Family-living and cooperative breeding in birds are associated with the number of avian predators

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Abstract

Cooperative breeding occurs when individuals contribute parental care to offspring that are not their own, and numerous intra- and inter-specific studies have aimed to explain the evolution of this behaviour. Recent comparative work suggests that family living (i.e., when offspring remain with their parents beyond independence) is a critical steppingstone in the evolution of cooperative breeding. Thus, it is key to understand the factors that facilitate the evolution of family living. Within-species studies suggest that protection from predators is a critical function of group living, through both passive benefits such as dilution effects, and active benefits such as nepotistic antipredator behaviours in kin groups. However, the association between predation risk and the formation and prevalence of family groups and cooperative breeding remains untested globally. Here we use phylogenetic comparative analyses including 2984 bird species to show that family living and cooperative breeding are associated with increased occurrence of avian predators. These cross-species findings lend support to previous suggestions based on intraspecific studies that social benefits of family living, such as protection against adult predation, could favour the evolution of delayed dispersal and cooperative breeding.

Introduction

Cooperative breeding is a form of cooperation where non-breeding individuals contribute to parental care to the offspring of others. It occurs across a wide range of taxa and is common in birds (Cockburn 2006). Many studies have examined its evolutionary drivers (Cockburn 2020), revealing an association with various ecological factors or life-history attributes (Arnold and Owens 1998; Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Feeney et al. 2013; Gonzalez et al. 2013; Griesser et al. 2017; Lukas and Clutton-Brock 2017; Cockburn 2020; Johnson et al. 2023). Across cooperative breeders, the majority of helpers are offspring or relatives of the breeding pair that have delayed the onset of dispersal and independent reproduction (Koenig et al. 1992; Kokko and Ekman 2002; Kingma et al. 2021), but unrelated individuals can also help (Riehl 2013). Thus, it is essential to understand the factors favouring the formation of families (or non-kin groups) (Covas and Griesser 2007; Drobniak et al. 2015), as it represents a stepping stone in the evolutionary transition towards cooperative breeding (Griesser et al. 2017). However, in spite of the large number of comparative analyses focusing on the factors associated with the evolution of cooperative breeding, only a single comparative study investigated the factors associated with family formation (Griesser et al. 2017).

Group living is an important behavioural mechanism to reduce predation risk (Alexander 1974; Ebensperger 2001; Beauchamp and Krams 2023) and increase survival rates (Zhu et al. 2023). Generally, individual group members can benefit through lower vigilance levels (Beauchamp 2019), thereby increasing foraging efficiency (Schoener 1971; Hintz and Lonzarich 2018), and can also benefit from risk dilution (Hamilton 1971; Foster and Treherne 1981). Additional benefits can also be gained in groups made of related individuals. Within-species studies suggest that protection from predators is an adaptive benefit of family living (regardless of whether there are helpers at the nest during breeding). For instance, in Siberian jay *Perisoreus infaustus* and Belding's ground squirrel *Spermophilus beldingi*, parents display increased vigilance, alarm calling, or mobbing behaviour specifically when accompanied by related individuals (Sherman 1977; Griesser 2003; Griesser and Ekman 2004, 2005). These nepotistic behaviours have been found to provide incentives for offspring to remain in their family group by increasing survival probabilities (Ekman et al. 2001; Griesser et al. 2006; Griesser 2013). Similar results were found in cooperatively breeding *Neolamprologus* cichlid fishes, where experimental and observational studies showed that increased predation risk was associated with delayed dispersal (Heg et al. 2004) and increased the benefits of group living (Tanaka et al. 2016), hence being the main factor explaining variation in social organisation in this taxon (Groenewoud et al. 2016). Altogether, these studies suggest that living in kin groups might be especially beneficial when predation risk is high.

Groups can be made of unrelated individuals, but can also be made of stable associations over long time periods, often consisting of family members. In family-living species, groups usually break-up before the breeding season, while in cooperative breeders the group is typically together all-year round (Koenig and Dickinson 2016). Thus, groups in family-living species break-up much faster than in cooperative breeding species (mean number of days beyond independence: 160 vs 360; Griesser unpublished data). Members can therefore reduce predation risk through risk dilution as well as via cooperative or nepotistic antipredator behaviours (Clutton-Brock et al. 1999; Griesser et al. 2006; Covas and Griesser 2007; Griesser 2013; Kingma et al. 2014), but we can therefore expect that these benefits will gradually increase from non-family living species, to family-living species, to cooperatively breeding species.

