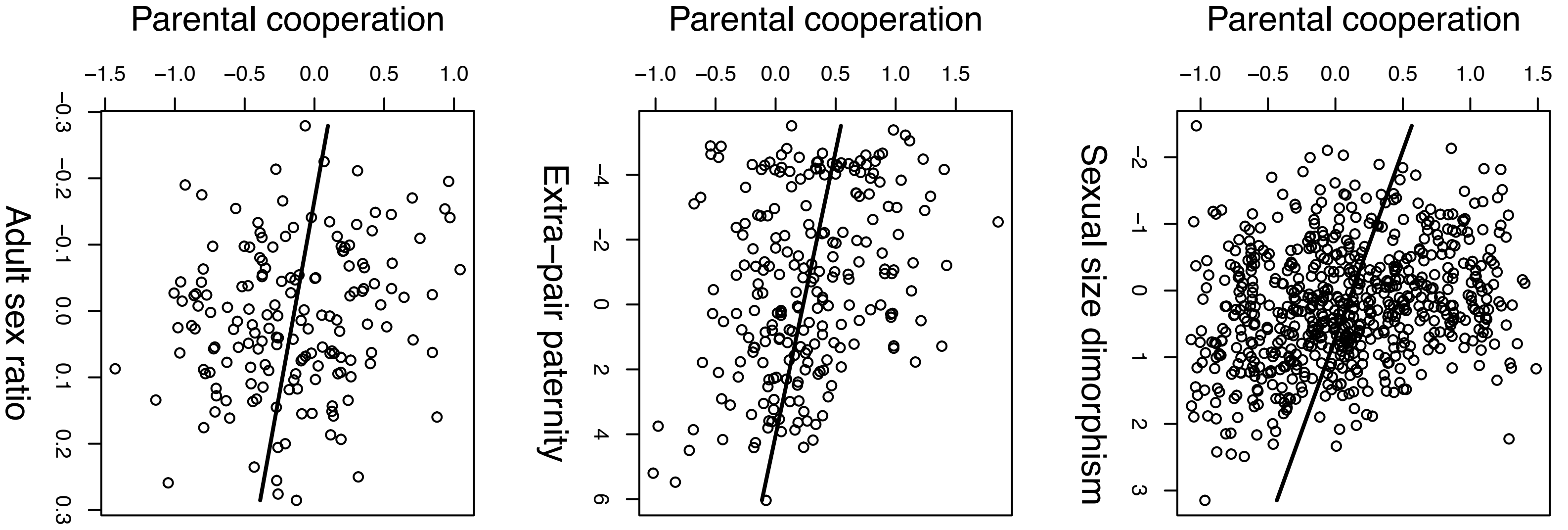
Fig. 3. Parental cooperation and relative male care (for their frequency distribution across 659 species of birds see SI Appendix, Fig. S1) in relation to sexual selection (orange), social environment (red), climate (green), and life-history traits (pink). The figure shows effect sizes (mean standardized regression coefficients ± 2SE) 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.

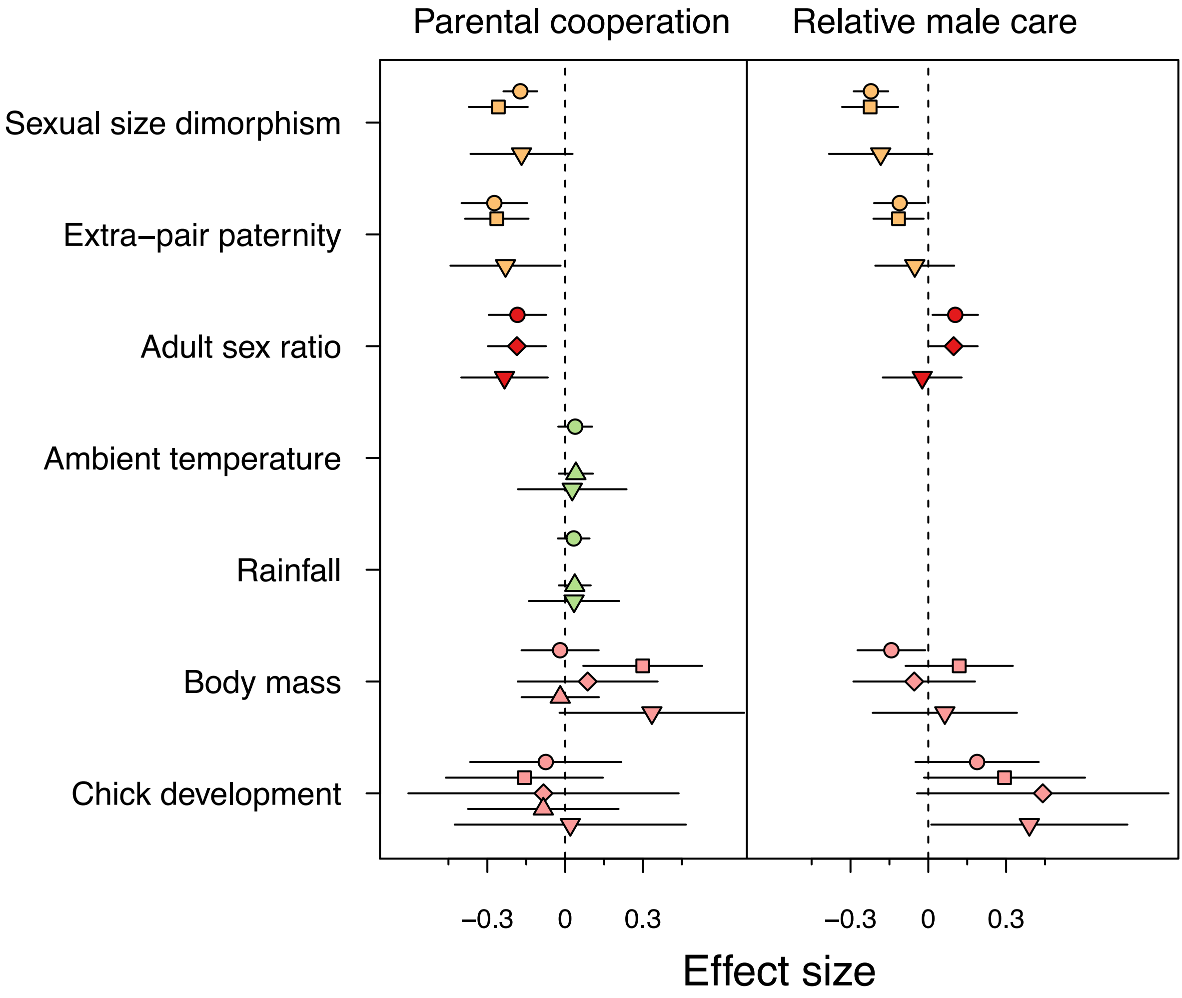
Table 1. Parental cooperation in relation to sexual selection, social environment, and climate in birds. In all models parental cooperation was the response variable and predictors included: sexual size dimorphism (log absolute Size Dimorphism Index), extra-pair paternity (sqrt EPP), adult sex ratio (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.

