

## Adaptation and Latitudinal Gradients in Species Interactions: Nest Predation in Birds

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Submitted February 11, 2020; Accepted May 27, 2020; Electronically published October 20, 2020

Online enhancements: supplemental PDF. Dryad data: <https://doi.org/10.5061/dryad.np5hqbzqg>.

**ABSTRACT:** Are biotic interactions stronger in the tropics? Here, we investigate nest predation in birds, a canonical example of a strong tropical biotic interaction. Counter to expectations, daily rates of nest predation vary minimally with latitude. However, life-history traits that influence nest predation have diverged between latitudes. For example, tropical species have evolved a longer average nesting period, which is associated with reduced rates of nest attendance by parents. Daily nest mortality declines with nesting period length within regions, but tropical species have a higher intercept. Consequently, for the same nesting period length, tropical species experience higher daily nest predation rates than temperate species. The implication of this analysis is that the evolved difference in nesting period length between latitudes produces a flatter latitudinal gradient in daily nest predation than would otherwise be predicted. We propose that adaptation may frequently dampen geographic patterns in interaction rates.

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

Since Darwin, ecologists have suggested that biotic interactions increase in strength toward the equator (Darwin 1859; Wallace 1869; Dobzhansky 1950; MacArthur 1972). Dobzhansky (1950, p. 220) expressed this viewpoint by arguing that “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 in the tropics (Schemske 2009). If so, strong biotic interactions in the

tropics may explain in part why there are far more species at low latitudes than in the temperate zone (Schemske 2009).

The biotic interactions hypothesis has inspired a growing number of studies that test the prediction that biotic interactions are indeed stronger in the tropics (Schemske et al. 2009; Moles and Ollerton 2016). There are two principal approaches to assess interaction strength across latitudes. The first is to place a standardized model at many sites and measure rates of biotic interactions experienced by this model (e.g., predator attack rates on green clay caterpillars or sunflower seeds; Roslin et al. 2017; Hargreaves et al. 2019). The second is to measure rates of biotic interactions that local wild populations actually experience, repeating this at a large number of sites across latitudes to account for variability (e.g., Kubelka et al. 2018). A fundamental difference between these two approaches is that standardized models do not participate in evolution. They are constant, so they cannot exhibit local adaptations to changing conditions across latitudes. By contrast, wild studies measure rates of biotic interaction experienced by populations that have had the opportunity to adapt to local species interactions. In this case, the possibility exists that adaptation in response to experienced species interactions could reduce any latitudinal gradient in interaction rates. This might explain why globally distributed experiments using standardized models often report higher interaction rates at low latitudes and elevations (Roslin et al. 2017; Camacho and Avilés 2019; Hargreaves et al. 2019; but see Roesti et al. 2020), whereas many observational studies of wild populations report latitudinal gradients in interaction rates that are flatter (reviewed by Moles and Ollerton 2016).

Here, we study rates of nest predation experienced by land birds. Nest predation rates in land birds are widely thought to be greatest at low latitudes (Skutch 1985; Robinson et al. 2000; Schemske et al. 2009; McKinnon et al.

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Am. Nat. 2020. Vol. 196, pp. E000–E000. © 2020 by The University of Chicago. 0003-0147/2020/19606-5976\$15.00. All rights reserved.

DOI: 10.1086/711415

2010; Remeš et al. 2012; DeGregorio et al. 2016; Kubelka et al. 2018; but see Martin et al. 2017). Tropical birds must deal with a distinct and diverse community of nest predators—a greater diversity of nest predators at low latitudes is one explanation for intense nest predation in the tropics (DeGregorio et al. 2016; Menezes and Marini 2017). To test whether nest predation rates are indeed higher in the tropics, we compiled published observational data on daily rates of nest survival for Western Hemisphere birds. We use published estimates of daily rates of nest survival to estimate daily rates of nest predation, as the bulk of nest failure in birds across latitudes is due to predation (Remeš et al. 2012; Martin et al. 2017; see the supplemental PDF, available online).

