




REVIEW AND SYNTHESES

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 949 estimates from 204 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 apparent survival compared to latitude alone, the relationship between apparent survival and latitude is strongly mediated by intrinsic traits – large-bodied species and species with smaller clutch size had the highest apparent survival. Our findings reveal that differences among intrinsic traits and whether species were passerines or nonpasserines surpass latitude and its underlying climatic factors in explaining global patterns of apparent avian survival.

Keywords

Birds, body mass, clutch size, demography, latitudinal gradient, life history.

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INTRODUCTION

Aves, a class represented by more than 10 000 species, display a broad diversity of morphologies and behaviours, 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 (i.e., > 0.95; 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 (i.e., < 0.25; DeSante *et al.* 2015; Johnston *et al.* 2016). While differences in body mass account for some of the variation in survival – 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 additional variation in survival rates (Williams 1966; Stearns 1992; Roff 2002). For instance, limited resources (i.e., time and/or energy) can result in an allocation trade-off between two competing vital functions; specifically, in this case, 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; Kremenetz *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 (Lebreton *et al.* 1992; 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 apparent survival between Central and North American birds (Karr *et al.* 1990), and lower than expected apparent survival for birds from South America (Blake & Loiselle 2008). Other studies have even found higher apparent survival 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 apparent survival of adults 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 generalise 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). Although many comparative studies of variation in life-history traits treat northern and southern latitudes equivalently (Jetz *et al.* 2008; Muñoz *et al.* 2018; Terrill 2018), this assumption is not always 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). Southern hemisphere and tropical passerines show extended periods of parental care and delayed dispersal compared to northern hemisphere species (Russell 2000; Russell *et al.* 2004), supporting the idea that greater parental care and increased juvenile survival balance the smaller clutch sizes observed in tropical and southern hemisphere species (Martin 1996). Consistent with this pattern, south temperate birds in Africa also tend to be longer lived than their north temperate European counterparts (Peach *et al.* 2001). A north-south hemispheric asymmetry in survival rates may in part be due to differing climatic conditions between northern latitudes and equivalent southern ones. Namely, with much of their landmass in close proximity to coastlines, south temperate latitudes are less seasonal and have higher minimum winter temperatures (Yom-Tov *et al.* 1994; Jahn *et al.* 2012), conditions which have been hypothesised 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 (Sillert & 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 largely focused on the north-temperate/tropical model (Martin 2004; Muñoz *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 review the literature on avian survival and synthesise survival data for 636 species of landbirds from around the world (Fig. 1). The

purpose of our meta-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 beyond using latitude alone? (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. By integrating data on macroecological processes with comparative biology, we address how the latitude-survival response may differ among species and across hemispheres.

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. We first searched for studies based on bibliographies compiled from previous publications of avian survival (Newton *et al.* 2016; Méndez *et al.* 2018; Muñoz *et al.* 2018). We then searched online using combinations of the following terms: 'survival', 'mortality', 'vital rate', or 'demography', and 'bird' or 'avian' in the Web of Science Core Collections and on Google Scholar. We also included data for apparent survival rates of North American birds downloaded from the Monitoring Avian Productivity and Survivorship (MAPS) programme (DeSante *et al.* 2015). Our initial survey resulted in over 2000 publications. We then screened titles and abstracts of publications and considered them for final inclusion in the meta-analysis if they met the following criteria: (1) the study provided estimates of adult survival, not juvenile or nestling, at the species level. (2) The species studied was from either the Old World (Afrotropical, Indomalaya, Palearctic) or the New World (Neotropical, Nearctic) biogeographical realm. (3) Estimates were from mainland populations of birds or, in a limited number of cases, large continental islands (e.g., Borneo, Trinidad, United Kingdom). We did not include estimates derived from populations on oceanic islands such as Hawaii. (4) The species studied was not pelagic. (5) The study did not include harvested or captive-bred populations, whose survival rates may not reflect those experienced under natural conditions. (6) Survival rate was estimated on the breeding grounds (i.e., we excluded estimates from studies of over-wintering or migratory stop-over sites). (7) The data were collected from marked populations of birds to estimate survival using live-encounter or dead-recovery data. (8) The study was conducted for at least 3 years, which is the minimum number of occasions needed to estimate the probability of encounter (p) from live-encounter data (Sandercock 2006). To avoid sex-biased differences in survival probability (Székely *et al.* 2014), we also required that (9) the estimate of survival included data from both males and females. In cases when studies had overlapping data, we retained the publication that presented the most information