Model and predictors	Estimate (SE)	F (P)
Sexual selection (R^2 = 0.17, λ = 0.76, df = 4,221)		
Sexual size dimorphism	−0.258 (0.057)	20.62 (<0.001)
Extra-pair 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, λ = 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, λ = 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)
Extra-pair 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)


Ratites
Gees & Swans
Ducks
Megapodes, Quail & allies
Pheasants, Grouse & allies
Sandgrouse & Grebes
Storks, Herons & allies
Cuckoos & Bustards
Cranes & Rails
Nightjars, Hummingbirds & allies
Plovers, Stilts & allies
Gulls, Terns & allies
Jacanas & allies
Snipes, Sandpipers & allies
Vultures, Hawks & Eagles
Owls
Woodhoopoes & Hornbills
Bee−eaters & Kingfishers
Barbets & Toucans
Woodpeckers
Falcons
Parrots
Antbirds, Cotingas & Manakins
Tyrant−flycatchers
Bowerbirds & Austr. Treecreepers
Fairy−wrens
Honeyeaters & Thornbills
Austr. Babblers & Logrunners
Crows, Vireos & allies
Australasian Robins
Tits & Chickadees
Larks
Swallows & Martins
Old W Warblers & allies
Wrens & allies
Starlings, Thrashers & allies
Thrushes & Flycatchers
Sunbirds
Waxbills & Weavers
Sparrows
Pipits & Wagtails
Finches & Honeycreepers
Cardinals & Tanagers
Wood Warblers
NW Blackbirds
Buntings & NW Sparrows


Parental cooperation
−1.5
−1.0
−0.5
0.0
0.5
1.0
Adult sex ratio
−0.3
−0.2
−0.1
0.0
0.1
0.2
0.3
Parental cooperation
−1.0
−0.5
0.0
0.5
1.0
1.5
Extra−pair paternity
−4
−2
0
2
4
6
Parental cooperation
−1.0
−0.5
0.0
0.5
1.0
1.5
Sexual size dimorphism
−2
−1
0
1
2
3


Parental cooperation
Relative male care
Sexual size dimorphism
Extra−pair paternity
Adult sex ratio
Ambient temperature
Rainfall
Body mass
Chick development
−0.3
0
0.3
−0.3
0
0.3
Effect size

Supporting Information for:

The evolution of parental cooperation in birds

Authors

Vladimír Remeš, Robert P. Freckleton, Jácint Tökölyi, András Liker, Tamás Székely

Supplement S1. Full Materials and Methods.

Fig. S1. Frequency distribution of parental cooperation and relative male care in birds.

Fig. S2. Scatterplots of parental cooperation in relation to predictors as modeled by PGLS multiple regressions.

Fig. S3. Scatterplots of relative male care in relation to predictors as modeled by PGLS multiple regressions.

Fig. S4. Scatterplots of the durations of different phases of breeding cycle (nest building, egg incubation, chick care before and after fledging) in relation to adult body mass.

Fig. S5. Estimates of semivariograms and Moran's I for residuals from i) the four PGLS models of parental cooperation with EPP, and ii) the three PGLS models of relative male care with EPP.

Table S1. Full results of PGLS models of parental cooperation run across 500 phylogenies.

Table S2. Summary of results of PGLS models of relative male care.

Table S3. Full results of PGLS models of relative male care run across 500 phylogenies.

Table S4. Factor loadings of climatic variables on the first two principal components.

Supporting Information for:

The evolution of parental cooperation in birds

Authors

Vladimír Remeš, Robert P. Freckleton, Jácint Tökölyi, András Liker, Tamás Székely

Supplement S1

Full 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). Although this scoring system does not quantify absolute parental effort, it quantifies relative participation of sexes, which is the metric we were interested in here. 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), post-fledging feeding of chicks, and post-fledging guarding of chicks (i.e., guarding and defending the brood after fledging, for details see (1)). Scoring was a necessity rather than preference, since quantitative data were not available for many species. This is a common practice in comparative studies; see (2–6) for similar approaches. Our scoring was significantly repeatable (sensu (7)) between two independent observers who scored a subset of species (intraclass correlation, repeatability of mean score of all care components: $r_{ICC} = 0.79$, $F = 8.6$, $p < 0.001$, $n = 31$ species). These scores also correlate with an independent measure of care (i.e., sex differences in the length of care, see (8)). 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. Sample size differed between individual analyses, because not all traits were available for all species (see below). There were too many missing values in some of the parental activities to allow data enhancement by imputation.

To represent the extent of biparental care, the eight parental activities were re-coded 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 extent of biparental care across the eight activities. However, not all activities were available for all species (average number of activities = 4.83, SD = 1.56, n = 659 species; all activities were available only for 28 species). At the same time, means for different parental activities ranged from 0.58 for incubation to 1.69 for post-fledging feeding across species. Consequently, differences between activity-specific means could have introduced bias into the calculation of parental cooperation for every species depending on which activity happened to lack for a particular species. Therefore, before averaging across activities we centered the extent of biparental care for each activity by subtracting the mean from the original score. The resulting parental cooperation ranged from minimum parental cooperation to maximum parental cooperation (frequency distribution of parental cooperation across 659 species of birds is available in 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, ca. 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 (ca. around the value of 1.5). To test specific hypotheses that predict effects on the scale from female-biased to male-biased care, we calculated in the same way as above centered values of the original scores of sex-specific engagement in parental care. Resulting values of this 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 Fig. S1). Note that for sake of simplifying the analyses, we worked with the ordinal scores as if they were continuous variables (for the necessity to work with ordinal scores see above).

We used two proxies of sexual selection that are widely available: sexual size dimorphism and extra-pair paternity (9). We calculated size dimorphism index as SDI = body mass of the heavier sex divided by body mass of the lighter sex minus one 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 value of the absolute SDI thus means greater difference in body masses between sexes, suggesting differential selection acting on males and females that may indicate sexual selection (10, 11). Indeed, when we quantified percentage of polygamous pairings of males and females and calculated absolute difference between the sexes, this difference correlated positively with absolute SDI (r = 0.28, n = 496 species). This showed that extensive sexual size dimorphism was correlated with divergent mating strategies of the two sexes indicating strong sexual selection. Extra-pair paternity was expressed as % of broods containing at least one extra-pair offspring (EPP), in accordance with recent studies (12). However, to check the sensitivity of our analyses to this particular choice, we also repeated all analyses with % of extra-pair offspring in the population (EPY). Although this variable dramatically decreased sample size, results were robust to the choice of EPP vs. EPY (details of these sensitivity analyses are available in Tables S1 and S2). This is probably not surprising, as evolutionary correlation between EPP and EPY was 0.92.

Social environment was characterized by adult sex ratio (ASR), which was expressed as the proportion of males in the adult population (13, 14). 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 (15) and global climatic layers (CRU Dataset, http://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 (˚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 years (1961-2009) of monthly averages for temperature and rainfall during the species' breeding season. Rainfall was log-transformed prior to all calculations. We excluded seabirds from all the analyses, as climatic variables do not affect their food supply in the same way as in terrestrial birds (Procellariiformes, Sphenisciformes, Alcidae, Fregatidae, Sulidae, Pelecanidae, some Sternidae, Laridae, Stercorariidae, and Phalacrocoracidae).

