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

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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, potentially blunting effects on evolutionary rates, has been largely ignored. Here we examine latitudinal patterns in nest predation in Western Hemisphere birds, a canonical example of a strong tropical biotic interaction. Surprisingly, daily rates of nest survival experienced by land birds vary minimally with latitude. Only when controlling for length of nesting period do tropical birds suffer higher predation than temperate zone birds. Tropical birds have evolved particularly long nesting periods, and long nesting periods are generally associated with reduced predation rates. Hence, long nesting periods may be a component of adaptation by tropical birds to a diverse community of nest predators. More generally, we suggest that adaptation to strong biotic interactions can alter observed latitudinal gradients in interaction strength, potentially equalizing evolutionary rates among latitudes. Moving forward, tests of the biotic interactions hypothesis should consider measuring 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; Dobzhansky 1950; MacArthur 1972; Wallace 2007). 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). If so, strong tropical biotic interactions may explain in part why there are far more species at low 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 (Schemske *et al.* 2009; Moles & Ollerton 2016). There are two principal approaches to measuring rates of biotic interactions. First, one can place a standardized model at many sites, and measure the frequency of biotic interactions experienced by this model (e.g., Roslin *et al.* 2017; Hargreaves *et al.* 2019). 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 (e.g., Kubelka *et al.* 2018). A fundamental difference between these two approaches is that standardized 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, standardized model studies neglect the possibility that adaptation in response to interaction strength and the perpetrators of these interactions could reduce, or 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 is thought to 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 appear to prey almost exclusively upon eggs (DeGregorio *et al.* 2016; Menezes & Marini 2017). Here, we test latitudinal patterns in nest predation using a newly compiled dataset of estimates of daily rates of nest survival experienced by land bird 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. Specifically, we examine the possibility that nesting period length is a component of adaptation to the higher predator diversity in the tropics. Our synthesis thus investigates not only latitudinal 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 continental 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, as predation on artificial nests is poorly correlated with predation on real nests (King *et al.* 1999; Burke *et al.* 2004; Moore & Robinson 2004; Robinson *et al.* 2005). Following previous studies investigating latitudinal trends in nest predation, we restricted our analysis to land birds that are not cavity nesters—primarily passerines, but also a small number of doves, hummingbirds, and other non-passerines (Robinson *et al.* 2000; Remeš *et al.* 2012; Martin *et al.* 2017). Several previous studies have analyzed nest predation data from the Americas (Nice 1957; Skutch 1985; Kulesza 1990; Conway & 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 only considered studies that reported the fate of at least 10 nests, and 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 & Young 1950).

We 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 data 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 each individual Central and South American country; (2) examined the entire publication records of 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 (the probability that an egg or nestling survives from one day to the next); (4) Latitude and longitude; (5) Elevation (meters above sea level, extracted using the Google Maps Platform); and (6) Clutch size, incubation and nestling periods, extracted from the paper itself or from Handbook of the Birds of the World Alive (del Hoyo *et al.* 2018).

Our final dataset included nest predation data for 515 unique species-site combinations (from 244 studies and representing 314 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 (269 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 (Fig 1). This dataset includes 369 estimates of fledging success and 267 estimates of daily survival rate (see Fig S1).

Quantifying nest predation vs. nest failure

Here we are interested in daily rates of nest predation, but researchers typically report daily rates of nest survival and do not parse out causes causes of nest failure. Predators are responsible for the large majority of nest mortality in most places

(Remeš *et al.* 2012), and previous syntheses have simply classified all nest failures as due to predation (Martin *et al.* 2017). In our dataset, around one quarter of studies (66 out of 244) attempted to identify causes of nest failure. Most nest failure was indeed attributed to predation (73%; $N = 112$ unique species-site combinations), a figure remarkably similar to that previously reported for Australian birds (72%; Remeš *et al.* 2012). Further, the percentage of nest failures due to predation was similar across latitudes (slope estimate for latitude in a linear model predicting the percentage of nest failure attributed to predation = -0.00083 ± 0.00074, $p = 0.27$). 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

We first assessed whether daily rates of nest survival vary as a function of latitude by fitting mixed effect meta-analytic models using the "metafor" package (Viechtbauer 2010) in R (R Development Core Team 2017). These models weight individual estimates by the inverse of their squared standard errors, and incorporate 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 (intercept-only); (2) a linear latitudinal gradient in predation (single slope term, equal slopes in both Northern and Southern hemispheres); and (3) a breakpoint linear model wherein predation differs categorically between the tropics and temperate zone (zero slope within the tropics, ≤ 23.4 degrees absolute latitude, equal slopes for temperate latitudes in both Northern and Southern hemispheres). We then compared model fits using AIC. After determining the best-fit model, we fit an expanded version of the best-fit model to test the influence of non-independence among effect sizes. This model included species as a random effect and 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

