Social complexity does not lead to more stable demographic histories across bird species

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Abstract

Species' responses to environmental variability can include evolutionary changes in social behaviours, leading to variation among species in characteristics including their mating systems, care systems (e.g., cooperative breeding), the rate of group formation, and the strength of interaction between individuals. These social traits can influence the physiology of individuals, potentially shielding them from adverse environmental conditions, and thus ultimately affect the demography of populations and species. However, the demographic consequences of sociality have rarely been studied and have been limited to ecological timescales. Across evolutionary timescales (thousands-to-millions of years), anecdotal comparative evidence based on a few species suggests that social traits lower effective population size while also buffering species demographic responses to environmental change. Here, we used whole-genome sequence data to reconstruct the deep-time demographic history of 630 populations of 322 bird species over half a million years. We then explored the role of different components of social complexity traits (social organisation, mating system, care system) in buffering the long-term demography of species to broad-scale environmental change. Contrary to previous studies, our analyses found no clear evidence of social complexity influencing and stabilising the long-term demographic patterns of bird populations. This finding highlights that the role of sociality on species' demography across evolutionary timescales might not be as widespread as previously assumed and instead be taxa-specific.

Introduction

Species can respond to environmental variation through adaptive changes in behaviours, which can include changes in the different components of social complexity itself (i.e., social organization, social structure, mating system, and care system) (Kappeler 2019) and in the expression of social behaviours (i.e., interactions between individuals) (Blumstein *et al.* 2023; Fisher *et al.* 2021; Komdeur & Ma 2021; Warrington *et al.* 2024). The social shielding hypothesis integrates the various potential benefits gained by individuals living in social groups, which can help to buffer them against environmental variability and thus lead to increased and more stable vital rates (Warrington *et al.* 2024). However, while extensive research has aimed to link social behaviors and individual vital rates, the consequences of sociality on population-level processes such as demographic trajectories are, to date, poorly understood.

Different components of social complexity are likely to alter several individual and population level parameters. Social organisation (i.e., group size and composition, relatedness patterns) can exert a direct influence on key physiological parameters of individuals, with proximity to other individuals or group living potentially reducing stress (Hennessy *et al.* 2009; Kikusui *et al.* 2006) and providing thermoregulatory benefits (Paquet *et al.* 2016). Social organisation can also have a direct influence on population-level parameters (e.g., survival rate), through mechanisms that could apply broadly to any socially-living species, such as cooperative foraging (Hintz & Lonzarich 2018) or passive dilution effects to reduce predation risks (Foster & Treherne 1981). In addition, individuals in kin groups are likely to gain additional benefits, for example through nepotistic anti-predatory strategies (Griesser & Ekman 2004, 2005; Sherman 1977). Accordingly, social

organisation has been found to be associated with longer lifespans (Griesser *et al.* 2017; Zhu *et al.* 2023) and can sometimes reduce the risk of reproductive failure.

Another component of social complexity, namely care systems through cooperative breeding, likely also plays a critical role in improving and stabilising reproductive rates. Cooperative breeding is a system whereby individuals ('helpers') provide parental care to the offspring of others, usually kin but also non-kin in some cases (Ben Mocha *et al.* 2023b; Cockburn 1998; Riehl 2013). Comparative research has established associations between the incidence of cooperative breeding and climatic, ecological, and life history variation (Bliard *et al.* 2024a; Cockburn 2020; Gonzalez *et al.* 2013; Griesser *et al.* 2017; Jetz & Rubenstein 2011; Shen *et al.* 2017), highlighting that cooperative breeding can be adaptive in the face of variable environmental conditions. Through alloparental care, helpers can buffer against the effects of unfavourable environmental conditions on reproductive success (Covas *et al.* 2008; Groenewoud & Clutton-Brock 2021), or compensate for poor breeding seasons through higher breeding success in favourable years (Bourne *et al.* 2020). Recent work has explored its effect on population dynamics as a whole, highlighting that the presence of helpers can promote population persistence and stave off local extinction under climate change (Busana *et al.* 2022; Paniw *et al.* 2019). However, since these studies are based on datasets spanning a few decades, they focus on short-term demographic changes but can miss the potential resilience of social species to longer-term fluctuations. This can be overcome by studying the demography of social species across evolutionary timescales that encompass hundreds-to-thousands of generations experiencing different periods of environmental change.

Coalescent-based methods coupled with increasingly available whole genome sequence data offer an unprecedented opportunity to study the deep-time demography of

species through changes in their effective population sizes *Ne* (Feng *et al.* 2020; Germain *et al.* 2023b; Li & Durbin 2011; Mather *et al.* 2020), allowing the exploration of the long-term consequences of sociality on population dynamics. The different components of social complexity are expected to have distinct consequences on the mean of *Ne* (Table 1). Mating systems are predicted to have a direct influence on *Ne*, mostly by determining the proportion of the population that reproduces and thus contributes genetically to the next generation (Nunney 1993; Waples 2024b). Strictly monogamous species with low rates of extra-pair paternity should have a low among-individual variance in reproductive success with most adults contributing to reproduction, theoretically leading to a higher average *Ne* than in frequently polygynous species where fewer individuals can monopolise reproduction. Polygynous bird species should therefore have lower *Ne* due to increased reproductive skews, but only when this is coupled with monoandry (Kvarnemo 2018). Indeed, an alternative could also be that high levels of promiscuity lead to extreme polygynandry (where most females mate with males and vice versa), which offers the largest proportion of individuals contributing to the next generation and thus higher *Ne*.

