



# Stronger negative species interactions in the tropics supported by a global analysis of nest predation in songbirds

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## Abstract

**Aim:** Species interactions are assumed to be stronger closer to the equator. However, numerous studies provided conflicting results and considerable controversy exists concerning the latitudinal patterns in the intensity of biotic interactions. Thus, the question of whether biotic interactions are stronger near the equator remains open. Here, we provide a global evaluation of latitudinal trends in nest predation in songbirds and their explanations.

**Location:** Worldwide.

**Taxon:** Songbirds (Aves: Passeriformes).

**Methods:** We collected published data on nest predation in 1297 populations of 659 species across the globe (124,958 nests). We quantified latitudinal trends in the intensity of nest depredation (daily predation rate, DPR) and in potential demographic impacts of nest depredation (the proportion of nests destroyed by predators). We also quantified the latitudinal trend in the proportion of failed nests destroyed by predators and assessed how nest depredation and latitudinal trends differed across nest types. We aimed at explaining spatial variation in nest predation by productivity and species richness of potential nest predators.

**Results:** All measures of nest predation increased towards the equator and the increase was stronger in the northern hemisphere. Nest predation also increased with time, and it was higher in open nests than in cavities. Nest predation increased with productivity (indexed by NDVI), independently of latitude. It also increased with species richness of potential nest predators, but this effect was confounded with latitude.

**Main conclusions:** Tropical songbirds faced both higher intensity of nest predation (higher DPR) and more detrimental demographic outcomes of nest depredation (higher proportion of nests lost to predators). Moreover, the proportion of nest failure caused by predators also increased towards the equator. Our results support the view that birds are subject to strong biotic interactions close to the equator. Nest predation increased with productivity and tended to increase with species richness of potential nest predators.

## KEYWORDS

biotic interactions, daily predation rates, nest failure, Normalized Difference Vegetation Index, latitudinal gradient, passerines

## 1 | INTRODUCTION

The received wisdom of ecology is that species interactions are stronger closer to the equator, including predation, herbivory and parasitism (reviewed in Schemske, 2009). If true, this should have important consequences for a number of ecological phenomena. For example, species distributions should be limited by biotic interactions close to the equator, while abiotic factors should be more important at higher latitudes (Gaston, 2007; MacArthur, 1972). Furthermore, herbivory should be more intense in the tropics (Baskett & Schemske, 2018; Longo et al., 2019) leading to herbivore specialization (Forister et al., 2015), stronger plant defences (Salazar & Marquis, 2012) and narrow, one-to-one coevolution between insects and host plants (Ehrlich & Raven, 1964). This should in turn boost the hyperdiversity of tropical insects (Novotny et al., 2006). Similarly, arthropod predation on herbivorous insects was shown to be higher in the tropics, selecting for better defence mechanisms in tropical arthropod herbivores compared to temperate ones (Roslin et al., 2017). However, the emerging picture is not clear-cut. On the contrary, numerous studies provide conflicting results and considerable controversy exists concerning the latitudinal patterns in the intensity of biotic interactions (Adams & Zhang, 2009; Chen & Moles, 2018; Moles, 2013; Moles et al., 2011; Moles & Ollerton, 2010; Zvereva et al., 2019). Thus, the question of whether biotic interactions are generally stronger near the equator remains open.

Predation on bird nests is an ideal system to study latitudinal gradients in species interactions. First, it is the most important factor responsible for nest failure in birds (Remeš et al., 2012a, 2012b; Ricklefs, 1969), and thus is a major selective force moulding parental behaviour at the nest and avian life histories (Lima, 2009; Martin & Briskie, 2009). Second, nest predation can have a sizeable impact on bird demography and population viability, with important implications for the conservation of endangered avian populations (Gibbons et al., 2007; Hilton & Cuthbert, 2010; Newton, 1998). Moreover, due to a long tradition of field ornithology, substantial data exist on the rates of nest destruction by predators. Previous studies capitalized on this tradition and analysed geographical trends in nest predation rates. Remeš et al. (2012a) showed that nest predation of passerine birds increased towards the equator in Australia, while Unzeta et al. (2020) confirmed this result for non-cavity breeding passerines of the world. Similarly, Kubelka et al. (2018) found out that rates of nest predation in shorebirds were higher close to the equator and in recent decades also in the Arctic. Thus, these studies suggest that overall nest predation rates may be higher in the tropics, but also leave some important questions unanswered.

We identify three questions worth careful evaluation. First, overall nest predation is a product of predation rate (intensity per day) and the duration of nest exposure to predators (the length of nest cycle). Many previous studies were unable to separate these two sources of predator-caused nest failure, because doing so is not easy in meta-analyses of published data (see discussion in Bulla et al., 2019; Freeman et al., 2020; Kubelka et al., 2018, 2019). We suggest that one remedy is to analyse how the importance of nest depredation

changes with latitude in comparison to other sources of nest failure. This approach naturally controls for the length of nest exposure and thus allows an unbiased evaluation of the latitudinal gradient in the importance of nest depredation. Second, the strength of species interactions might be modified by plant and animal structures, for example seed hardness and leaf toughness in case of herbivory (Lucas et al., 2000; Van Der Meij et al., 2004) or shell strength in case of predation (Rosin et al., 2013). In case of nest predation, the structure of bird nests is thought to modify predator-prey interaction strength. More specifically, nests in cavities and crevices usually suffer from lower nest predation (Auer et al., 2007; Martin, 1995; Oniki, 1979). While the same has been traditionally claimed for domed nests (Hall et al., 2015; Oniki, 1985; Skutch, 1985), recent evidence suggests that domed nests have thermoregulatory rather than anti-predator advantages (Martin et al., 2017). Given the potential effect of nest structure on the probability of nest depredation, studying whether the latitudinal gradient in nest predation differs among nest types should be a research priority. Third, while increasing nest predation rates towards the equator have been identified previously (Kubelka et al., 2018; Remeš et al., 2012a; Unzeta et al., 2020), we currently lack broad-scale explanations for spatial patterns in nest predation. We suggest testing two biogeographical hypotheses, namely environmental productivity and predator diversity. High productivity enables high densities of consumers, including potential nest predators (Storch et al., 2018; Tallavaara et al., 2018). We thus predict a positive correlation between productivity and nest predation rates. Moreover, high species richness of potential nest predators can also lead to high nest predation rates because it is difficult to avoid nest depredation when prey faces many predator species with diverse search strategies (Martin, 1993).

