Adaptation and latitudinal gradients in species interactions: nest predation in birds

Benjamin G. Freeman[1,2*], Micah N. Scholer[1,2], Mannfred M. A. Boehm[1,3], Julian Heavyside[1,2], Dolph Schluter[1,2]

[1] Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T1Z4, Canada

[2] Department of Zoology, University of British Columbia, Vancouver, BC V6T1Z4, Canada

[3] Department of Botany, University of British Columbia, Vancouver, BC V6T1Z4, Canada

*Corresponding author: freeman@zoology.ubc.ca

Abstract

The "biotic interactions" hypothesis—that stronger interspecific interactions in the tropics drive faster evolution and speciation, giving rise to the latitudinal diversity gradient—has inspired many tests of whether certain biotic interactions are indeed stronger in the tropics. However, the possibility that populations have adapted to latitudinal differences in species interactions, blunting effects on evolutionary rates, has been largely ignored. Here we show that mean rates of nest predation experienced by land birds vary minimally with latitude in the Western Hemisphere. This result is surprising because nest predation in birds is a canonical example of a strong tropical biotic interaction. We explain our finding by demonstrating that (1) rates of nest predation are in fact higher in the tropics, but only when controlling for the length of the nesting period, (2) long nesting periods are associated with reduced predation rates, and (3) tropical birds have evolved particularly long nesting periods. We suggest this is a case example of how adaptation to a biotic interaction can alter observed latitudinal gradients in interaction strength, potentially equalizing evolutionary rates among latitudes. More broadly, we advocate for tests of the biotic interactions hypothesis to consider both latitudinal patterns in interaction strength *and* evolutionary responses to these interactions.

Keywords: biotic interaction, latitudinal gradient, latitudinal diversity gradient, nest predation, predation, species interactions

Since Darwin, ecologists have suggested that biotic interactions increase in strength towards the Equator (Darwin 1859, Wallace 1869, Dobzhansky 1950, MacArthur 1972). Dobzhansky (1950) expressed this viewpoint by arguing "Where physical conditions are easy, interrelationships between species become the paramount adaptive problem…This is probably the case in most tropical communities." Strong biotic interactions in the tropics are hypothesized to generate strong selection that, in turn, leads to faster rates of evolution and speciation (Schemske 2009). Hence, the idea that biotic interactions are strongest in the tropics might help to explain why there are far more species at lower latitudes than in the temperate zone (the "biotic interactions hypothesis; (Schemske 2009)).

The biotic interactions hypothesis has inspired a growing number of studies that test the prediction that total biotic interactions are indeed strongest in the tropics (for reviews that present opposing perspectives on this literature see; (Schemske et al. 2009, Moles and Ollerton 2016)). There are two principal approaches to measuring rates of biotic interactions. First, one can place the same naïve model at many sites, and measure the frequency of biotic interactions experienced by this standardized model (Roslin et al. 2017). Second, one can measure the intensity of biotic interactions that wild local populations actually experience, repeating this across a large number of sites to account for variability (Kubelka et al. 2018). A fundamental difference between these two approaches is that naïve model studies attempt to measure the biotic interaction as experienced by populations that have not adapted to local interactions, whereas wild studies measure biotic interactions as experienced by populations that have had the opportunity to adapt to local interactions (i.e., "naïve" vs. "adapted"). Hence, naïve model studies neglect the possibility that adaptation in response to interaction strength and the perpetrators of these interactions could reduce, and perhaps even eliminate, any gradient. If so, adaptations could blunt any differential effects of interactions on evolutionary rates in the tropics vs. the temperate zone.

Here, we examine the biotic interactions hypothesis by studying nest predation in land birds. Nest predation experienced by birds is widely held to be most intense at lower latitudes (Skutch 1985, Robinson et al. 2000, Schemske et al. 2009, Mckinnon et al. 2010, Remeš et al. 2012, DeGregorio et al. 2016, Kubelka et al. 2018), but see (Martin et al. 2017). High nest predation in the tropics may be related to the fact that the tropics are home to both more species and more types of nest predators than the temperate zone, including some tropical species that prey almost exclusively upon eggs (DeGregorio et al. 2016, Menezes and Marini 2017). We test whether rates of nest predation are indeed stronger in the tropics using a newly compiled dataset of > 500 estimates of daily rates of nest predation experienced by land birds populations across the Western Hemisphere. Our study measures interactions experienced by populations in nature (i.e., “adapted” interactions). We therefore explore whether tropical birds, which must deal with a distinct and diverse community of nest predators, might have evolved adaptations that reduce the rates of nest predation they experience in nature. To evaluate potential adaptations to nest predation, we focus on length of the nesting period, because longer nesting periods are associated with reduced daily rates of nest predation both within and across sites (Martin 2002). Specifically, we examine the possibility that prolonged nesting periods are a component of adaptation to the higher predator diversity in the tropics. Our synthesis thus investigates not only geographic patterns in the intensity of a biotic interaction, but also the interplay between ecological interaction and evolutionary consequence across latitudinal gradients.

Methods

Assembling nest predation data

We searched the peer-reviewed literature to find studies that have measured nest predation for land bird populations breeding in North, Central or South America. We focus on the Western Hemisphere because nest predation data for tropical birds outside of the Americas (e.g., the Asian and African tropics) is scarce (but see (Remeš et al. 2012) for an analysis of Australian birds). We included only studies of real nests because we were interested in biotic interactions experienced by populations in nature, and because predation on artificial nests is poorly correlated with predation on real nests (King et al. 1999, Burke et al. 2004, Moore and Robinson 2004, Robinson et al. 2005). We did not include studies from oceanic islands (e.g., the Galapagos) because oceanic islands often differ ecologically from nearby continents (e.g., oceanic islands typically have lower diversity of predators). We restricted our analysis to land birds—primarily passerines, but also a small number of doves, hummingbirds, and other non-passerines—, following previous studies that have investigated latitudinal trends in nest predation (Robinson et al. 2000, Remeš et al. 2012, Martin et al. 2017). In addition, we did not include cavity nesters, which differ dramatically in their nesting biology from non-cavity nesters (Martin and Li 1992). Last, we only considered studies that reported the fate of at least 10 nests, as metrics of nest success based on small sample sizes are more prone to error.

We compiled nest predation data by searching the peer-reviewed published literature. Several previous studies have analyzed nest predation data from the Americas (Nice 1957, Skutch 1985, Kulesza 1990, Conway and Martin 2000, Robinson et al. 2000, Boyle et al. 2016, Martin et al. 2017). These syntheses are valuable summaries of relevant studies, but did not always present the complete set of data that we were interested in for each study. Hence, we extracted data from the original publications in all cases. We then located additional studies by conducting a

Web of Science search in February 2018 with the keywords “Nest predation” OR “Breeding ecology” OR “Nest success” AND “bird.” Because there is a latitudinal gradient in data availability (more in the temperate zone, less in the tropics), we expended additional effort to more exhaustively search for tropical studies. Specifically, we: (1) conducted additional country-specific Web of Science searches for each nation in Central and South America, with keywords “Nest predation” OR “Nest success” AND “Country Name”, where “Country Name” was the name of every Central and South American country; (2) examined the entire publication records of individual scientists who have extensively studied Neotropical bird breeding biology; and (3) followed citation webs to search for additional relevant studies from the tropics and southern temperate zone.