Despite longstanding support for the idea that nest predation is more intense in the tropics, we found minimal variation in daily survival rates with latitude (see Results). To explore this surprising result, we examined latitudinal patterns in nesting period duration. We calculated nesting period as the number of days from the laying of the first egg until fledging, assuming that species begin incubating upon laying the final egg. We first plotted species' nesting period durations vs. latitude (N = 292 species). Upon observing clear latitudinal patterns in nesting period duration, with longer nesting periods in the tropics (see Results), we tested the evolutionary association between latitude and nesting period duration by fitting a phylogenetic generalized least squares (PGLS) 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, Pagel's λ was estimated using maximum likelihood, and we used . a majority rules consensus tree from 1000 phylogenies downloaded from birdtree.org ("Hackett" backbone; Jetz *et al.* 2012). In both reality and our dataset, oscine passerines predominate in the temperate zone while suboscines are more common in the tropics. To explore whether our overall results are mirrored within these groups, we repeated the PGLS for oscines only (N = 175 species) and for suboscines only (N = 86 species).

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 first fit a model that estimated different slopes and intercepts for different latitudinal zones (predictor variables = nesting period duration, latitudinal zone [north temperate, tropical, south temperate], 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 expanded version of the "same slopes" model that included species as a random effect and incorporated phylogeny by specifying phylogenetic branch length as the variance-covariance matrix. Again, 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

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. Upon plotting the data for the best-fit model (breakpoint regression with equal slopes in Northern and Southern temperate zones), we noticed that this model provided a poor fit to data from the Southern temperate zone. We therefore fit an additional breakpoint regression model where we allowed slopes to differ between Northern and Southern temperate zones, and compared model fits using AIC. Last, we fit an expanded version of the best-fit model that included species as a random effect and specified 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 similar across latitudes within the Western Hemisphere. The most supported model of daily nest survival fit a line with equal daily survival rate (0.96) across the entire latitudinal gradient (Fig 2, Table 1). Alternative models that fit symmetric, non-zero slopes to the relationship between latitude and daily survival rates were less well supported ($\Delta AIC \sim 7$; Table 1). These less supported models were similar to the best-fit model in that they estimated slopes that were nearly flat (Table S1), with estimated daily nest survival at 60° North only slightly greater (by ~ 0.006) than at the equator. Our results did not change when including phylogenetic relationships and species identity in our model (Table S2), indicating that our findings are robust to sources of non-independence in our data.

Thus, unlike in tests that have used standardized models to measure predation in other systems (e.g., Mckinnon *et al.* 2010; Roslin *et al.* 2017; Hargreaves *et al.* 2019), we conclude that natural rates of nest predation experienced by land birds in the Americas 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 trait that varies considerably between the tropics and the North temperate zone—the length of the nesting period (Fig 3). Eggs and chicks remain longer in the nest in the tropics compared to the North temperate zone (Martin 2002; Chalfoun & Martin 2007); in our dataset, tropical nesting periods average approximately 15% longer than in the North temperate zone (~ 32 days vs ~ 28 days; Fig 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 S3), and patterns are similar when analyzing only oscines (temperate origin, predominate in the temperate zone) or suboscines (tropical origin, predominate in the tropics; Table S3).

Is nesting period length an adaptation to predation?

We hypothesize 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 if nestling period length remained unchanged. 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 $p < 0.0001$; Fig 4, Table S4), which was marginally better supported than a model that fit different slopes to different latitudinal zones ($p = 0.092$), and is also present in the different slopes model (comparing estimates for North temperate zone vs. tropics for the mean nesting period of 29 days, $p < 0.001$; Table S5, Fig S2). Again, this result is robust to sources of non-independence in our dataset (Table S6).

