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Daily Nest Predation Rates Decrease with Body Size in Passerine Birds

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abstract: Body size evolution is generally framed by the benefits of being large, while costs are largely overlooked. An important putative cost of being large is the need to extend development periods, which should increase exposure to predation and potentially select against larger size. In birds, this selection pressure can be important because predation is the main source of offspring mortality and predators should more readily detect the larger nests associated with larger body sizes. Here, we show for diverse passerine birds across the world that counter to expectations, larger species suffer lower daily nest predation rates than smaller species. This pattern is consistent despite latitudinal variation in predation and does not seem to reflect a tendency of larger species to use more protected nests or less exposed nest locations. Evidence instead suggests that larger species attack a wider array of predator sizes, which could reduce predation rates in nests of large-bodied species. Regardless of the mechanism, the lower daily nest predation rates of larger species yield slightly lower predation rates over the entire development period compared with smaller species. These results highlight the importance of behavior as a mechanism to alter selection pressures and have implications for body size evolution.

Keywords: body size evolution, nest predation, antipredator behavior, life history, passerines.

Introduction

Body size influences much of an organism's biology, affecting almost all aspects of its ecology (Blueweiss et al. 1978; Peters 1983; Calder 1984; Saether 1989). For example, most life-history traits scale allometrically with body size, which suggests that much variation in life history across species is the result of selection for different sizes (Bielby et al. 2007). Given the importance of body size, understanding its effects has long been considered a central issue in many biological fields.

Past theoretical and empirical work has largely focused on the benefits of larger bodies, perhaps influenced by the observed trend of organisms to increase in size over evolutionary time (Cope's rule). Benefits include increased success in mating and intraspecific competition, the possibility of using a broader range of foods, and a greater resistance to environmental variation (Watson 1949; Rensch 1959; Gould 1966; Schoener and Janzen 1968; Hone and Benton 2005). While larger body size may provide benefits, it may also create costs, and such costs have more rarely been explored (Blanckenhorn 2000).

A potential cost of larger bodies is the need to extend the development period, which makes offspring more exposed to predation, parasitism, and starvation (Blanckenhorn 2000). In birds, this cost can be particularly relevant because predation is one of the most important sources of offspring mortality (Ricklefs 1969; Martin 1992*a*). In addition, larger species may be more exposed to nest predators because of the need to construct larger conspicuous nests that are more likely to be detected by predators (Snow 1978; Slagsvold 1989; Biancucci and Martin 2010).

Current evidence for a link between body size and nest predation rates is contradictory. Some studies of relatively small numbers of species found that larger species and nests experience higher nest predation rates (Murphy and Fleischer 1986; Møller 1990; Biancucci and Martin 2010; Mouton and Martin 2019), but other studies found lower predation rates (Ricklefs 1969; Weidinger 2004; Remeš et al. 2012*a*). Thus, the influence of body size and associated nest size on nest predation rates remains unclear.

One issue that may have hindered progress in disentangling the relationship between body size and nest predation rates is the existence of substantial geographic variation in nest predation (Martin 1992*b*; Chalfoun et al. 2002; Thompson et al. 2002; Thompson 2007; Martin et al. 2017). At broad geographic scales, latitudinal and elevational differences in predator diversity and abundance (Fischer 1960; Brown 2001) may lead to substantial

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variation in nest predation pressures (Skutch 1949, 1985; Snow 1978; Thompson et al. 2002; Thompson 2007; Boyle 2008; Nana et al. 2015). At local scales, habitat type and landscape configuration can also affect nest predation (Chalfoun et al. 2002; Renfrew and Ribic 2003; Thompson and Burhans 2003). Such variation in the exposure to predators may obscure a body size–nest predation relationship, highlighting the need for broad tests across a large array of species, habitats, and geographic locations.

Another possible influence on a body size–nest predation relationship is the potential of animals to proactively reduce predation risk through behavioral responses (Montgomerie and Weatherhead 1988; Martin 1992*b*). Birds, for instance, commonly respond to predators through a variety of active defense behaviors (e.g., direct attacks, distraction and defensive displays, alarm calls), which are chosen according to the risk that a predator entails (Gochfeld 1984; Pietz and Granfors 2005). Evidence suggests that larger species engage in more vigorous defense against intruders (Ricklefs 1977; Weidinger 2002), although other strategies are also possible such as harassing predators by joining larger groups (Hoogland and Sherman 1976; Wiklund and Andersson 1994; Krams et al. 2009). However, under new predation pressures such as introduced exotic predators, species can lack antipredator behaviors to novel predators, thus being more vulnerable to nest predation risk (Salo et al. 2007; Remeš et al. 2012*b*).