A conceivable demographic consequence of cooperative breeding is also a reduction in average *Ne*. Similarly to eusocial species (e.g., Hymenoptera, naked mole-rats), albeit to a lesser extent, cooperative breeders are often characterized by a strong reproductive skew (but see Ben Mocha *et al.* 2026), especially in birds (Ben Mocha *et al.* 2023a; Raihani & Clutton-Brock 2010), leading to lower *Ne* (Romiguier *et al.* 2014). This effect could be compounded, with cooperative breeding leading to more frequent contact among kin, potentially increasing the risk of inbreeding (Craig & Jamieson 1988; Nichols *et al.* 2014; Reeve *et al.* 1990; Richardson *et al.* 2004). Such interactions are expected to further decrease *Ne* (Charlesworth 2009), even though inbreeding avoidance mechanisms might be

strong in social species (Koenig & Haydock 2004; Nichols 2017; Pike *et al.* 2021). This overall reduction in genetic diversity and *Ne* has been found in eusocial insects (Romiguier *et al.* 2014; Shell *et al.* 2021; Weyna & Romiguier 2021), as well as in comparative studies on snapping shrimps (Chak *et al.* 2021, 2022) and social spiders (Settepani *et al.* 2017), but contrasting results have been found across more varied taxa (Bromham & Leys 2005). However, such studies did not include more than a dozen species, and are thus taxonomically limited in their scope and conclusions.

Another potential consequence of sociality on the demographic history of species is related to the long-term variability of *Ne* (Table 1). This is a result of group living and cooperative care systems being expected to buffer populations against environmental fluctuations and ecological stressors (Jetz & Rubenstein 2011; Lv *et al.* 2023; Rubenstein & Lovette 2007; Salguero-Gómez *et al.* 2025), which can lead to more stable survival rates and allow individuals to breed even during bouts of harsher ecological conditions (Cockburn 2020), thus relaxing strong events of directional selection (Mashoodh *et al.* 2023). The potential consequence thereof is that species which breed cooperatively and have a higher degree of social organisation might have more stable population dynamics and thus be more likely to persist through time (Busana *et al.* 2022). This could potentially result in more stable *Ne* through evolutionary times (Chak *et al.* 2022; Mashoodh *et al.* 2023). The effect of cooperative behaviours buffering *Ne* variability has also been found comparatively in the demographic histories of 12 species of snapping shrimps (Chak *et al.* 2022), with species with a higher degree of social organisation having more stable long-term population dynamics. However, the link between different components of social complexity and the long-term variability of *Ne* remains untested in vertebrates using a cross comparative framework encompassing a large number of species.

Here, we use a global demographic dataset of 630 samples from 322 bird species based on high-coverage whole genome sequence data. Using the demographic history of these populations over the last half million years reconstructed through coalescent methods, alongside detailed trait-based data and phylogenetic comparative analyses, we test whether cooperatively breeding species and more promiscuous species exhibit lower average *Ne* over evolutionary timescales. We further expect that social traits of bird species related to social organisation and offspring care systems will be associated with the temporal variability of *Ne* through time, such that more social species exhibit markedly lower demographic variability, thus being more buffered against long term environmental variation. We use varied proxies of social organisation and care systems, which allows us to assess different aspects of social complexity that could potentially be advantageous regarding demographic buffering. On the one hand, the propensity of joining mixed-species flocks will inform whether the potential benefits for demographic stability depend on individuals being part of groups, regardless of kinship or species composition. On the other hand, intraspecific flock size for each species will inform on the relevance of being part of conspecific groups in particular. Finally, using family living and cooperative breeding will show the importance, or lack thereof, of associations among kin and alloparental care for demographic buffering.

Methods

Demographic data

Whole genome sequence data were initially collected for 634 individuals from 322 species (1-7 samples per species). The initial 322 individual data samples (one sample per species) originated from the B10k genome project (Feng *et al.* 2020). An additional 312 samples were

collected to have repeated samples for 105 species of the total 322 species (Germain *et al.* in prep). These additional samples were collected throughout the range of these species to maximize geographic representation. In 4 species (*Acrocephalus arundinaceus*, *Cuculus canorus*, *Certhia familiaris*, *Piprites chloris)*, two individuals were related, and subsequently one individual of each pair was excluded from further analyses, resulting in a final dataset of 630 individuals from 322 species.

To minimize reference bias and maximize mappability across diverse species, reads from each individual were mapped to their respective de novo assemblies using BWA-MEM v.0.7.17 (Li & Durbin 2009). Variant calling was performed using the standard GATK pipeline v.4.4.0.0, including HaplotypeCaller, GenotypeGVCFs, SelectVariants, and VariantFiltration (McKenna *et al.* 2010). Following Germain et al. (2023a), we used several filtering steps to remove SNPs: (1) applying hard filters according to the GATK manual with parameters "QD<2.0 || MQ<40.0 || FS>60.0 || SOR>3.0 || MQRankSum<–12.5 || ReadPosRankSum<–8.0"; (2) filtering homozygous sites and multiallelic SNPs; (3) filtering sites with an inter-SNP distance < 10 bp; (4) filtering sites with sequencing depth below 1/3 or exceeding twice the genome-wide average depth; (5) filtering sites located in repetitive regions annotated by RepeatMasker, RepeatModeler, LTR_Finder, ProteinMasker, and TRF; (6) filtering sites located on sex chromosomes, identified by aligning assemblies to the chicken (*Gallus gallus*) genome using LastZ and classifying scaffolds with >60% alignment coverage against chicken Z/W chromosomes as sex-linked (Hansen *et al.* 2022); (7) filtering sites with mappability < 1 as calculated by GenMap.