Predation can favour group formation through delaying dispersal, and the importance of delayed dispersal for the evolution of cooperative breeding is usually well accepted (Covas and Griesser 2007; Griesser et al. 2017; García-Ruiz et al. 2022). However, the effect of predation as an evolutionary driver of family formation and cooperative breeding has not yet been tested at a large scale using a comparative cross-species framework. Here, using a global dataset of 2984 bird species and a phylogenetic comparative analysis, we test the hypothesis that species facing higher risk from avian predators should be more likely to live in family groups or to be cooperative breeders. We further expect that the effect of predation on sociality will be stronger for species living in more open habitats due to higher exposure to predators.

Methods

Data collection

Data for social systems, climatic variables and body mass were taken for 2984 species from a published data set (Griesser et al. 2017). Social systems of species were categorised as (i) non-family living when offspring disperse away from their parent(s) within less than 50 days beyond nutritional independence, (ii) family living when offspring remain at least 50 days beyond nutritional independence with their parent(s) but do not engage in cooperative breeding, and (iii) cooperative breeding when offspring remain with their parents and engage in parental care behaviours (see also Drobniak et al. 2015).

To estimate predation pressure, we collected data on the breeding and resident distribution (excluding the wintering range of migratory species) of all focal species in our dataset (N=2984) and their avian predators (N=553) from BirdLife International and Handbook of the Birds of the World (2018). These data were gridded at a 10-min resolution, to be able to analyse the distribution of species with narrow and fragmented ranges. Avian predators have been shown to be the main drivers of predation on juveniles outside the nest and adult birds (Caro 2005; Lima 2009; Valcu et al. 2014). We acknowledge that other taxa could also be locally important predators in some cases. We considered all avian predators mentioned in the literature as predators of adult birds (Valcu et al. 2014; Billerman et al. 2022). However, out of these 553 avian predator species, we only included 302 species here, as we excluded avian predators that rarely prey upon adult birds (e.g., *Circaetus gallicus*). In addition, we obtained the average weight of the lightest (n=84) and heaviest (n=176) possible prey for all these predators and performed a predator-prey body mass allometry (Figure 1a) to infer the range of suitable prey mass for each predator species (Gravel et al. 2013; Valcu et al. 2014; Bliard et al. 2020). This method has been shown to produce prey richness estimates for each predator that correlate strongly with bibliographical records (Valcu et al. 2014). Then, we calculated the number of grid cells shared between each predator species and a focal species of suitable mass, and estimated the average specific richness of potential sympatric avian predators across the range of each focal species (Figure 1b). The breeding latitude of each focal species was also computed as the mean latitude across all grid cells (breeding and resident distributions) of a species distribution.

Analysis

We assessed whether predation risk is associated with sociality, while accounting for potential confounders. We used N=2984 bird species with known social system. Due to the ordered nature of the social system data (see Griesser et al. 2017), we analysed the data using an ordinal cumulative logistic regression with the three levels of sociality. A cumulative logistic regression is a regression that allows for more than two categories that are ordered. It estimates several intercepts, but a single slope per predictor variable. We used the average richness of potential predators faced by each species as an explanatory variable. We also included habitat openness because it was shown to be a correlate of sociality using a similar dataset (Griesser et al. 2017), and its interaction with predation richness because we expect the effect of predation to be stronger in open habitats. We also included the following explanatory variables that could act as confounders: absolute latitude, and for both rainfall and temperature we calculated mean, variance, and predictability (obtained from Griesser et al. 2017). Note that some collinearity might exist among these environmental variables, but collinearity of predictors is not an issue in multiple regression analyses (Morrissey and Ruxton 2018; Vanhove 2021). We also included log body mass and its quadratic effect, as it could have an influence on species sociality and is also likely influencing our proxy of predation risk through the predator-prey body mass allometry, with intermediate species more likely to have higher estimated predation risk. Because few cooperative breeders occur in the Holarctic (Cockburn 2020), we also performed the same model on a subset of N=2299 bird species, excluding all Holarctic and widespread species (Appendix B). In addition, since migratory species are less social (Griesser et al. 2017), and because our metric of predation pressure did not account for predation risk on wintering grounds, we also ran the model excluding migratory species, on a subset of N=2503 species (Appendix C). All continuous variables were centred and scaled before analysis (mean-centred and divided by their standard deviation).