Behavior can also proactively reduce predation risk in yet another way, that is, by mediating the decisions about how, when, and where it is best to reproduce. Birds can, for instance, reduce nest predation by selecting less exposed nest locations (Martin 1993; Martin and Joron 2003; Colombelli-Négrel and Kleindorfer 2009) and by building more protected nests (Nice 1957; Snow 1978; Oniki 1985; Martin 1995; but see Martin et al. 2017; Mouton and Martin 2019). The link of these latter mechanisms to body size is less obvious, but they still have the potential to obscure the relationship between body size and nest predation.

Here, we examine possible relationships between body size and nest predation rates by means of a phylogenetic-based comparative analysis. We focus on passerine birds, a group that exhibits substantial body size variation (4–1,135 g) while sharing a similar altricial development. Our analyses are based on a nest predation data set of unusually large spatial extent and taxonomic diversity, comprising 509 populations of 321 species distributed across the world. A multiscale analysis of this large data set allowed us to rigorously test the relationship between body size and nest predation and to investigate the extent to which this relationship is explained by spatial variation and/or behavioral mechanisms that confer protection against predators.

Methods

Data Collection on Nest Predation

We used nest predation data on passerine birds based on our personal field studies in five sites (88 species and 88 populations) and from studies reported in the literature (243 species and 421 populations; fig. S1; figs. S1–S5 are available online). Our personal field studies included nest predation data from the following five intensively studied field sites: (i) a mixed conifer forest (at 2,300 m elevation) in Arizona (34°N, 111°W) studied for 28 years; (ii) a rain forest (between 1,400 and 2,000 m elevation) in Yacambu National Park, Venezuela (9°N, 69°W), studied for 7 years; (iii) a rain forest (between 1,450 and 1,950 m elevation) in Kinabalu Park, Malaysian Borneo (6°N, 116°E), studied for 9 years; (iv) a semievergreen subtropical montane forest, which forms part of the Andean tropical forest types (between 1,000 and 2,000 m elevation) in El Rey National Park, Argentina (24°S, 64°W), studied for 3 years; and (v) a Mediterranean dwarf shrubland (between 0 and 60 m elevation) in Koeberg Nature Reserve, Western Cape Province, South Africa (33°S, 18°E), studied for 7 years. In each field site, nest predation rates were obtained from a large number of nests monitored following standardized long-term protocols (Martin 1993; Martin et al. 2017). Nests were checked every 2–4 days to determine their status and predation events but were checked daily or twice daily during egg laying, near hatching, and near fledging to obtain exact durations of developmental periods. Nest predation was assumed when all eggs or nestlings disappeared more than 2 days prior to average fledging age and parents could not be found in the area feeding fledglings (Martin et al. 2017).

To further generalize the results, we added information on nest predation rates extracted from the literature, including both field studies (detailed in data deposited in the Dryad Digital Repository [https://doi.org/10.5061/dryad.4f4qrfj8z; Unzeta et al. 2020]) and comparative studies (Martin 1993, 1995; Martin and Clobert 1996; Robinson et al. 2000; Remeš and Martin 2002; Remeš 2007; Matysioková et al. 2011; Remeš et al. 2012*a*, 2012*b*). A literature search was performed through Google Scholar using the following terms: “nesting success,” “reproductive success,” “breeding success,” “nest predation,” and “nest survival.” Hole nesters were not considered in our analyses because they exhibit low nest predation rates (i.e., Lack 1954; Nice 1957; Martin 1995) that can obscure any body size relationships in more exposed nest types. Altogether, the complete database comprised passerine species from 58 different families. Also, populations varied in their spatial distribution across tropical regions (50% north-temperate, 15% tropical, and 35% south-temperate) and zoogeographic regions (47% Nearctic, 12% Neotropic, 5% Palearctic, 5% Afrotropic, 5% Oriental, and 26% Australian).

Data Collection on Body Size

Body size of species was characterized in terms of adult body mass. For the species in the intensively studied field sites, body mass was measured with GemPro 250 portable electronic scales (MyWeigh, Phoenix, AZ) in birds captured by mist nets (Martin 2015). For species for which nest predation data were obtained from published sources, adult body mass was obtained from Dunning (2007).