Here, we provide a global evaluation of the latitudinal trend in nest predation in passerine birds and its explanations. We collected the largest and most detailed dataset on nest failure caused by predators in passerines from literature. We addressed four questions. First, we quantified latitudinal trends in both the intensity of nest depredation (daily predation rates) and in potential demographic impact of nest depredation (the proportion of nests destroyed by predators). Second, we quantified the latitudinal trend in the proportion of failed nests destroyed by predators. This approach avoids potential biases of different nest exposure duration across species. Third, we assessed how nest depredation differed across nest types (open, domed and cavity) and whether latitudinal trends differed between nest types. Fourth, we tested two biogeographical explanations for the latitudinal trend in nest predation: environmental productivity and species richness of potential nest predators.

## 2 | MATERIALS AND METHODS

We collected data for this study from the literature. To find articles with data on the nest predation rates in songbirds (Passeriformes), we searched major ornithological compendia (Ali & Ripley, 2002; Cramp, 1998; Fry et al., 2000; Fry & Keith, 2004; Higgins et al., 2001,

2006; Higgins & Peter, 2002; Hockey et al., 2005; Keith et al., 1992; Poole & Gill, 1992; Safford & Hawkins, 2013; Skutch, 1954, 1960, 1969; Urban et al., 1997) and examined all volumes of major local zoological journals (Appendix S1 in Supporting Information). We located additional articles from literature cited in the articles obtained in the above-mentioned ways. We ignored populations breeding in nest boxes.

From articles resulting from the literature search we extracted the number of nests studied, the total number of nests failed, and the number of nests which failed due to nest predation. Using those numbers, we calculated (1) overall failure as the fraction of nests that failed, (2) nest predation as the fraction of depredated nests out of total nests found and (3) predator-caused nest failure as the fraction of depredated nests out of all nests that failed. Where possible, we also extracted information on daily predation rates calculated using the Mayfield method (DPR Mayfield; Mayfield, 1975). In cases when the authors did not provide DPR calculated in this way but provided information on the number of exposure days and the number of depredated nests, we used those numbers to calculate DPR Mayfield as nest depredated/exposure days.

We transformed the proportion of nests lost to predators to daily predation rates (DPR) using the method of Ricklefs (1969). The method gives  $DPR = -[\ln(1 - PR)]/T$ , where PR is nest predation intensity (i.e. the fraction of nests destroyed by predators out of the nests found) and T is the length of the nest cycle. For all the estimates of daily rates, the length of the nest cycle was calculated as the sum of incubation period, nestling period and clutch size. It should be noted that this method does not estimate true daily rates that can be obtained only by applying the Mayfield method (Mayfield, 1975) on the original datasets, and these are mostly not available when working with data from literature. We thus analysed the relationship between DPR Mayfield extracted from original studies and DPR calculated using the Ricklefs method (Figure S2.1). As expected, we found that calculated DPR underestimated DPR Mayfield but the correlation between the two was high ( $r = 0.87$ ,  $N = 162$ ). Due to this reasonable correlation, we analysed daily predation rates on a global scale using the calculated DPR, while being sure that calculated DPR values closely reflected unbiased daily predation rates in the populations (DPR Mayfield). However, we also report the relationship of DPR Mayfield to latitude and year to provide regression estimates of the two most interesting predictors for comparison with our main models. Additionally, the fraction of depredated nests out of total nests found (our measure of potential demographic impact of predation) can be also underestimated. We thus calculated also its unbiased version for the subsample of populations where DPR Mayfield was available as:  $1 - (1 - DPR \text{ Mayfield})^{\text{nest cycle duration}}$ . The correlation of the value reported in literature with that calculated using DPR Mayfield was reasonably high, with  $r = 0.83$  (Figure S2.2).

Using the original studies, we obtained the geographical latitude of the study location using Google Earth. Using the Handbook of the Birds of the World (del Hoyo et al., 2020), we obtained data on nest type (open, domed and cavity). Previous studies showed that nest predation intensity can increase with the year of study (Kubelka

et al., 2018; Remeš et al., 2012a). Thus, we also extracted the midpoint of the years when the study was conducted. In case this information was missing ( $N = 48$ ), we used the year of publication minus 6 years (the average difference between the year of the study and publication in our dataset;  $N = 1230$  populations for which both the year of publication and the year of study were known). Similarly, we also included adult body mass as one of the predictors in our analyses, since it is a common correlate of life-history traits and behaviour (Dial et al., 2008; Schmidt-Nielsen, 1984) and can predict nest predation intensity (Unzeta et al., 2020). Adult body mass (g) was obtained from Dunning (2008) and the compendia listed above. Finally, we excluded all studies where less than 10 nests had a known outcome and included sample size into our models to take care of varying samples of nests across studies (see below).