We were surprised to find minimal latitudinal variation in daily nest predation rates. To explore this result, we asked whether tropical birds have evolved life-history traits that might reduce the rates of nest predation they experience, focusing on one specific trait—nesting period length. Nesting periods are substantially longer in the tropics. Moreover, longer nesting periods are associated with reduced rates of nest attendance that, in turn, are linked to reduced rates of nest predation, perhaps because nest predators locate nests in part on the basis of parental activity at the nest (Martin 2002; Chalfoun and Martin 2007; Martin et al. 2007; Matysioková and Remeš 2018; note that many other breeding biology traits are also involved in adaptation to nest predation). We then asked whether daily nest predation is predicted to differ between the tropics and the temperate zone when observed differences in mean nesting period length are statistically removed. This represents an attempt to estimate the latitudinal gradient in interaction strength when removing local adaptation, akin to the standardized model approach. Our synthesis thus investigates not only latitudinal patterns in the rate 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, and South America (see the supplemental PDF). Our final data set included nest predation data for 515 species-site combinations (from 244 studies and representing 314 species; fig. S1; figs. S1–S5 are available online), including 267 estimates of daily survival rate (fig. S2) and 369 estimates of fledging success. The data set and R scripts to perform analyses and produce figures have been deposited in the

Dryad Digital Repository (<https://doi.org/10.5061/dryad.np5hqbzqg>; Freeman et al. 2020). Estimates of daily nest predation are based on methods, including the Mayfield method, and fitting logistic exposure models to observations of exposure days and survival (Shaffer 2004). Fledging success estimates are based on observed numbers of initiated nests fledging at least one offspring. Most studies were conducted between  $\sim 40^{\circ}\text{S}$  and  $\sim 50^{\circ}\text{N}$  (northern temperate zone: 269 species-site combinations; tropics [absolute latitude,  $<23.4$ ]: 187 species-site combinations; southern temperate zone: 59 species-site combinations). We estimated daily predation rate as one minus the daily survival rate (see the supplemental PDF).

### *Latitudinal Variation in Daily Rates of Nest Predation*

We conducted all analyses using R (R Development Core Team 2020). We fit three mixed effects meta-analytic models in the metafor package (Viechtbauer 2010). The models correspond to distinct biological hypotheses (data = 267 estimates of daily predation rate: 132 north temperate, 90 tropical, and 45 south temperate): (1) no latitudinal gradient in predation (intercept-only model), (2) a linear latitudinal gradient in predation (equal slopes in Northern and Southern Hemispheres), and (3) a breakpoint linear model wherein predation is the same within the tropics but differs between the tropics and temperate zone (zero slope within the tropics, equal slopes for temperate latitudes in Northern and Southern Hemispheres). We compared model fit using the Akaike information criterion (AIC). We then fit additional models to investigate the influence of covariates and to test whether incorporating phylogenetic relationships or including multiple estimates per species influenced our result (see the supplemental PDF).

### *Latitudinal Variation in Nesting Period Length*

We found minimal variation in daily predation rates among latitudes (see “Results”). To explore potential causes of this surprising result, we examined patterns in the duration of nesting periods. We calculated nesting period length for the 292 species in our data set for which full information was available 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 tested the evolutionary association between latitude and nesting period length by fitting a phylogenetic generalized least squares regression with nesting period length as the response variable and absolute value of latitude as a fixed effect, and we estimated Pagel’s  $\lambda$  using maximum likelihood using the ape package (Paradis et al. 2004).

To quantify the relationship between nesting period length and daily predation rates, we fit additional meta-analytic models (data = 252 estimates of daily predation rate for which we had data on the species' nesting period length: 132 north temperate, 84 tropical, and 36 south temperate). We fit two models to predict daily predation rate that included nesting period length and latitudinal zone as predictor variables; the first model did not include an interaction between these fixed effects, while the second model included this interaction. We compared fit of these two models using a likelihood ratio test (anova function in R).

*Latitudinal Variation in Fledging Success*

We examined latitudinal patterns in fledging success by repeating the three meta-analytic models and methods described above for latitudinal patterns in daily predation rate but with fledging success as the response variable (data = 369 estimates of fledging success: 187 north temperate, 152 tropical, and 30 south temperate). On the basis of visual inspection of patterns, we fit an additional breakpoint regression model where we allowed slopes to differ between northern and southern temperate zones.

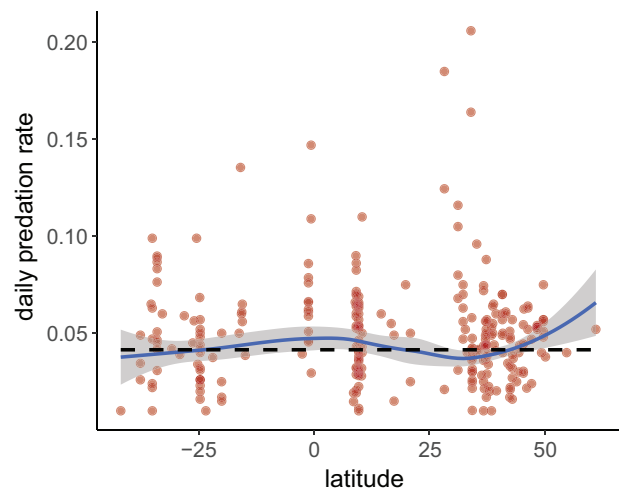
*Testing Additional Drivers of Nest Predation*