Nesting period duration is generally positively related to daily survival rate (Fig 4). For example, the equal slopes model estimated that a 10-day increase in nesting period is associated with a 1.9% increase in daily survival rates within each latitudinal zone (Table S4). The suspected reason is that a longer nesting period is associated with fewer visits to the nest per day by attending parents, reducing rates of detection by nest predators that cue on parental activity to locate and depredate the nest (Matysioková & 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 fledging success (~ daily survival rate * number of days in nesting period) is lower in the tropics compared to the temperate zone. Indeed, we found strong evidence that fledging success of nests is highest in the Northern temperate zone (Fig 5, Tables 2), and a breakpoint regression estimated ~33% of nests successfully fledge nestlings within the tropics while ~ 62% of nests successfully fledge nestlings at 60° (Table S7). Plotting this data revealed that this breakpoint regression model poorly fit data from the Southern temperate zone. Indeed, a breakpoint regression model that fit different slopes to the Southern and Northern temperate zones was better supported (Table 2); this model estimated that ~34% of nests successfully fledge nestlings within both the tropics *and* the Southern temperate zone, while ~ 66% of nests successfully fledge nestlings at 60° N, a result that is robust to sources of non-independence in our data (Table S8). Fledging success in the tropics vs. the Northern temperate zone is based on mortality accumulated over different time spans. Hence, our fledging success results are not a demonstration of higher overall predation in the tropics vs. the Northern temperate zone.

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. Nest predation has long been known to be intense in the tropics (Skutch 1985) such that nest predation is an archetypical example illustrating the more general pattern that biotic interactions are stronger at low latitudes (Schemske 2009). Moreover, recent well-designed globally distributed

experiments have shown that predation rates on standardized models (clay caterpillars, sunflower seeds) are indeed higher in the tropics (Roslin *et al.* 2017; Hargreaves *et al.* 2019). Why do clay caterpillars and sunflower seeds get gobbled up rapidly in the tropics, while tropical birds appear to suffer nest predation at similar rates to temperate zone birds? We propose that adaptation may explain this discrepancy, and hypothesize that adaptation to local predation regimes may generate relatively flat latitudinal gradients in predation experienced by wild populations.

The biotic interactions hypothesis proposes that strong biotic interactions in the tropics generate strong selection that results in faster evolution in the tropics. Here we argue that strong biotic interactions in the tropics do not invariably lead to faster rates of evolution (and ultimately speciation) in the tropics. Instead, strong selection may lead to adaptations that reduce experienced interaction strength (for the link between interaction strength and strength of selection see Benkman 2013). For example, caterpillars living within tropical forests may respond to high rates of predation by adapting anti-predator traits that reduce the rates at which they are eaten in nature. It seems noteworthy to us that caterpillars in tropical forests—at least those noticed by an entomologically-naïve ornithologist— tend not to be green inchworms but instead are often covered with spikes, brightly colored and presumably poisonous, or exquisitely camouflaged (BGF pers. obs). The idea that strong negative interactions drives adaptations that have consequences for the interaction is pervasive in evolutionary ecology, but has seldom been considered in the context of latitudinal gradients in interaction strength (but see Rasmann & Agrawal 2011; Chen *et al.* 2017).

Here we hypothesize that tropical birds have adapted to the greater diversity of nest predators in the tropics, and that these adaptations in part explain the observation that the latitudinal gradient in daily rates of nest survival is relatively flat.

Specifically, we hypothesize that one component of tropical bird adaptation against the diversity of tropical nest predators is the evolution of longer nesting periods. 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. However, nesting periods are not equivalent between the tropics and temperate zone. Instead, tropical birds have repeatedly evolved nesting periods that are longer than those of their relatives that live in the temperate zone. Thus, we hypothesize that tropical birds have achieved higher daily survival rates in part by evolving longer nesting periods (i.e., moving to the right and upwards along the regression line for daily survival vs. nesting period in Fig 4). We note that this link between daily survival rate and nesting period duration is based on observational data, so unmeasured correlated traits (e.g., adult survival; Martin 2002) may also be involved. Further, many factors likely exert selection on nesting period duration, and the evolutionary association we document between tropical birds and long nesting periods could reflect a combination of tropical birds evolving prolonged nesting periods (as described above) and temperate zone birds evolving shorter nesting periods (e.g., if shorter breeding seasons in the temperate zone select for faster nesting periods).

High predation risk could potentially drive tropical populations to evolve longer nesting periods via reductions in rates of parental care that lead to longer nesting periods. Previous studies provide support for these correlations. When confronted with high predation risk, there is a general pattern for birds to reduce their rates of activity at the nest (nest attentiveness), and this correlation appears to be especially strong in tropical environments (Matysioková & Remeš 2018). In addition, less parental care per day at the nest is associated with longer nesting periods (Chalfoun & Martin 2007; Martin *et al.* 2007) but see (Tieleman *et al.* 2004). Future studies that include data on nest attendance (and other relevant breeding biology and

life history traits) are needed to more directly test these relationships.