We used the Normalized Difference Vegetation Index (NDVI) as a proxy of environmental productivity, which is commonly used in broad-scale biogeographical analyses (Pettorelli et al., 2011). We obtained Modis-based NDVI from <https://search.earthdata.nasa.gov>. Specifically, we used the MOD13C2.006 version of data spanning 2001–2020. This is monthly NDVI index in the resolution of 0.05 degrees. We aggregated the layers to obtain the resolution of 0.2 degrees (ca. 20 km at the equator). We calculated monthly averages of NDVI across the 20 years of data. For tropical species, we used the average NDVI across all months. For northern temperate species (north of 23.5 degrees), we used average NDVI from March to June. For southern temperate species (south of -23.5 degrees), we used average NDVI from September to December. The months were chosen to represent the breeding season of most passerine species living in each latitudinal band. We then extracted NDVI values of raster cells (0.2-degree resolution) that were intercepted by geographical coordinates of the study sites. In this way, we obtained an index of environmental productivity for all 776 study sites.

To estimate species richness of potential nest predators, we first identified avian and mammalian families holding the most species of nest predators. To do that, we searched studies that identified nest predators, usually using video taping of nests (Allcorn et al., 2012; Bellamy et al., 2018; Bolton et al., 2007; Brown et al., 1993; Cerón-Cardona et al., 2018; Chen et al., 2015; Chmel, 2018; DeGregorio et al., 2016; Eggers et al., 2005; Fulton, 2019; Grendelmeier et al., 2015; Hoset et al., 2009; Innes & Watts, 2004; Kelly et al., 2005; King & Degraaf, 2006; Kirby et al., 2018; Li et al., 2012; Lima, 2009; Lloyd et al., 2016; Mallord et al., 2012; Maziarz et al., 2018; Menezes & Angelo, 2017; Morgan et al., 2011; Morris & Gilroy, 2020; Nietmann & Ha, 2018; Pierce & Pobprasert, 2013; Praus et al., 2014; Praus & Weidinger, 2010, 2015; Ribeiro-Silva et al., 2018; Samsonov et al., 2018; Schaefer, 2004; Thibault & Villard, 2005; Weidinger, 2009; Zduniak & Kuczynski, 2003). We selected taxonomic families with at least two species documented as nest predators. We then used digitized ranges of the birds and mammals of the world (BirdLife International and NatureServe, 2014; IUCN, 2021) to obtain presence-absence matrices for all species of these families for the 776 study sites across the world. We calculated species richness of potential nest predators for each location as the

sum of all species from these families whose ranges overlapped with the geographical coordinates of a particular study site.

We modelled nest predation using phylogenetic mixed models implemented in the MCMCglmm package (Hadfield, 2010) for the R computing environment (Core Team, 2020). This approach allowed us to analyse the data on the population level while accounting for the random effects of phylogeny, species identity and study location. We also tested several other statistical methods and made sure that they gave results similar to those of MCMCglmm (see Appendix S3). To fit the MCMCglmm models, we downloaded 1000 phylogenies from the birdtree.org archive using the Hackett constraint and version 2 of the database (Jetz et al., 2014). We calculated one Bayesian maximum credibility tree using TreeAnnotator (Drummond et al., 2016) and used this tree in all subsequent analyses. We ran four parallel MCMC chains for 6 million generations, with the first 1 million discarded as a burn-in and sampled every 1000th value. Our final sample size to generate summary statistics was thus 20,000 (5000 × 4 chains).

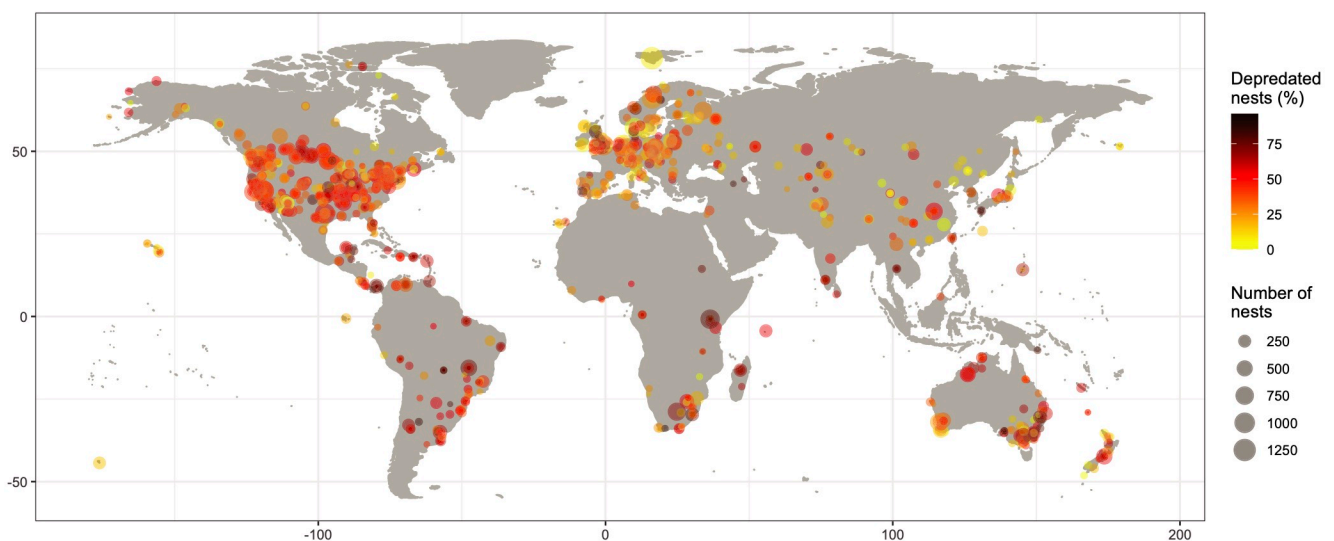
We modelled four dependent variables: (1) The proportion of failed nests out of total nests, coded as the binomial proportion; (2) the proportion of depredated nests out of total nests (binomial proportion); (3)  $\log_{10}(\text{daily nest predation rate} + 0.005)$ , fit as a Gaussian variable and (4) the proportion of depredated nests out of the failed nests, that is, predator-caused nest failure (binomial proportion). Models using the binomial proportion as a response take automatically care of unequal sample sizes across studies. They are exactly equivalent to simple logistic model with 0/1 response weighted by sample size. The only method that allowed to incorporate sample size into models of the gaussian variable (DPR) was the random effects model as implemented in Kubelka et al. (2018). These models gave very similar results to those from the MCMCglmm function (Figure S2.3) and thus for consistency we present here only the MCMCglmm estimates. Finally, there was virtually no spatial autocorrelation in