The models were deployed in R v.4.0.5 (R Core Team 2021), using the R packages *brms* v.2.14.4 (Bürkner 2017, 2018) as a frontend and *cmdstanr* (Gabry and Češnovar 2020) as a backend, using a Bayesian framework by implementing Hamiltonian Monte Carlo simulation in *Stan* (Carpenter et al. 2017). The model ran on 3 chains of 2000 iterations, with a warm-up period of 1000 iterations, and no thinning, resulting in a total of 1000 samples per chain. We applied a phylogenetic correction in the model by including the phylogeny in the form of an inverse variance-covariance matrix as a random effect. We did not account for phylogenetic uncertainty (Villemereuil et al. 2012) due to computational limitations. Instead, we used a composite tree of the phylogeny of Prum et al. (2015) as backbone and adding the tips of the maximum clade credibility tree from Jetz et al. (2012), constructed following the method described in Cooney et al. (2017). We also conducted the same model with maximum clade credibility trees computed from a random sample of 100 trees with the Ericson backbone and the Hackett backbone (Jetz et al. 2012) to ensure robustness of the results (Appendix D). Convergence and mixing of the 3 chains were confirmed visually and using the Gelman-Rubin diagnostic (Gelman and Rubin 1992), with potential scale reduction factors all inferior to 1.01.

Results

Phylogenetic comparative models indicated a likely association between richness of potential avian predators and bird sociality. Species in sympatry with a larger number of potential predator species were more likely to occur in family groups or cooperatively breeding groups (Table A1, Figure 2, Figure 3). Excluding Holarctic species did not change the mean effect size of predator richness on sociality (Appendix B). Similar results for the effect of predator richness were also found when excluding migratory species (Appendix C). Habitat openness was found to be negatively associated with sociality (see also Griesser et al. 2017). However, the interaction between predation richness and habitat openness was negligible, with no evidence for an effect (Table A1, Figure 2), even though the mean estimate was slightly positive. Body mass, latitude, and environmental variables (Table A1) were included to control for their effect as they are potential confounders (Westreich and Greenland 2013).

Discussion

Our results suggest that species living in areas with a higher number of avian predator species tend to live more often in family groups and breed cooperatively. This association suggests a potential role of adult predation on the evolution of family living and cooperative breeding, providing inter-specific support for results previously found at the intra-specific level (Griesser et al. 2006; Groenewoud et al. 2016; Tanaka et al. 2016). Hence, our results also provide support for previous hypotheses suggesting that benefits of delayed dispersal and philopatry are in themselves an important route to cooperative breeding (Griesser et al. 2006; Covas and Griesser 2007; García-Ruiz et al. 2022).

We acknowledge that the metric we computed for predation pressure, i.e., the average richness of potential predators, is imperfect. As argued by Suraci *et al.* (2022), a spatial overlap between predators and preys does not necessarily results in actual predator-prey interactions, as many ecological and environmental factors can influence encounter and depredation probabilities. For instance, dissimilar activity patterns for species of predator and prey could reduce the true predation risk (Smith et al. 2019). Nonetheless, despite its limitations, predation richness is a commonly used proxy of predation pressure (Valcu et al. 2014; Ciccotto and Mendelson 2016; Kotrschal et al. 2017; Matthews et al. 2018; Bliard et al. 2020), and the only one available for such a large-scale comparative study, where information on predator-prey encounters or predator densities is lacking. In addition, we computed predation richness as the average of potential predators across the geographical range of species using a method that does not inflate the predation pressure of wide-ranging species (Bliard et al. 2020; in contrast with e.g., Valcu et al. 2014). This leads to a more meaningful proxy of predation pressure for a study at the global scale and, given the data available, it arguably represents the best possible approach.