For each species from each study that met our criteria described above, we extracted the following information: (1) Species name; (2) Sample size of nests; (3) Nest success, presented either as fledging success (often termed “apparent success”, an estimate of the percentage of nests that successfully fledge young) or as daily survival rate (or, rarely, daily predation rate); (4) Latitude and longitude; (5) Elevation (meters above sea level, extracted using the Google Maps Platform); (6) Incubation and nestling periods (extracted either from information in the paper itself, from other papers studying the breeding biology of the same species, or from Handbook of the Birds of the World Alive (del Hoyo et al. 2018); (7) Habitat. Following Tobias et al. (Tobias et al. 2013), we used standard published sources (del Hoyo et al. 2018) to classify species’ preferred habitats into three categories: “open”, for grasslands and deserts, “semi-open” for open-canopy woodland and shrubby landscapes, and “closed” for closed-canopy forest; and (8) Nest type (open vs. enclosed). We used standard published sources (del Hoyo et al. 2018) to assign categories of nest type, following Martin et al. (Martin et al. 2017) who defined open cups as “cups or platforms exposed from above and the sides” and enclosed nests as those with “a constructed or natural roof that provides cover in all directions except the entrance.” While some nests do not fit clearly into one of these two categories, this binary classification is a useful way to contrast nest types that may differ in nest predation (Martin et al. 2017).

Our final dataset included nest predation data for 516 unique species-site combinations (from 244 studies and representing 315 species). The bulk of this dataset comes from studies conducted between ~40° South and ~50° North. The majority of studies come from the Northern Hemisphere temperate zone (270 unique species-site combinations), but the tropics (187 unique species-site combinations) and Southern Hemisphere temperate zone (59 unique species-site combinations) are also well represented (Figure 1). We note that though this dataset is larger than previous analyses of nest predation in the Western Hemisphere, this dataset is not exhaustive. In particular, there is an extensive gray literature for the northern temperate zone that we did not attempt to include.

Quantifying nest predation vs. nest failure

In this study we are interested in daily rates of nest predation, but researchers are seldom able to precisely quantify rates of predation compared to rates of other causes of nest failure. Predators are responsible for the large majority of nest mortality in most places (Remeš et al. 2012). As a consequence, previous syntheses have simply classified all nest failures as due to predation (Martin et al. 2017). This methodology could lead to error if predation does not account for most nest failure. More worryingly for our purposes, this methodology could lead to bias if the proportion of nest failure due to predation varies systematically along latitudinal gradients. We investigated these possibilities by extracting the cause of failure (predation vs.

abandonment vs. other factors) from the subset of studies that reported causes of failure. We did not include studies where authors explicitly described that nest failure was due to human activities such as mowing (e.g., birds nesting in hay fields), or, in one case, when “much of the predation is known to have been by young boys” (Peterson and Young 1950).

We found that the large majority of nest failures are indeed caused by predation, and that the percentage of nest failures caused by predation does not vary with latitude. Only 26% of studies (64 out of 246) attempted to identify the cause of nest failure. The mean percentage of nest failures attributed to predation from these studies was 73% ($N = 106$ unique species-site combinations), supporting the assertion that predation accounts for the large majority of nest failure in land birds. This figure remarkably similar to that for Australian birds, where nest predation accounts for ~72% of nest failure (Remeš et al. 2012). We found no evidence that the percentage of nest failures due to predation varies as a function of latitude (slope estimate for latitude in a linear model predicting the percentage of nest failure attributed to predation = -0.00075 ± 0.00078, $p = 0.343$). Hence, analyzing a dataset of studies that report nest success appears to be appropriate for our goal of analyzing latitudinal patterns in nest predation.

Latitudinal variation in nest predation

Our first goal was to assess whether daily rates of nest predation vary as a function of latitude. As previously mentioned, studies reported nest predation as either fledging success (the percentage of nests that successfully fledged young; $N = 368$ unique species-site combinations) or daily survival rates (the probability that an egg or nestling survives from one day to the next; $N = 267$ unique species-site combinations). Some studies reported both metrics. Daily survival rates can be calculated from fledging success when the length of the nesting period (incubation + nestling periods) is known. We found published information for nesting periods for most but not all species, and converted fledging success to daily survival rates by taking fledging success to the exponent of 1/(total days of nesting period). Hence we were able to compile a complete dataset of 501 unique species-site combinations measuring daily survival rates. We note that calculating daily survival rates based on fledging success can be problematic. We therefore repeated our analysis using the smaller dataset that directly report daily survival rates, and report that our main results remain unchanged when we analyzed only the subset of our dataset ($N = 269$) that directly reported daily survival rates (Table S1). We analyzed daily survival rate and not daily predation rate because the majority of studies in our dataset report daily survival rates. All analyses were conducted in R (R Development Core Team 2017).

To estimate nest predation along the latitudinal gradient, we fit mixed effect meta-analytic models to predict daily survival rate using the “metafor” package in R (Viechtbauer 2010), which weights individual estimates by their squared standard errors, and incorporates the estimated variance among the study-specific effect sizes. We fit three models that correspond to different biological hypotheses: (1) no latitudinal gradient in predation; (2) a linear latitudinal gradient in predation; and (3) a breakpoint linear model wherein predation differs categorically between the tropics and temperate zone. We compared model fits using AIC. The first model was an intercept-only model that did not include a slope term. The second model included a single slope term that described symmetric linear regressions relating survival rate to latitude. The third model fit a breakpoint regression with zero slope for tropical latitudes (≤ 23.4 degrees absolute latitude), and equal slopes for temperate latitudes. We fit an additional, fourth, model to account for non-independence among effect sizes. This model included study ID for the 244 studies (the between-study effect), and species (the within-study effect) as random effects. We incorporated phylogeny into this model by specifying phylogenetic branch length as the variance-covariance matrix. Branch lengths were measured from a majority rules consensus tree calculated from 1000 phylogenies pruned to our study taxa and downloaded from birdtree.org ("Hackett" backbone; (Jetz et al. 2012)).

Latitudinal variation in nesting period duration

We found that daily survival rates varied minimally with latitude (see Results), a finding seemingly at odds with previous analyses that evaluated fledging success across latitudes (Robinson et al. 2000, Schemske et al. 2009). To better understand this apparent discrepancy, we examined latitudinal patterns in the duration of nesting periods for species within our dataset. We first plotted species' nesting period durations vs. latitude for the 295 species for which we had information on both variables. We observed clear latitudinal patterns in nesting period duration, with longer nesting periods in the tropics (see Results). Consequently, we tested the evolutionary association between latitude and nesting period duration by fitting a phylogenetic generalized least squares regression using the "ape" package (Paradis et al. 2004). The response variable in this model was nesting period duration. Absolute value of latitude was a fixed effect, and Pagel's λ was estimated using maximum likelihood. We estimated evolutionary relationships for the 295 species in this analysis using a majority rules consensus tree from 1000 phylogenies downloaded from birdtree.org ("Hackett" backbone; (Jetz et al. 2012)).