To control for potential confounds, we included the following life-history traits in the models. For every species in our dataset, we obtained estimates of body mass of males and females (g) and used their average, and chick development (altricial vs. precocial). Body mass captures many aspects of species’ life history, including adult mortality (16), and thus pair bond duration and divorce rate (17, 18). Demanding chicks (i.e. altricial) preclude the evolution of reduced parental care (19–21). In a previous study of shorebirds, species with less demanding (i.e. precocial) young exhibited uniparental care with higher probability than species with more demanding (i.e. semiprecocial) young (20). Thus, chick development could influence parental cooperation by setting overall offspring demand. Since the length of breeding cycle might influence parental cooperation (22), we also recorded durations of breeding cycle phases (nest building, incubation, chick feeding, post-fledging care). However, we were able to find durations of all four phases only for 214 out of our 659 species. All these durations correlated well with body mass (for the relationship of breeding cycle duration to adult body mass in our dataset see Fig. S4) and thus to avoid decreasing the sample size, we modeled only adult body mass.

Phylogenetic analyses

We used phylogenetic generalized least squares (PGLS) approach implemented in a fast likelihood algorithm (23) in the R language (24). In PGLS models, we estimated the phylogenetic signal by optimizing the λ parameter (25). We used 500 phylogenetic trees extracted from www.birdtree.org (Hackett constraint, (26)). We ran the PGLS analyses across all the trees and then summarized the resulting 500 parameter estimates. In Table 1 in the main text, we present average values of parameters and test statistics, whereas in this Supporting Information we also present their 95% CIs. The non-random distribution of species ranges across the globe could potentially introduce spatial autocorrelation, therefore we checked for spatial autocorrelations in residuals from our models by i) fitting semi-variograms and ii) estimating Moran's I based on the latitude and longitude of the centroid of each species' range. Indeed, there was no indication of significant spatial autocorrelation in residuals from our models (Fig. S5).

Parental cooperation and relative male care were the main response variable in our models. First, we fitted bivariate PGLS models between parental cooperation and the following predictors: sexual size dimorphism (log absolute SDI), extra-pair 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 reduce the number of predictors in these multiple regression models, we performed a Principal Components Analysis on all six climatic variables and extracted the first two PCs, which represented temperature (PC.temperature: higher values mean hot environments with low temperature variability) and rainfall (PC.rainfall: higher values mean dry environments with high rainfall variability), respectively (Table S4). These two axes explained 76.4% of variation in climatic variables. We used these PCs as predictors in multiple PGLS regression models to reduce multicollinearity of predictors.

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 – PC.temperature, PC.rainfall, adult body mass, chick development (n = 659 species); Full model – absolute SDI, EPP, ASR bias, PC.temperature, PC.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.

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Fig. S1. Frequency distribution of parental cooperation and relative male care in birds (n = 659 species). Parental cooperation varies between 1.5 when the male and the female parent share care provisioning approximately equally and −1.5 when only one parent (the male or the female) provides all care, with most species clustered around 0 when the share of the two sexes is roughly 2:1. Relative male care varies from strongly female-biased (ca. −2) to strongly male-biased (ca. 3). The bottom panel shows graphically how relative male care was recoded to express parental cooperation. Note that the scales of both parental cooperation and relative male care are arbitrary and based on our system of scoring (Supplement S1).

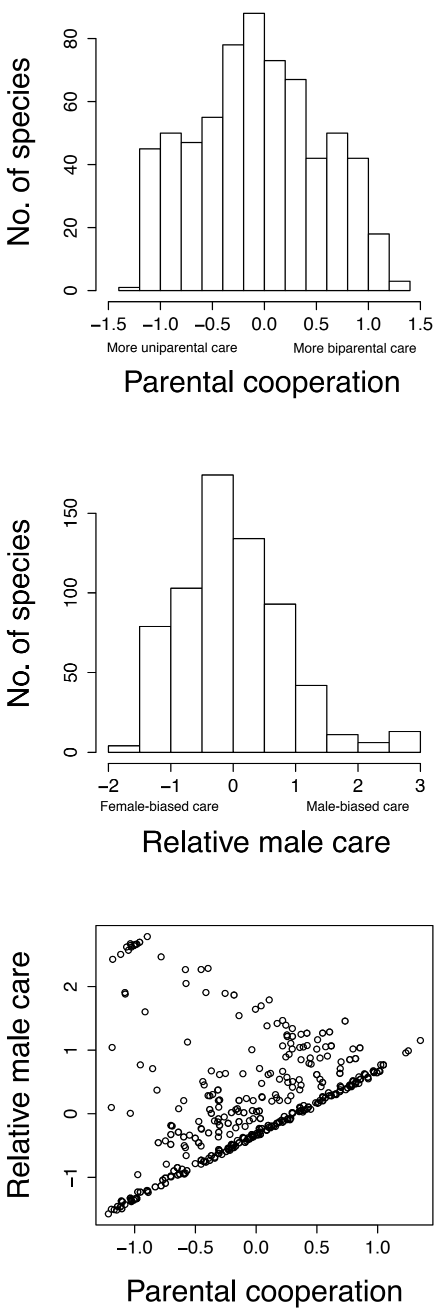


Fig. S2. Parental cooperation in relation to predictors (see Table 1): sexual size dimorphism ($\log_{10}$-transformed absolute Sexual Dimorphism Index), extra-pair paternity (square-root transformed EPP), adult sex ratio (square-root transformed ASR bias), ambient temperature (PC1 from PCA on climatic variables, factor loadings available in Table S4), rainfall (PC2 from PCA on climatic variables, factor loadings available in Table S4), body mass ($\log_{10}$-transformed adult body mass), and chick development (categorical variable coded as altricial vs. precocial). Raw data and a lowess smoother line are depicted.