Our results provide evidence that the richness of potential predators is likely associated with increased sociality across bird species. This study being correlational, results could also have arisen from unaccounted confounders favouring simultaneously increased sociality and increased predator richness, and the directionality of the relationship can only be hypothesised. However, group formation as a response to predator pressure is well established in birds and other animals. Predation risk was found to be a driver of delayed dispersal in Siberian jays and cichlid fishes (Heg et al. 2004; Griesser et al. 2006; Tanaka et al. 2016), and work comparing cichlid populations experiencing different predation risk found that predation pressure influenced social structure (Groenewoud et al. 2016) by increasing the benefits of staying in the natal group. The direct fitness benefits of living in groups were also found to be more important than indirect fitness benefits as evolutionary drivers of delayed dispersal (García-Ruiz et al. 2022). Predation risk has therefore the potential to favour the evolution of family living (Griesser et al. 2017). Since cooperatively breeding groups usually live together throughout the year, group members can be expected to receive longer benefits in terms of protection from predators. Thus, the formation of family groups as a response to predation risk could pave the way towards the evolution of cooperative breeding.

Despite our finding of a likely positive association between average predation richness and sociality, the estimated effect size is small (Møller and Jennions 2002), although similar to what is commonly found in broad-scale comparative studies (Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2017; Stoddard et al. 2017; Mikula et al. 2021; but see Griesser et al. 2023). Small effect sizes can be expected if several distinct, possibly antagonistic, processes are leading to a similar outcome, which is the case for cooperative breeding and its evolutionary drivers (Griesser et al. 2017; Shen et al. 2017). Therefore, scaling down and studying the role of predation risk on the evolution of sociality focusing on a smaller geographical scale (Cockburn and Russell 2011) could potentially offer additional insights. Here, we conducted an analysis excluding Holarctic species, where the frequency of cooperative breeding is low compared to other geographic regions (Cockburn 2006, 2020), but obtained a similar effect size for the association of predator richness and sociality. An alternative would be to conduct studies within specific avian families with varying degrees of sociality (e.g., Gonzalez et al. 2013). Smaller scale studies would also allow to collect more detailed data on predation risk, to estimate predator densities based on bird surveys or citizen-science data (Sullivan et al. 2009; Fink et al. 2020).

Contrary to our expectations, there was no clear effect of habitat openness on the association between predation risk and sociality. The effect of predators in open habitats, like savannahs or grasslands, was expected to be stronger given the lower availability of refuges when escaping from predators, and hence leading to the expectation that forming groups would be an important strategy for predator avoidance in these habitats. However, other factors could influence this relationship. For instance, many species inhabiting open areas appear to rely on being cryptic to avoid predators (Negro et al. 2019; Nokelainen et al. 2020; but see Somveille et al. 2016), in which case group formation would not be favoured. We did, however, find an effect of habitat openness on sociality, with species being more social in habitats with denser vegetation. This is similar to what was found with an almost identical dataset by Griesser et al. (2017), and supports an association of delayed dispersal and family group formation with more vegetated, and hence productive, environments. This result is in line with the findings of Gonzalez et al. (2013) for hornbills (Bucerotidae), but contrasts with previous results based on a global dataset that found higher prevalence of cooperative breeding in regions characterized by low rainfall and high precipitation uncertainty (Jetz and Rubenstein 2011). These contrasting results may arise from the different categorisation of social systems, as climatic variables do not have the same effects on the prevalence of non-family and family-living species (Griesser et al. 2017), but they were merged in the same category in previous analyses.

Previous comparative studies on the evolution of cooperative breeding have focused on associations of various factors with alloparental care. However, associations among individuals before the onset of breeding are required for cooperative breeding to occur. Drivers of group formation can be varied (e.g., Lin et al. 2019) and can differ from those that make helping at the nest beneficial (Covas and Griesser 2007; Griesser et al. 2017). This study provides cross-species support for the hypothesis that predation risk is associated with group formation, a pattern which was previously shown within species. Thus, predation might be an evolutionary driver of family living by increasing benefits of delayed dispersal, thereby favouring the evolution of cooperative breeding. We suggest that future studies combining predation risk alongside other known factors associated with family-living and cooperative breeding could improve our understanding of the relative importance of each driver for the evolution of these social behaviours.