We used Pairwise Sequentially Markovian Coalescent (PSMC) analysis to infer the regional demographic histories of each individual sample. The rate of coalescent events is inversely proportional to *Ne*, thus this method allows us to reconstruct the temporal

changes in *Ne* for each population through time (Germain *et al.* 2023b; Li & Durbin 2011; Nadachowska-Brzyska *et al.* 2016). We used the PSMC settings "-N30 -t5 -r5 -p 1+1+1+1+800+4+6+10", where the first time window was segmented for more accurate estimates of early *Ne* and to avoid artifacts of false *Ne* peaks (Hilgers *et al.* 2025). To scale PSMC output, we used data on species generation time from Bird et al. (2020). Data on mutation rate per site per generation was estimated following Germain et al. (2023b), using substitution rates inferred from branch lengths of the dated phylogeny of B10k as a proxy (Stiller *et al.* 2024). Because the scaling of PSMC output is sensitive to the accuracy of the mutation rates used, we compared recently estimated synonymous substitution rates obtained through a similar method (Duchêne *et al.* 2025), rates used in past studies (Brüniche-Olsen *et al.* 2021), as well as directly measured mutation rates from parent-offspring trios (Bergeron *et al.* 2023). Mutation rates per site per generation estimates and their comparisons are provided in the supplementary materials (Figure S1).

Given the uncertainty of PSMC estimates for recent times, we restricted our analyses to older time periods (30 kya to 500 kya), keeping only samples with full demographic coverage during that time interval (607 individuals for 308 species). From the *Ne* time series, we estimated two demographic metrics: (1) the harmonic mean of *Ne* across time (Waples 2024a, 2025) and (2) the coefficient of variation (CV) of *Ne* as a metric of demographic stability, which represents *Ne* variability independent from its mean, with lower values indicating more stable demographic histories (Bliard *et al.* 2024b; Chak *et al.* 2022; Postuma *et al.* 2020).

Social complexity data

We gathered four types of sociality data to be used to test for the effect of sociality on both the mean and temporal variability (CV) of *Ne* (Figure 1). First, we collected data from

Griesser et al. (2017) and additionally from the literature on the offspring care systems of birds, with information available for 243 of the species of our dataset, characterized in three categories representing incremental degrees of offspring care: non-family living, family living, and cooperative breeding (Bliard *et al.* 2024a; Drobniak *et al.* 2015; Griesser *et al.* 2017). Non-family living was defined as species where offspring dispersing away from their parents within 50 days of nutritional independence, family living when offspring stay at least 50 days beyond nutritional independence but do not provide alloparental care (do not breed cooperatively), and cooperative breeding when offspring remain with their parents and provide alloparental care.

Second, we used data on mating systems and the frequency of extra-pair parentage from Barber et al. (2024), which is categorised by five levels of increasing frequency in polgyny and extra-pair parentage, with the highest level corresponding to lekking species.

Third, we estimated the average flock size for each species following Callaghan et al. (2021) and Dufour et al. (2024) using citizen science data (Sullivan *et al.* 2009). In these previous studies, a proxy of flock size was estimated for each species using all complete eBird checklists only made of count data, with flock size for a species defined as its mean observed abundance per checklist, averaged across all months. This calculation is likely to lead to upward biased estimates due to the inclusion of eBird checklists of long duration, as there is no way to tell if individual birds observed in a checklist were part of the same group or observed at different times during the search effort. Therefore, we decided to re-estimate Callaghan's (2021) proxy of flock size using the most up-to-date eBird dataset (version of March 2025), but restricting the calculation to complete stationary and travelling checklists of less than 10 minutes and 500 meters, keeping only estimates for species observed in at least 10 independent checklists. This restricted dataset consisted of more than 24 million

bird observations across 282 species (mean per species = 85818 count data observations; median = 1456 observations).

Fourth, we collected data on mixed-species flocking from published handbooks and Birds Of the World (Billerman *et al.* 2025), and recorded whether they took part in mixed-species flocking and at which frequency, with data available for 269 of our focal species. The propensity of joining mixed-species flocks was characterised following 5 categories of incremental frequencies: “never”, “rare”, "occasional”, “frequent”, and “obligate”, with the latter category representing species almost always found as part of mixed-species flocks.

Functional traits

We obtained additional data on functional traits (body mass, hand-wing index as a proxy of dispersal ability), as well as data on habitat characteristics (habitat type, vegetation density) for all species from the AVONET database (Tobias *et al.* 2022).

Analyses

We first assessed whether cooperative breeding, mating systems and promiscuity are associated with an overall lower mean *Ne* of populations over the last 500 kya. We used a total of 473 individual demographic histories from 232 species with known mating systems and offspring care systems, with species classified for the latter as either cooperative breeders or non-cooperative breeders. The response variable was the mean of *Ne*, and we analyzed this data using a lognormal regression model with a log link function. The explanatory variables were the care system (cooperative breeding / non-cooperative breeding), the mating system (frequency of polygyny and EPP) as well as variables that could act as confounder: log body mass and absolute latitude of the sampling location.