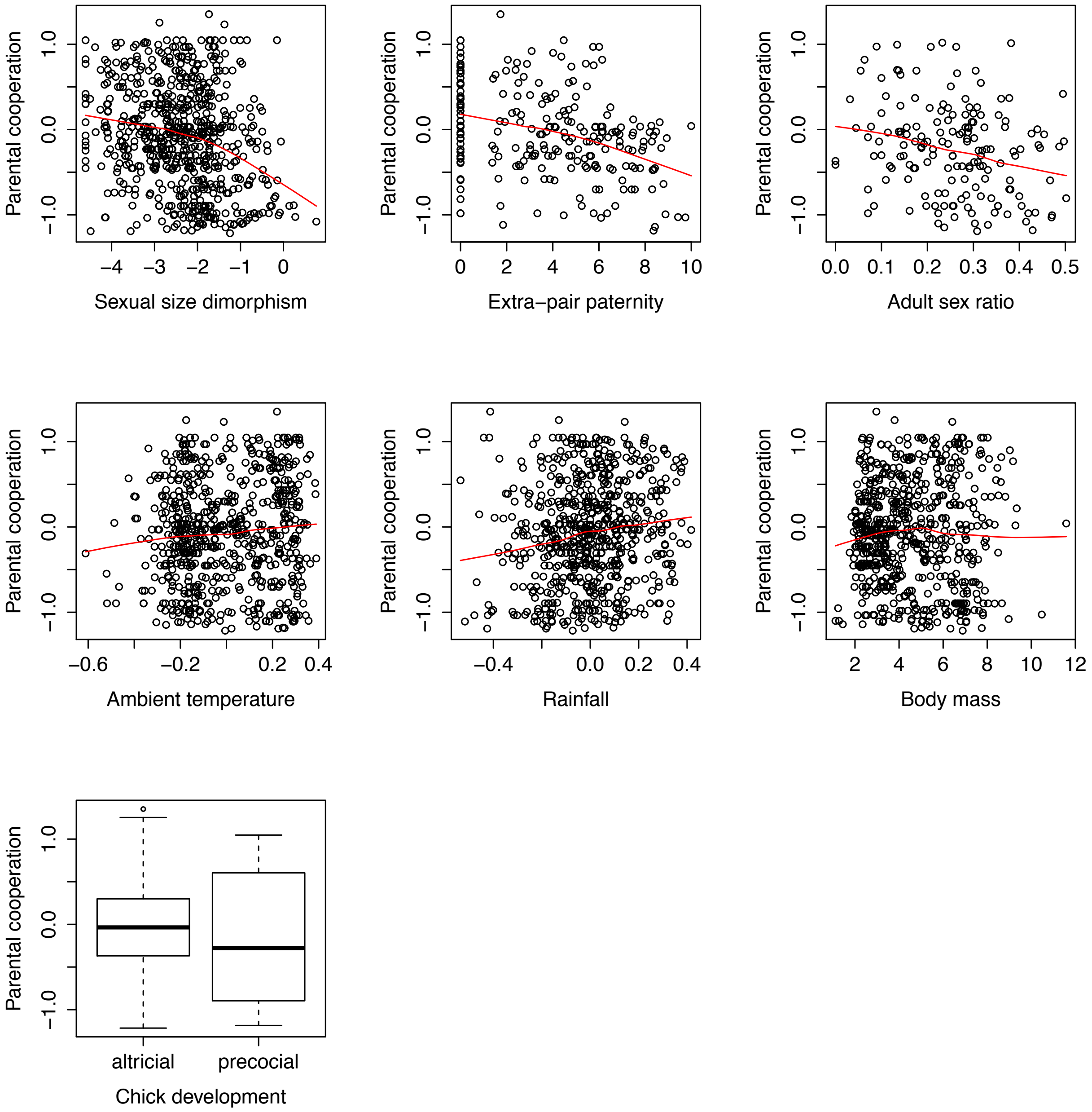


Fig. S3. Relative male care in relation to predictors (see Table S2): sexual size dimorphism (Sexual Dimorphism Index), extra-pair paternity (square-root transformed EPP), adult sex ratio (ASR), body mass ($\log_{10}$- transformed adult body mass), and chick development (categorical variable coded as altricial vs. precocial). Raw data and a lowess smoother line are depicted. An extreme value of Sexual Dimorphism Index = 2.14 (Great Bustard *Otis tarda*) is excluded from the first panel.

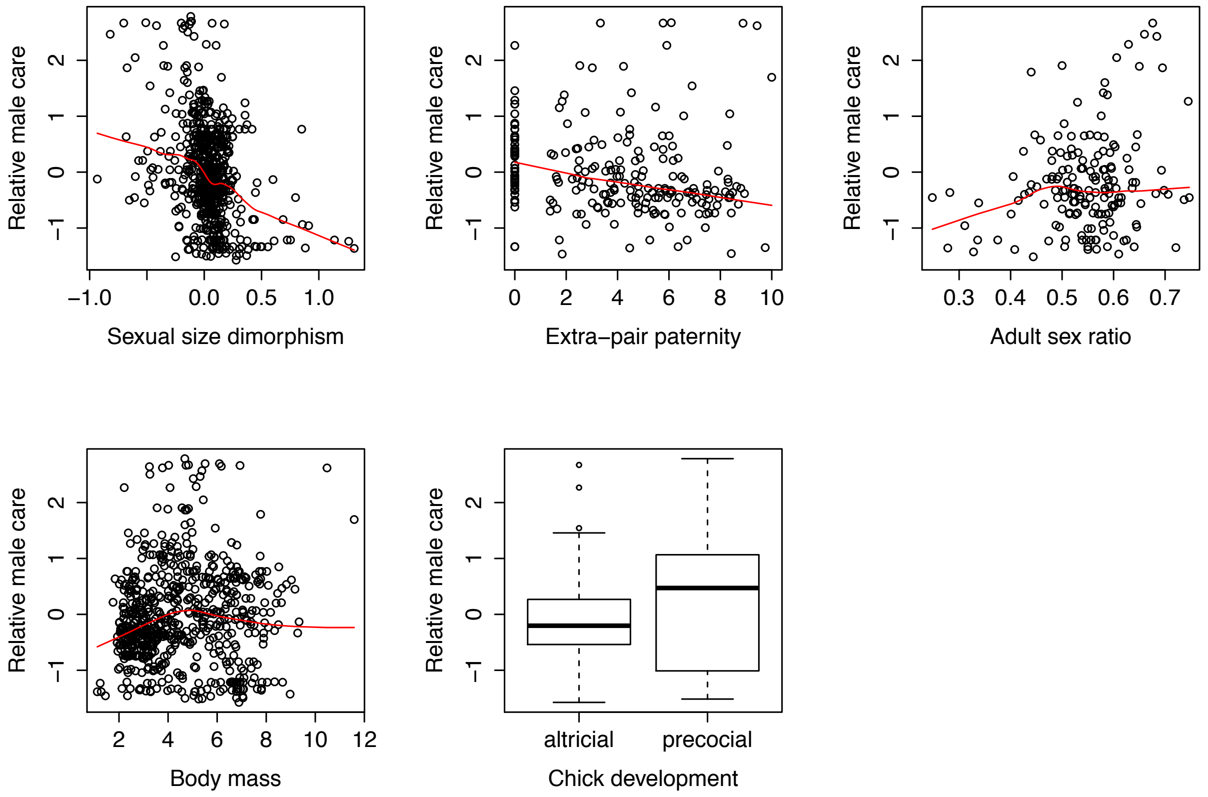


Fig. S4. Durations of different phases of breeding cycle (nest building, egg incubation, chick care before fledging, post-fledging care, and total duration of the whole breeding cycle) in relation to adult body mass (n = 199-214 species depending on the phase of breeding cycle). All variables $\log_{10}$-transformed. All correlations were significant at $p < 0.001$.