data (explaining only 0.1%–1% of variance in data; Appendix S3) and we thus ignored it.

In the life-history models, we used four predictors: geographical latitude, nest type (open, domed and cavity), adult body mass ( $\log_{10}$ -transformed) and the year of study. To obtain robust results, we coded latitude in three different ways. First, we used it as a quadratic predictor. Second, we fit the absolute value of latitude as a linear predictor. Here we also fit interactions between absolute latitude and hemisphere, and between absolute latitude and nest type. Third, we assigned every population in our dataset into one of three latitudinal bands based on their geographical latitude (northern temperate – above 23.5°N, tropical – between 23.5°N and 23.5°S, and southern temperate – below 23.5°S). Here we also tested the interaction between the latitudinal band and nest type. If the highest probability density intervals (95%) of interaction terms included zero, we omitted the interaction from the model. If the interaction of absolute latitude with hemisphere was to be omitted, we also excluded the main hemisphere term. In the biogeographical models, we used three predictors: absolute value of the geographical latitude, species richness of potential nest predators and environmental productivity (NDVI index). We also fit the biogeographical models without latitude to evaluate the other two predictors alone.

### 3 | RESULTS

Altogether, we collected data on nest predation from 1297 songbird populations belonging to 659 songbird species and distributed across 776 study sites, while data on predator-caused nest failure were available for 1117 populations (603 species). In total, we worked with 124,958 nests. The data came from years between 1934 and 2018 and latitudinal span from 48.12°S to 78.18°N (Figure 1). Most of the species in our dataset were open nesters (67.7%,  $N = 659$ ),



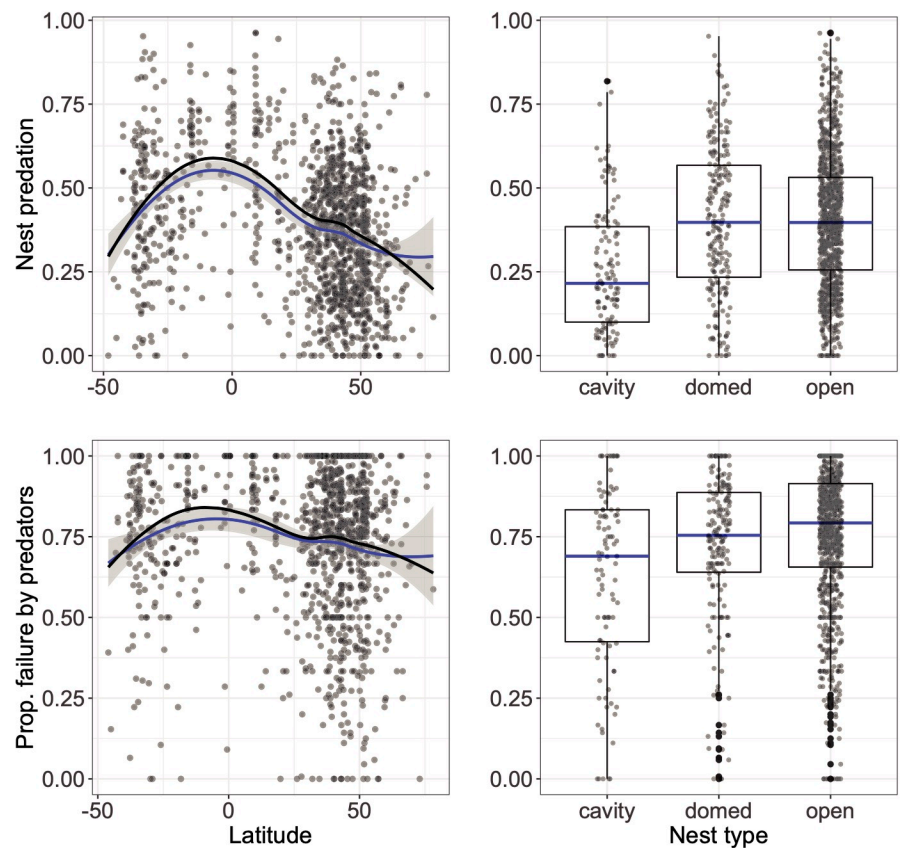
**FIGURE 1** The distribution of study sites ( $n = 776$ ) across the globe. Since our literature search was not confined to readily available databases, but included books and grey literature, blank spaces should be considered true gaps in our knowledge of nest predation patterns in passerines. The map is in the equirectangular projection



