A meta-analysis of global avian survival across species and latitude

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Abstract

Tropical birds are purported to be longer lived than their temperate counterparts, but it has not been shown whether avian survival rates covary with latitude worldwide. Here, we perform a global-scale meta-analysis of 1,007 estimates from 249 studies of avian survival and demonstrate that a latitudinal survival gradient exists in the northern hemisphere, is dampened or absent for southern hemisphere species, and that differences between passerines and nonpasserines largely drive these trends. We also show that while extrinsic factors related to climate were poor predictors of survival compared to latitude alone, the relationship between survival and latitude is strongly mediated by intrinsic traits – larger species with smaller clutch size had the highest survival. Taken together, our results suggest that interactions between intrinsic traits and lineage-specific effects surpass latitude and its underlying climatic factors in explaining global patterns of avian survival.

INTRODUCTION

Aves, a class represented by around 10,000 species, display a broad diversity of morphologies and behaviors, and also show considerable variation in their lifespan and annual survival. For example, in large-bodied landbirds, such as some raptors and parrots, annual survival is often high (Newton *et al.* 2016; Maestri *et al.*2017) and individuals are long lived, but for small-bodied species like warblers and kinglets, rates of annual survival can be low (DeSante*et al.* 2015; Johnston *et al.* 2016). While differences in body mass account for some of this variation – larger species tend to live longer than smaller ones (Lindstedt & Calder 1976, 1981; Promislow 1993; Speakman 2005) – many species live longer or shorter lives than predicted given their body mass (Healy *et al.* 2014). Other aspects of a species' life history, particularly the demographic cost of reproduction, may explain this residual variation in survival rates (Williams 1966; Stearns 1992; Roff 2002). This view stems from the hypothesis that limited resources (i.e., time and / or energy) result in an allocation trade-off between two competing vital functions; specifically, current reproduction reduces future reproduction and survival. The pivotal survival-reproduction trade-off has been well documented in birds (Ricklefs 1977, 2000; Saether 1988; Linden & Møller 1989; Martin 1995; Ghalambor & Martin 2001), and with the observations of early investigators that the number of eggs laid declines from the poles towards the equator (Moreau 1944; Lack 1947; Skutch. 1949), it has given rise to the expectation that tropical species should offset a reduced clutch size by having higher adult survival (Murray 1985).

There are many studies that suggest high adult survival in tropical birds, the majority of which focus on comparisons between north-temperate systems and the tropics (Martin 2004). Early reports of high survival came from studies equating survival estimates with return rates (Snow 1962; Fogden 1972; Fry 1980; Bell 1982; Dowsett 1985). While these studies deepened our understanding of life-history strategies in tropical birds, estimates based on return rates are problematic because they confound estimation of complicated functions of survival rate and capture probability (Nichols & Pollock 1983; Krementz *et al.*1989; Sandercock 2006). More recently, studies employing improved methods for estimating survival via Jolly-Seber (JS) and Cormack-Jolly-Seber (CJS) models, which separate apparent survival (i.e., Φ: the product of true survival

and site fidelity) from encounter probability (Sandercock 2006), have reinforced the idea of higher adult survival at lower latitudes (Faaborg & Arendt 1995; Johnston *et al.* 1997; Francis *et al.* 1999; Peach *et al.* 2001; McGregor *et al.* 2007). The generality of these findings, however, has been questioned based on comparisons showing negligible differences in survival between Central and North American birds (Karr *et al.*1990), and lower than expected survival rates for birds from South America (Blake & Loiselle 2008). Other studies have even found higher survival rates for south temperate birds compared to tropical species in Africa (Lloyd *et al.* 2014). Only one quantitative review has formally addressed latitudinal patterns in adult survival rates of birds across a broad range of latitudes. Muñoz *et al.* (2018) showed that adult survival was higher for species in the tropics compared to those in five sites across the north temperate zone, supporting the hypothesis of a latitudinal gradient in survival, at least for forest-dwelling passerines in the western hemisphere. Yet, despite longstanding interest in the idea of a latitudinal gradient in survival, we still lack an empirical synthesis at the global scale, which stands as a limiting factor in our ability to generalize these relationships to the diverse life history of birds found worldwide (Martin 2004).