Comparison with previous studies of latitudinal gradients in nest predation

Tropical birds have long been thought to suffer greater nest predation than temperate zone birds (e.g., Robinson *et al.* 2000; Schemske *et al.* 2009; Kubelka *et al.* 2018), but not all previous studies have supported this idea (e.g., Martin *et al.* 2017). Here we show that one important factor generating disparate results is the choice of metric of nest predation, as in temperate-tropical comparisons, daily rates vs. fledging success are measured over non-equivalent time periods. Our finding that fledging success is much lower in the tropics compared to the North temperate zone 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. In addition, we find that fledging success in temperate South America is similar to that within the tropics (and that nesting periods are similarly long in the tropics and Southern temperate zone), consistent with previous global studies highlighting that temperate-tropical comparisons in bird breeding biology may differ between Northern and Southern Hemispheres (Martin *et al.* 2007, 2017). However, this finding should be treated as provisional given the small amount of data from latitudes > 35° S in our analysis.

The degree to which our findings can be extrapolated to other regions remains uncertain. A previous global study found little latitudinal variation in daily rate of nest predation (Martin *et al.* 2017), consistent with our results. In contrast, rates of nest predation are indeed higher in the tropics in Australia (Remeš *et al.* 2012; this study also found much greater longitudinal variation in nest predation than latitudinal

variation). Here we show that for the Western Hemisphere, 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 vs. the Northern temperate zone do not adequately measure overall survival rates in these two latitudinal zones.

Conclusions

The biotic interactions hypothesis invokes strong biotic interactions in the tropics to explain in part 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 present evidence that the lack of a latitudinal gradient in nest predation suffered by birds may be in part a result of adaptation on the part of tropical birds. 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.

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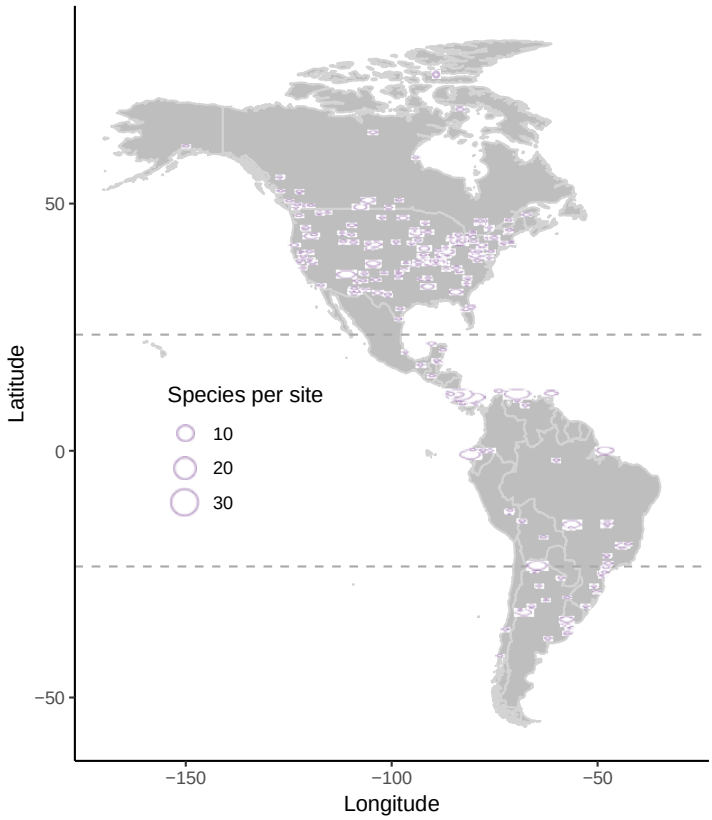

Figure 1. Map of studies measuring nest predation experienced by land birds in the Americas (dataset = 244 studies). Many studies report data for multiple species from the same site, illustrated by the size of the circle. The Tropics of Cancer and Capricorn (at 23.4° N and S, respectively) delimit the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