We then assessed the link between three proxies of sociality and the temporal variability of *Ne* in the last 500 kya. We performed one model for each of the sociality variables, which are care systems (non-family-living / family-living / cooperative breeding), the log of estimated flock size, and the propensity to join mixed-species flocks (5 incremental frequency categories). In each model, we modelled the response variable — the coefficient of variation of *Ne* — with a Gaussian distribution. First, using 473 individuals from 232 species, we included as covariates the offspring care system, log body mass, absolute latitude, and hand-wing index (i.e., a measure of a species dispersal capacity), which could act as a confounder if more dispersive species can stabilise their demographic histories by changing environments during unfavourable periods. Second, using 553 individuals from 270 species, we ran a model with log flock size as a covariate, and included log body mass, absolute latitude, hand-wing index, as well as vegetation density of the habitat, which is likely to influence both flock size and the demographic variability of species. Third, we used 498 individuals from 257 species to estimate the effect of joining mixed-species flocks. Given the incremental nature of this variable (5 categories representing increasing frequencies), we parametrized this ordinal predictor as a monotonic effect (Bürkner & Charpentier 2020), ensuring that predictions increase or decrease monotonically across categories, while the change between adjacent categories is allowed to vary. The variables that could act as confounders and that were included in this model were log body mass, absolute latitude, and hand-wing index as a proxy of dispersal capability.

In all the models, we controlled for the phylogenetic relationships between species (see below for more details). Given that the data include multiple observations per species, we also included a species random effect to account for any species effect that would be

independent of the phylogenetic relationship between species. All continuous variables were scaled before analyses (mean centered and divided by their standard deviation).

All analyses were conducted in R v.4.5.0 (R Core Team 2025) using the R package *brms* v.2.22.0 (Bürkner 2017, 2018), which itself uses *cmdstanr* (Gabry & Češnovar 2020) as an interface to the Bayesian data analysis software *Stan* v.2.36.0 (Carpenter *et al.* 2017) to implement Hamiltonian Monte Carlo simulations. All models ran on 4 chains with 1000 burn-in iterations per chain, saving the subsequent 1000 iterations with no thinning (Link & Eaton 2012). For all models, good mixing and convergence of the 4 chains were confirmed visually as well as using the Gelman-Rubin diagnostic (Gelman & Rubin 1992). We accounted for phylogenetic relationships between species in all the models. Thus, we included the phylogeny as a variance-covariance matrix of species as a random effect. We used the R package *clootl* (Miller *et al.* 2025) to access the latest bird phylogenetic information (v.1.4) from McTavish et al. (2025), consisting of a sample distribution of 100 complete dated trees aligned with the Clements taxonomy (Clements *et al.* 2023). We ran each model on 50 of these alternative phylogenetic trees, which is enough to account for phylogenetic uncertainty (Nakagawa & de Villemereuil 2019; de Villemereuil *et al.* 2012) and then merged the posterior samples of all these alternative models, thus obtaining a single posterior distribution of 200000 samples (50*4*1000) for each parameter.

Results

We did not find any clear evidence that cooperatively breeding species have a lower mean *Ne*. While the mean effect size is negative as initially hypothesised, the posterior distribution widely overlaps zero, highlighting large uncertainty in the estimated effect, such that there is no clear difference in long-term mean *Ne* for both cooperatively breeding and

non-cooperatively breeding bird species (Figure 2a-b). However, for mating systems, we found a trend where more promiscuous species tend to display higher average *Ne* (Figure 2c-d).

Similarly, we did not find any clear association patterns between a species' care system and its temporal variability of *Ne* (Figure 3a-d). While we expected a lower CV of *Ne* with an increase in offspring care, we found that family living species have the lowest *Ne* variability, but contrary to our expectations cooperative breeders had the most temporally variable demographic histories.

While we expected a negative effect of estimated flock size on demographic variability, we found no effect of flock size on the CV of *Ne*, with the estimated effect of flock size being close to null (Figure 3e-f).

Contrary to our initial expectations, we found that the mean estimated monotonic effect of the propensity to join mixed-species flocks on the long-term variability of Ne tends to be close to zero, with no influence of mixed-species flocking on the CV of *Ne* (Figure 3g-h).

Discussion

Our results suggest that across a diverse array of species and broad geographic ranges, sociality was not associated with more stable demographic histories in birds. This finding could indicate that social and affiliative behaviours might not act as a long-term demographic buffer across bird species. Hence, using a large-scale comparative analysis, we provide evidence against previous hypotheses that were formulated based on studies on invertebrates, which had suggested that sociality leads to lower variability in *Ne* (Chak *et al.* 2022). Therefore, our study highlights that the role of social behaviours on long-term demography might depend on ecological conditions and be taxa specific.

We found that species mating systems tended to influence the mean of *Ne*. Since more promiscuous species and species with higher polygamy tend to have increased *Ne*, it might suggest that the mating system of these species, rather than increase reproductive variance, tend to increase polygynandry, whereby both males and females have multiple partners, thus increasing effective population size (Kvarnemo 2018). However, we did not find any clear effect of cooperative breeding on the mean *Ne* of species (Figure 2). This result was surprising given that this pattern of lower genetic diversity and lower *Ne* for (eu)social species is well supported across invertebrate species, with compelling evidence in taxa as varied as ants, bees, spiders, and shrimps (Chak *et al.* 2021, 2022; Romiguier *et al.* 2014; Settepani *et al.* 2017; Shell *et al.* 2021; Weyna & Romiguier 2021). The different pattern found for birds might be explained by less extreme reproductive skews in cooperative birds than eusocial insects. It might be argued that eusociality and cooperative breeding are distinctive social systems, though ultimately these two systems exist on the same sociality continuum, with the main difference being the strength of reproductive skews experienced in the populations (Sherman *et al.* 1995). However, a less extreme reproductive skew in cooperatively breeding birds than in eusocial insects could attenuate the differences in genetic diversity and *Ne* when comparing social and non-social species. Reproductive skews in cooperatively breeding birds have been found to be higher than in mammals (Raihani & Clutton-Brock 2010), but nonetheless, extreme skews are rare, with most cooperatively breeding birds experiencing at least some degree of reproductive sharing (Ben Mocha *et al.* 2023a; Riehl 2017), which could explain that we did not detect lower *Ne* for cooperative breeders in this study.