Most explanations for a latitudinal survival gradient are based on the assumption of consistent latitudinal variation in survival and other life history traits with which it covaries, such as clutch size (Karr *et al.* 1990; Faaborg & Arendt 1995; Johnston *et al.* 1997; Peach *et al.* 2001; McGregor *et al.* 2007). Indeed, most comparative studies of variation in life history traits treat northern and southern latitudes equivalently (Jetz *et al.* 2008; Muñoz *et al.* 2018; Terrill 2018). However, this assumption may not always be met, since latitude itself does not directly influence organisms per se; rather, environmental factors that covary with latitude exert selective pressures on life history traits. For example, although there exists a global latitudinal gradient in clutch size (Cardillo 2002; Jetz *et al.* 2008), this trend is dampened in the southern hemisphere – south temperate species lay smaller clutches than those in the north temperate hemisphere (Yom-Tov *et al.* 1994; Martin 1996; Evans *et al.* 2005). Consistent with this pattern, south temperate birds in Africa also tend to be longer lived than their north temperate European counterparts (Lloyd *et al.* 2014). This hemispheric asymmetry may in part be due to differing climatic conditions between northern latitudes and equivalent southern ones. Namely, south temperate latitudes are less seasonal and have higher minimum winter temperatures, both of which have been hypothesized to decrease adult mortality and lead to smaller clutch size (Ricklefs 1980). Similarly, clades and their intrinsic traits that may influence survival rates are also distributed nonrandomly across environmental gradients (Jetz *et al.* 2008; Sibly *et al.* 2012). Migratory habit, for instance, arises at least in part from species occupying higher latitudes and experiencing seasonal environments with lower minimum winter temperatures, and there can be substantial deleterious effects on survival over the migratory phase of the annual cycle (Sillett & Holmes 2002; Rockwell *et al.* 2017). Thus, the geographic variation in survival rates reflects a composite of extrinsic factors, intrinsic traits, and historical events related to a species' lineage.

Because previous analyses of the latitudinal gradient in survival have focused on the north-temperate / tropical model (Martin 2004; Munoz *et al.* 2018) and have relied on a relatively narrow group of taxa, our current perspective of the biological underpinnings of the geographic variation in survival rates remains somewhat limited. Here, we present data on survival rates for 681 species of landbirds gathered from around the world (Fig. 1). The purpose of our analysis was to test the relative importance of latitude and extrinsic climate factors (temperature, precipitation, and seasonality) in explaining geographic patterns of avian survival rates, and to ask whether including intrinsic traits (body mass, clutch size, migratory habit) improved model predictions. Specifically, we ask: (1) Is there a latitudinal gradient in adult survival and, if so, are there differences between hemispheres? (2) Do climate measurements (extrinsic factors) explain differences in survival rates as well as latitude? (3) Do intrinsic traits explain additional variation in species-level survival rates? We tested for these relationships in both passerines and nonpasserines and between Old World and New World birds from mainland and island populations. By integrating data on macroecological processes with comparative biology, our modeling approach provides a powerful tool for understanding the diversity of life histories that have evolved across the globe.

METHODS

Assembling a global dataset of avian survival rates

We conducted a search of the peer-reviewed literature for studies that measured survival rate in birds, relying primarily on Web of Science Core Collections and Google Scholar. We also included data for survival rates of North American birds downloaded from the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante *et al.*2015). For each study, we extracted information on species' annual survival rates and their standard error. When the same study provided separate estimates for males and females, or where estimates were made for different time periods, ages of adult birds, or circumstances (e.g., successful breeders vs. unsuccessful, brood parasites present vs. absent) we took the geometric mean of those estimates. When estimates were available from different habitat types within the same study (e.g., logged vs. unlogged forest), we took the geometric mean of those estimates, provided that the study found no significant differences between groups. If group estimates were reported as significantly different, we chose the estimate from the control group for our analysis. A list of the 249 studies included in our analysis and a detailed account of our selection criteria is available in Supporting Information S1 and S2, respectively.