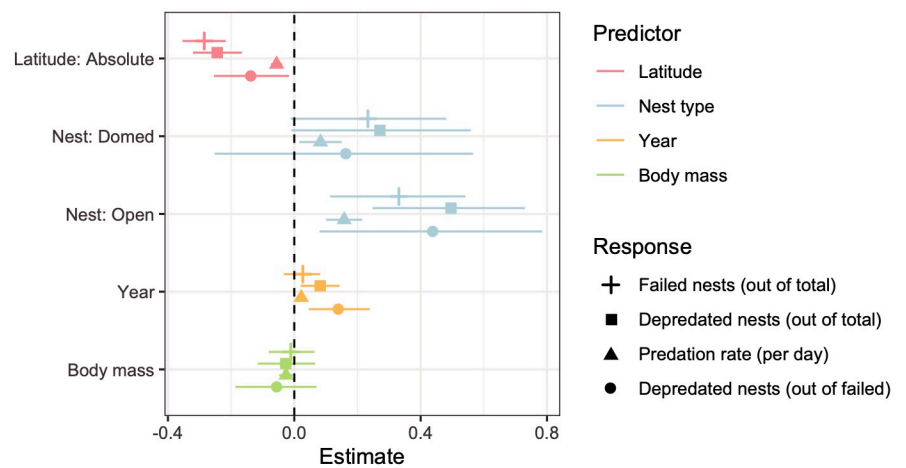
while 20.9% and 11.4% of the species were domed and cavity nesters, respectively. Roughly equal proportion of populations came from the New ( $n = 669$ ) versus Old World ( $n = 628$ ).

All three measures of nest predation intensity (the proportion of depredated nests, daily predation rate and predator-caused nest failure) increased towards the equator and across the 84 years (Figures 2 and 3; Figure S2.4 and Tables S4.1–S4.3). Since the interaction of absolute latitude with a hemisphere was not statistically significant (it was excluded from all models), the decline of nest predation intensity seemed to be similar in both hemispheres (Figure 2). However, when split into latitudinal bands, the decline

of nest predation intensity was stronger in the north, except for predator-caused nest failure where it was similar across hemispheres (Table S4.3). To make sure that latitudinal differences in nest predation intensity were not biased by temporal trends, we split temporal trends by latitudinal bands. Visual inspection of these plots showed that the difference between northern temperate and tropical regions was consistent across time, with southern temperate regions having steeper temporal trends than the other two latitudinal bands (Figure S2.5). Overall, this showed that latitudinal differences in nest predation were robust with respect to temporal trends.



**FIGURE 2** Relationships of the proportion of depredated nests (top) and the proportion of failed nests that failed due to predation (bottom) in relation to latitude (left) and nest type (right). Loess smoother was used to depict relationships on the left panels, with black lines depicting loess smoother weighted by sample size. Data points for all populations are depicted together with boxplots on the right panels, jittered horizontally for better visibility



**FIGURE 3** Mean effect sizes (with 95% highest posterior density intervals, HPD) from the life-history models fitted using phylogenetic mixed models. If the HPD interval does not include zero, the effect can be considered different from zero

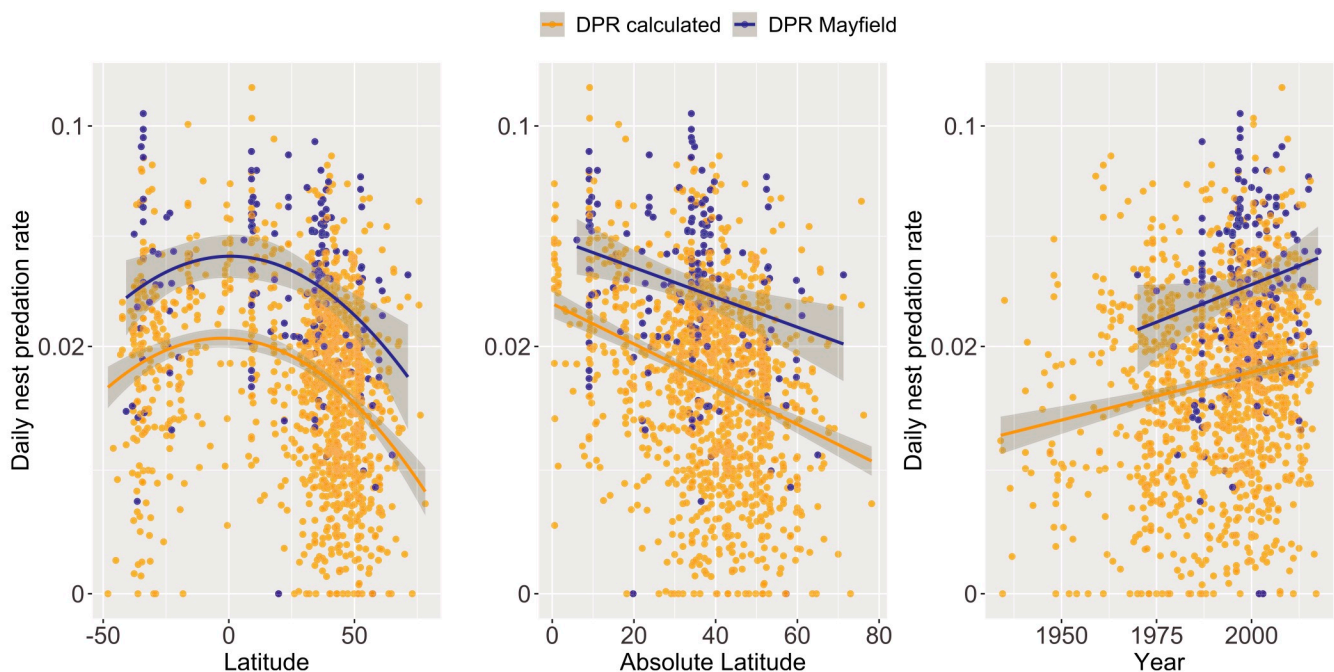
We had only 162 estimates of daily nest predation rates obtained using the Mayfield method (DPR Mayfield). We thus did not fit full models with this variable. However, to see whether effect sizes were comparable for our main predictor of interest, namely geographical latitude, we evaluated the relationship between DPR Mayfield and latitude (Figure 4). The estimate of the linear relationship between DPR and absolute geographical latitude was  $-0.061$  (95% highest posterior density, HPD, interval  $-0.080$  to  $-0.043$ ) for calculated DPR, while it was  $-0.043$  ( $-0.088$  to  $0.004$ ) for DPR Mayfield. Out of interest, we did the same also for the year of study (Figure 4). Estimates for the linear relationship between DPR and year of the study were  $0.029$  ( $0.014$ – $0.043$ ) for calculated DPR and  $0.040$  ( $-0.032$  to  $0.113$ ) for DPR Mayfield, respectively. Thus, estimates for calculated DPR and DPR Mayfield were comparable for both predictors, suggesting that our results for DPR were not biased by the method used to calculate this variable (see also Figure 4).