Methodological issues could also have led to imprecise *Ne* estimates, thus potentially blurring the differences in mean *Ne* between cooperative and non-cooperative breeders.

PSMC estimates need to be scaled with species mutation rates to obtain results in a unit of *Ne* (Li & Durbin 2011), and using inaccurate mutation rates will lead to imprecise values of mean *Ne*. Direct measurements of germline mutation rates requires data from parents-offspring trios, which have only been measured in a handful of bird species (Bergeron *et al.* 2023), and are unavailable for most species used in our dataset. In addition, mutation rates can even vary within species and as a consequence of life history differences (Bergeron *et al.* 2023; Majic *et al.* 2026). Nonetheless, we relied on species-level substitution rates estimated from branch length of the most up-to-date phylogeny (Duchêne *et al.* 2025; Feng *et al.* 2020). Given that these estimates were correlated with the direct measurements of Bergeron et al. (2023) (Figure S1), we are confident that our results reflect a biological lack of mean *Ne* difference between cooperatively and non-cooperatively breeding birds rather than being the outcome of methodological caveats related to imprecise mutation rates. In addition, mutation rates influence *Ne* estimates in a predictable fashion, and the overall qualitative shape of *Ne* curves through time will remain unaffected (Nadachowska-Brzyska *et al.* 2015). Therefore, our proxy of demographic variability (CV of *Ne*) should not be influenced by the uncertainty of species mutation rates, as this metric represents the variability of *Ne* time series independent of their mean.

We did not find any stabilising effect of the different sociality metrics on long-term population demography (Figure 3). This result is surprising given the strength of the effect found across snapping shrimp species (Chak *et al.* 2022). Our study used sample sizes that were manyfold larger than previous studies (Bromham & Leys 2005; Chak *et al.* 2022; Shell *et al.* 2021; Weyna & Romiguier 2021), thus it is unlikely the lack of association between sociality and demographic stability in birds could not be detected due to underpowered analyses. Biological differences between social invertebrates and birds might potentially

explain the discrepancies between our results and past findings. For instance, compared to snapping shrimps and social insects, bird life histories are characterized by longer lifespan, overlapping generations, and more pronounced iteroparity. These differences could buffer bird species against environmental variability (Ellner & Hairston 1994; Lippé *et al.* 2006; Orzack & Tuljapurkar 1989), thus making any potential effect from social shielding less pronounced than in species with shorter generation time, no overlapping generation, and semelparous reproduction.

Several other hypotheses could explain the patterns observed from our analyses. First, albeit surprising, the results could simply reflect that these various social traits do not bring any true benefits for demographic stability over evolutionary timescales. Second, such analyses rely on contemporary trait data, while we know that traits could potentially have evolved over the timescale studied here. Some morphological traits can shift in a matter of decades (Ozgul *et al.* 2009; Weeks *et al.* 2020), and behavioral traits such as mixed-species flocking propensity or parental care systems can be evolutionarily labile (Griesser *et al.* 2017). However, given the large phylogenetic coverage of our study with most species belonging to different families (Figure 1), we expect among-species differences in traits to dominate over any potential evolutionary changes in traits within the timespan of the study. Finally, not detecting associations between sociality metrics and demographic stability could also be due to differences in the environment where species are present. Sociality could have enabled some species to inhabit and persist in harsher, more variable environments, while keeping similarly stable demographic histories. This is in part supported by the geographical distribution of some cooperatively breeding species, with global analyses finding them to be more prevalent in regions with open habitats and scarce, unpredictable rainfall (Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017). However, this might be

unlikely for birds, as some taxa-specific analyses have found social species to be more prevalent in stable and productive environments (Gonzalez *et al.* 2013; Johnson *et al.* 2023). In addition, our overall knowledge of species sociality is rife with biases (Farine 2026), with little known for species inhabiting denser, more benign environments (Cockburn 2020).

Altogether, our results on bird long-term demography contrast with previous findings on invertebrates, calling into question the generalisability of social buffering patterns across varied taxa. We hope that the increasing amount of whole-genome sequence data in other taxa displaying a wide range of social traits (Vizueta *et al.* 2025) will help shed light on the long-term demographic consequences of social evolution.

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Author contributions

LB conceived the study, performed the comparative analyses, and wrote the first draft of the manuscript. DNB, ABO, RG led the demographic sampling. JX ran the PSMC. MG collected the data on offspring care systems. YC and DF collected the data on mixed-species flocks.

Data and code availability

Data and R code are publicly available on GitHub (https://github.com/lbiard/sociality_comparative_Ne), and will be uploaded to Zenodo upon acceptance.