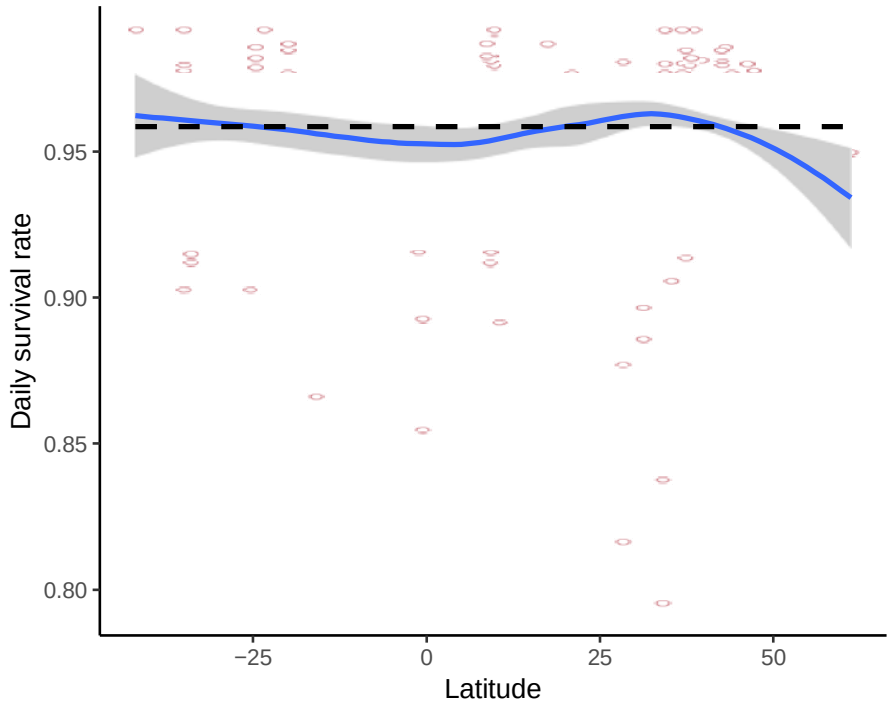

Figure 2. The latitudinal gradient in daily survival rates for land birds in the Americas (N = 267). Predictions from the best-fit metafor model are plotted as a dashed line—this simple model fit a constant value for daily survival rates across latitudes. For comparison, the loess fit, which used the 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.

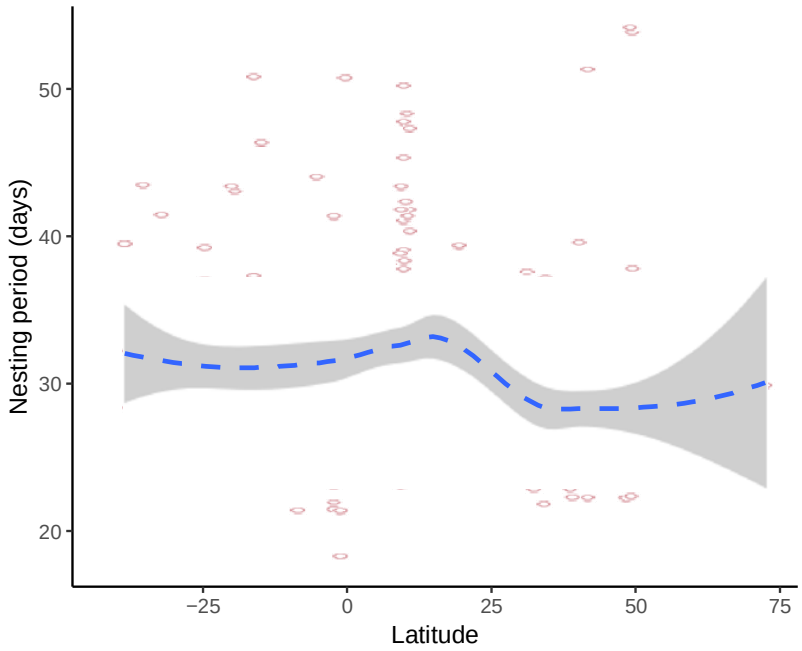

Figure 3. The latitudinal gradient in nesting period length for land birds in the Americas (N = 292 species). The dashed line illustrates the loess trendline, with 95% confidence intervals shaded in gray. Nesting periods average ~ 32 days within the tropics and Southern temperate zone but ~28 days within the Northern temperate zone.