We also used our data set to test three additional hypotheses: that nest predation rates are (1) highest at low elevations (Jankowski et al. 2012; Boyle et al. 2016), (2) higher in species with open-cup nests than in species with enclosed nests (Martin et al. 2017), and (3) variable across different habitats (Martin 1993). For each of these three covariates, we fit our set of three models both with and without the covariate and compared model fit using AIC. We followed this procedure for both daily predation rate and fledging success analyses. In addition to testing hypothesized environmental drivers of nest predation, these analyses serve to test whether the latitudinal patterns that are the focus of this article are robust to the inclusion of covariates.

**Results**

*Latitudinal Variation in Daily Rates of Nest Predation Is Minimal*

We found evidence that daily rates of nest predation in land birds are similar across latitudes within the Western Hemisphere. The most strongly supported model of daily nest survival fit a line with equal daily predation rate (~0.04) across the entire latitudinal gradient (fig. 1). Models that fit slopes to the relationship between latitude and



**Figure 1:** Latitudinal gradient in daily rates of nest predation for land birds in the Americas is approximately flat ( $N = 267$ ). Daily rates of nest predation estimate the probability per day that a predator consumes eggs or nestlings. Fitted values from the best-fit univariate metafor model are plotted as a dashed line—this simple model fit a constant value for daily predation rates across latitudes. For comparison, the loess fit, which uses 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. Daily rates of nest predation are estimated from daily survival rates reported in the literature. The finding that the latitudinal gradient in daily predation rates is approximately flat is robust to both the inclusion of elevation and nest shape, two covariates that also impact predation rates (table S2), and to sources of nonindependence in our data (table S3).

daily survival rates were less supported ( $\Delta AIC \sim 7$ ; table S1; tables S1–S10 are available online) and estimated shallow slopes, with estimated daily rates of nest predation at 45° latitude only slightly lower (by ~0.004) than at the equator (table S1). Our finding that latitudinal variation in daily rates of nest predation is minimal is robust to the inclusion of three environmental variables hypothesized to drive nest predation rates (elevation, nest shape, and habitat type; see table S2) and to sources of nonindependence in our data (table S3).

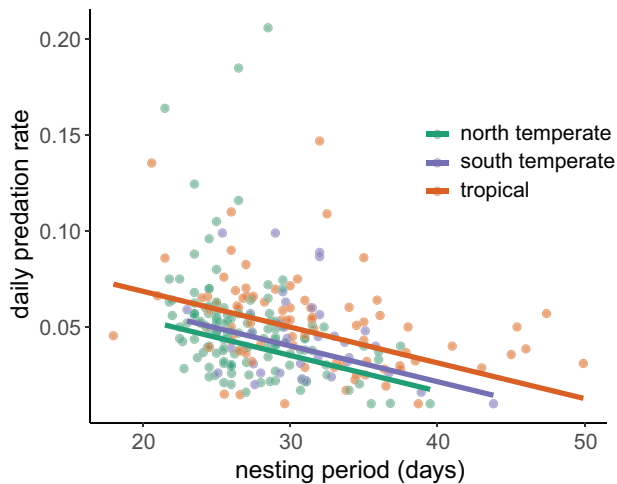
*Nesting Period Length Is a Key Covariate*

In our data set, tropical nesting periods average approximately 15% longer than those in the northern temperate zone (~32 days vs. ~28 days; figs. S3, S4; see also “Supplemental methods” in the supplemental PDF; table S4). Longer nesting period is thought to be in part an adaptation to reduce daily mortality rate on eggs and chicks. In agreement, nesting period length is negatively associated with daily predation rates within latitudinal zones,