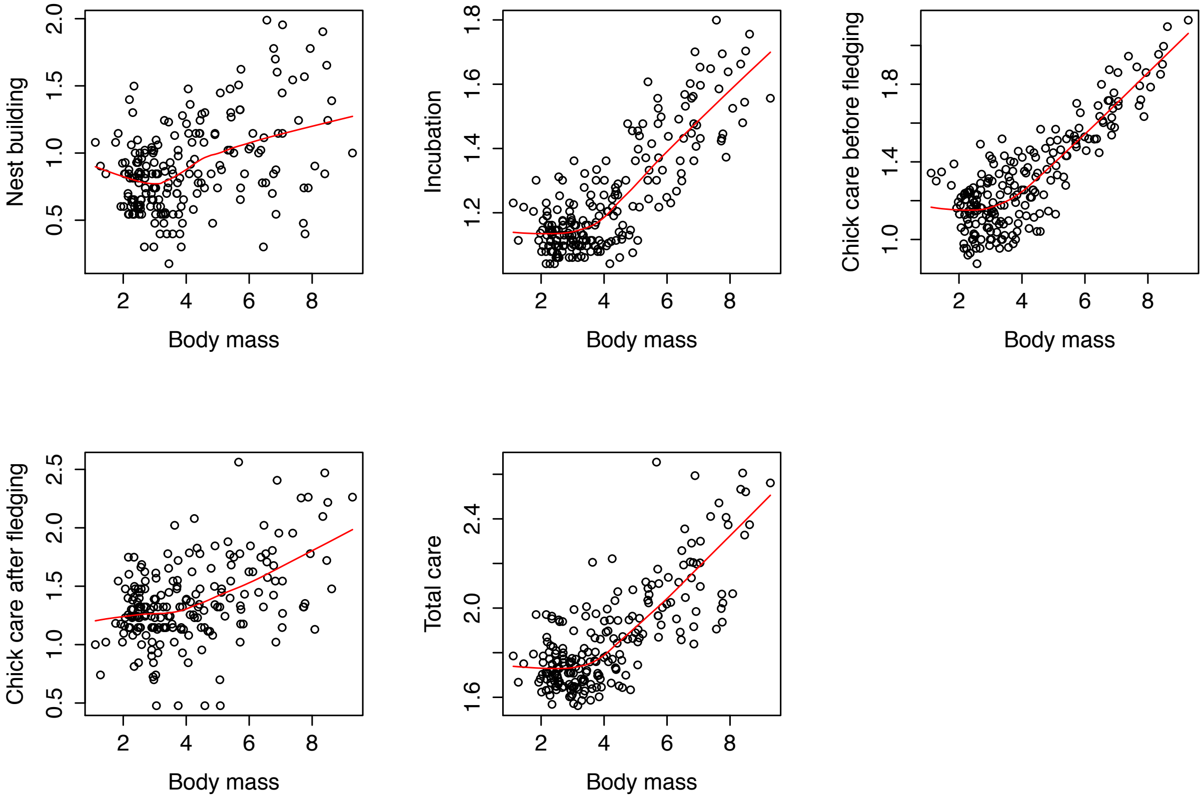
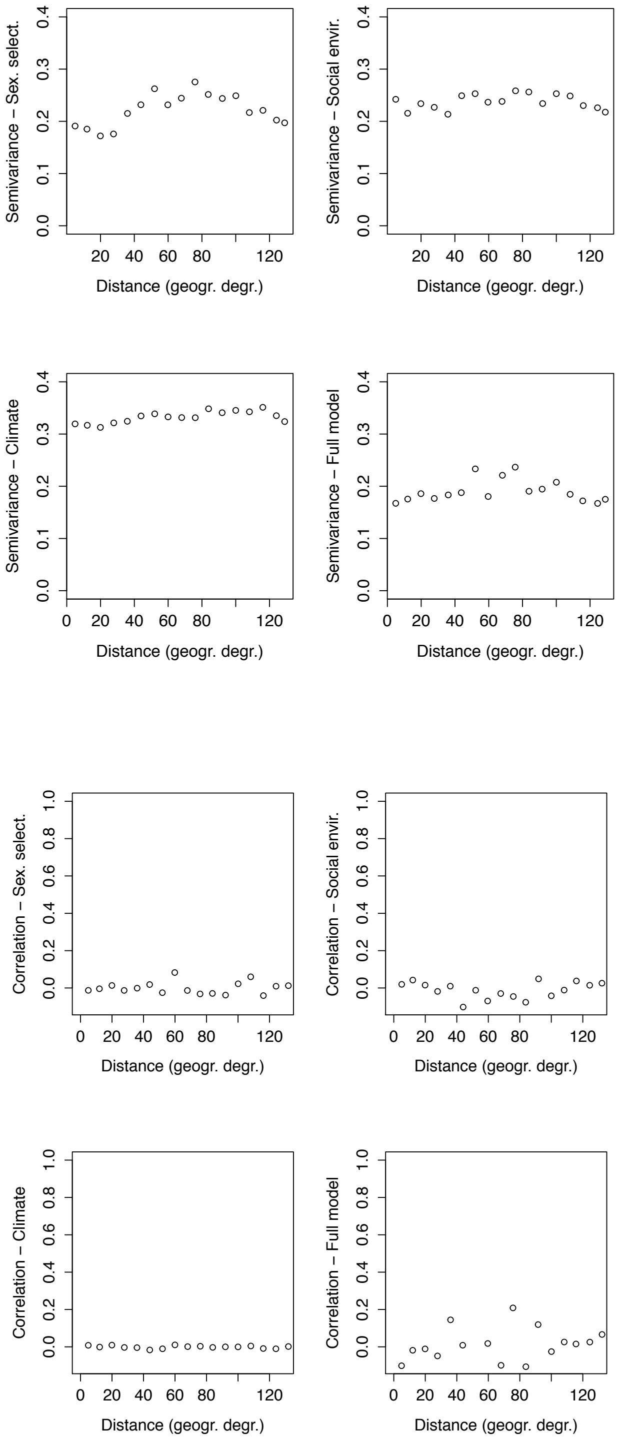


Fig. S5

Estimates of semivariograms and Moran's I for residuals from the four PGLS models of **parental cooperation** with EPP. Distance is expressed in geographic degrees. All the estimates indicate lack of spatial autocorrelations in residuals.



Estimates of semivariograms and Moran's I for residuals from the three PGLS models of **relative male care** with EPP. Distance is expressed in geographic degrees. All the estimates indicate lack of spatial autocorrelations in residuals. Note that the climatic model was not fit for relative male care.