Extracting data for latitude, climate, and species' intrinsic traits

In order to assess the relationship between survival and latitude, we recorded the geographic coordinates for each species in each study from information provided in the paper itself or by locating the study area on Google Maps. For 26 studies that measured survival over broad spatial scales, such as at the national or continental level (e.g., the MAPS dataset; DeSante *et al.* 2015), we calculated the centroid of the breeding range for each species within the area specified by the study with occurrence data extracted from eBird using the *auk* package (Strimas-Mackey *et al.* 2018) in R (v.3.5.3; R Core Team 2019). This allowed us to estimate a unique latitude and longitude for the centroid of each species' realized breeding range rather than simply selecting an unweighted point in the study area itself. As latitude is often used as a surrogate for variation in climatic conditions between the north and south poles, we evaluated the predictive power of three key extrinsic factors that characterize the environment of a species and are hypothesized to influence avian survival: annual precipitation (Rockwell *et al.* 2017; Shogren *et al.* 2019), minimum winter temperature (Robinson *et al.* 2007; Salewski *et al.*2013), and temperature seasonality (Ricklefs 1980; Lloyd *et al.*2014). We also tested whether species' intrinsic traits explained global patterns in avian survival rates by collecting data on body mass, clutch size, and species' migratory habit, which we obtained from information contained in the paper, published reference databases (i.e., Jetz *et al.* 2008 for clutch size; Wilman *et al.*2014 for body mass; Barcante *et al.* 2017 for migration), or the Handbook of birds of the World Alive (del Hoyo *et al.* 2018). Further details describing our data compilations methods are available in Supporting Information S2.

Statistical analysis

We used logit survival as the response variable in our models to account for nonlinearassociations with extrinsic and intrinsic predictors. Prior to analysis, we $\log_{10}$ transformed body mass and clutch size due to skewness, and scaled latitude and climate data to z scores by subtracting their mean and dividing by their standard deviation. Most variables were weakly correlated, although both measures of temperature reached Spearman rank correlations >0.75 (Table S1). To estimate adult survival rates along the latitudinal gradient, we used a multi-level meta-analytical framework using the R package *metafor*(Viechtbauer 2010), which fits random and fixed effects models, weighting effect sizes by the inverse of their squared standard error. For each model developed, we accounted for sources of non-independence in our dataset that can arise when multiple survival estimates are extracted from the same study, are available for the same species, and / or due to common ancestry, by fitting study identity, species identity, and phylogeny as random intercepts. To incorporate phylogeny, we used a majority rules consensus tree derived from a set of 1,000 randomly-selected trees based on the global phylogeny of birds (Jetz*et al.* 2012), and pruned to our study taxa (Fig. S1) with the R package *phytools* (Revell 2012). We used the branch length from this consensus tree to specify values for the model variance-covariance matrix.

We first ran a random effects only model on the entire dataset using the*rma.mv* function to estimate a pooled effect size of global avian survival rates. Given potential differences in selection pressures experienced by

3

passerines vs. nonpasserines, species from Old World (Afrotropics, Indomalayan, Palearctic) vs. New World (Neotropics, Nearctic) biogeographic realms, and mainland vs. island bird populations, we also evaluated separate meta-analytic models using effect sizes for these six data subsets. We considered point estimates to be different from one another if their 95% confidence intervals (CI) did not overlap. We quantified total heterogeneity of each dataset by calculating Cochran's Q and I^2 statistics (Higgins & Thompson 2002).

To test for publication bias in our global dataset we used three complimentary methods: (1) We visually assessed asymmetry of funnel plots (Fig. S2); they appeared close to symmetrical. (2) We removed studies that reported survival estimates for >10 species, and which accounted for 64% of effect sizes, and reran the analysis. We repeated this procedure for studies conducted for <10 years to examine the effects of study duration on survival estimates. (3) We fit additional models where study method (i.e., live-recapture, dead recovery, or both) was used as a moderator or whether package *auk* was used to calculate the geographic coordinates. Results of this sensitivity analysis were all qualitatively similar to the global mean survival rate based on the entire dataset (Fig. S3).