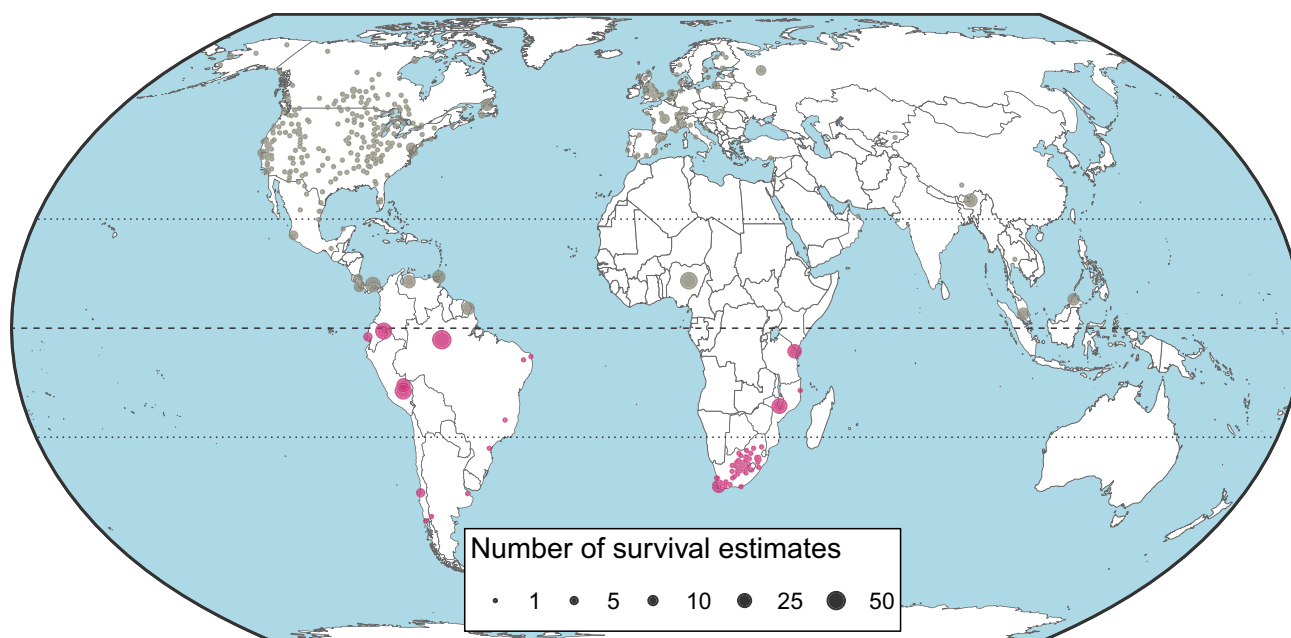


Figure 1 Location of effect sizes from 204 studies used in the meta-analysis of avian survival rates. The number of survival estimates reported at each location is illustrated by the size of the circle. Grey indicates studies collected from the northern hemisphere and pink studies from the southern hemisphere. 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.

(i.e., had more precise estimates or used a larger dataset). This second review narrowed the window of appropriate publications to < 350. However, many of these papers did not report measurement error on survival rate, which is required to weight individual effect sizes in meta-analyses. Our global dataset therefore consisted of 949 effect sizes extracted from 204 publications.

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 excluded the estimate from the habitat more altered by anthropogenic factors (i.e., logged forest) or, in one case, from a population of Barn Swallows (*Hirundo rustica*) breeding in the Chernobyl nuclear disaster site. A list of the 204 studies included in our analysis is available in Supporting Information S1.

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). Our modelling approach allowed us to estimate a unique latitude and longitude for the centroid of each species' realised 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 characterise the environment of a species and are hypothesised to influence avian survival: annual precipitation (Rockwell *et al.* 2017; Shogren *et al.* 2019) in mm, and minimum winter temperature (Robinson *et al.* 2007; Salewski *et al.* 2013) and temperature seasonality (Ricklefs 1980; Lloyd *et al.* 2014) measured in °C. 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; Barçante *et al.* 2017 for migration), or the Handbook of Birds of the World Alive (del Hoyo *et al.* 2019). Further details describing our data compilation methods as well basic features of the data used in our analysis are available in Supporting Information S2 and Table S1, respectively.

Statistical analysis

We used logit survival as the response variable in our models to account for nonlinear associations 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; however, both measures of temperature (i.e., $Temp_{Winter}$ and $Temp_{Seasonality}$) reached Spearman rank correlations > 0.90 (Table S2). To avoid issues of multicollinearity, we included only one of these variables for use in our modelling framework, using AIC_C values to guide selection of the stronger predictor (Burnham & Anderson 2002). Minimum winter temperature ($Temp_{Winter}$) provided the best model fit, but only marginally so compared to temperature seasonality ($\Delta AIC_C < 2$, Table S3).

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. Because differences in the field methods used to generate survival can lead to substantially different estimates (Martin et al. 2017, Mendez et al. 2018), we included estimation method as a random effect in each of our models. Specifically, we categorised survival as being derived from mark-recapture (i.e., from standard-effort netting), mark-resight, dead-recovery, or more complex models that use a combination of these data types. For each model developed, we also 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-rule consensus tree derived from a set of 1000 randomly selected trees based on the global phylogeny of birds (Jetz et al. 2012), and pruned to our study taxa (Fig. 2) with the R package *phytools* (Revell 2012). We specified values for the model variance-covariance matrix using the branch lengths from the consensus tree developed with *phytools*. We performed all statistical analyses in R environment 3.5.0 (R Core Team 2019).