To explore the relationship between nesting period duration and daily survival rates, we fit a meta-analytic model to predict daily survival rate using the "metafor" package. We included only data from studies that reported daily survival rates (N = 254; i.e., not including estimates of daily survival rates calculated using fledging success and duration of nesting period). We first fit a model that estimated different slopes and intercepts for different latitudinal zones (predictor variables = nesting period duration, latitudinal zone, and an interaction between nesting period duration and latitudinal zone). We next fit a model where latitudinal zones had different intercepts but the same slope (i.e., without the interaction term between nesting period duration and latitudinal zone), and compared fit of the "different slopes" and "same slopes" models using the "anova" function. Last, we fit an additional model that included species and study as random effects, and incorporated phylogeny by specifying phylogenetic branch length as the variance-covariance matrix. Branch lengths were measured from a majority rules consensus tree calculated from 1000 phylogenies pruned to our study taxa and downloaded from birdtree.org ("Hackett" backbone; (Jetz et al. 2012)).

Latitudinal variation in fledging success

Last, we examined latitudinal patterns in fledging success by repeating the three meta-analytic models described above for latitudinal patterns in daily survival rate, but with fledging success as the response variable. There were 148 estimates of nest predation in our dataset with daily survival rates but not fledging success. We had information on species' nesting periods for most but not all (132 out of 148) cases. For these 132 cases, we converted daily survival rate estimates to fledging success by taking the daily survival rate to the exponent of the nesting period, which is the sum of incubation and nestling periods. We then evaluated model fit using AIC. As before, we fit an additional fourth model to account for non-independence by including study ID and species as random effects, specifying phylogenetic branch lengths as the variance-covariance matrix (calculated as previously described).

Results

Latitudinal variation in nest predation

We found evidence that daily rates of nest predation in land birds are largely invariant with latitude within the Western Hemisphere. The most supported model fit a line with equal daily survival rate (0.97) across the entire latitudinal gradient (Figure 2, Table 1). Alternative models that fit symmetric, non-zero slopes to the relationship between latitude and daily survival rates were less well supported (ΔAIC ~ 3; Table 1). These less supported models were similar to the best-fit model in that they estimated slopes that were nearly flat (Table S2)—these models estimated daily nest survival at 60° North only slightly greater (by 0.006 to 0.012) than at the equator. Our results did not change when including phylogenetic relationships and species identity in our model (Table S3), indicating that our findings are robust to sources of non-independence in our data (e.g., phylogenetic relationships). In addition, we found support for the hypotheses that nest predation varies minimally with elevation, is similar in open nests compared with enclosed nests, and is similar in forested and open habitats (Appendix 1).

Thus, unlike in tests that have used naïve models to measure predation (Mckinnon et al. 2010, Roslin et al. 2017), we conclude that natural rates of nest predation are similar across latitudes. A possible explanation for this contrast between real nests and experimental nests is that adaptation to contrasting predation regimes has equalized observed rates in wild birds across latitudes.

Latitudinal variation in nesting period duration

Birds exhibit many adaptations to deter nest predators. We investigated the role of one specific adaptation, the length of the nesting period, which also varies considerably between the tropics and the North temperate zone (Figure 3). Here we focus on the North temperate zone, because data are sparse from the South temperate zone. Eggs and chicks remain longer in the nest in the tropics compared to the North temperate zone (Martin 2002, Chalfoun and Martin 2007). Nesting periods in the tropics average ~ 30 days, approximately 20% longer than in the North temperate zone (average = ~ 25 days; Figure 3). This difference reflects repeated patterns of evolution across a diversity of avian lineages—latitude is negatively related to nesting period in a phylogenetic generalized least squares regression model ($p < 0.0001$, Table S4).

Evidence that nesting period is an adaptation to predation

We suggest that longer nesting periods in the tropics are in part an adaptation to tropical predation regimes. In this view, longer nesting periods in the tropics lead to lower daily mortality levels on tropical nests than would be expected without a change in nestling period. Supporting this idea, when we compare species of similar nesting duration, daily survival rates are lower in the tropics than in the temperate zone. This comparison is simplest when we compare intercepts from the equal slopes model (North temperate zone vs. tropics $p < 0.0001$; Figure 4, Table S5). The equal slopes model was marginally better supported than a model that fit different slopes to different latitudinal zones ($p = 0.078$). When we analyze the different slopes model, we find the same result that daily survival rates are higher in the temperate zone than the tropics when controlling for nesting period (comparing estimates for North temperate zone vs. tropics for the mean nesting period of 27 days, $p < 0.0001$; Table S6, Figure S1). Moreover, this result is robust to sources of non-independence in our dataset (Table S7).

Nesting period duration is generally positively related to daily survival rate within and across latitudinal zones (Figure 4). For example, the equal slopes model estimated that a 10-day increase in nesting period is associated with a 1.7% increase in daily survival rates (Table S5; equivalent estimates from the different slopes model are a 1.1 – 2.5% increase in daily survival rates, depending on latitudinal zone; Table S6, Figure S1). The suspected reason is that a longer nesting period is associated with fewer visits to the nest per day by attending parents, reducing nest detection by nest predators (Matysioková and Remeš 2018).

Latitudinal variation in fledging success

The observation that nesting periods are longer in the tropics, while daily survival rates are similar across latitudes, implies that fledgling success is higher in the temperate zone compared to the tropics. Indeed, we found strong evidence that fledging success of nests is highest in the temperate zone (Figure 5, Tables 2). The best-fit model was a breakpoint regression that estimated ~32% of nests successfully fledge nestlings within the tropics while ~ 56% of nests successfully fledge nestlings at 60° North (Table S8). This result that is robust to sources of non-independence in our data (Table S9). We note that this pattern is not a demonstration of higher overall predation in the tropics because fledging success in the tropics and the temperate zone is based on mortality accumulated over different time spans.

Discussion

We report that natural rates of nest predation experienced by land birds are similar along a latitudinal gradient in the Americas stretching from ~ 40° South to ~ 60° North. This result is surprising, because nest predation has long been known to be intense in the tropics (Skutch 1985). Indeed, nest predation in land birds has been put forth as a good example of the more general pattern that biotic interactions are stronger at low latitudes (Schemske 2009). We suggest that similar rates of nest predation in nature between tropical and temperate zone birds may be explained if populations have adapted to local predation regimes.