Figures and tables

Mechanism	Effect	Components of social complexity	Explanatory variable	Effect on *Ne*	References
Group living	↓ temporal variance in survival	Social organisation, care system	Flock size, mixed-flocking propensity, family living & cooperative breeding	↓ CV *Ne*	Waples 2016
Cooperative care	↓ temporal variance in reproduction	Care system	Cooperative breeding	↓ CV *Ne*	Chak et al. 2022
Reproductive skew	↓ share of population reproducing	Care system, mating system	Cooperative breeding, extra-pair paternity	↓ *Ne*	Romiguer et al. 2014
Kin structuring and inbreeding	↑ coalescence rate	Social organisation, care system	Family living & cooperative breeding	↓ *Ne*	Charlesworth 2009
Promiscuity	↑ polygyny (with monoandry) or ↑ polyandry (with monogyny)	Mating system	Extra-pair paternity	↓ Ne	Kvarmeno 2018
	↑ polygynandry			↑ *Ne*	

Table 1: Summary of expected mechanisms through which social complexity could potentially influence effective population size (*Ne*) and its temporal variability (CV *Ne*). Each mechanism can be ascribed to one or more components of social complexity, following Kapeller's (2019) categorisation, and to one or more explanatory variables of our dataset.

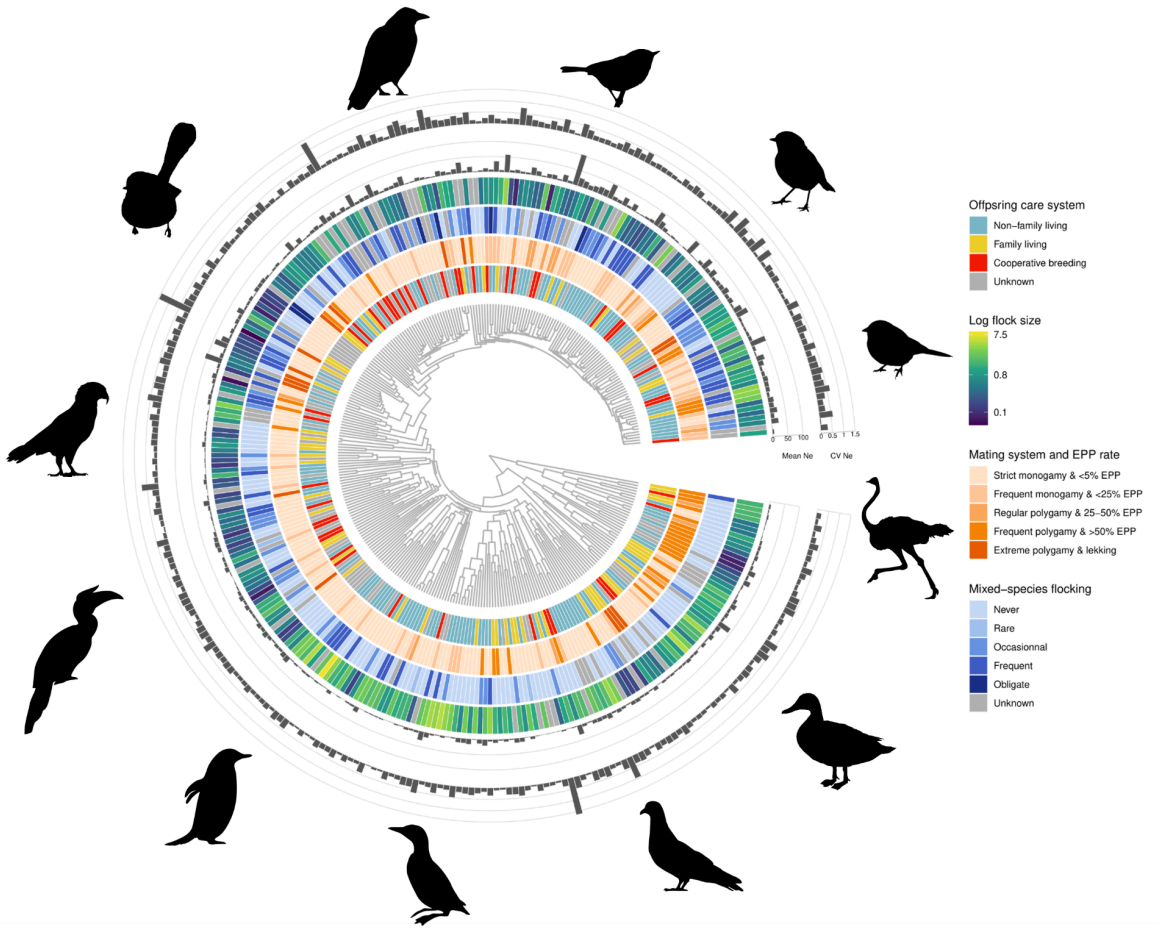

Figure 1: Phylogenetic distribution of social traits and summary statistics of bird demographic histories at the species level. The four colored inner circles highlight different components of species-level social complexity data for each of the four social traits used in this study, with gray bands representing missing data. The two outer circles represent respectively the harmonic mean and coefficient of variation of *Ne* in the last 500 kya, averaged at the species level. A total of 322 species are displayed on this phylogenetic tree, which was generated from v.1.4 of McTavish et al. (2025). The figure was produced using the R package *ggtree* (Yu *et al.* 2017) and all the bird silhouettes were obtained from PhyloPic under a public domain license.