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 life histories of passerines vs. nonpasserines, and environmental conditions experienced by species from Old World vs. New World biogeographic realms, we also evaluated separate meta-analytic models using effect sizes for these four data subsets. We considered point estimates to differ if their 95% confidence intervals (CI) did not overlap. For each dataset we calculated Cochran's Q to test for a difference between the individual study effects and the meta-analytical mean survival rate (Higgins & Thompson 2002). We further examined heterogeneity using the I^2 statistic, which provides a measure of the extent of the total variability in a set of effect sizes due to differences among studies (Higgins et al. 2003).

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. Previous research has

largely focused on either a macroecological approach, relating extrinsic environmental factors such as latitude to survival rates, or a comparative approach correlating survival rates to species' intrinsic traits, such as clutch size and body mass. We therefore began by comparing multi-predictor models of extrinsic moderators (latitude, annual precipitation, and minimum winter temperature) and intrinsic traits (body mass, clutch size, and migratory habit) separately to explore their relative contribution to predicting patterns of global avian survival. We then combined both sets of moderators into a joint extrinsic/intrinsic model and repeated the analysis using the global dataset and each of the four data subsets. As the majority of studies did not distinguish between losses due to mortality vs. emigration from the study area, we interpret all of our results in terms of apparent survival.

To test for publication bias in our global dataset, we used three complementary methods: (1) We visually assessed asymmetry of funnel plots (Fig. S1); they appeared to be close to symmetrical. (2) We removed studies that reported survival estimates for > 10 species, which accounted for 73% 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. Results of this sensitivity analysis were qualitatively similar to the global mean survival rate based on the entire dataset (Fig. S2). (3) Since extracting latitude and climate data from the centroid of a species' breeding range may obscure relationships between survival and explanatory factors, we repeated analysis of the global dataset after excluding studies where survival was estimated over broad spatial scales (i.e., studies in which package *auk* was used to calculate the geographic coordinates). We found no difference between effect sizes estimated using this reduced dataset compared to the global joint model (Fig. S3).

RESULTS

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

The global meta-analytic mean estimate of survival calculated over 949 effect sizes, representing 636 species and extracted from 204 publications, was 0.67 (95% CI = 0.46 to 0.83; Table S4). This estimate represents the back-transformed mean apparent 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 four data subsets, we found similar values with overlapping 95% confidence intervals between the global mean and mean effect sizes calculated for passerines vs. nonpasserines and Old World vs. New World biogeographic realms (Fig. 3; 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 evident in the northern hemisphere. When we examined model predictions of latitude based on extrinsic moderators only, the odds