We hypothesize that the evolution of longer nesting periods is one way that tropical birds have adapted to the greater diversity of nest predators in the tropics. Supporting this hypothesis, when we compare species with similar nesting periods, rates of nest predation are higher on average in the tropics than in the temperate zone. We further show that longer nesting periods are generally associated with higher daily survival rates even within the tropics and within the temperate zone, and that bird lineages repeatedly evolve longer nesting periods within the tropics. Thus, we hypothesize that tropical birds have achieved higher daily survival rates in part by evolving longer nesting periods (moving to the right and upwards along the regression line for daily survival vs. nesting period in Figure 4). We wish to make clear that many factors likely exert selection on nesting periods (e.g., shorter breeding seasons in the temperate zone may select for faster nesting periods in high latitude birds). In addition, the evolutionary association we document between tropical birds and long nesting periods could reflect a combination of tropical birds evolving prolonged nesting periods and temperate zone birds evolving shorter nesting periods. Overall, and despite these caveats, our results suggest that adaptation to different predation regimes may largely equalize observed rates of nest predation in land birds.

One possible mechanism by which populations evolve longer nesting periods is simply by reducing the time they spend at their nest (nest attentiveness). Indeed, bird species that seldom visit their nest have longer nesting periods (Chalfoun and Martin 2007, Martin et al. 2007) but see (Tieleman et al. 2004). In turn, reduced nest attentiveness has repeatedly evolved in association with increased nest predation risk (Matysioková and Remeš 2018). The negative correlation between evolved nest attentiveness and ambient predation risk is particularly strong in the tropics, consistent with the idea that predation risk for nesting birds is especially high in tropical environments (Matysioková and Remeš 2018). These observations are consistent with the possibility that birds experiencing high predation risk (e.g. in the tropics) tend to evolve longer nesting periods. We note that other life history traits, such as adult survival, can explain variation in nesting period durations (Martin 2002), and that disentangling drivers of evolution of life history traits is a difficult task.

Implications for the biotic interactions hypothesis

The biotic interactions hypothesis posits that high species richness in the tropics generate strong biotic interactions that lead to faster evolutionary rates—and ultimately faster speciation—in the tropics. Our results are inconsistent with this hypothesis. While predation on naïve models in the tropics may be higher in the tropics where there are more predators (Roslin et al. 2017), we find that predation experienced by nesting tropical birds in nature is not higher than in the temperate zone. We attribute our finding of similar rates of predation across latitudes in part to anti-nest predator adaptations of tropical birds.

It remains an open question whether our results are unique to nest predation in land birds. However, three arguments that represent difficulties for the biotic interactions hypothesis are: (1) the direction of causality may be reversed—it is possible that stronger total biotic interactions in the tropics are a consequence of higher tropical species diversity rather than its cause; (2) Stronger total interactions do not necessarily lead to stronger selection (Benkman 2013); and (3) Recent speciation rates appear to be highest in the temperate zones (and lower in the tropics), at least for birds and marine fishes (Weir and Schluter 2007, Schluter and Pennell 2017, Rabosky et al. 2018).

Comparison with previous studies of latitudinal gradients in nest predation

While tropical birds have long been thought to suffer greater nest predation than temperate zone birds (Robinson et al. 2000, Schemske et al. 2009, Kubelka et al. 2018), not all previous studies have supported this idea (Martin et al. 2017). This discrepancy may result from using different metrics of nest predation—daily rates vs. fledging success—that are measured over non-equivalent time periods. Our finding that fledging success is much lower in tropical birds is in agreement with previous analyses of fledging success (Robinson et al. 2000, Schemske et al. 2009). However, this pattern is deceptive because daily mortality rates are in fact similar across latitudes. We suggest that lower fledging success in the tropics results mainly because tropical birds accumulate mortality over a greater number of days in the tropics than in the temperate zone. The degree to which our findings can be extrapolated to other regions remains uncertain: While a previous global study found no latitudinal gradient in daily rate of nest predation (Martin et al. 2017), rates of nest predation are indeed higher in the tropics in Australia (Remeš et al. 2012); note that this study found much greater longitudinal variation in nest predation than latitudinal variation). Here we focus on the Western Hemisphere, where we conclude that the long-held view that nest predation is higher in the tropics is mainly derived from the reduced fledging success of tropical birds (Skutch 1985, Schemske 2009), which is more a consequence of a longer nesting period than a lower daily survival rate. Since they are measured over different time periods on average, fledging success rates in the tropics and the temperate zone do not adequately measure overall survival rates at the two latitudes.

Conclusions

The biotic interactions hypothesis invokes strong biotic interactions in the tropics to explain the origin of high tropical species richness. This intriguing proposal has spawned intense interest in documenting latitudinal clines in interaction strength. We add to this literature by showing evidence that a latitudinal gradient in rates of nest predation suffered by land birds in the Americas is weak or absent. Yet documenting gradients in interaction strength is only part of the story. The idea that species can adapt to strong interactions, potentially blunting their effects, has been comparatively ignored. Here we report that rates of predation suffered by land birds are similar across latitudes, and present evidence that this lack of a latitudinal gradient is in part due to adaptation on the part of tropical birds. Specifically, tropical birds experience greater daily risk of predation, but only when holding nesting period constant; tropical birds have evolved long nesting periods that reduce the daily risk of predation they experience in nature. We suggest this is an example of how an adaptation to strong negative biotic interactions can flatten the observed latitudinal gradient in interaction strength. More broadly, we advocate for an increased focus on the evolutionary consequences of biotic interactions.

Acknowledgements

This research was supported by postdoctoral fellowships from the Biodiversity Research Centre and Banting Canada (#379958) to BGF. None of our funders had any influence on the content of the submitted manuscript, and none of our funders required approval of the final manuscript to be published. Comments from the Schluter lab group and Ralf Yorque greatly improved this manuscript.

Author contributions

BGF conceived of this project; BGF, MNS, MAB and JH conducted the literature search; BGF and DS conducted analyses with input from all authors. BGF wrote the manuscript with input from all authors.

References

Badyaev, A. V, and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. Ecology 82:2948–2960.

Benkman, C. W. 2013. Biotic interaction strength and the intensity of selection. Ecology Letters 16:1054–1060.

Boyle, A. W., B. K. Sandercock, and K. Martin. 2016. Patterns and drivers of intraspecific variation in avian life history along elevational gradients: A meta-analysis. Biological Reviews 91:469–482.

Burke, D. M., K. Elliott, L. Moore, W. Dunford, E. Nol, J. Phillips, S. Holmes, K. Freemark, J. Phiitips, and K. Freemarktt. 2004. Patterns of Nest Predation on Artificial and Natural Nests in Forests. Conservation Biology 18:381–388.

Chalfoun, A. D., and T. E. Martin. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. Animal Behaviour 73:579–585.

Conway, C. J., and T. E. Martin. 2000. Evolution of Passerine Incubation Behavior : Influence of Food , Temperature , and Nest Predation. Evolution 54:670–685.

Darwin, C. 1859. On the origin of species by means of natural selection. J. Murray, London,.

DeGregorio, B. A., S. J. Chiavacci, T. J. Benson, J. H. Sperry, and P. J. Weatherhead. 2016. Nest Predators of North American Birds: Continental Patterns and

Implications. BioScience 66:655–665.

Dobzhansky, T. 1950. Evolution in the tropics. American Scientist 38:209–221.

del Hoyo, J., A. Elliott, J. Sargatal, D. Christie, and de J. E. 2018. Handbook of the Birds of the World Alive.