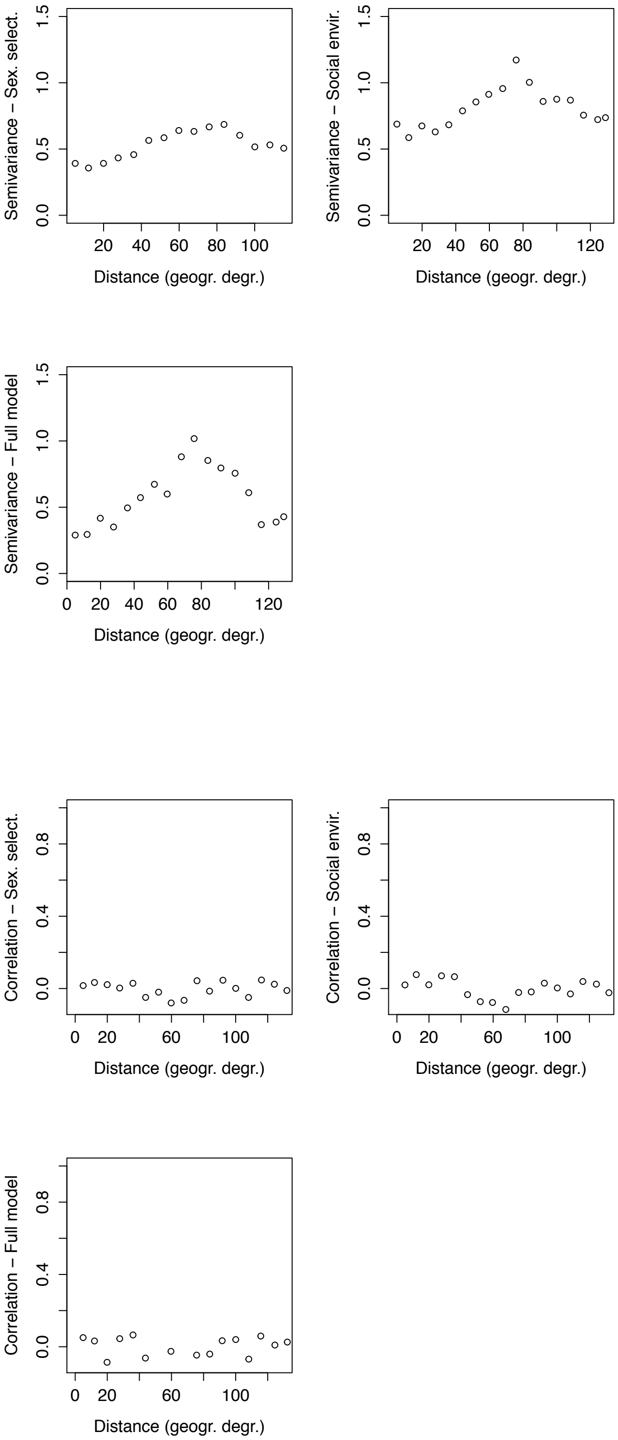


Table S1. Full results of PGLS models of **parental cooperation** run across 500 phylogenies

PGLS bivariate models

	Coef			SE			Stand Coef			Stand Coef SE			F			p			Rsq			lambda			DF	
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
Body mass (log)	-0.006	-0.014	0.001	0.024	0.024	0.025	-0.020	-0.043	0.004	0.074	0.073	0.075	0.09	0.00	0.33	0.790	0.566	0.980	0.000	0.000	0.001	0.902	0.875	0.923	1	657
Chick development	-0.101	-0.145	-0.058	0.196	0.185	0.205	-0.075	-0.108	-0.043	0.146	0.138	0.153	0.28	0.09	0.56	0.609	0.454	0.767	0.000	0.000	0.001	0.901	0.874	0.922	1	657
Absolute SDI (log)	-0.105	-0.111	-0.098	0.020	0.019	0.020	-0.173	-0.183	-0.162	0.033	0.032	0.033	28.12	24.81	31.34	0.000	0.000	0.000	0.041	0.036	0.046	0.881	0.854	0.904	1	657
EPP (sqrt)	-0.049	-0.051	-0.047	0.011	0.011	0.012	-0.273	-0.284	-0.262	0.063	0.062	0.065	18.68	16.92	20.43	0.000	0.000	0.000	0.077	0.070	0.084	0.813	0.767	0.852	1	224
EPY (sqrt)	-0.064	-0.067	-0.061	0.020	0.020	0.020	-0.289	-0.303	-0.274	0.090	0.089	0.091	10.306	9.279	11.401	0.002	0.001	0.003	0.083	0.075	0.091	0.817	0.788	0.845	1	114
ASR bias (sqrt)	-0.876	-0.916	-0.835	0.264	0.258	0.270	-0.184	-0.192	-0.175	0.055	0.054	0.057	11.03	9.79	12.26	0.001	0.001	0.002	0.063	0.057	0.070	0.907	0.890	0.922	1	163
PC.temperature	0.113	0.088	0.139	0.096	0.093	0.098	0.039	0.030	0.047	0.033	0.032	0.033	1.41	0.85	2.09	0.242	0.148	0.356	0.002	0.001	0.003	0.901	0.875	0.922	1	657
PC.rainfall	0.114	0.086	0.142	0.106	0.104	0.108	0.033	0.025	0.041	0.031	0.030	0.031	1.19	0.67	1.80	0.284	0.181	0.413	0.002	0.001	0.003	0.899	0.871	0.921	1	657
Temp mean	0.003	0.002	0.004	0.003	0.003	0.003	0.031	0.022	0.039	0.033	0.032	0.034	0.88	0.45	1.34	0.355	0.248	0.502	0.001	0.001	0.002	0.901	0.874	0.922	1	657
Temp var among	-0.052	-0.065	-0.040	0.049	0.048	0.050	-0.033	-0.040	-0.025	0.031	0.030	0.032	1.15	0.67	1.71	0.291	0.191	0.414	0.002	0.001	0.003	0.903	0.877	0.924	1	657
Temp var within	0.010	0.003	0.018	0.031	0.030	0.032	0.009	0.003	0.017	0.029	0.029	0.030	0.11	0.01	0.33	0.758	0.567	0.923	0.000	0.000	0.000	0.901	0.874	0.922	1	657
Prec mean	-0.074	-0.090	-0.059	0.059	0.058	0.060	-0.038	-0.046	-0.030	0.030	0.029	0.031	1.58	0.99	2.29	0.216	0.131	0.320	0.002	0.002	0.003	0.899	0.872	0.921	1	657
Prec var among	0.400	0.323	0.481	0.286	0.280	0.292	0.045	0.036	0.054	0.032	0.032	0.033	1.97	1.29	2.77	0.167	0.096	0.257	0.003	0.002	0.004	0.900	0.873	0.921	1	657
Prec var within	0.107	0.069	0.141	0.120	0.118	0.122	0.029	0.019	0.038	0.032	0.032	0.033	0.81	0.34	1.37	0.380	0.242	0.562	0.001	0.001	0.002	0.900	0.872	0.921	1	657

PGLS multiple regression models

Sexual selection model with EPP (% of nests with at least one extra-pair young)

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Absolute SDI (log)	-0.136	-0.143	-0.130	0.030	0.029	0.031	-0.258	-0.270	-0.247	0.057	0.056	0.058
EPP (sqrt)	-0.047	-0.049	-0.046	0.011	0.011	0.011	-0.264	-0.272	-0.254	0.061	0.060	0.062
Body mass (log)	0.083	0.074	0.093	0.032	0.031	0.032	0.299	0.269	0.339	0.115	0.113	0.116
Chick development	-0.204	-0.277	-0.135	0.197	0.188	0.205	-0.157	-0.213	-0.104	0.151	0.145	0.158

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
20.62	19.21	21.96	0.000	0.000	0.000	0.168	0.161	0.174	0.762	0.718	0.801	4	221
18.55	16.92	20.08	0.000	0.000	0.000								
6.83	5.45	8.81	0.011	0.003	0.021								
1.12	0.46	2.04	0.308	0.154	0.498								

Sexual selection model with EPY (% of extra-pair young in the population)

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Absolute SDI (log)	-0.182	-0.189	-0.175	0.044	0.044	0.045	-0.329	-0.341	-0.317	0.080	0.079	0.081
EPY (sqrt)	-0.059	-0.062	-0.057	0.020	0.019	0.020	-0.268	-0.280	-0.256	0.089	0.088	0.090
Body mass (log)	0.067	0.060	0.075	0.042	0.042	0.043	0.239	0.213	0.265	0.151	0.148	0.153
Chick development	-0.180	-0.241	-0.117	0.197	0.191	0.204	-0.141	-0.188	-0.092	0.154	0.149	0.159