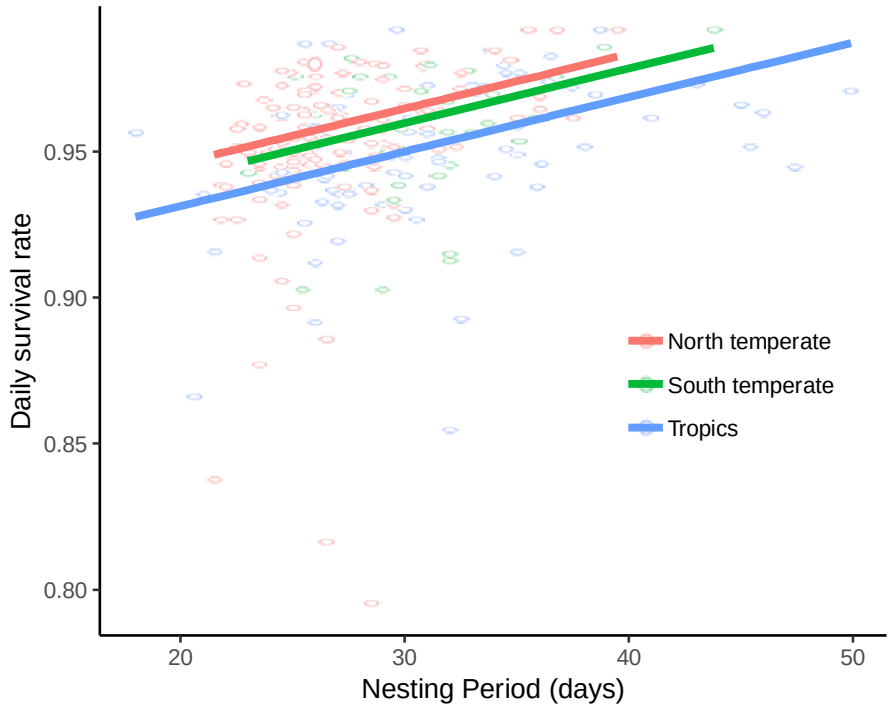

Figure 4. The relationship between daily survival rate and nesting period duration among latitudinal zones. Daily survival rate increases with nesting period length in each latitudinal zone, but with different intercepts. Predictions from a metafor model are plotted as solid lines; values from individual studies are plotted in colors corresponding to their latitudinal zone (N = 252).

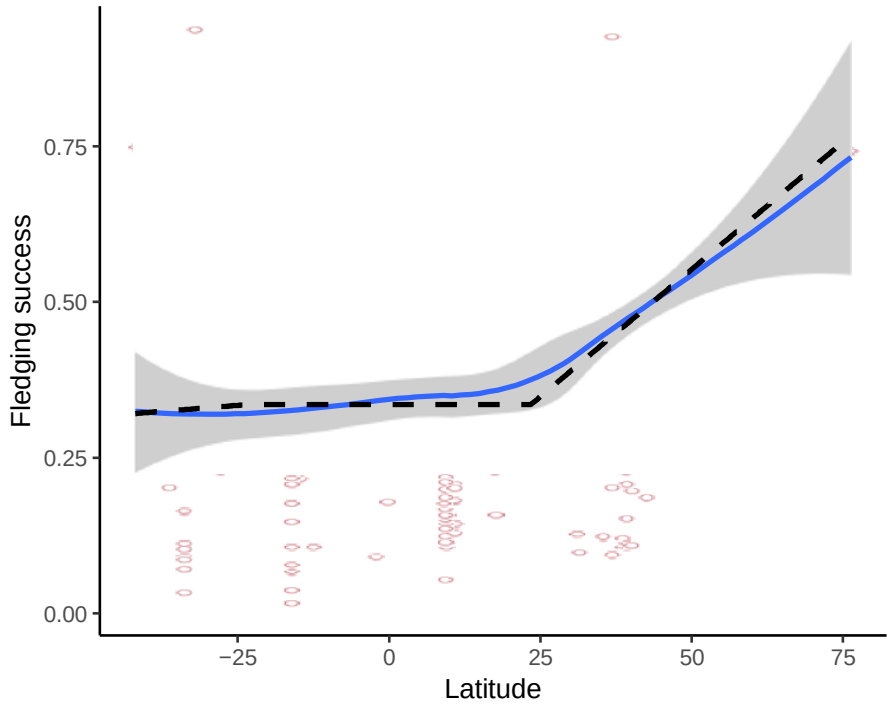

Figure 5. The latitudinal gradient in fledging success for land birds in the Americas (N = 367). Predictions from the best-fit model in metafor—a breakpoint regression that fit a flat line within the tropics and different slopes in the Northern and Southern Hemisphere temperate zones—, are plotted as a dashed line. 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	6.89
Breakpoint regression (breakpoint = 23.4°)	7.54

Table 2. Model comparison of metafor models with fledging success as the response variable. The best-fit model was a breakpoint regression that fit one slope within the tropics and unequal slopes in the Northern and Southern temperate zones.