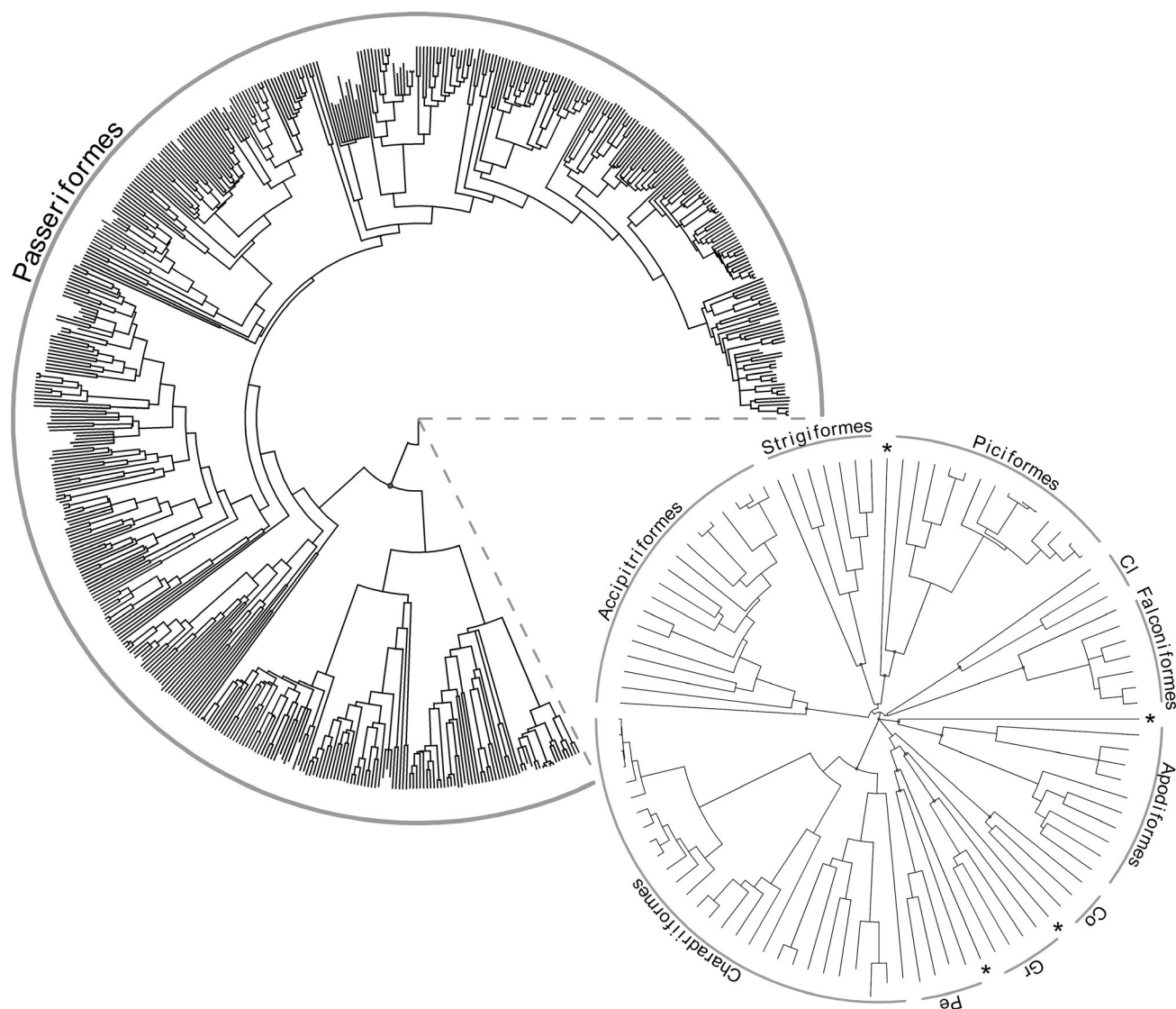


Figure 2 Phylogenetic relationships of the 636 species of birds used in the global meta-analysis of survival rates. Most species (83%) were in order Passeriformes. The call out shows nonpasserine orders used in the analysis. Red circles indicate nodes demarking branches for each of the orders. Abbreviations are: Cl = Coliiformes, Co = Columbiformes, Gr = Gruiformes, Pe = Pelcaniformes. From clockwise from top right, asterisk symbols show orders represented by a single species: Coraciiformes, Caprimulgiformes, Cuculiformes, Ciconiiformes.

of apparent survival decreasing were 1.2 times greater for every 1° increase in latitude in the northern hemisphere compared to the southern hemisphere (Table 1). After accounting for intrinsic traits in the global joint model, however, latitude retained relatively little residual effect, and estimates for northern hemisphere species ($\beta = -0.081$, 95% CI = -0.262 to 0.100), as well as for those inhabiting the southern hemisphere ($\beta = -0.042$, 95% CI = -0.161 to 0.076), were small and nonsignificant (Table 1, Fig. 5a). Only when we examined passerines and nonpasserines separately did we find a significant negative effect size of northern latitudes on apparent survival for passerine birds ($\beta = -0.261$, 95% CI = -0.473 to -0.048 ; Fig. 5b). In the southern hemisphere, we found New World species (i.e., birds from South America) also showed a significant negative association with latitude ($\beta = -0.185$, 95% CI = -0.344 to -0.026 ; Fig. 5c). Of the extrinsic climate moderators we considered, minimum winter temperature was

the most competitive within our AIC_C model selection framework (Table S3), although only marginally so compared to temperature seasonality. Regardless of whether minimum winter temperature (Fig. 5) or temperature seasonality (Fig. S5) was used in the joint model, the effect of climate moderators calculated over the global dataset were nonsignificant. We found similar results across the four data subsets, with the exception of the Old World, where milder winters and less seasonal environments appeared to have a marginally significant effect on apparent survival (Fig. 5c and S5c).

In general, the relationship between apparent survival and intrinsic life-history traits was stronger than those of either climate or latitude (Figs 4 and 5; Table 1). Both body mass and clutch size continued to have strong effects in the joint model, but this was less true of migratory habit. Effect size estimated from the global model was positive for body mass ($\beta = 0.251$, 95% CI = 0.201 to 0.301 ; Figs 4d and 5a) and