Nest predation intensity was always higher in open nests than in cavity nests, irrespective of the response variable used (Figures 2 and 3; Tables S4.1–S4.3). The findings for domed nests differed according to the response variable: daily nest predation rates were higher than in cavity nests, while other variables did not differ significantly. However, 95% highest posterior density intervals for the effects for overall nest failure and the proportion of depredated nests included zero only by a very small

margin (Figures 2 and 3; Tables S4.1–S4.3). Daily predation rates also negatively correlated with adult body mass, while overall nest failure, the proportion of depredated nests and predator-caused nest failure did not change with body mass (Figure 3; Tables S4.1–S4.3).

The proportion of depredated nests and daily predation rate increased with both environmental productivity (indexed by NDVI) and the number of potential nest predators (birds and mammals; Figures 5 and 6; Tables S4.4 and S4.5). However, for potential nest predators, this was true only in models without absolute latitude. When latitude was included into the model as one of the predictors, the effect size of potential nest predators included zero (Figure 6; Tables S4.4 and S4.5). This might have been caused by a higher correlation between absolute latitude and potential nest predators ( $r = -0.58$ ) than between absolute latitude and productivity ( $r = -0.34$ ; Figure S2.6). Predator-caused nest failure did not depend on productivity, while it increased with the number of potential nest predators, but only in the model without latitude (Figure 6; Tables S4.4 and S4.5).

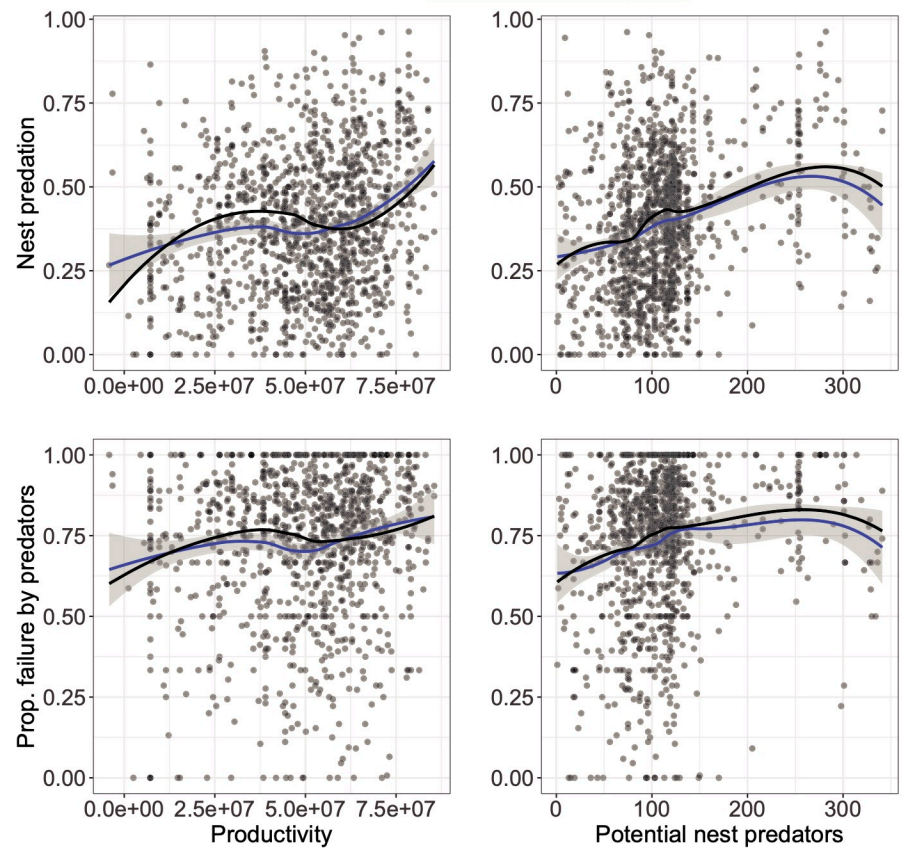
Major part of the variability in our data was explained by phylogeny (39.3% on average across life-history models and 44.9% across biogeographical models) and study site (34.9% and 34.1%), while only small proportion was accounted for by species identity (2.9% and 1.6%, Tables S4.1–S4.5).