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Data availability

The datasets and R scripts needed to reproduce the results and figures can be found on Github (https://github.com/lbiard/predation_sociality_birds) and will be uploaded to Zenodo upon acceptance.

Figures and tables

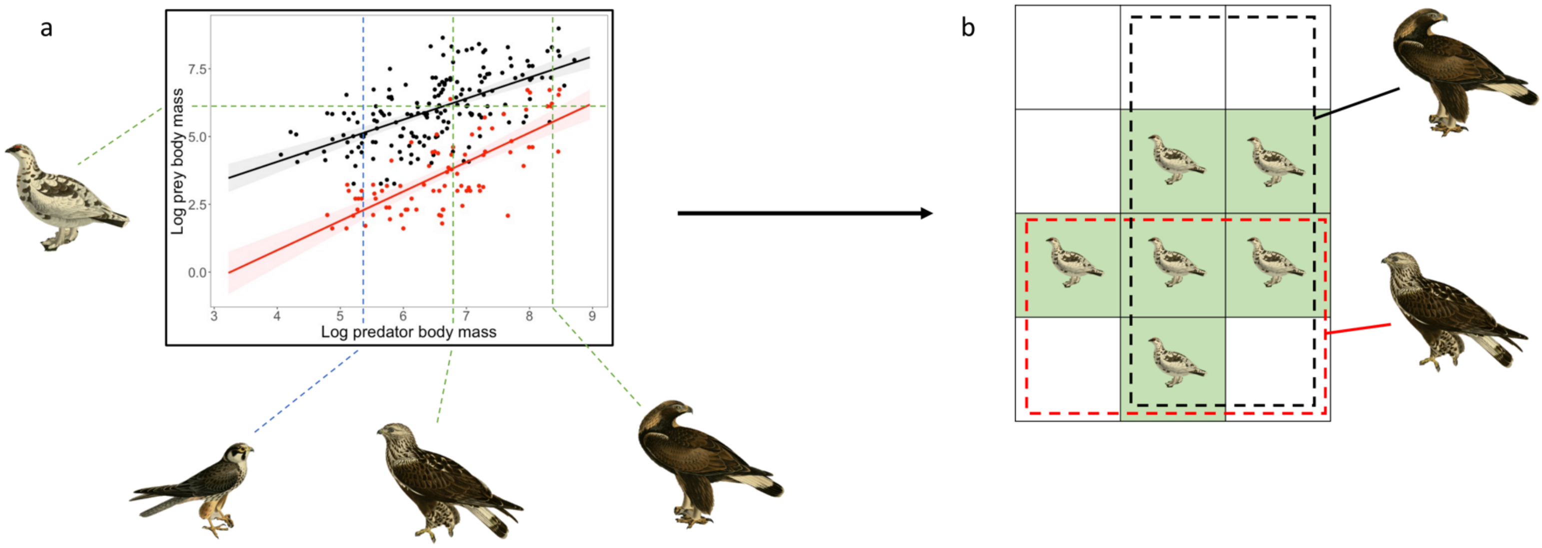

Figure 1: Schematic representation explaining how average predation richness was computed for each species (n=2984). (a) Predator-prey body mass allometry showing the lightest (red, n=84) and heaviest prey (black, n=176) targeted by predator species depending on their mass, used to infer a range of prey mass for each predator species (n=302). For instance, considering a given species (e.g., *Lagopus muta*) and several predator species (e.g., *Falco subbuteo, Buteo lagopus, Aquila chrysaetos*), a predator will be considered only if a given species fall within its predation mass range (*F. subbuteo* will not be considered a potential predator of *L. muta*). (b) Geographical range overlap, to compute the average richness of predators in each grid cell for each species of the dataset (in this hypothetical case, *L. muta* has an average predator richness of 1.5). *Bird illustration credits: Magnus & Wilhelm von Wright (1828).*