We conducted meta-regressions (meta-analyses incorporating explanatory variables, hereafter referred to as "moderators") whereby we determined the effects on species-specific adult survival rates of (1) latitude, (2) extrinsic climatic factors, and (3) intrinsic traits in accordance with hypotheses described from the primary literature. We began by comparing fit of a latitude-only model, where regression slopes varied between hemispheres, to single-predictor linear models testing the influence of moderators on adult survival rates (Table S2). We next used AIC_C values (Burnham & Anderson 2002) to guide selection of a multi-predictor model of extrinsic climatic factors and intrinsic traits separately. Starting with the moderator that had the lowest AIC_C value, we sequentially added the next strongest moderator until AIC_C was no longer improved (Table S3). We considered the model that minimized AIC_C the most appropriate if it had fewer parameters and was at least 2 AIC_C less than the next most competitive model (Arnold 2010). All of the intrinsic moderators we assessed improved model fit and were carried forward to the next step of model development. Temperature seasonality ($Temp_{Seasonality}$) provided the best model fit for extrinsic moderators. We then combined both sets of moderators into a joint extrinsic / intrinsic model and repeated analysis using the global dataset and each of the six data subsets.

RESULTS

Meta-analytic means and the relationships between intrinsic and extrinsic moderators

The global meta-analytic mean calculated over 1007 effect sizes and representing 681 species and extracted from 249 publications, was 0.68 (95% CI = 0.48 to 0.83; Table S4). This is the back-transformed mean survival rate of all birds included in the analysis. Overall, the joint extrinsic / intrinsic model explained variation in survival well (Fig. S4, adjusted $r^2 = 0.43$). When we estimated separate meta-analytical means for the six data subsets, we found similar values with overlapping 95% confidence intervals between the global mean and mean effect sizes calculated for passerines vs. nonpasserines, Old World vs. New World biogeographic realms, and estimates from mainland vs. island birds (Fig. 2; Table S4). In addition, all models had values of P <0.0001 for Q_E and I^2 >90%, which indicated that substantial heterogeneity remained unexplained among studies and warranted our subsequent step of evaluating moderator variables.

We found evidence supporting the hypothesis of a latitudinal gradient in survival, and this effect was most apparent in the northern hemisphere. When we examined model predictions from a single-predictor model of latitude over the entire dataset, the odds of survival decreasing were 1.35 times greater for every 1deg increase in latitude in the northern hemisphere compared to the southern hemisphere (Fig. 3a). Similarly, the global joint model showed a negative, albeit nonsignificant, effect of latitude on survival for northern hemisphere species ($\beta = -0.121$, 95% CI = -0.293 to 0.050), while estimates for those inhabiting the southern hemisphere were close to zero ($\beta = -0.016$, 95% CI = -0.130 to 0.097; Table 1, Fig. 4). Driving this global trend at northern latitudes was a significant negative effect size for passerine birds ($\beta = -0.252$, 95% CI = -0.448 to -0.056; Fig. 4b) and a marginally significant effect of species / populations from the mainland ($\beta = -0.142$, 95% CI = -0.315 to 0.031; Fig. 4d). In contrast, effect sizes calculated for southern latitudes

4

were generally smaller, and the overall slope of the meta-regression line of the global model was shallower compared to the northern hemisphere (Figs 3a and 4). Only New World species (i.e., birds from South America) showed a significant negative association with latitude (β = -0.211, 95% CI = -0.378 to -0.045; Fig. 4c). Of the extrinsic climate moderators we considered, temperature seasonality was the most competitive within our AIC model selection framework (Table S2 and S3), although only marginally so compared to minimum winter temperature. Regardless of which climate moderator was used in the joint model, the effect calculated over the global dataset and for all data subsets was nonsignificant (Fig. 4).