Jankowski, J. E., G. A. Londoño, S. K. Robinson, and M. A. Chappell. 2012. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography 36:1–12.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

King, D. I., R. M. DeGraaf, C. R. Griffin, and T. J. Maier. 1999. Do Predation Rates on Artificial Nests Accurately Reflect Predation Rates on Natural Bird Nests? Journal of Field Ornithology 70:257–262.

Kubelka, V., M. Šálek, P. Tomkovich, Z. Végvári, R. Freckleton, and T. Székely. 2018. Global pattern of nest predation is disrupted by climate change in shorebirds. Science 362:680–683.

Kulesza, G. 1990. An analysis of clutch size in New World passerine birds. Ibis 132:407–422.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proceedings of the Royal Society B: Biological Sciences 269:309–316.

Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. Evolution 61:2558–2569.

Martin, T. E., A. J. Boyce, K. Fierro-Calderón, A. E. Mitchell, C. E. Armstad, J. C. Mouton, and E. E. Bin Soudi. 2017. Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. Functional Ecology 31:1231–1240.

Martin, T. E., and P. Li. 1992. Life history traits of open-vs. cavity-nesting birds. Ecology 73:579–592.

Matysioková, B., and V. Remeš. 2018. Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species. Evolution 72:2214–2224.

Mckinnon, L., P. A. Smith, E. Nol, J. L. Martin, F. I. Doyle, K. F. Abraham, H. G. Gilchrist, R. I. G. Morrison, and J. Bêty. 2010. Lower Predation Risk for Migratory birds. Science 327:6–8.

Menezes, J. C. T., and M. Â. Marini. 2017. Predators of bird nests in the Neotropics: a review. Journal of Field Ornithology 88:99–114.

Moles, A. T., and J. Ollerton. 2016. Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? Biotropica 48:141–145.

Moore, R. P., and W. D. Robinson. 2004. Artificial Bird Nests , External Validity, and Bias in Ecological Field Studies. Ecology 85:1562–1567.

Nice, M. 1957. Nesting Success in Altricial Birds. The Auk 74:305–321.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Peterson, A., and H. Young. 1950. A nesting study of the Bronzed Grackle. The Auk 67:466–476.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J. Near, M. Coll, and M. E. Alfaro. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559:392–395.

Remeš, V., B. Matysioková, and A. Cockburn. 2012. Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. Journal of Avian Biology 43:435–444.

Robinson, W. D., T. R. Robinson, S. K. Robinson, and J. D. Brawn. 2000. Nesting Success of Understory Forest Birds in Central Panama. Journal of Avian Biology 31:151–164.

Robinson, W. D., J. N. Styrsky, and J. D. Brawn. 2005. Are artificial bird nests effective surrogates for estimating predation on real bird nests? A test with tropical birds. The Auk 122:843–852.

Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus, I. C. Barrio, Y. Basset, A. L. Boesing, T. C. Bonebrake, E. K. Cameron, W. Dáttilo, D. A. Donoso, P. Drozd, C. L. Gray, D. S. Hik, S. J. Hill, T. Hopkins, S. Huang, B. Koane, B. Laird-Hopkins, L. Laukkanen, O. T. Lewis, S. Milne, I. Mwesige, A. Nakamura, C. S. Nell, E. Nichols, A. Prokurat, K. Sam, N. M. Schmidt, A. Slade, V. Slade, A. Suchanková, T. Teder, S. van Nouhuys, V. Vandvik, A. Weissflog, V. Zhukovich, and E. M. Slade. 2017. Higher predation risk for insect prey at low latitudes and elevations. Science 356.

Schemske, D. 2009. Biotic interactions and speciation in the tropics. Page (Butlin R, Bridle J, and Schluter D, Eds.) Speciation and patterns of diversity. Cambridge University Press.

Schemske, D. W., G. G. Mittelbach, H. V Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–269.

Schluter, D., and M. W. Pennell. 2017. Speciation gradients and the distribution of biodiversity. Nature 546:48–55.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of

Neotropical birds, reviewed. Ornithological Monographs 36:575–594.

Tieleman, B. I., J. B. Williams, and R. E. Ricklefs. 2004. Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds. Functional Ecology 18:571–577.

Tobias, J. A., C. K. Cornwallis, E. P. Derryberry, S. Claramunt, R. T. Brumfield, and N. Seddon. 2013. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. Nature 506:359–363.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36:1–48.

Wallace, A. R. 1869. The Malay Archipelago. Cosimo Classics.

Weir, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. Science 315:1574.