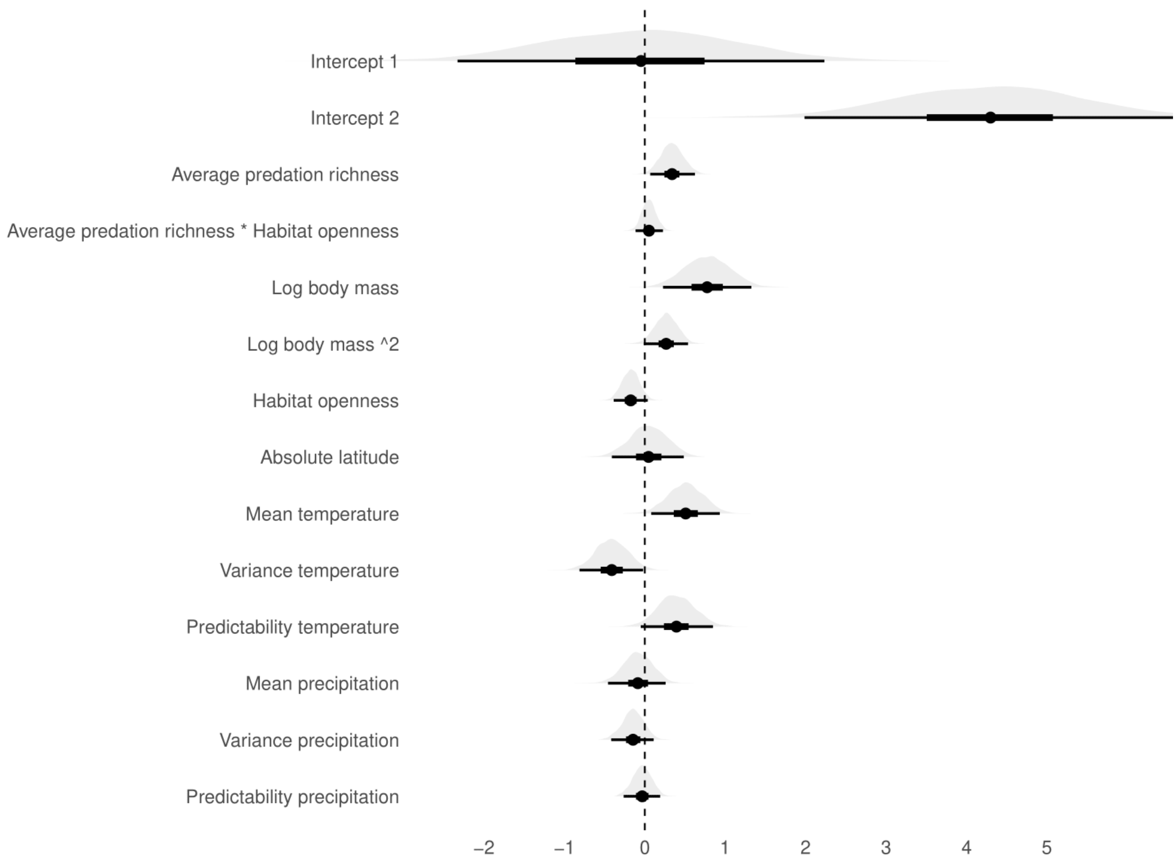

Figure 2: Estimated effects of standardized predictors on bird sociality. The figure displays the posterior distributions estimated by the ordinal model, alongside the mean, 50%, and 95% credible intervals. A summary of the posterior distributions can also be found in Table A1.