In general, the relationship between survival and intrinsic life history traits was stronger than those of either climate or latitude (Fig. 4; Table 1). Effect size estimated from the global model was positive for mass (β = 0.236, 95% CI = 0.189 to 0.284; Fig 3c) and negative for clutch size (β = -0.507, 95% CI = -0.641 to -0.373; Fig 3d), which means that avian survival was higher for larger birds and for those with smaller clutch sizes. With the exception of mass for island species, similar results for both moderators were found for all data subsets (Fig. 4). When we included nonmigrant as a moderator in the global model, the effect size was small and positive, with confidence intervals marginally overlapping zero (β = 0.016, 95% CI = -0.005 to 0.039; Fig. 4), suggesting higher survival for year-round residents. This effect was strongest for passerines (β = 0.147, 95% CI = 0.011 to 0.254; Fig. 4b) and Old World birds (β = 0.237, 95% CI = 0.062 to 0.412; Fig. 4c).

DISCUSSION

Global-scale patterns of avian survival with latitude

We found support for the oft-toted latitudinal survival gradient, but this depended on both the geographic region and taxa being considered. Specifically, we demonstrate that the previously noted inverse relationship between latitude and survival is only weakly borne out across northern hemisphere avifauna overall, but that this effect is strengthened when considering only passerines or species inhabiting the mainland. In contrast, the relationship was only evident in the southern hemisphere for survival estimates from New World birds, the vast majority of which were passerines. When considered independently, there was no indication that nonpasserines had higher survival with decreasing latitude in either hemisphere. Overall, our meta-analysis reveals that while some tropical birds may be longer lived than their temperate counterparts, the shape of the latitude-survival response is likely to differ among species and between hemispheres.

Our synthesis is the first to assess global-scale patterns in avian survival rates; previous studies have either been limited geographically (Karr *et al.* 1990; Peach *et al.* 2001; Lloyd *et al.*2014), or have focused on a narrower range of species, such as raptors (Newton *et al.* 2016) or shorebirds (Méndez *et al.* 2018). To date, the most extensive analysis of avian survival and latitude comes from a study of 12 locations spanning 60° across the Americas (Muñoz *et al.* 2018). Our global-scale analysis compliments that of Muñoz *et al.* (2018), who reported a linear decrease in survival of roughly 2.1% for every 10° increase in latitude for passerine birds from Alaska to Peru, similar to what we observed for northern hemisphere species worldwide. Granted both our studies used a meta-analytical approach, Muñoz *et al.* (2018) conducted their analysis using a Bayesian mode of inference and considered only forest-dwelling passerines, while our study includes survival estimates of both passerines and nonpasserines from a variety of habitats, which we investigated using a maximum-likelihood approach. We also fit regression lines for latitude both north and south of the equator rather than testing the relationship between survival and absolute latitude. This latter point is particularly important, given that one general explanation for spatial patterns in life-history traits is that they arise from natural selection imposed by latitudinal gradients in environmental conditions (Cardillo 2002), which differ between hemispheres (Chown *et al.* 2004). Despite our use of different methods, the fact that we obtained some common results lends increased support to the overall relationship. Moreover, with our analysis, we provide a strong mechanistic basis for understanding variation in survival rates, as it better reflects the climatic variables that underlie latitude in the northern and southern hemispheres.

Hemispheric asymmetries in other patterns of avian life-history traits, such as timing of reproduction (Covas *et al.* 1999), clutch size (Moreau 1944; Martin *et al.* 2006; Lloyd *et al.* 2014), and parental care (Russell *et al.*

5

2004; Llambías *et al.* 2015), are well documented. The global patterns we identified are also congruent with the idea of a differential response of life-histories between hemispheres – we detected an inverse relationship between survival and latitude in the northern hemisphere but found little indication that this association was mirrored by southern hemisphere species overall. Only when we analyzed biogeographic realms in the southern hemisphere separately did we find that New World birds showed higher survival with decreasing latitude. This pattern is deceptive, however, since southern hemisphere nonpasserines account for little more than 1% of the effect sizes analyzed in the New World data subset. We therefore interpret this result as evidence of the latitudinal survival gradient in South American passerines. This means that for Old World birds, tropical species had similar survival rates to birds from the austral zone, and this was likely to be true regardless of whether they were passerines or nonpasserines. Survival estimates from Australasia and Oceania, biogeographic realms not traditionally included in the New / Old world classification, also reflected this same pattern and showed no evidence of a negative relationship with latitude.