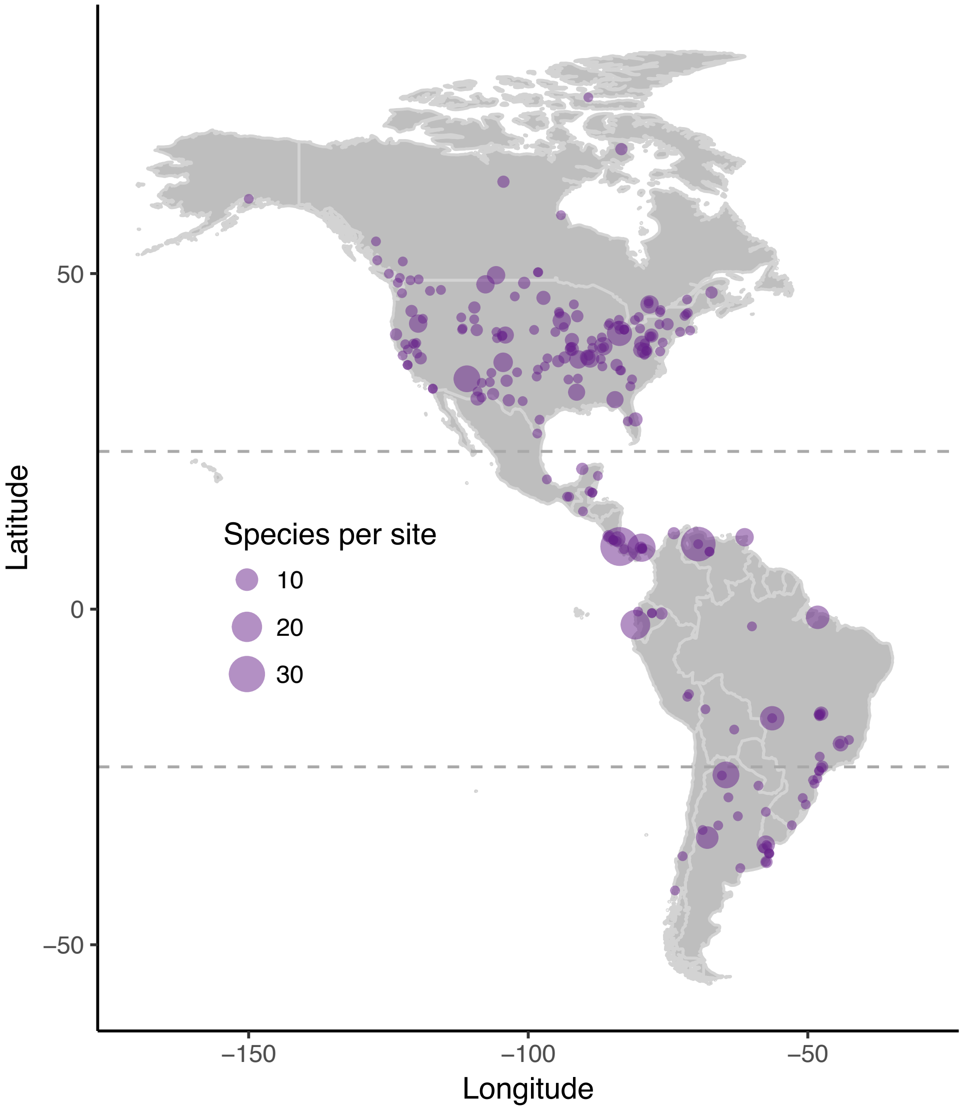

Figure 1. Map of the 244 studies included in our dataset that measured nest predation experienced by land birds in the Americas. Many studies report data for multiple species from the same site, illustrated by the size of the circle. The Tropics of Cancer and Capricorn (at 23.4° N and S, respectively) delimit the tropics, and are illustrated with dashed lines.

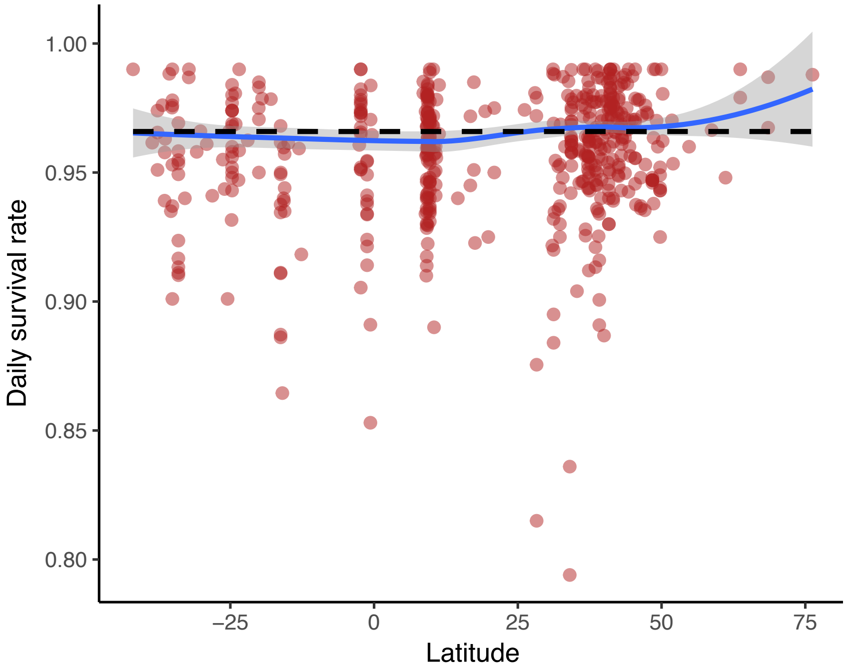

Figure 2. Daily survival rates of nesting birds along latitudinal gradients in the Americas. Predictions from the best-fit metafor model are plotted as a dashed line—this simple model fit a constant value for daily survival rates across latitudes. Summary statistics from individual studies are plotted (N = 501). For comparison, the loess fit, which used the same weights for each data point as the best-fit model, and incorporates the same estimated variance among the study-specific effect sizes, is plotted in blue with shaded 95% confidence intervals.

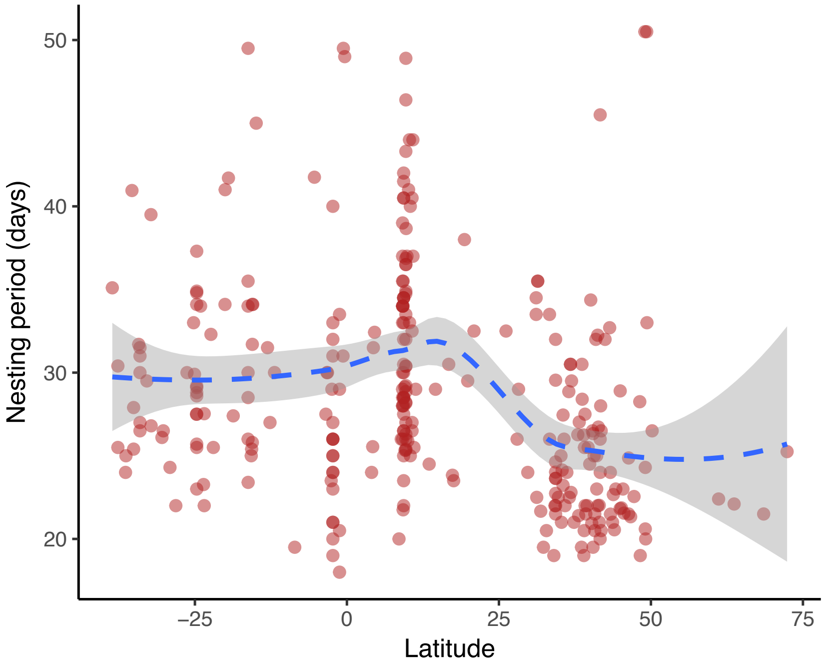

Figure 3. Mean nesting period duration varies predictably with latitude. Species in our dataset with known nesting period duration (N = 295) are plotted. The dashed line illustrates the loess trendline, with 95% confidence intervals shaded in gray. Nesting periods average ~ 30 days within the tropics but ~25 days within the North temperate zone.