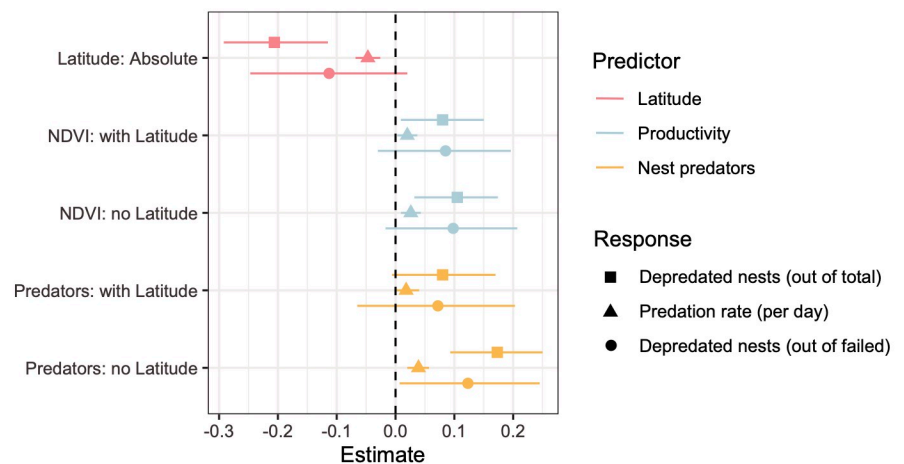
**FIGURE 4** Relationships of daily nest predation rates (DPR) in passerines to latitude and year, separately for DPR calculated from the proportion of depredated nests using the Ricklefs method and for DPR directly estimated using the Mayfield method. We show a quadratic relationship with latitude (left), a linear relationship with absolute latitude (middle) and a linear relationship with the year of study (right). Although DPR calculated using the Ricklefs method underestimates true DPR obtained with the Mayfield method, their trends with latitude and year were very similar. More specifically, the estimate for DPR Mayfield was less steep in case of Absolute Latitude and steeper in case of Year, but all DPR Mayfield effects had wider confidence intervals due to smaller sample size. Note the log<sub>10</sub>-transformation of the y-axis



**FIGURE 5** Relationships of the proportion of depredated nests (top) and the proportion of failed nests that failed due to predation (bottom) in relation to productivity indexed by NDVI (left) and the number of potential nest predators (birds and mammals) occurring in each study site (right). Loess smoother was used to depict relationships on the panels, with black lines depicting loess smoother weighted by sample size



**FIGURE 6** Mean effect sizes (with 95% highest posterior density intervals, HPD) from the biogeographical models fitted using phylogenetic mixed models. If the HPD interval does not include zero, the effect can be considered different from zero. 'With Latitude' means that absolute latitude was included into the model as one of predictors, while 'no Latitude' means that NDVI and nest predators were tested without absolute latitude



## 4 | DISCUSSION

All measures of nest failure and depredation increased towards the equator, but this increase was stronger in the northern hemisphere. An increase in nest predation rates towards the equator was previously documented on smaller samples in Australian and non-cavity breeding songbirds (Remeš et al., 2012a; Unzeta et al., 2020), while other studies of songbirds did not find this pattern (Jahn et al., 2014; Martin, 1995). Thus, due to our exceptionally complete, worldwide sampling, our study is an up-to-date rejoinder of these and previous studies and provides a major synthesis, at least for passerines. We confirmed that tropical passerines faced both higher intensity

of nest predation (higher daily predation rate, although this effect was weaker with the Mayfield DPR estimates) and potentially more detrimental demographic outcomes of nest depredation (higher proportion of nests being lost to predators). Confirming the potential demographic impact, overall nest failure also increased towards the equator, which is not surprising given the most common source of nest failure is depredation (Remeš et al., 2012a, 2012b; Ricklefs, 1969). Moreover, for the first time we revealed that the proportion of nest failure caused by predators also increased towards the equator. This result further supports the view that species are more affected by biotic interactions close to the equator, while abiotic factors can be more important at higher latitudes

(MacArthur, 1972; reviewed in Schemske, 2009). Moreover, this view is further reaffirmed by stronger declines of nest predation in the northern hemisphere (Table S4.3), which has harsher climate than the southern hemisphere.

Nest predation did not only change with geographic space, but also in time. It increased over the last eight decades, from 25.7% before 1950 ( $n = 37$  studies) to 42.3% after 2000 ( $n = 421$ ). Similar trend was previously found by Remeš et al. (2012a) in Australian songbirds and by Kubelka et al. (2018) in shorebirds. Previous studies also identified increases in densities of nest predators (Langgemach & Bellebaum, 2005; Panek & Bresiński, 2002), which probably resulted from habitat fragmentation (Chalfoun et al., 2002), availability of additional food resources from agriculture (Cove et al., 2014; Wood, 1998) and in some species also from changes in hunting practices (Panek & Bresiński, 2002). Moreover, introduction of new species by humans or expansion of their ranges due to climatic changes can locally increase the diversity of potential nest predators (Iverson et al., 2014; Kauhala & Kowalczyk, 2011; Madsen et al., 2019; Prop et al., 2015). Thus, the increase in nest predation intensity in passerines that we document here might have been the result of gradually increasing predation pressure caused by habitat fragmentation or changes in predator communities. This would agree with our finding that the strongest temporal increase was identified in the proportion of failed nests that failed due to depredation, while the overall nest failure did not increase (Figure S2.4; Tables S4.1–S4.3). However, for at least two reasons it can also be an artefact of data collection methods (Bulla et al., 2019). First, nest predation studies have become more common in recent decades (Figure S2.7). Hence, more studies may have been conducted in fragmented places or places impacted by anthropogenic disturbance, which in general suffer from higher nest predation (Andrén et al., 1985; Batáry & Báldi, 2004; Gates & Gysel, 1978). Second, over the years, researchers have probably improved their searching methods and/or searching effort (e.g. sample size of nests increased with years, Figure S2.8). This could lead to researchers finding also nests that have failed early in the nesting cycle. Including those nests would lead to an increase in the calculated nest predation rate, provided early nest failure is more commonly caused by nest predators than by other causes. It is fair to note that this potential source of bias has been accounted for in at least one earlier study (Kubelka et al., 2019). Moreover, this problem could be avoided by analysing daily predation rates calculated using the Mayfield method and original exposure days. Unfortunately, this information was available only for 12% of populations. However, encouragingly, results for latitude and year obtained with these more reliable estimates were very similar to those obtained using calculated daily predation rates (although statistical estimates were weaker and had wider confidence intervals). Taken together, increasing nest predation rates have been repeatedly documented (Kubelka et al., 2018; Remeš et al., 2012a; Roodbergen et al., 2012; this study), but it is often unclear to what extent this finding might be the result of temporal biases in research methodology.