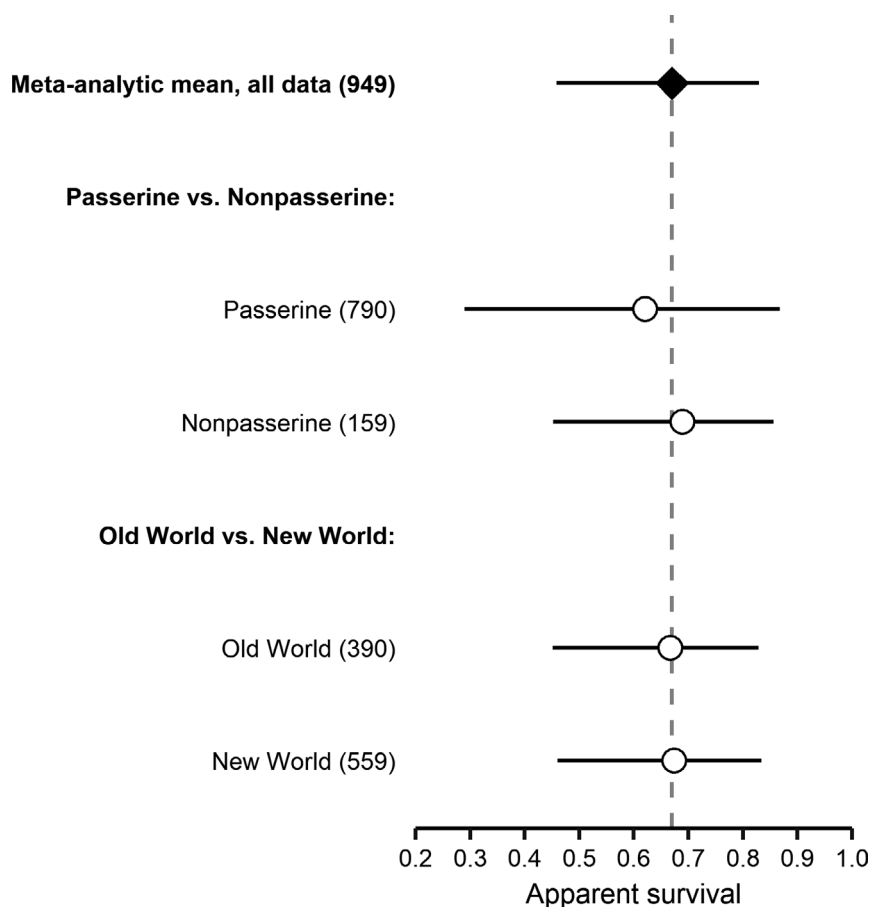


Figure 3 Back transformed mean avian survival and 95% confidence limits calculated over the entire dataset and from meta-regression models, which estimated intercepts independently for data from passerines versus nonpasserine birds, and Old World vs. New World biogeographic realms. Number of effect sizes used in each data subset is shown in parentheses. Dashed line is positioned to show difference from the overall meta-analytical mean.

negative for clutch size ($\beta = -0.506$, 95% CI = -0.646 to -0.366 ; Figs 4e and 5a), which means that apparent survival was higher for larger birds and for those with smaller clutch sizes. Similar results for both moderators were found for all data subsets (Fig. 5). When we included nonmigrant as a moderator in the global model, the effect size was small and

positive, with confidence intervals marginally overlapping zero ($\beta = 0.111$, 95% CI = -0.002 to 0.225 ; Fig. 5), suggesting higher apparent survival for year-round residents. This effect was strongest for passerines ($\beta = 0.142$, 95% CI = 0.008 to 0.276 ; Fig. 5b) and Old World birds ($\beta = 0.279$, 95% CI = 0.107 to 0.451 ; Fig. 5c).

Table 1 Multi-predictor meta-regression models of apparent avian survival based on only extrinsic factors or intrinsic traits or a joint model that included both sets of moderators

Variable	Extrinsic ΔAIC_C	Intrinsic ΔAIC_C	Multi-predictor models					Joint model					
			β	LCL	UCL	Z	P	ΔAIC_C	β	LCL	UCL	z	P
<i>Latitude</i> _{Northern}	4.07		-0.22	-0.42	-0.02	-2.17	*	-0.42	-0.08	-0.26	0.10	-0.88	
<i>Latitude</i> _{Southern}			-0.02	-0.15	0.12	-0.25			-0.04	-0.16	0.07	-0.70	
<i>Precip</i>	0.08		0.03	-0.04	0.11	0.85		-0.90	-0.01	-0.07	0.06	-0.20	
<i>Temp</i> _{winter}	1.15		0.05	-0.06	0.15	0.84		-0.50	0.03	-0.06	0.12	0.60	
<i>Body mass</i>		84.43	0.24	0.19	0.29	9.73	***	87.13	0.25	0.20	0.30	9.86	***
<i>Clutch size</i>		60.19	-0.56	-0.69	-0.44	-8.61	***	41.97	-0.51	-0.65	-0.37	-7.08	***
<i>Nonmigrant</i>		7.78	0.16	0.06	0.26	3.03	**	2.28	0.11	0.00	0.23	1.92	
Model AIC_C	1448.12	1297.41						1296.27					

Latitude was fitted with separate intercepts for the northern and southern hemispheres, *Precip* is the total annual precipitation, *Temp*_{winter} is the minimum temperature measured over the coldest month, and *Nonmigrant* is a binary variable representing species migratory habit. Model AIC_C is the AIC_C for each fully parameterised model. ΔAIC_C columns represent the increase in model AIC_C when a moderator is dropped relative the full model. Model coefficients (β), and lower (LCL) and upper (UCL) 95% confidence limits 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 of the random effects only model was 1468.74