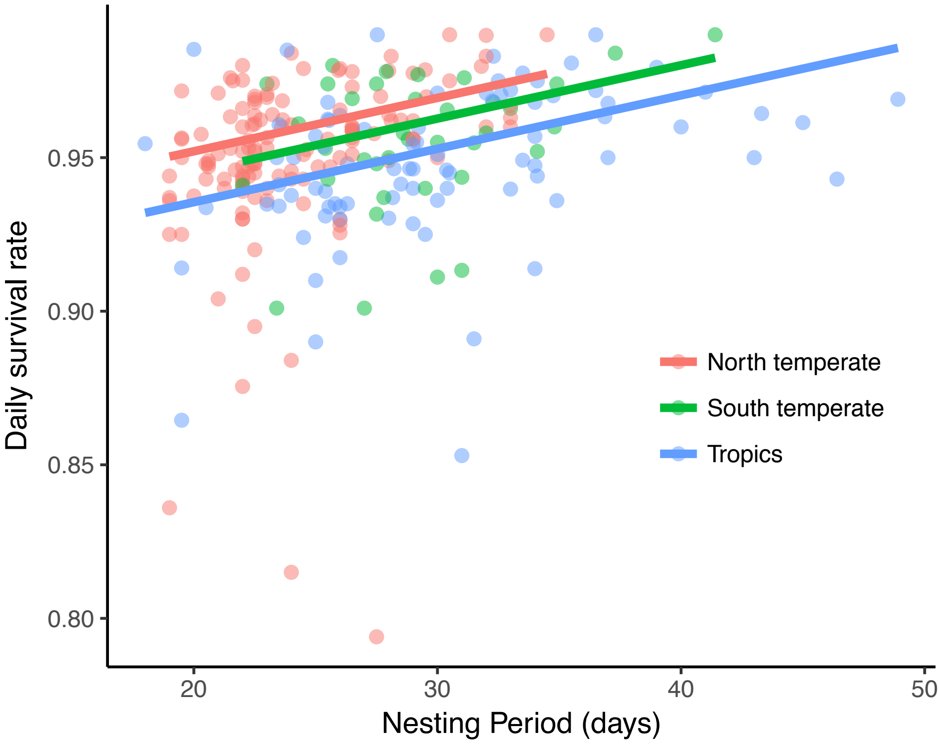

Figure 4. Daily survival rate increases with nesting period length, but with different intercepts for different latitudinal zones. Predictions from a metafor model are plotted as solid lines, and values from individual studies are plotted in colors corresponding to their latitudinal zone (N = 254; including only studies that reported daily survival rates).

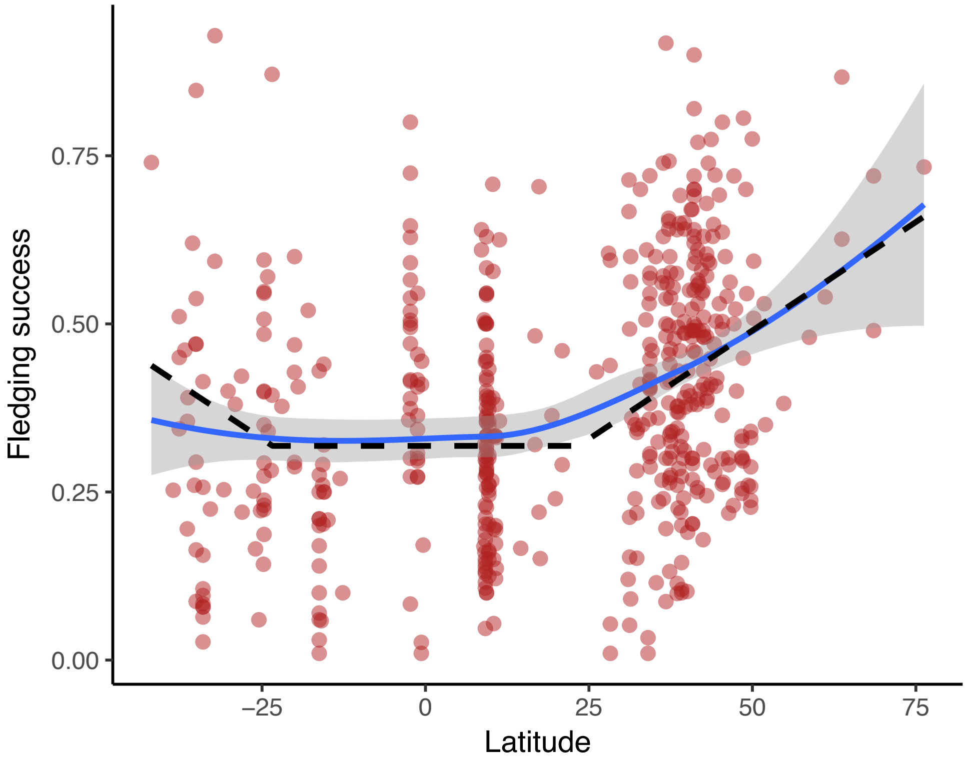

Figure 5. Fledging success of nesting birds along latitudinal gradients in the Americas. Predictions from the best-fit model in metafor—a symmetric breakpoint regression that fit a line with zero slope within the tropics and a positive slope within the temperate zone—, are plotted as a dashed line. Values from individual studies are plotted (N = 500). For comparison, the loess fit, which used the same weights for each data point as the best-fit model, and incorporated the same estimated variance among the study-specific effect sizes, is plotted in blue with shaded 95% confidence intervals.

Table 1. Model comparison of metafor models with daily survival rate as the response variable. The best-fit model fit a constant value of daily survival rate across the entire latitudinal expanse of the dataset.

Model	**ΔAIC**
Constant (daily survival rates do not vary with latitude)	--
Linear regression	3.68
Breakpoint regression (breakpoint = 23.4°)	3.86

Table 2. Model comparison of metafor models with fledging success as the response variable. The best-fit model was a symmetric breakpoint regression that fit a line with zero slope within the tropics and a positive slope within the temperate zone.

Model	**ΔAIC**
Breakpoint regression (breakpoint = 23.4°)	--
Linear regression	11.95
Constant (fledging success does not vary with latitude)	51.40

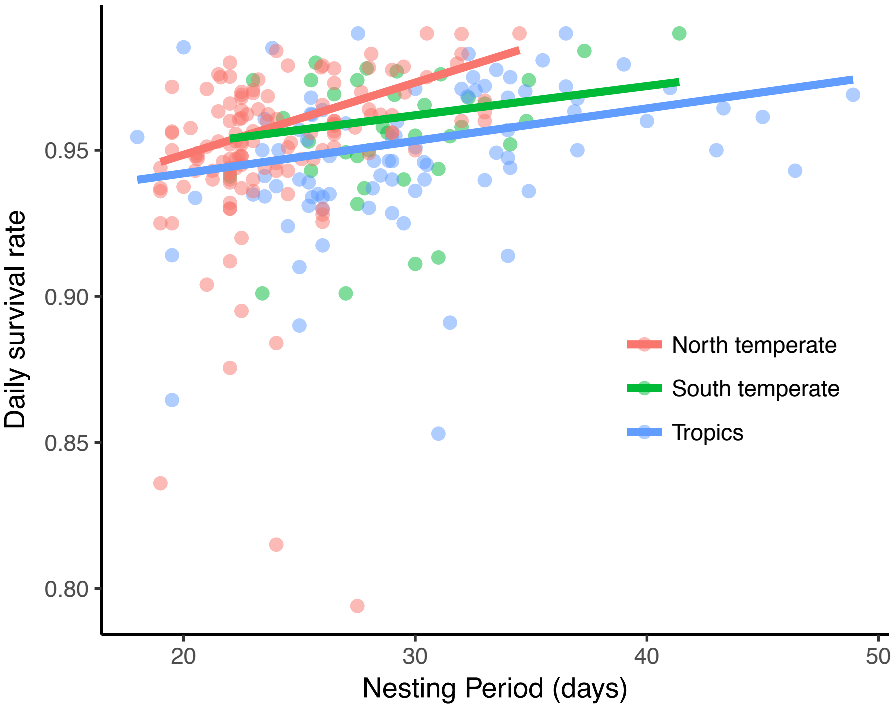

Figure S1. The relationship between nesting period length and daily survival rate in the North temperate zone, the tropics, and the South temperate zone (different slopes model). Predictions from a metafor model are plotted as solid lines, and values from individual studies are plotted in colors corresponding to their latitudinal zone (N = 254; including only studies that reported daily survival rates).