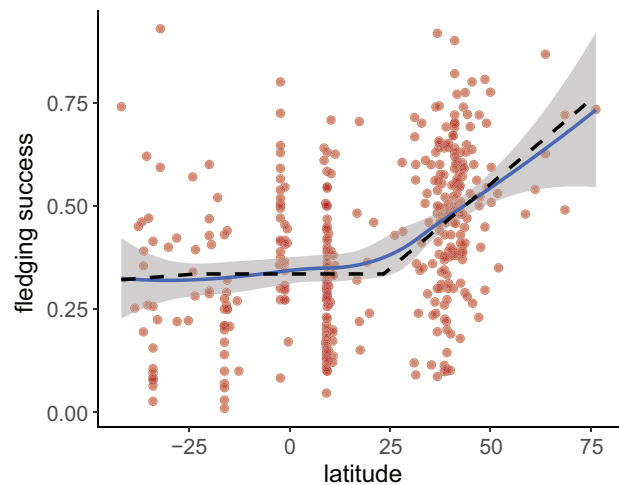
with the best-fit model estimating that a 10-day increase in nesting period results in a drop in predation rates of 1.9 percentage points (table S5). However, the relationship between daily predation and length of nesting period has a higher intercept in the tropics than in the temperate zone (fig. 2; table S5; northern temperate zone vs. tropics:  $P < .0001$ ; see also fig. S7; table S6). If we examine those tropical species having a relatively short nesting period—equal to the mean value of species in the temperate zone (28 days)—we find that the tropical species have a higher predicted nest predation rate than temperate zone species with the same nesting period lengths (fig. 2; table S5). In other words, statistically removing the evolved difference in mean nesting period length between the tropics and the temperate zone predicts higher predation on average in the tropics. This suggests that divergent adaptation of nesting period between the two zones contributes to the flat latitudinal gradient in observed daily nest predation rates. Again, this result is robust to potential sources of nonindependence in our data set (table S7).

#### *Fledging Success Is Lower in the Tropics*

The observation that nesting periods are longer in the tropics, while daily predation rates are similar across latitudes, implies that fledging success (the cumulative probability that nests survive to fledging) is lower in the tropics com-



**Figure 2:** Daily predation rate is higher in the tropics when controlling for nesting period length ( $N = 252$ ). Within each latitudinal zone, daily predation rate decreases with nesting period length in each latitudinal zone. Fitted values from a metafor model are plotted as solid lines; values from individual studies are plotted in colors corresponding to their latitudinal zone. Daily predation rates are estimated from daily survival rates reported in the literature; nesting period is calculated as the number of days from the laying of the first egg to fledging.



**Figure 3:** Latitudinal gradient in fledging success for land birds in the Americas ( $N = 367$ ). Fitted values 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 uses 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.

pared with the temperate zone. Indeed, independently derived estimates of fledging success provide strong evidence that fledging success is highest in the northern temperate zone (fig. 3; table S8). The best-fit breakpoint regression model fit different slopes to the southern and northern temperate zones (table S8); this model estimated that ~34% of nests successfully fledge nestlings within both the tropics and the southern temperate zone, while ~53% of nests successfully fledge nestlings at 45°N (table S8), a result that is robust to sources of nonindependence in our data (table S10).

#### *Elevation and Nest Shape Drive Nest Predation*

Daily rates of nest predation were higher for open-cup nests compared with enclosed nests (4.4% vs. 3.1%; table S2) and higher at 2,000 m compared with sea level (4.6% vs. 3.4%; table S2). However, daily rates of nest predation did not consistently differ between habitat types (table S2). We found no evidence that covariates (e.g., elevation, nest shape) explained variation in fledging success (table S9).

## Discussion

Daily rates of nest predation are similar between tropical and temperate birds in the Western Hemisphere. At the



same time, daily rates of nest predation decline with increasing nesting period length in both zones but with a higher intercept in the tropics. Thus, when we statistically eliminated differences in nesting period length between zones, daily rates of nest predation were higher in the tropics. Reconciling these results requires explicit consideration of the fact that birds at different latitudes possess different life-history adaptations and that these different traits affect nest predation rates. Specifically, tropical birds have longer nesting periods on average. The implication is that local adaptation in traits such as nesting period can mitigate differences in predation rate that would otherwise be more apparent and, in so doing, yield a relatively flat latitudinal gradient in predation rate.

If predator pressure is higher in the tropics, as is often hypothesized, this implies selection on tropical birds to reduce predation rates, for example, by lowering nest attendance. A higher predation pressure in the tropics could be experimentally tested by placing artificial nests across a large range of latitudes. Such an experiment would eliminate adaptive life-history differences between tropical and temperate birds. An underlying assumption of using artificial nests to test these ideas is that predators use the same cues to locate nests across latitudes. Within the Arctic, daily predation rates on artificial nests are higher at lower latitudes (latitudinal extent: 53°–82°; McKinnon et al. 2010). This is consistent with our expectations, but a similar test across a larger range of latitudes has not yet been done. However, correlative evidence comes from the observation that nesting periods and hence overall predation rates on nests are higher in the tropics. Apparently, evolution that has reduced daily predation rates has come at the expense of longer nesting periods. We emphasize that the exact mechanism by which predator-driven selection, among many sources of selection on life-history traits, favors longer nesting periods in tropical birds is not yet clear. Three additional notes are that (1) we focus on the longer nesting periods of tropical birds here, but temperate zone predator assemblages could equally select for shorter nesting periods in temperate zone birds; (2) we are unable to explain why there is substantial variation in nesting period length within latitudinal zones; and (3) other life-history differences between tropical and temperate birds may contribute to the relatively flat latitudinal gradient in nest predation rates.