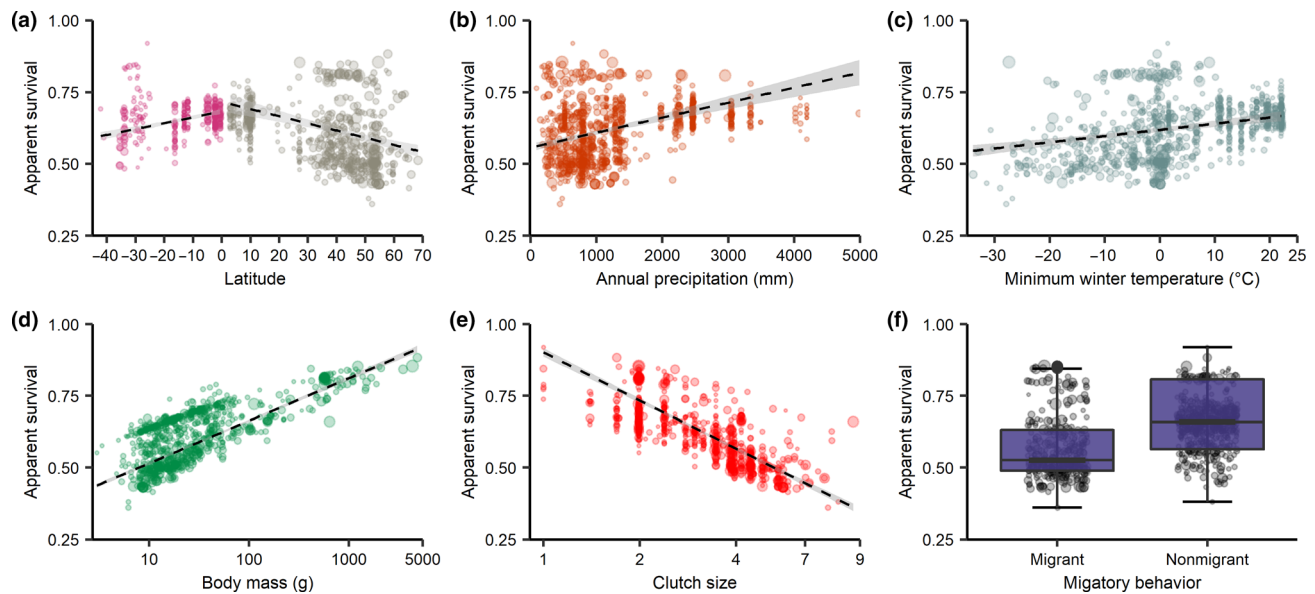


Figure 4 Relationship between apparent adult survival and each moderator used in the meta-analysis (Table 1). Dashed lines represent the best linear fit based on predictions estimated from the joint extrinsic/intrinsic model and using the global dataset of 949 effect sizes. Grey shading indicates 95% confidence limits. Point sizes reflect the inverse of the standard error used to weight data points (i.e., more precise estimates appear as larger points). Body mass and clutch size are reported on the \log_{10} scale.

DISCUSSION

Global-scale patterns of avian survival with latitude

We found support for a latitudinal gradient in avian survival, but this depended on both the taxa and geographic region 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. In contrast, the relationship was only evident in the southern hemisphere for apparent 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 apparent survival; 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 apparent 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 passerines 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 apparent 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. Analysing the northern and southern hemispheres separately 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), and 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 apparent survival, 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.* 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 apparent survival and latitude in northern hemisphere passerines but found little indication that this association was mirrored by southern hemisphere species overall. Only when we analysed biogeographic realms in the southern hemisphere separately did we find that New World birds showed higher apparent survival with decreasing latitude. This pattern is deceptive, however, since southern

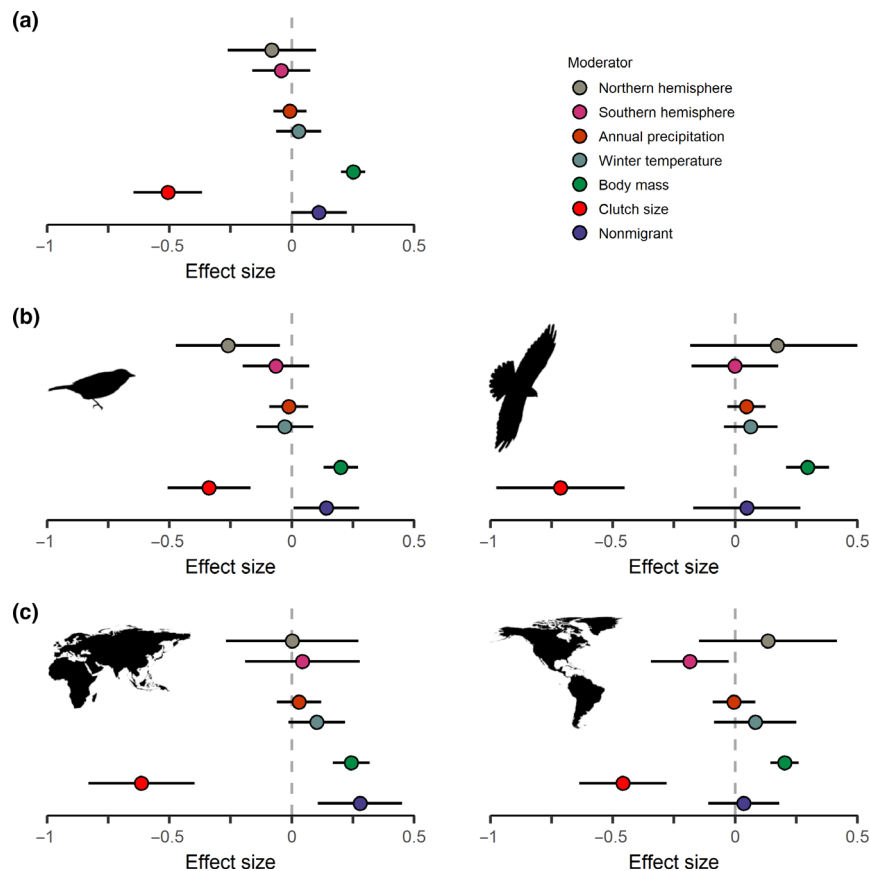


Figure 5 Overall effect sizes for the six moderators considered in the joint extrinsic/intrinsic model for the global dataset (a) and over data subsets, including passerine and nonpasserine (b), and Old World and New World biogeographic realms (c). Bars indicate 95% confidence limits. Effect sizes are considered significant where confidence limits do not overlap zero (dashed line).