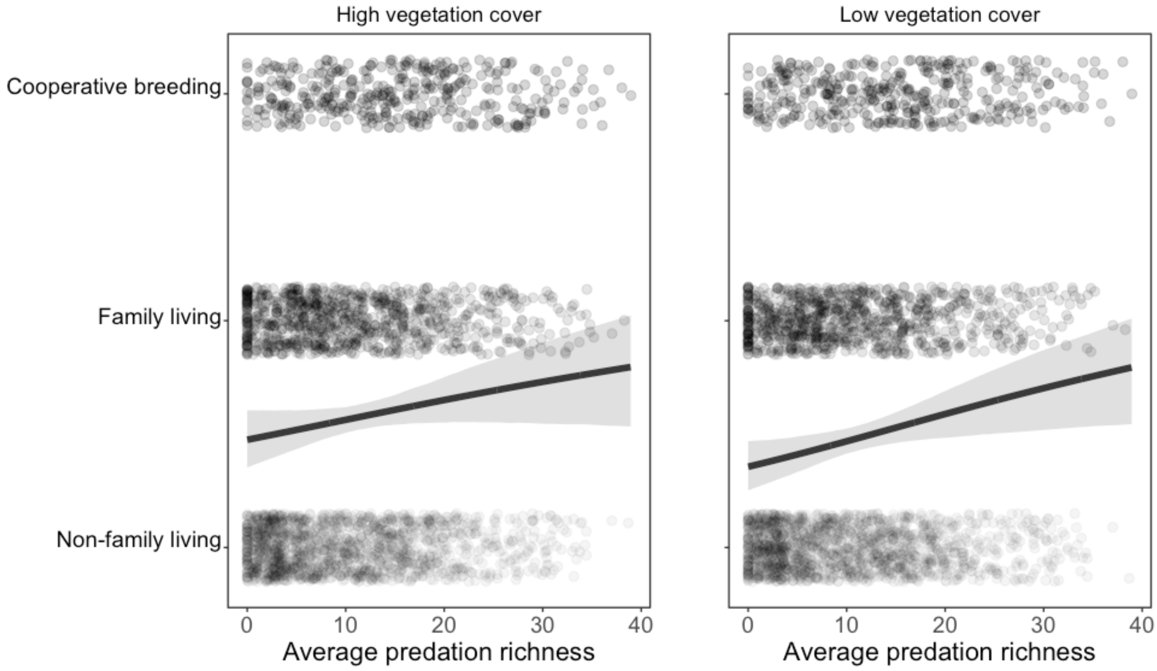

Figure 3: Effect of average predation richness on the social system of bird species. The left panel shows this association for habitats with high vegetation cover (habitat openness set to -1 SD) and the right panel shows this association for habitats with low vegetation cover (habitat openness set to +1 SD). The social system is represented as a graded scale. The regression lines and their associated 95% CI are those predicted by the ordinal logistic regression model, accounting for phylogenetic relationship between species. For display purposes only, the uncertainty associated with the intercepts was not accounted for. Each circle represents a species (N=2984 species). Average predation richness was transformed back to its original scale.

Appendix A

Table A1: Result of the ordinal logistic regression model exploring the effect of predation risk on sociality in birds (N=2984 species), accounting for phylogenetic relationship between species using a composite maximum clade credibility tree of the Prum et al. (2015) and Jetz et al. (2012) phylogenies. Estimates and effect sizes are presented on the logit scale. All continuous variables were scaled.

Response variable	Explanatory variable	Mean estimate	95% Credible intervals
Social system	Intercept 1	-0.05	-2.33; 2.23
	Intercept 2	4.30	1.99; 6.61
	Average predation richness	0.34	0.07; 0.62
	Average predation richness * Habitat openness	0.05	-0.11; 0.23
	Log body mass	0.78	0.23; 1.32
	Log body mass ^ 2	0.27	-0.01; 0.54
	Habitat openness	-0.18	-0.39; 0.04
	Absolute latitude	0.05	-0.41; 0.48
	Mean temperature	0.51	0.08; 0.93
	Variance temperature	-0.41	-0.81; -0.02
	Predictability temperature	0.39	-0.05; 0.85
	Mean precipitation	-0.09	-0.46; 0.26
	Variance precipitation	-0.15	-0.42; 0.11
	Predictability precipitation	-0.03	-0.26; 0.19

Appendix B

Table B1: Result of the ordinal logistic regression model excluding Holarctic species exploring the effect of predation risk on sociality in birds (N=2299 species), accounting for phylogenetic relationship between species using a composite maximum clade credibility tree of the Prum et al. (2015) and Jetz et al. (2012) phylogenies. Estimates and effect sizes are presented on the logit scale. All continuous variables were scaled.