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
16.92	15.76	18.01	0.000	0.000	0.000	0.217	0.207	0.227	0.726	0.694	0.755	4	111
9.06	8.22	9.86	0.003	0.002	0.005								
2.53	2.00	3.12	0.117	0.080	0.160								
0.86	0.35	1.54	0.369	0.218	0.554								

Social environment model

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
ASR bias (sqrt)	-0.886	-0.926	-0.846	0.267	0.260	0.273	-0.186	-0.194	-0.178	0.056	0.055	0.057
Body mass (log)	0.024	0.015	0.034	0.037	0.037	0.038	0.087	0.055	0.122	0.135	0.132	0.137
Chick development	-0.094	-0.162	-0.028	0.295	0.279	0.310	-0.084	-0.144	-0.025	0.261	0.247	0.274

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
11.05	9.90	12.24	0.001	0.001	0.002	0.066	0.060	0.073	0.905	0.888	0.922	3	161
0.43	0.17	0.82	0.524	0.368	0.682								
0.12	0.01	0.31	0.750	0.577	0.925								

Climate model

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
PC.temperature	0.121	0.095	0.147	0.096	0.094	0.098	0.041	0.032	0.050	0.033	0.032	0.034
PC.rainfall	0.128	0.101	0.157	0.107	0.104	0.109	0.037	0.029	0.045	0.031	0.030	0.031
Body mass (log)	-0.006	-0.014	0.001	0.024	0.024	0.025	-0.019	-0.042	0.004	0.074	0.073	0.076
Chick development	-0.113	-0.157	-0.067	0.195	0.184	0.204	-0.084	-0.117	-0.050	0.145	0.137	0.152

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
1.60	0.99	2.33	0.214	0.127	0.320	0.005	0.003	0.006	0.898	0.870	0.920	4	654
1.47	0.90	2.16	0.233	0.142	0.344								
0.09	0.00	0.33	0.795	0.568	0.980								
0.35	0.12	0.69	0.564	0.407	0.729								

Full model with EPP (% of nests with at least one extra-pair young)

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Absolute SDI (log)	-0.080	-0.090	-0.072	0.047	0.045	0.048	-0.168	-0.189	-0.151	0.098	0.095	0.102
EPP (sqrt)	-0.042	-0.044	-0.039	0.019	0.019	0.020	-0.230	-0.244	-0.214	0.106	0.104	0.108
ASR bias (sqrt)	-0.943	-1.004	-0.883	0.336	0.326	0.346	-0.234	-0.249	-0.219	0.083	0.081	0.086
PC.temperature	0.070	0.030	0.115	0.270	0.265	0.275	0.027	0.012	0.044	0.105	0.103	0.107
PC.rainfall	0.096	0.062	0.131	0.244	0.238	0.250	0.034	0.022	0.047	0.087	0.085	0.089
Body mass (log)	0.088	0.080	0.097	0.047	0.046	0.048	0.334	0.301	0.366	0.178	0.175	0.181
Chick development	0.021	-0.040	0.082	0.238	0.227	0.248	0.020	-0.037	0.077	0.223	0.212	0.233

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
2.93	2.46	3.53	0.093	0.064	0.121	0.291	0.278	0.305	0.817	0.759	0.865	7	72
4.70	4.07	5.41	0.034	0.023	0.047								
7.88	6.90	8.80	0.007	0.004	0.011								
0.08	0.01	0.18	0.796	0.675	0.910								
0.16	0.06	0.30	0.696	0.583	0.802								
3.54	2.81	4.30	0.066	0.042	0.098								
0.03	0.00	0.12	0.900	0.732	0.994								

Full model with EPY (% of extra-pair young in the population)

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Absolute SDI (log)	-0.142	-0.156	-0.131	0.075	0.063	0.078	-0.281	-0.308	-0.259	0.148	0.124	0.155
EPY (sqrt)	-0.023	-0.031	0.013	0.033	0.027	0.034	-0.105	-0.143	0.059	0.150	0.124	0.157
ASR bias (sqrt)	-0.901	-0.982	-0.725	0.580	0.543	0.595	-0.211	-0.230	-0.170	0.136	0.127	0.139
PC.temperature	0.820	0.722	1.171	0.475	0.466	0.485	0.256	0.225	0.366	0.148	0.145	0.151
PC.rainfall	0.225	0.178	0.386	0.423	0.392	0.438	0.069	0.055	0.119	0.131	0.121	0.135
Body mass (log)	0.045	0.031	0.090	0.066	0.062	0.068	0.163	0.112	0.326	0.241	0.224	0.246
Chick development	0.122	0.065	0.207	0.277	0.260	0.340	0.120	0.063	0.203	0.271	0.255	0.333

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
3.64	3.10	5.66	0.067	0.023	0.087	0.350	0.316	0.602	0.764	0.662	1	7	35
0.62	0.04	0.85	0.455	0.362	0.835								
2.42	1.71	2.91	0.131	0.097	0.200								
3.04	2.36	5.98	0.101	0.020	0.134								
0.31	0.17	0.94	0.600	0.338	0.685								
0.53	0.21	2.07	0.513	0.159	0.649								
0.20	0.06	0.40	0.666	0.533	0.810								

Table S2. Relative male care in relation to sexual selection and social environment in birds. In all models relative male care was the response variable and predictors included: sexual size dimorphism (Size Dimorphism Index), extra-pair paternity (sqrt EPP), adult sex ratio (ASR), body mass (log-transformed), and chick development (altricial vs. precocial). Climatic variables were not fitted due to the lack of specific predictions. We use phylogenetic generalized least squares approach and present means from 500 analyses using different phylogenetic trees (see detailed statistical results in SI Appendix, Table S3). Estimates are standardized regression coefficients and λ indicates the strength of the phylogenetic signal in the analyses.

Model and predictors	Estimate (SE)	F (P)
Sexual selection (R^2 = 0.11, λ = 0.91, df = 4,221)		
Sexual size dimorphism	−0.224 (0.054)	17.25 (<0.001)
Extra-pair paternity	−0.115 (0.048)	5.64 (0.019)
Body mass	0.119 (0.103)	1.35 (0.257)
Chick development	0.294 (0.155)	3.61 (0.062)
Social environment (R^2 = 0.05, λ = 0.97, df = 3,161)		
Adult sex ratio	0.098 (0.046)	4.47 (0.039)
Body mass	−0.054 (0.117)	0.23 (0.645)
Chick development	0.441 (0.242)	3.34 (0.072)
Climate		
Not fitted		
Full model (R^2 = 0.12, λ = 0.88, df = 5,74)		
Sexual size dimorphism	−0.184 (0.100)	3.40 (0.070)
Extra-pair paternity	−0.052 (0.076)	0.48 (0.496)
Adult sex ratio	−0.024 (0.076)	0.12 (0.760)
Body mass	0.064 (0.139)	0.22 (0.650)
Chick development	0.390 (0.189)	4.28 (0.045)

Table S3. Full results of PGLS models of **relative male care** run across 500 phylogenies