Model	**ΔAIC**
Breakpoint regression, unequal slopes (breakpoint = 23.4°)	--
Breakpoint regression, equal slopes (breakpoint = 23.4°)	4.68
Linear regression	21.29
Constant (fledging success does not vary with latitude)	66.35

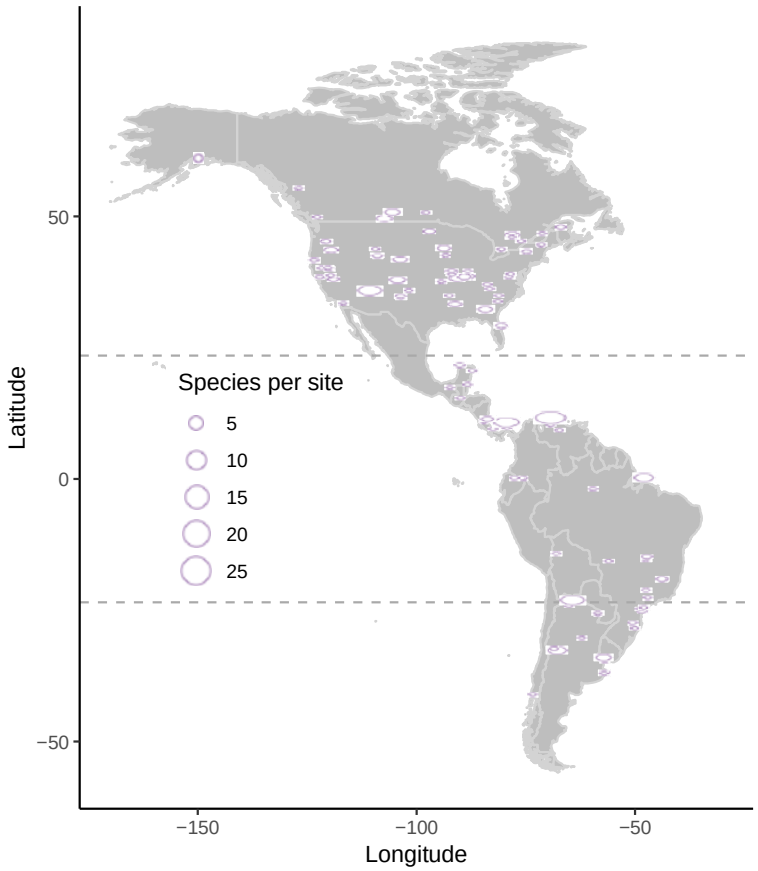

Figure S1. Map of studies measuring daily rates of nest survival for land birds in the Americas (dataset = 110 studies). Many studies report data for multiple species from the same site, illustrated by the size of the circle. The Tropics of Cancer and Capricorn (at 23.4° N and S, respectively) delimit the tropics, and are illustrated with dashed lines.