Response variable	Explanatory variable	Mean estimate	95% Credible intervals
Social system	Intercept 1	-0.34	-2.61; 1.97
	Intercept 2	4.09	1.83; 6.38
	Average predation richness	0.32	0.02; 0.65
	Average predation richness * Habitat openness	0.05	-0.13; 0.24
	Log body mass	0.42	-0.19; 1.02
	Log body mass ^ 2	0.28	-0.04; 0.61
	Habitat openness	-0.14	-0.38; 0.09
	Absolute latitude	0.10	-0.24; 0.45
	Mean temperature	0.30	0.05; 0.56
	Variance temperature	-0.36	-0.65; -0.08
	Predictability temperature	-0.12	-0.48; 0.23
	Mean precipitation	0.06	-0.33; 0.47
	Variance precipitation	-0.27	-0.56; 0.01
	Predictability precipitation	-0.06	-0.33; 0.21

Appendix C

Table C1: Result of the ordinal logistic regression model excluding migratory species exploring the effect of predation risk on sociality in birds (N=2503 species), accounting for phylogenetic relationship between species using a composite maximum clade credibility tree of the Prum et al. (2015) and Jetz et al. (2012) phylogenies. Estimates and effect sizes are presented on the logit scale. All continuous variables were scaled.

Response variable	Explanatory variable	Mean estimate	95% Credible intervals
Social system	Intercept 1	-0.17	-2.55; 2.18
	Intercept 2	4.14	1.84; 6.53
	Average predation richness	0.34	0.08; 0.64
	Average predation richness * Habitat openness	0.11	-0.07; 0.29
	Log body mass	0.64	0.07; 1.25
	Log body mass ^ 2	0.24	-0.04; 0.51
	Habitat openness	-0.15	-0.37; 0.05
	Absolute latitude	0.15	-0.27; 0.56
	Mean temperature	0.39	0.05; 0.76
	Variance temperature	-0.41	-0.76; -0.08
	Predictability temperature	0.17	-0.24; 0.59
	Mean precipitation	0.05	-0.33; 0.44
	Variance precipitation	-0.25	-0.53; 0.02
	Predictability precipitation	-0.05	-0.29; 0.19

<u>Appendix D</u>

Table D1: Result of the ordinal logistic regression model exploring the effect of predation risk on sociality in birds, accounting for phylogenetic relationship between species using Ericson backbone. Estimates and effect sizes are presented on the logit scale. All continuous variables were scaled.

Response variable	Explanatory variable	Mean estimate	95% Credible intervals
Social system	Intercept 1	-0.54	-3.01; 1.91
	Intercept 2	3.75	1.36; 6.18
	Average predation richness	0.32	0.07; 0.57
	Average predation richness * Habitat openness	0.04	-0.13; 0.21
	Log body mass	0.71	0.17; 1.23
	Log body mass ^ 2	0.25	0.00; 0.52
	Habitat openness	-0.19	-0.40; 0.02
	Absolute latitude	0.13	-0.33; 0.57
	Mean temperature	0.59	0.18; 1.01
	Variance temperature	-0.37	-0.74; 0.01
	Predictability temperature	0.46	0.04; 0.89
	Mean precipitation	-0.10	-0.44; 0.24
	Variance precipitation	-0.16	-0.42; 0.09
	Predictability precipitation	-0.04	-0.26; 0.19

Table D2: Result of the ordinal logistic regression model exploring the effect of predation risk on sociality in birds, accounting for phylogenetic relationship between species using Hackett backbone. Estimates and effect sizes are presented on the logit scale. All continuous variables were scaled.

Response variable	Explanatory variable	Mean estimate	95% Credible intervals
Social system	Intercept 1	-0.42	-2.92; 2.03
	Intercept 2	3.85	1.39; 6.29
	Average predation richness	0.33	0.08; 0.62
	Average predation richness * Habitat openness	0.03	-0.14; 0.20
	Log body mass	0.74	0.20; 1.27
	Log body mass ^ 2	0.24	-0.02; 0.51
	Habitat openness	-0.19	-0.40; 0.02
	Absolute latitude	0.17	-0.27; 0.61
	Mean temperature	0.61	0.20; 1.03
	Variance temperature	-0.34	-0.75; 0.04
	Predictability temperature	0.49	0.06; 0.93
	Mean precipitation	-0.13	-0.48; 0.22
	Variance precipitation	-0.15	-0.41; 0.11
	Predictability precipitation	-0.02	-0.24; 0.20

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