Such differences may be explained, in part, by the historical geography and latitudinal positions of the continents. For the last 15 million years, South America has extended roughly 20deg further into the southern hemisphere than continental landmasses in the Old World. Thus, one reason we may have detected a negative trend in survival for southern hemisphere birds, but only in the New World, could simply be due to the greater range of latitudes and climatic conditions available to landbirds from South America with which to adapt. For example, latitudes greater than 35deg S are characterized by higher seasonality and mean annual temperatures [?]0degC (Chown *et al.* 2004); thus, this result may be indicative of a threshold response of avian survival to freezing temperatures and / or a more seasonal environment. Supporting this idea, mean survival of South American passerines that occurred at latitudes higher than 35deg S (survival rate = 0.38, n = 8) was lower on average than those from the highest latitudes occupied by birds in Africa (Old World survival at 34deg S = 0.69, n = 19). Only one other study has addressed the question of a latitudinal survival gradient in the southern hemisphere; Lloyd *et al.* (2014) found no indication of higher survival for birds living in tropical Malawi compared to austral South Africa. Our results are congruent with those findings and suggest that higher survival of tropical birds may be a pattern localized primarily to passerines from the northern hemisphere and in South America, where factors such as a more seasonal environment may limit resource availability and constrain species survival.

Influence of Climate on Survival

Our results suggest that temperature seasonality, at least at the resolution that we examined it, is a poor predictor of avian survival. Indeed, latitude-only models out-performed single-predictor models of extrinsic climate factors for each of the moderators we considered by a minimum of >4.88 ΔAIC_C (Table S2). Although temperature seasonality was not significant, our finding of higher survival in the southern hemisphere, but only for New World birds, is in accordance with reported asymmetries in climate between hemispheres. Compared to north-temperate latitudes, austral latitudes are characterized as less seasonal in general, having higher minimum winter temperatures and higher, less variable patterns of precipitation (Chown *et al.* 2004). That said, South America does posses environments with climates closer to those of the northern hemisphere (e.g., mean temperatures [?]0°C, higher temperature seasonality) compared to Africa and Asia, which lack such climate analogs at their southern-most latitudes. Although latitudinal variation in life history traits arises in part from natural selection imposed by complex interactions among environmental factors, latitude as a 'catch-all' variable provided a more complete picture of global variation in survival. For example, temperature seasonality fails to capture the negative latitude-survival relationship in passerines because this effect is counter-acted by pooling data for taxa from different regions; specifically, combining data with estimates for southern hemisphere passerines from the Old World. It appears, therefore, that latitude remains one of the best methods to portray the suite of climatic constraints that characterize a species' environment and leads to variation in life histories, but only when northern and southern hemispheres are examined independently.

Intrinsic traits mediate variation in the latitudinal survival gradient

We find that the association between body mass and survival and reproduction and survival – two of the

cornerstone trade-offs of life history theory (Stearns 1992) – are well supported by our meta-analysis, suggesting higher survival for larger birds and those with smaller clutch sizes. Notably, when mass and clutch size were included in the joint model, the strength of the latitudinal survival gradient was diminished (Table 1). Similarly, we found general support for the idea that sedentary behavior favors higher survival and, hence, shifts towards slower life-histories often associated with tropical latitudes. These results highlight the importance of considering the interplay between intrinsic and extrinsic variables when investigating macroecological processes. Latitude of course is associated with the changes in many aspects of avian life history, including migratory behavior (Alerstam *et al.* 2003), clutch size (Cardillo 2002; Jetz*et al.* 2008) and body mass (Olson *et al.* 2009), all of which have been demonstrated to increase globally with increasing latitude. Combined with these findings, our results are in accordance with the theory of a slow-fast life-history continuum (Ricklefs & Wikelski 2002) and suggest that while birds at tropical latitudes tend to be longer lived and have reduced clutches given their body size, this is far from the full picture. Global patterns of avian survival are driven by interactions between intrinsic traits and lineage-specific effects of latitude and their associated climatic factors.