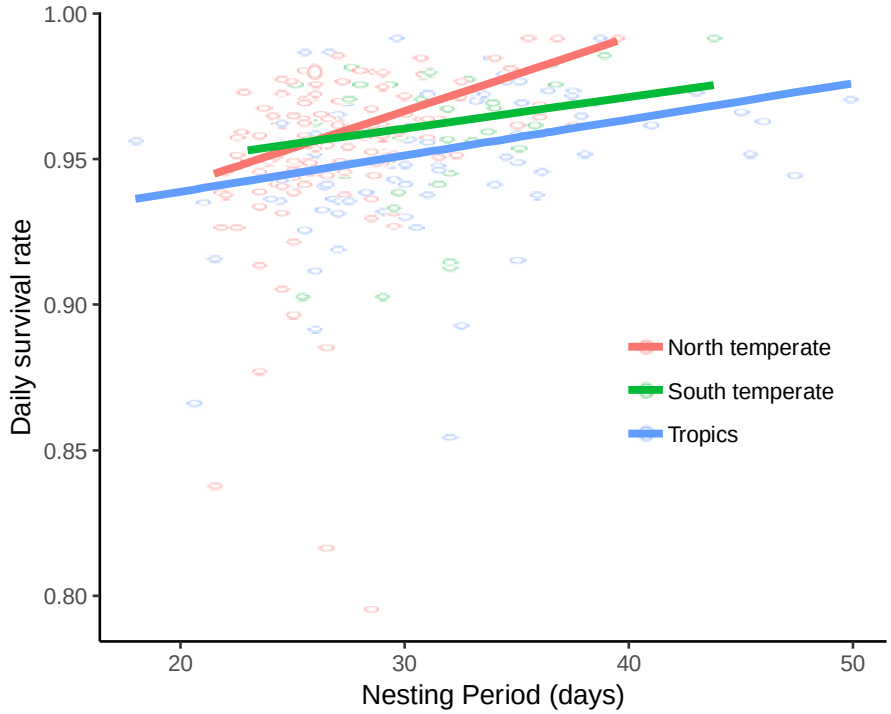

Figure S2. The relationship between daily survival rate and nesting period duration among latitudinal zones (different slopes model). Daily survival rate increases with nesting period length, but with different intercepts and slopes for different latitudinal zones. Predictions from a metafor model are plotted as solid lines; values from individual studies are plotted in colors corresponding to their latitudinal zone (N = 252).

Table S1. 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)	0.96 ± 0.0015	NA
Linear regression	0.96 ± 0.0039	0.0001 ± 0.0001
Breakpoint regression (breakpoint = 23.4°)	0.96 ± 0.0024	-0.0001 ± 0.0002

Table S2. Model summary of intercept-only metafor model with daily survival rate as the response variable and species and phylogeny as random effects.

Effect	**Estimate**
Intercept (fixed)	0.96 (se = 0.0083)
Species (random)	0.0000 (sqrt = 0.0067)
Phylogeny (random)	0.0003 (sqrt = 0.016)

Table S3. Parameter estimates for fixed effects from phylogenetic generalized least squares regression models with nesting period as the response variable. Pagel's λ for these model was 0.99 (entire dataset), 1.00 (oscines) and 0.94 (suboscines).

Model	**Parameter**	**Estimate ± SE**
Entire dataset	Intercept	27.29 ± 2.90
	Absolute value (latitude)	-0.040 ± 0.015
Oscines only	Intercept	34.92 ± 2.86
	Absolute value (latitude)	-0.026 ± 0.016
Suboscines only	Intercept	35.45 ± 2.99
	Absolute value (latitude)	-0.065 ± 0.039

Table S4. Parameter estimates from a metafor model with daily survival rate as the response variable. This is the "equal slopes" model where different latitudinal zones have the same slope. The reference category is the North temperate zone; parameter estimates for the South temperate zone and tropics represent deviations from this reference category.

Parameter	**Estimate ± SE**
Intercept	0.91 ± 0.0084
Nesting period	0.0019 ± 0.0003
South temperate zone	-0.0049 ± 0.0047
Tropics	-0.015 ± 0.0037

Table S5. Parameter estimates from a metafor model with daily survival rate as the response variable. This is the "different slopes" model where different latitudinal zones have different slopes. The reference category 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	0.89 ± 0.012
Nesting period	0.0025 ± 0.00043
South temperate zone	0.038 ± 0.035
Tropics	0.024 ± 0.019
Nesting period: South temperate zone	-0.0015 ± 0.0012
Nesting period: Tropics	-0.0013 ± 0.00063

Table S6. 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. 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	0.91 ± 0.0084
Nesting period	0.0019 ± 0.00030
South temperate zone	-0.0050 ± 0.0047
Tropics	-0.015 ± 0.0037
Species (random)	0.0 (sqrt = 0.0064)
Phylogeny (random)	0.0 (sqrt = 0.0)

Table S7. 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. Breakpoint regressions fit either equal slopes (same slope value in both Northern and Southern temperate zones) or unequal slopes (different slopes in Northern vs. Southern temperate zones).

Model	**Intercept ± SE**	**Slope ± SE**
Intercept-only (constant)	0.41 ± 0.010	NA
Linear regression	0.29 ± 0.019	0.0043 ± 0.0006
Breakpoint regression, equal slopes (breakpoint = 23.4°)	0.33 ± 0.013	0.0080 ± 0.001
Breakpoint regression, unequal slopes (breakpoint = 23.4°)	0.34 ± 0.013	-0.0008 ± 0.0032 (S Hemisphere) 0.0089 ± 0.0031 (N Hemisphere)

Table S8. Model summary of unequal slopes breakpoint regression metafor model with fledging success as the response variable, and species and phylogeny included as random effects.

Effect	**Estimate**
Intercept (fixed)	0.34 (se = 0.013)
Slope (fixed)	-0.0008 ± 0.0032 (S Hemisphere)
	0.0089 ± 0.0031 (N Hemisphere)
Species (random)	0.026 (sqrt = 0.16)
Phylogeny (random)	0 (sqrt = 0.0000)