hemisphere nonpasserines account for < 1% of the effect sizes analysed 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 apparent survival rates to birds from the austral zone, and this was likely to be true regardless of whether they were passerines or nonpasserines.

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 20° further into the southern hemisphere than continental landmasses in the Old World. Thus, one reason we may have detected a negative trend in apparent 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 35° S are characterised by mean annual temperatures $\leq 0^{\circ}\text{C}$ and higher seasonality (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 apparent survival of South American passerines that occurred at latitudes higher than 35° 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 34° 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 apparent survival for birds living in tropical Malawi compared to austral South Africa. Our results are congruent with those findings and suggest that higher apparent survival of tropical birds may be a pattern localised primarily to passerines from the northern hemisphere and in South America, where factors such as a lower minimum winter temperature and more seasonal environment may limit resource availability and constrain species survival.

Influence of climate moderators on apparent survival

Our finding of an inverse, albeit weak, relationship between apparent survival and minimum winter temperature and temperature seasonality in Old World birds is consistent with results from other studies comparing avian survival across latitudes within the Afrotropics (Lloyd *et al.* 2014) and between African and European birds (Peach *et al.* 2001). While we found no significant effect of climate moderators for the New World, our finding of higher apparent survival in South American birds is in accordance with reported asymmetries in climate between hemispheres. Compared to north-temperate latitudes, austral latitudes are characterised 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 possess environments with climates closer to those of the northern hemisphere (e.g., mean temperatures $\leq 0^{\circ}\text{C}$, higher temperature seasonality) compared to Africa and Asia, which lack such climate analogues at their southernmost latitudes. In a study spanning northern and southern hemispheres, Ricklefs (1997) found a strong correlation between survival rates and the difference between maximum and minimum mean monthly temperatures, (i.e., temperature seasonality) in New World thrushes, particularly in the northern hemisphere. We might expect studies from focused datasets to show stronger relationships, particularly those examining a single genus or group of closely related species whose ranges span latitudes, since lineage-specific variation in survival rates is minimised.

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, climate moderators failed to capture the negative latitude-survival relationship in passerines because this effect is counteracted 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 characterise 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 apparent survival for larger birds and those with smaller clutch sizes. Notably, when body 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 behaviour favours 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 behaviour (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 and limitations in evaluating avian survival

Survival rates are inherently difficult to study in free-living populations of birds because they require the initial capture and subsequent recapture, resighting, or recovery of marked individuals throughout their lifetime (Lebreton *et al.* 1992). One of the drawbacks of mark-recapture and mark-resighting 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). The vast majority (88%) of our estimates were reported as apparent survival. Thus, the variation in apparent survival we report between hemispheres, biogeographical realms, and passerines and nonpasserines is also affected by site fidelity. For example, if the differential costs of dispersal and territory exploration are absorbed by seasonal migratory movements, then differences in site fidelity could offer an alternative explanation for the patterns in apparent survival between migrants and residents we observed, particularly in Old World birds. The perception of lower apparent survival among birds at high latitudes in the northern hemisphere might also be explained by lower site fidelity if a higher proportion of the species in the community were migratory or more likely to disperse to find resources. In tropical species, behaviours such as altitudinal migration are more common than in temperate regions (Barçante *et al.* 2017) and can also lead to temporary emigration from study plots. Our observed patterns in apparent survival should therefore be interpreted as minimum estimates of true survival.

Underestimation of true survival can also result from differences in the estimation method used by researchers. Our dataset consisted primarily of studies that used standard-effort mark-recapture techniques (72% of effect sizes), which have been shown to lead to consistently lower estimates of apparent survival compared to studies that use a combination of mark-recapture and resighting data (Lloyd *et al.* 2014; Martin *et al.* 2017; Méndez *et al.* 2018). For example, in a study of tropical passerines Martin *et al.* (2017) was able to verify that a high proportion of colour-marked individuals remained in the study area, but were never recaptured using standard-effort netting. Biases in survival estimates may therefore be strong for birds from tropical regions in general, which consisted mostly of standard-effort netting data. Our study also makes use of the very extensive mark-recapture estimates generated by the MAPS program in North America. While these estimates may be biased low (Ricklefs *et al.* 2011), they also provide a more balanced comparison to data for Central and South American species, which were often derived using similar field techniques. Although we included estimation method as a random effect in our models, we acknowledge that methodological differences among studies may have masked our ability to detect patterns in apparent survival.