Challenges in evaluating avian survival

Adult survival estimates are affected by several methodological caveats that we consider here. First, a general problem with comparing survival studies is that differences between estimates derived from old versus new methods and between live recaptures and dead recoveries may mask trends in the data (Roodbergen *et al.* 2012). Our dataset consisted primarily of studies that used live capture-mark-recapture techniques (83% of effect sizes) and most of these were conducted since 2000; nearly all studies were conducted after 1990 when modern statistical tools for analyses of marked animals were developed (Lebreton *et al.* 1992). One of the drawbacks of capture-mark-recapture data is that the reported metric, apparent survival, is a product of true survival and site fidelity and as such will always be biased low, whereas estimates of survival from dead recovery models are often interpreted as true survival (Sandercock 2006). Biases in survival estimates may therefore be strong for birds from tropical regions, which consisted exclusively of live-recapture data, and where behaviors such as altitudinal migration are more common than in temperate regions (Barcante *et al.* 2017) and can lead to temporary emigration from study plots. Another issue affecting the comparison of survival studies is the study duration. This, too, may be particularly problematic for tropical regions, where data collection is often hampered by sampling conducted over irregular or insufficiently long intervals to produce robust estimates of survival (Ruiz-Guiterrez*et al.* 2012). For example, in our meta-analysis 62% and 69% of effect sizes from austral and temperate latitudes, respectively, were calculated from datasets spanning >10 years, compared to only 34% from tropical latitudes. However, in a study of tropical birds comparing survival estimates derived from 6 vs.12 years of data, Blake & Loiselle (2013) reported an improvement in precision, but no change in point estimates for survival. Still, other authors argue that longer time frames are needed to generate reliable survival estimates for tropical resident species (i.e., 10–30 years), given their expected longevity and low recapture probabilities ($p <0.25$; Ruiz-Guiterrez *et al.* 2012). Despite these problems with the comparability of the data, we found no indication that difference in methodological approaches strongly biased our results (Fig. S3).

CONCLUSION

Based on a global-scale synthesis of avian survival rates, we find evidence that survival increases with decreasing latitude, but that this phenomenon is more nuanced than previous descriptions have characterized. Specifically, we demonstrate that the latitudinal survival gradient is stronger in northern hemisphere species, where climate seasonality may be greater. By including aspects of species life history traits in our models, we could explain a greater portion of the variation in survival rates than with latitude alone. These results indicate the importance of considering an organism's intrinsic traits as well as the extrinsic factors of their environment when describing broad-scale macroecological patterns. Where peaks in survival occur, how they relate to climatic variables, and how these patterns are likely to change through time and space given the effects of climate change, are of major importance for conservation. We hope that in assembling this database and dissecting some of the global patterns in survival across avian groups and hemispheres, we

7

can provide a platform for future work to target underrepresented regions and taxa and also make a clear path forward to better understanding variation in survival rates, and how it intersects with other life history traits across the world's avifauna.