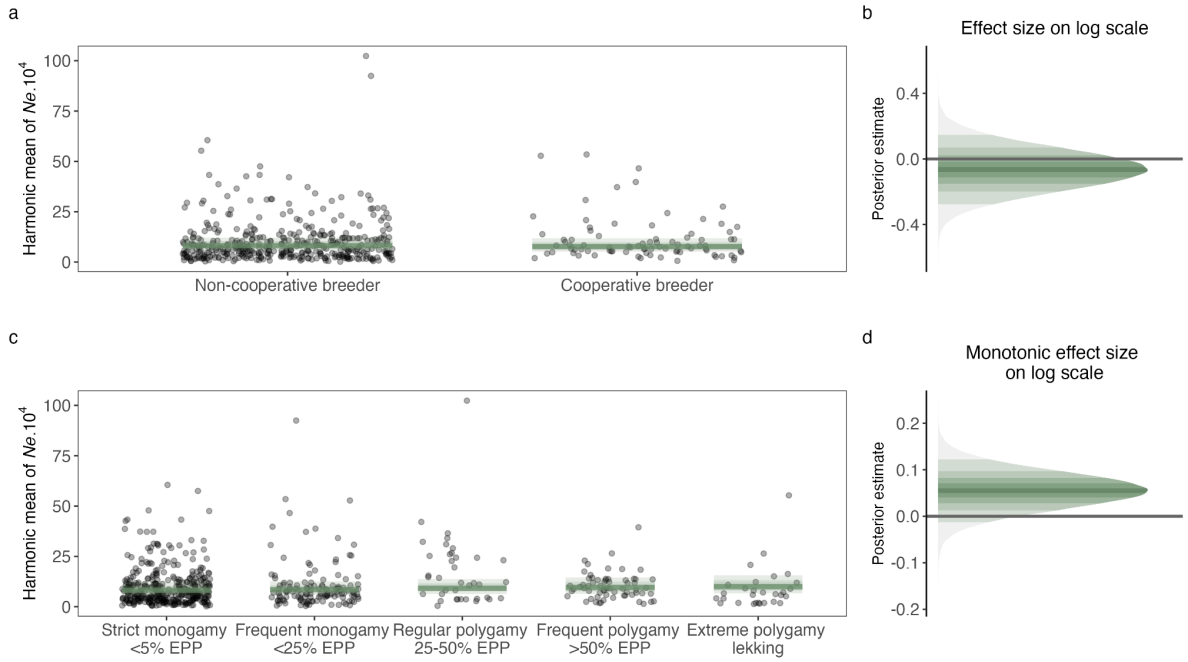

Figure 2: Effect of (a) offspring care system (cooperative breeding vs. non-cooperative breeding) and (c) mating systems (Frequency of polygamy and promiscuity) on the harmonic mean *Ne*. Posterior median effect sizes from the phylogenetic regression are represented by the darker lines, alongside their 10% to 90% credible intervals represented by the shaded bands. Each circle represents a sample (N = 473 samples from 232 species). Effect size of care system (b) and mating system (d) on the log scale from the lognormal phylogenetic regression, highlighting the estimated difference in the mean *Ne* between non-cooperative and cooperative breeders, and across mating systems and degrees of promiscuity..