#### *Nest Shape and Elevation Influence Predation Rates*

We report strong evidence in support of the hypotheses that elevation and nest shape drive daily rates of nest predation. Daily rates of nest predation decline with increasing elevation, and enclosed nests are associated with lower daily rates of nest predation compared with open-cup nests. Importantly, including these covariates does not alter our

main finding—that latitudinal variation in nest predation rates is minimal.

#### *Daily Predation Rate versus Fledging Success*

Nest predation in birds has classically been used to support the more general hypothesis that biotic interactions are stronger at low latitudes (Schemske 2009). Here, we show that daily predation rates hardly differ with latitude for Western Hemisphere land birds. Instead, the long-held view that nest predation is higher in the tropics appears to be derived from observations of reduced fledging success of tropical birds. However, fledging success is integrated over a different nesting duration in the tropics than in the temperate zone, so fledging success is not an accurate measure of predation rates (Bulla et al. 2018). Whether the pattern we document for the Americas applies to other continents remains uncertain; for example, nest predation rates within Australia are slightly higher in the tropics (Remeš et al. 2012; note that this study found greater longitudinal variation than latitudinal variation).

#### *Conclusions*

The biotic interactions hypothesis invokes strong biotic interactions in the tropics to explain in part the high species richness of the tropics. However, whether interactions are stronger in the tropics remains hotly debated. On one hand, an influential review reported general support for stronger biotic interactions in the tropics (Schemske et al. 2009). On the other hand, a recent review suggested that the notion that interactions are stronger in the tropics is a “zombie idea”—an idea not supported by empirical data but that nevertheless refuses to die (Moles and Ollerton 2016). We propose that these opposing viewpoints may be reconciled in part by considering how adaptation alters interaction rates. Our argument builds on similar ideas proposed within the plant defense and herbivory literature (Rasman and Agrawal 2011; Chen et al. 2017). For example, one possible outcome of higher rates of herbivory at low latitudes is that investment in leaf chemical defenses is greater at low latitudes, leading to a rate of herbivory that is more similar between the tropics and the temperate zone than would otherwise be expected (Anstett et al. 2015; Baskett and Schemske 2018).

More broadly, we argue that documenting geographic patterns in observed interaction strengths represents a weak test of the biotic interactions hypothesis. The biotic interactions hypothesis is intriguing precisely because it links ecological interactions to evolutionary rates in order to explain geographic patterns in species richness. The idea is that stronger biotic interactions in the tropics exert

selection that leads to faster evolutionary rates in the tropics and hence faster speciation. We propose that selection could equally lead to differential adaptations along the gradient that reduce or flatten latitudinal gradients in interaction rates. That is, the “ghost of strong interactions past” may influence rates of interactions that we measure today. If so, such adaptations could potentially flatten any latitudinal gradient in evolutionary rates as well, though this remains untested. We advocate for an increased focus on the evolutionary consequences of variation in the strength of biotic interactions (Benkman 2013). Moving forward, we suggest that the most rigorous tests of the biotic interaction hypothesis will consider how both biotic interaction strength and evolutionary rates of trait divergence vary across latitude.

### Acknowledgments

We thank all of the researchers who have studied nest predation in the field and published their hard-won data. This research was supported by postdoctoral fellowships from the Biodiversity Research Centre and Banting Canada (379958) to B.G.F. None of our funders had any influence on the content of the manuscript, and none of our funders required approval of the manuscript to be published. Comments from Renee Duckworth, Trevor Price, Craig Benkman, two anonymous reviewers, Martin Bulla, Jeroen Reneerkens, the Schluter lab group, and Ralf Yorke greatly improved the manuscript.

### Statement of Authorship

B.G.F. conceived of this project; B.G.F., M.N.S., M.M.A.B. and J.H. conducted the literature search; B.G.F. and D.S. led data analysis with input from all authors; B.G.F. wrote the original draft; and all authors contributed to editing and revising the manuscript.

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Associate Editor: Renée A. Duckworth  
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