PGLS bivariate models

	Coef			SE			Stand Coef			Stand Coef SE			F			p			Rsq			lambda			DF	
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
SDI	-0.824	-0.857	-0.786	0.124	0.122	0.127	-0.221	-0.230	-0.211	0.033	0.033	0.034	43.97	40.80	47.08	0.000	0.000	0.000	0.063	0.058	0.067	0.815	0.775	0.853	1	657
EPP (sqrt)	-0.031	-0.034	-0.027	0.014	0.013	0.014	-0.110	-0.124	-0.096	0.049	0.048	0.051	5.01	3.80	6.20	0.028	0.014	0.052	0.022	0.017	0.027	0.933	0.913	0.950	1	224
EPY (sqrt)	-0.047	-0.053	-0.040	0.024	0.024	0.025	-0.140	-0.160	-0.120	0.073	0.071	0.075	3.669	2.662	4.821	0.061	0.030	0.106	0.031	0.023	0.041	0.930	0.910	0.947	1	114
ASR	1.022	0.849	1.200	0.432	0.406	0.461	0.104	0.086	0.122	0.044	0.041	0.047	5.63	4.12	7.34	0.021	0.007	0.044	0.033	0.025	0.043	0.970	0.935	0.986	1	163
Body mass (log)	-0.066	-0.074	-0.056	0.030	0.030	0.031	-0.143	-0.161	-0.122	0.065	0.064	0.066	4.78	3.50	6.03	0.031	0.014	0.062	0.007	0.005	0.009	0.837	0.800	0.874	1	657
Chick development	0.358	0.298	0.421	0.226	0.213	0.239	0.188	0.156	0.221	0.119	0.112	0.126	2.53	1.70	3.55	0.118	0.060	0.193	0.004	0.003	0.005	0.828	0.789	0.867	1	657

Climatic variables were not fitted due to the lack of specific predictions

PGLS multiple regression models

Sexual selection model with EPP (% of nests with at least one extra-pair young)

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
SDI	-0.970	-1.054	-0.891	0.234	0.228	0.238	-0.224	-0.244	-0.206	0.054	0.053	0.055
EPP (sqrt)	-0.032	-0.035	-0.028	0.013	0.013	0.014	-0.115	-0.126	-0.102	0.048	0.047	0.050
Body mass (log)	0.051	0.038	0.068	0.044	0.043	0.045	0.119	0.090	0.159	0.103	0.102	0.105
Chick development	0.590	0.507	0.663	0.311	0.297	0.326	0.294	0.253	0.330	0.155	0.148	0.163

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
17.25	14.53	20.17	0.000	0.000	0.000	0.106	0.095	0.118	0.914	0.892	0.935	4	221
5.64	4.46	6.73	0.019	0.010	0.036								
1.35	0.76	2.36	0.257	0.126	0.385								
3.61	2.62	4.58	0.062	0.034	0.107								

Sexual selection model with EPY (% of extra-pair young in the population)

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
SDI	-0.954	-1.041	-0.866	0.410	0.400	0.420	-0.182	-0.199	-0.165	0.078	0.076	0.080
EPY (sqrt)	-0.043	-0.049	-0.037	0.025	0.025	0.026	-0.129	-0.146	-0.112	0.076	0.075	0.078
Body mass (log)	0.029	0.020	0.039	0.062	0.061	0.063	0.069	0.046	0.093	0.146	0.144	0.149
Chick development	0.480	0.415	0.547	0.312	0.299	0.326	0.249	0.216	0.284	0.162	0.155	0.169

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
5.42	4.55	6.31	0.023	0.013	0.035	0.091	0.083	0.100	0.892	0.864	0.915	4	111
2.86	2.13	3.68	0.097	0.058	0.148								
0.23	0.10	0.40	0.641	0.528	0.754								
2.38	1.74	3.14	0.129	0.079	0.190								

Social environment model

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
ASR	0.960	0.782	1.145	0.456	0.428	0.486	0.098	0.080	0.116	0.046	0.044	0.049
Body mass (log)	-0.024	-0.036	-0.013	0.052	0.051	0.054	-0.054	-0.080	-0.029	0.117	0.114	0.120
Chick development	0.804	0.737	0.886	0.441	0.404	0.474	0.441	0.404	0.487	0.242	0.222	0.260

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
4.47	3.16	6.05	0.039	0.015	0.077	0.053	0.044	0.064	0.966	0.927	0.986	3	161
0.23	0.06	0.46	0.645	0.501	0.804								
3.34	2.69	4.44	0.072	0.037	0.103								

Climate model

There is no climate model due to the lack of specific predictions

Full model with EPP (% of nests with at least one extra-pair young)
Full model does not include climate due to the lack of specific predictions.

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
SDI	-0.689	-0.753	-0.628	0.374	0.362	0.386	-0.184	-0.201	-0.167	0.100	0.097	0.103
EPP (sqrt)	-0.015	-0.019	-0.012	0.022	0.022	0.023	-0.052	-0.066	-0.039	0.076	0.074	0.078
ASR	-0.215	-0.403	-0.021	0.693	0.673	0.713	-0.024	-0.044	-0.002	0.076	0.074	0.078
Body mass (log)	0.027	0.015	0.041	0.060	0.059	0.061	0.064	0.035	0.096	0.139	0.136	0.142
Chick development	0.677	0.588	0.769	0.328	0.313	0.343	0.390	0.339	0.443	0.189	0.180	0.197

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
3.401	2.766	4.038	0.070	0.048	0.101	0.119	0.102	0.136	0.881	0.845	0.914	5	74
0.480	0.273	0.734	0.496	0.394	0.603								
0.116	0.001	0.326	0.760	0.570	0.970								
0.222	0.063	0.476	0.650	0.492	0.803								
4.279	3.171	5.692	0.045	0.020	0.079								

Full model with EPY (% of extra-pair young in the population)
Full model does not include climate due to the lack of specific predictions.

	Coef			SE			Stand Coef			Stand Coef SE		
Predictors	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
SDI	-1.578	-1.658	-1.487	0.618	0.609	0.628	-0.317	-0.332	-0.298	0.124	0.122	0.126
EPY (sqrt)	-0.018	-0.022	-0.014	0.041	0.040	0.042	-0.049	-0.060	-0.037	0.111	0.108	0.114
ASR	-0.650	-0.778	-0.526	1.086	1.060	1.111	-0.062	-0.074	-0.050	0.103	0.101	0.106
Body mass (log)	0.011	0.000	0.023	0.085	0.083	0.087	0.023	-0.001	0.049	0.182	0.178	0.185
Chick development	0.627	0.558	0.704	0.326	0.313	0.338	0.361	0.321	0.405	0.187	0.180	0.195

F			p			Rsq			lambda			DF	
Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	DF model	DF residual
6.52	5.85	7.15	0.015	0.011	0.021	0.261	0.237	0.282	0.796	0.744	0.837	5	37
0.20	0.11	0.29	0.664	0.591	0.740								
0.36	0.23	0.53	0.554	0.473	0.635								
0.02	0.00	0.07	0.897	0.790	0.995								
3.72	2.86	4.78	0.064	0.035	0.099								

Table S4. Factor loadings of climatic variables on the first two principal components. These two axes explained 76.4% of variation in the original climatic variables. Temperature is in °C, rainfall in mm.

	PC1 - PC.temperature	PC2 - PC.rainfall
Mean temperature	0.87	-0.16
Temperature variability among years	-0.86	0.33
Temperature variability within years	-0.65	0.64
Mean rainfall	-0.20	-0.86
Rainfall variability among years	0.57	0.61
Rainfall variability within years	0.62	0.52