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-Gutiérrez *et al.* 2012). For example, in our meta-analysis 63% and

73% of effect sizes from austral and temperate latitudes, respectively, were calculated from datasets spanning > 10 years, compared to only 46% from tropical latitudes. However, in a study of tropical birds comparing survival estimates derived from 6 versus 12 years of data, Blake & Loiselle (2013) reported an improvement in precision, but no change in point estimates for survival. Our results support this finding, and indicate that confidence limits are smaller for apparent survival estimated from studies that were conducted for > 10 years, but mean apparent survival differs little from that of the overall meta-analytical mean (Fig. S2). 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-Guitérrez *et al.* 2012).

Future directions

The case studies included in our meta-analysis cover all of the world's major terrestrial biomes on every continent of the Old World and New World biogeographic realms. However, there remain substantial gaps in our spatial coverage, particularly for regions of North and Central Africa, and much of continental Asia. More than 3700 species are found throughout Asia alone – more than a third of the world's avifauna – yet the number of survival estimates from Asian countries number less than 100 in our meta-analysis. We also did not consider species from the Australasian biogeographical realm in our study, in part because we found very few estimates of apparent survival from Australia that met the appropriate criteria for inclusion in our meta-analysis. Oceania in general contains lineages of birds that have evolved under very different ecological circumstances, and thus may be expected to deviate from the patterns we generally observed. For instance, many temperate-breeding Australian birds display a suite of slow life-history characteristics (i.e., high survival and small clutch size), but these traits are not accompanied by low BMR (Bech *et al.* 2016). A focus on survival estimates from these parts of the world is therefore needed to achieve a coherent picture of global variation in survival. Although many countries have regional or nationwide banding programs capable of producing estimates of survival rates, regrettably, the data remain unavailable, unanalysed, or both. In part, our ability to bridge macroecological and evolutionary processes to describe life-history variation has been limited because of this lack of data accessibility. A laudable goal, therefore, is for banding/ringing programs throughout the world to work towards making these data more readily available (e.g., following the MAPS banding database model) and to better equip researchers with the ability to analyse data for marked populations of birds. Towards this goal, Figure 1 can offer a roadmap to identifying data deficient areas around the globe where we know very little about avian survival and its intrinsic and extrinsic correlates.

Another fruitful direction for future research, given the hemispheric and biogeographic differences we found, is to design studies of survival covering other environmental gradients; for instance, examining life-history trade-offs and

variation across gradients like altitude within the tropics or temperate zone. Many temperate species appear to show shifts towards slower life-history strategies at high elevations, including higher survival and smaller clutch size (Hille & Cooper 2015; Boyle *et al.* 2016), while tropical species may not (Scholer *et al.* 2019). Understanding why montane species differ in their response to high elevation conditions may lend additional insights into the relationships of extrinsic factors and intrinsic traits with apparent survival.

Our latitudinal comparison does not incorporate other aspects of species natural history or behaviors that may significantly impact survival rates. For instance, social behaviours vary widely among bird species, particularly within the tropics. Many estimates of apparent survival for tropical birds represent species that utilise leks or territories, where individuals exhibit high survival and site fidelity (Sandercock *et al.* 2000). Mixed-species flocks within the tropics show high stability in space and time (e.g., Jullien & Thiollay 1998), unlike their temperate counterparts, and in some cases maintain consistent territory positions over decades (Martínez & Gomez 2013). Furthermore, a number of tropical and southern hemisphere species are cooperative breeders, which may show distinct demographic characteristics (Edwards & Naeem 1993; Poiani & Jeremiin 1994). One method to address such variation and to effectively evaluate trends in survival, or other life-history traits, across latitudes is to focus on phylogenetic lineages with species represented across tropical and temperate habitats (Ricklefs 1977, Martin 2002; Boyce & Martin 2017). Such approaches offer ways to both complement and provide additional insights into the complexities of latitude-survival relationships, which may be otherwise concealed by variation found across distantly related lineages within a broad meta-analysis.

CONCLUSION

Based on a global-scale synthesis of apparent avian survival rates, we find evidence that survival increases with decreasing latitude, but that this phenomenon is more nuanced than previous descriptions have characterised. Specifically, we demonstrate that the latitudinal survival gradient is stronger in northern hemisphere species, where minimum winter temperature and climate seasonality may be greater. When including aspects of species life-history traits in our models, we could explain a greater portion of the variation in apparent survival than with latitude alone. By revealing that there are stronger relationships among intrinsic traits, this study also underscores the 'pace of life' syndrome in birds – notably, where species fall out along the slow-fast life history continuum is particularly important in predicting apparent survival across species globally. Where peaks in survival occur, how they relate to climatic variables, and how these patterns are likely to evolve 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 apparent survival across avian groups and hemispheres, we 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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AUTHORSHIP

MNS and JEJ conceived of the ideas, MNS designed the study, collected data, and performed the meta-analysis, MSM modelled eBird data and assisted with data visualisation. MNS and JEJ wrote the manuscript with contributions from MSM.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data used in this manuscript will be archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.qv9s4mwbwbs>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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