Larger species had lower daily nest predation rates, which indicates that they are probably better able to defend their nests

against predators (Larsen, 1991; Unzeta et al., 2020). However, unlike the daily nest predation rates, the proportion of nests destroyed by predators did not change with species body mass. This presumed contradiction is probably the result of developmental periods being longer in larger species of birds (Cooney et al., 2020; Rahn & Ar, 1974; Yom-Tov & Ar, 2016). Daily predation rates thus accumulate for a longer time, which might result in the proportion of depredated nests being independent of body mass. Thus, although the intensity of predator–prey interactions seems to be stronger in smaller species (daily nest predation rate), potential demographic impact of predation might be similar across divergent body masses (the proportion of nests depredated).

It has long been established that different nest structure and nest placement can have important consequences for avian reproductive performance. Traditionally, closed nests (either domed or cavity nests) were believed to provide better protection against nest predators (Nice, 1957; Skutch, 1985). However, empirical evidence suggests that while this may be true for species breeding in cavities (Martin, 1995; Martin & Li, 1992), the adaptive function of domed nests may be different, probably providing energetic benefits via improved thermal environment (Martin et al., 2017; Mouton & Martin, 2019). In our study, daily predation rates in domed and open nests were similar while cavity nesters had lower rates. This would support the view that while there is a clear benefit for breeding in cavities, domed nests do not protect clutches and broods against predators much better than open nests do (Martin et al., 2017). However, the proportion of depredated nests and the fraction of failed nests due to predators were not higher in domed nests than in cavity nests, although only by a very small margin (Figure 3; Tables S4.1–S4.3). Overall, it seems that domed nests bring at least partial protection against nest predators, although not so much as cavity nests. Thus, domed nests might bring advantages both in terms of improved thermal environment (Mouton & Martin, 2019) and, at least partly, better nest protection against predators (this study).

There are at least two potential explanations of latitudinal trends in nest predation: first, high productivity might enable high densities of consumers (Storch et al., 2018; Tallavaara et al., 2018), resulting in strong predation pressure on nests. Second, high species richness of potential nest predators can preclude finding enemy-free space with consequent high nest predation intensity (Martin, 1993). We found support for both these hypotheses, because nest predation rate in our dataset increased with both environmental productivity (indexed by NDVI) and the estimated number of potential nest predators. However, unlike productivity, the latter relationship disappeared when latitude was included in the model, suggesting a dependency of the statistical signals of the number of nest predators and geographical latitude. Another factor weakening the signal of the number of nest predators might have been that, for practical reasons, we included only potential mammalian and avian nest predators while omitting other taxa. However, other taxa, for example snakes in the tropics (Berkunsky et al., 2011; Degregorio et al., 2014; Weatherhead & Blouin-Demers, 2004),



might be important nest predators. We were also able to include only entire families of potential nest predators without knowing what proportion of their constituent species is actually involved in nest depredation. Despite these reservations, we revealed surprisingly persuasive statistical effects of potential nest predators and productivity on nest predation intensity. Consequently, we did not stop at simply describing spatial patterns but succeeded in at least partly explaining the spatial trend in avian nest predation rates on a biogeographical scale.

There are some limitations of our study we would like to address here. First, since only limited data on DPR calculated by the Mayfield method were available, we mostly calculated it from the proportion of depredated nests provided by authors. This approach underestimates true nest predation rates (Mayfield, 1975; Figure 4) and thus provides a relative index, rather than absolute estimate, of nest predation intensity. However, we show that the correlation between those two measurements is high (Figure S2.1) and that the results for latitude and year of study are fairly robust to the way of calculating DPR. Second, for similar reasons, our measure of potential demographic impacts of nest depredation can be underestimated. Thus, we calculated also its unbiased version for the subsample of populations where DPR Mayfield was available and showed that the correlation between those two measures was again quite high (see Methods and Figure S2.2). However, to avoid those problems in the future, we recommend researchers studying nest predation in birds to use standardized methods and cover a large range of geographical latitudes. This would allow for direct and unbiased comparison of nest predation across latitudes, as has been done for example with insect predation (Roslin et al., 2017). Third, unlike in precocial species where all nest predation data come from incubation period only, data on nest predation in songbirds come from both the incubation and nestling period. It is difficult to obtain data separately for those stages from literature and thus our estimates lump those two periods. However, this is not a problem since lumping the incubation and nestling stage is a common approach and it makes our study comparable with other comparative studies of songbirds.

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#### CONFLICT OF INTEREST

There is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

All data can be accessed on Zenodo under <https://doi.org/10.5281/zenodo.5817338>.

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#### BIOSKETCH

**Beata Matysioková** is interested in life histories and parental care of birds. **Vladimír Remeš** is interested in large-scale ecology and evolution. In particular, he studies biogeography of avian communities, species coexistence, and the evolution of morphology, signalling traits, life histories and parental care.

**Authors' contributions:** Designed the study: BM and VR; Collected the data: BM; Analysed the data: VR; Wrote the MS: BM and VR.

#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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