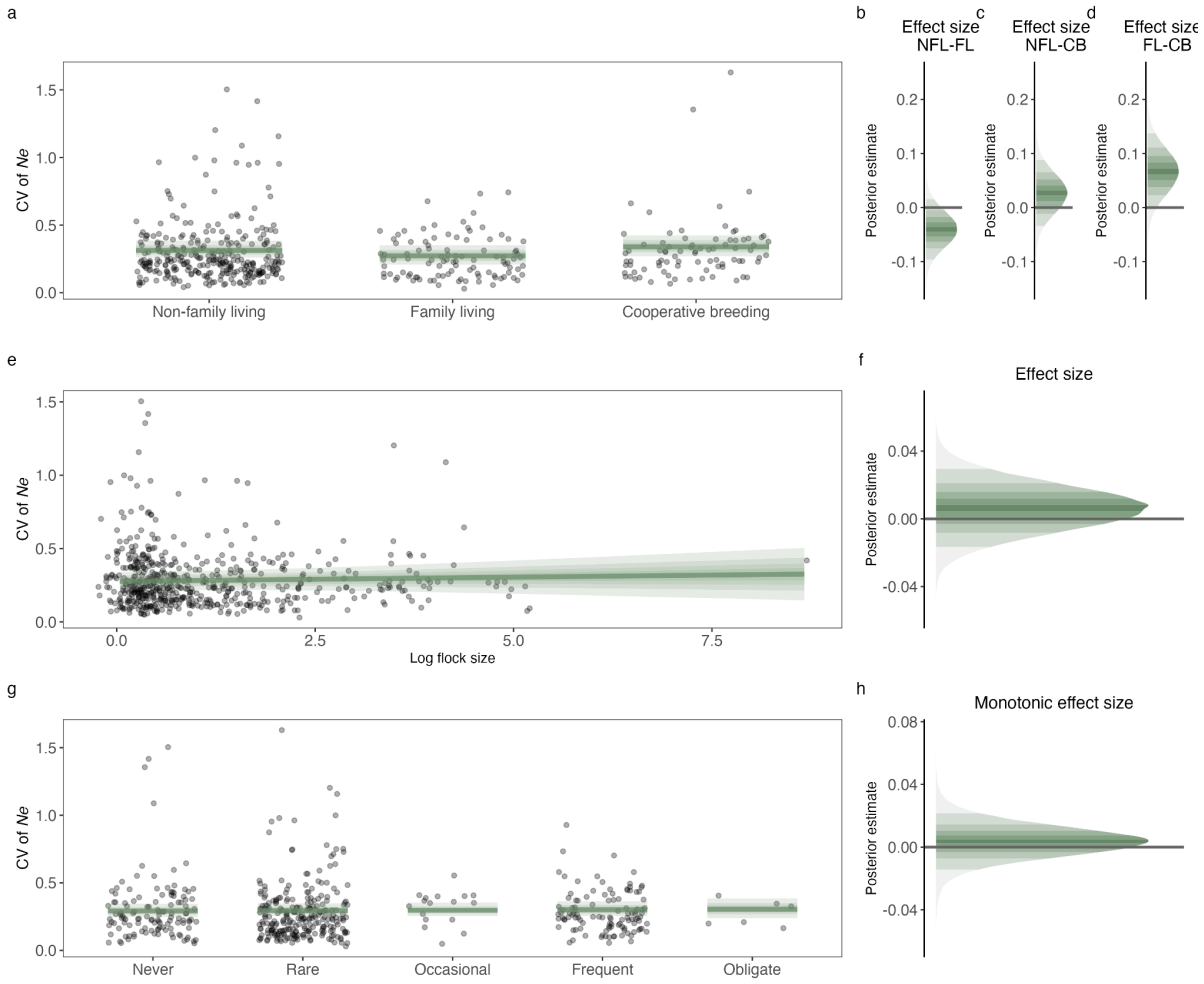

Figure 3: Top panels: (a) Effect of offspring care system (non-family living vs. family living vs. cooperative breeding) on the CV of *Ne* (N = 473 samples from 232 species), alongside the posterior distributions for the estimated difference between non-family and family living birds (b), non-family living and cooperatively breeding birds (c), and family living and cooperatively breeding birds (d). Middle panels: (e) Effect of average flock size on the CV of *Ne* (N = 553 samples from 270 species), alongside the posterior distribution for the estimated effect of flock size (f). Bottom panels: (g) Effect of the propensity of joining mixed-species flocks on the CV of *Ne* (N = 498 samples from 257 species), alongside the posterior distribution for the estimated monotonic effect of mixed-species flocking propensity (h). Posterior median effect sizes from the phylogenetic regression are

represented by the darker lines, alongside their 10% to 90% credible intervals represented by the shaded bands, and each circle represents a sample.

Supplementary materials

We compared the mutation rate estimates we used to calibrate the PSMC trajectories in this study with family-levels substitution rates recently estimated by Duchêne et al. (2025) using the same methodology as in our study, highlighting strong concordance between both. In addition, we compared the family-level estimates from Duchêne et al. (2025) to both direct measurements of mutation rates from parent-offspring trios from Bergeron et al. (2023), as well as previously used mutation rates in the comparative study of Bruniche-Olsen et al. (2021), highlighted that all these measures are positively correlated.

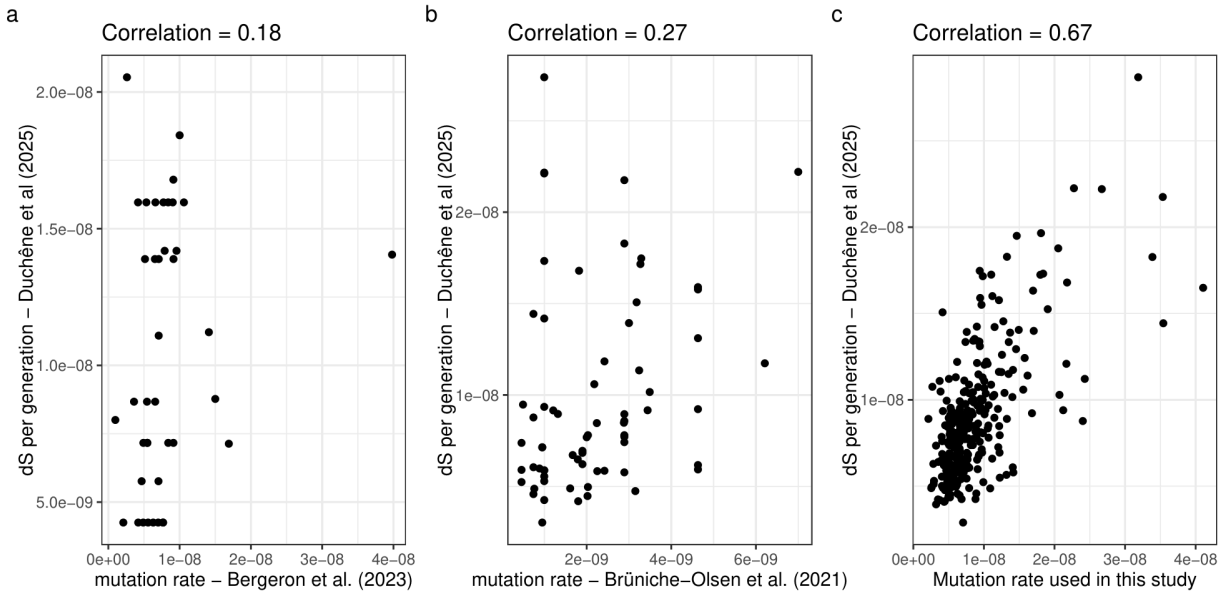

Figure S1: (a) Comparison of estimated family-level mutation rates and direct measurements from parent-offspring trios. (b) Comparison of estimated family-level mutation rates and previously used mutation rate estimates. (c) Comparison of our estimated mutation rates and family-level estimates from Duchêne et al. (2025).

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