Table S1. Model comparison of metafor models with daily survival rate as the response variable for only studies that directly reported daily survival rate (N = 269). The best-fit model was a simple model that fit a constant value of daily survival rate across the entire latitudinal expanse of the dataset.

Model	**ΔAIC**
Constant (daily survival rates do not vary with latitude)	--
Linear regression	6.98
Breakpoint regression (breakpoint = 23.4°)	7.52

Table S2. Parameter estimates for fixed effects from metafor models with daily survival rate as the response variable. Slope estimates for the linear regression are for straight lines outward from the equator towards higher latitudes; slope estimates for breakpoint regression are for straight lines outward from the tropics (23.4 degrees latitude) towards higher latitudes.

Model	**Intercept ± SE**	**Slope ± SE**
Intercept-only (constant)	0.97 ± 0.001	NA
Linear regression	0.96 ± 0.0025	0.0001 ± 0.0001
Breakpoint regression (breakpoint = 23.4°)	0.96 ± 0.0017	0.0002 ± 0.0001

Table S3. Model summary of intercept-only metafor model with daily survival rate as the response variable and study, species and phylogeny as random effects.

Effect	**Estimate**
Intercept (fixed)	0.97 (se = 0.0049)
Study (random)	0.0001 (sqrt = 0.0093)
Species (random)	0.0000 (sqrt = 0)
Phylogeny (random)	0.0001 (sqrt = 0.0099)

Table S4. Parameter estimates for fixed effects from phylogenetic generalized least squares regression model with nesting period as the response variable. Pagel's λ for this model was 0.99.

Parameter	**Estimate ± SE**
Intercept	31.57 ± 2.91
Absolute value (latitude)	-0.074 ± 0.015

Table S5. Parameter estimates from a metafor model with daily survival rate as the response variable, based on data from studies that reported daily survival rates (i.e., not including studies where we calculated daily survival rates from fledging success using the known nesting period). This is the “equal slopes” model where different latitudinal zones have the same slope. The reference category for the intercept is the North temperate zone; parameter estimates for the South temperate zone and tropics represent deviations from this reference category.

Parameter	**Estimate ± SE**
Intercept	0.92 ± 0.0075
Nesting period	0.0017 ± 0.0003
South temperate zone	-0.0067 ± 0.0047
Tropics	-0.017 ± 0.0039

Table S6. Parameter estimates from a metafor model with daily survival rate as the response variable, based on data from studies that reported daily survival rates (i.e., not including studies where we calculated daily survival rates from fledging success using the known nesting period). This is the “different slopes” model where different latitudinal zones have different slopes. The reference category for “Nesting period” is the North temperate zone; parameter estimates for “Nesting Period: South temperate zone” and “Nesting Period: Tropics” represent deviations from this reference category.

Parameter	**Estimate ± SE**
Intercept	0.90 ± 0.011
Nesting period	0.0025 ± 0.0004
South temperate zone	0.033 ± 0.033
Tropics	0.021 ± 0.018
Nesting period: South temperate zone	-0.0015 ± 0.0012
Nesting period: Tropics	-0.0014 ± 0.0006

Table S7. Parameter estimates from a metafor model with daily survival rate as the response variable and study, species and phylogeny as random effects, based on data from studies that reported daily survival rates (i.e., not including studies where we calculated daily survival rates from fledging success using the known nesting period). This is the “equal slopes” model where different latitudinal zones have the same slope. The reference category for the intercept is the North temperate zone; parameter estimates for the South temperate zone and tropics represent deviations from this reference category.

Parameter	**Estimate ± SE**
Intercept	0.92 ± 0.0079
Nesting period	0.0016 ± 0.0003
South temperate zone	-0.0088 ± 0.0059
Tropics	-0.016 ± 0.0042
Study (random)	0.001 (sqrt = 0.008)
Species (random)	0.0 (sqrt = 0.0)
Phylogeny (random)	0.0 (sqrt = 0.0)

Table S8. Parameter estimates for fixed effects from metafor models with fledging success as the response variable. Slope estimates for the linear regression are for straight lines outward from the equator towards higher latitudes; slope estimates for breakpoint regression are for straight lines outward from the tropics (23.4 degrees latitude) towards higher latitudes.

Model	**Intercept ± SE**	**Slope ± SE**
Intercept-only (constant)	0.39 ± 0.0085	NA
Linear regression	0.28 ± 0.018	0.0036 ± 0.0005
Breakpoint regression (breakpoint = 23.4°)	0.32 ± 0.012	0.0065 ± 0.0008

Table S9. Model summary of breakpoint regression metafor model with fledging success as the response variable and study, species and phylogeny as random effects.

Effect	**Estimate**
Intercept (fixed)	0.31 (se = 0.017)
Slope (fixed)	0.0081 (se = 0.0011)
Study (random)	0.015 (sqrt = 0.12)
Species (random)	0.012 (sqrt = 0.11)
Phylogeny (random)	0 (sqrt = 0.0040)

Appendix 1

Other hypothesized drivers of nest predation

We additionally evaluated three additional hypotheses in the literature that have proposed nest predation is; (1) higher at low elevations than at high elevations; (Jankowski et al. 2012); (2) higher in species that build open cup nests than in species that build enclosed nests; reviewed in (Martin et al., 2017); and (3) higher in forest habitats than open habitats; (Skutch, 1985). Specifically, we added the pertinent covariate (elevation, nest type, or habitat type) to the best-fit latitudinal model one at a time and used AIC to compare model fit with and without the covariate.

We found little evidence to support existing hypotheses that elevation, nest type and habitat explain variation in daily survival rates (Table A1). Nest predation was unrelated to elevation, though we caution that our dataset included few studies from high elevations (e.g., only 27 estimates of nest predation were from above 2,000 m) and that the relationship between nest predation and elevation may not necessarily be linear, as we assume in our analysis. Despite these caveats, our results are consistent with previous meta-analyses that have found minimal influence of elevation on nest predation within temperate zone species (Badyaev and Ghalambor 2001, Boyle et al. 2016). In addition, daily survival rates were similar in enclosed vs. open cup nests, consistent with the findings of a recent study that argued predation is unlikely to drive the evolution of enclosed nests (Martin et al. 2017). Last, daily survival rates were generally similar among habitats (e.g. closed canopy forests vs. more open habitats). At a broad scale, this does not support Skutch's (1985) suggestion that "the real contrast may be, not between tropical and temperate regions, but between wild woodland, where predators abound, and man-made habitats, where predation is much reduced." However, the habitat categories we used may be too coarse to capture the habitat differences that Skutch hypothesized to be relevant to nest predation.

Table A1. Model comparison to assess three covariates (nest shape, elevation and habitat type) hypothesized to influence rates of nest predation. We compared the best-fit model—a simple intercept-only model— with and without each covariate.

Model	**ΔAIC**
Best fit model	--
Best fit model + Nest shape	3.47
Best fit model + Elevation	6.15
Best fit model + Habitat	6.47