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Table 1 Multi-predictor meta-regression models of avian survival based on only extrinsic factors (*Latitude* and *Temp* $_{\text{Seasonality}}$ combined) or intrinsic traits (*Mass* , *Clutch size* , and *Nonmigrant*) or a joint model that included both sets of moderators. *Latitude* was fitted with separate intercepts for the northern and southern hemispheres, *Temp* $_{\text{Seasonality}}$ is the difference in mean temperature of the three warmest vs. three coldest months, and *Nonmigrant* is a binary variable representing species migratory habit. $\Delta\text{AIC}_\text{C}$ columns represent the increase in model AIC_C when a moderator is dropped relative to the fully parameterized model. Model coefficients (β), 95% confidence intervals are shown for the full models. Significant effects are denoted as $p <$ 0.0001, ***; $p <$ 0. 01, **; or $p <$ 0. 05, *. For comparison, AIC_C for the random effects only model was 1613.66.
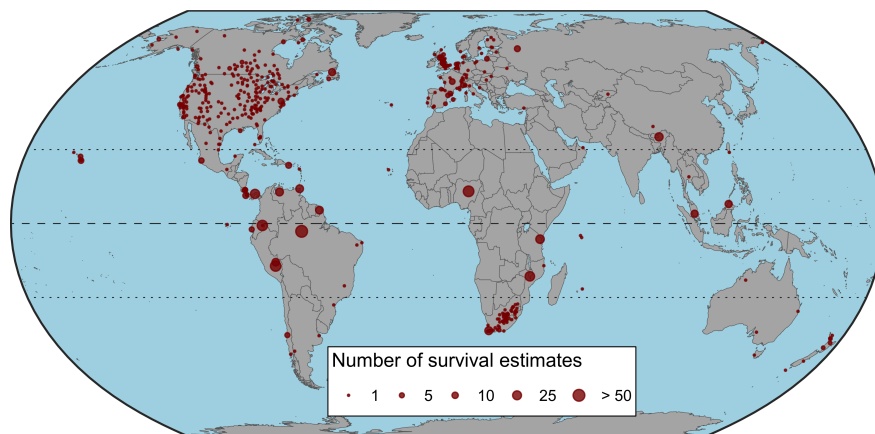
Variable	Extrinsic $\Delta\text{AIC}_\text{C}$	Intrinsic $\Delta\text{AIC}_\text{C}$	Multi-predictor models β	Multi-predictor models 95% LCL	Multi-predictor models 95% UCL	Multi-predictor models z	Multi-predictor models p	Joint model $\Delta\text{AIC}_\text{C}$	Joint model β	Joint model 95% LCL	Joint model 95% UCL	Joint model z
Latitude$_{\text{Northern}}$	6.07		-0.23	-0.41	-0.05	-2.51	*	0.74	-0.12	-0.29	0.05	-1.39
Latitude$_{\text{Southern}}$			-0.01	-0.14	0.12	-0.16			-0.02	-0.13	0.10	-0.29
Temp$_{\text{Seasonality}}$	1.12		-0.06	-0.14	0.03	-1.27		0.72	0.00	-0.09	0.08	-0.07
Body mass		79.40	0.23	0.18	0.27	9.57	***	82.05	0.24	0.19	0.28	9.69
Clutch size		67.53	-0.56	-0.68	-0.44	-8.99	***	46.81	-0.51	-0.64	-0.37	-7.43
Nonmigrant		6.69	0.15	0.04	0.25	2.79	**	1.54	0.1	-0.02	0.22	1.69

Figure 1 Location of effect sizes from 249 studies used in the meta-analysis of avian survival rates. The number of survival estimates reported at each location is illustrated by the size of the circle. Dashed line represents the equator while dotted lines at 23.4°N and S indicate the Tropic of Cancer and Capricorn, respectively, and delineate the tropics.

Figure 2 Mean avian survival and 95% confidence limits calculated over the entire dataset and from meta-regression models, which estimated intercepts independently for data from passerines vs. nonpasserine birds, Old World vs. New World biogeographic realms, and mainland vs. islands. Number of effect sizes used in each data subset is shown in parentheses. Dashed line indicates the difference from the overall meta-analytical mean.

Figure 3 Relationship between adult survival rate of birds from the entire dataset and moderator variables included in the joint extrinsic / intrinsic model (Table 1). Dashed lines represent the best linear fit based on model predictions estimated from single-predictor meta-regression models in *metafor* with 95% confidence intervals plotted as solid lines. Point sizes reflect the inverse of the standard error used to weight data points (i.e., more precise estimates appear as larger points).

Figure 4 Overall effect sizes for the six moderators considered in the joint extrinsic / intrinsic model for the global dataset (a) and over data subsets (b–d). Bars indicate 95% confidence limits. Effect sizes are considered significant where confidence limits do not overlap zero (dashed line).