Processing Data on Nest Predation

Because not all nests were found at the beginning of the nesting cycle, nest predation was estimated as daily nest predation rates (Mayfield 1961). For the species from the intensively studied field sites, we estimated daily predation rates using the logistic exposure method (Shaffer 2004; Martin et al. 2017). However, most of the original sources for literature data provided nest predation estimates as the percentage of depredated nests. Following Ricklefs (1969), we transformed percentage of depredated nests to daily nest predation rates (DPRs) by the formula $\mathrm{DPR} = -(\ln(1 - \mathrm{PR}))/T$, where PR is the proportion of depredated nests and T is the duration of the nesting cycle. The method of Ricklefs (1969) assumes that all nests are found at the beginning of the nesting cycle, but estimates using this method correlate well with those calculated by an alternative method (i.e., Beintema 1996) that varied T for simulated nests found at the middle stage of the nesting cycle (Matysioková et al. 2011; Remeš et al. 2012*a*). Following Remeš et al. (2012*a*), we estimated the duration of the nesting cycle by summing clutch size (assuming one egg laid per day), incubation period, and nestling period. The information on these life-history traits was collected from *Handbook of the Birds of the World Alive* (Del Hoyo et al. 2018), *The Birds of North America* (Rodewald 2018), and original sources. Finally, because daily predation rates may underestimate total predation pressure over the entire nesting cycle (Pietz et al. 2012), we estimated nest predation rates during the entire development period (hereafter, total nest predation rates) by the formula $\mathrm{TotalPred} = 1 - \mathrm{DSR}^T$ (Mayfield 1961), where T is the duration of the nesting cycle and DSR is the daily survival rate (i.e., $\mathrm{DSR} = 1 - \mathrm{DPR}$).

Data Collection on Nest Size

Measures of the outer height and diameter of nests were collected from Higgins et al. (2001, 2006), Higgins and Peter (2002), Del Hoyo et al. (2018), and Rodewald (2018). These measures were then used to estimate both nest side surface area, as the half of an ellipse area (for open nests) and as the whole ellipse area (for domed nests), and nest top surface area, as the area of a circle. Nest side surface area and nest top surface area were highly correlated, so we used the latter to maximize sample size.

Data Collection for Behavioral Response to Predators

A good surrogate of the antipredatory potential of a species is to assess the body size of the predators that parents of the prey species can attack. Consequently, we scored defense behavior as the body mass (range and maximum) of the bird and mammal predators that adults of the prey species have been reported to attack. The information on species agonistic behaviors was obtained from Higgins et al. (2001, 2006), Higgins and Peter (2002), and Rodewald (2018), while the information on predator body mass was collected from the Animal Ageing and Longevity Database (Tacutu et al. 2018). We defined attacking behaviors as those agonistic interactions implying an aggressive approach to predators, described in the literature with some of the following terms: "attacking," "chasing," "harassing," "diving," "pecking," "striking," "fighting," "aggressive interaction," and "physical contact." Moreover, we considered as predators those species that were cited as nest or adult predators by Higgins et al. (2001, 2006), Higgins and Peter (2002), and Rodewald (2018). The type of predator (bird or mammal) did not affect the relationship between body mass and maximum body size of predators, so predator types were pooled together in the final analyses. Data on body sizes of predators that the prey species can successfully attack are provided in the Dryad Digital Repository (https://doi.org/10.5061/dryad.4f4qrfj8z; Unzeta et al. 2020).

Data Collection on Covariates

For each species in our data set, we extracted information on several factors that could affect the relationship between body size and nest predation, as follows: (1) nest structure (open vs. domed), (2) nest location (ground, shrub, or canopy), (3) habitat of the study site (open vs. forested), and (4) social organization (solitary vs. group breeders, the latter including cooperative breeding and colonial species). Information was obtained from original sources, Del Hoyo et al. (2018), Rodewald (2018), and Cockburn (2006). We also collected data on the mean latitude, longitude, and elevation of the study sites. Whenever the original articles did not provide coordinates or elevation of the study sites, we extracted the information based on the reported localities by using Google Earth software. Moreover, we considered the possible presence of exotic predators in those study sites present in human-disturbed habitats (Hugo and van Rensburg 2009), such as urban and rural habitats, and when exotic predators were detected in the study sites. Finally, we used research effort estimates from Ducatez and Lefebvre (2014) to account for the fact that detection of agonistic behaviors can be increased in species that are more commonly studied. Research effort was based on the number of articles published for each species from 1978 to 2008 in the Zoological Record database.

Phylogeny

Phylogenetic trees were obtained from the global phylogeny of birds, available at http://www.birdtree.org (Jetz et al. 2012). To account for phylogenetic uncertainty, we built a maximum clade credibility tree (summary tree) for the first chunk of 1,000 phylogenetic trees for each backbone, using the Ericson et al. (2006) backbone and TreeAnnotator (a program included in the software BEAST ver. 1.8.0; Drummond et al. 2012).

Modeling Body Size and Daily Nest Predation

To investigate the relationship between body size and daily nest predation, we used Bayesian phylogenetic mixed models (BPMMs) with Gaussian error structures, as implemented in the MCMCglmm R package version 2.20 (Hadfield 2010). The use of this approach allowed us to perform mixed models while accounting for phylogenetic effects. We first used BPMMs to test the association between body size and daily nest predation. Nest predation rate measures were not totally independent from each other because of shared inheritance among species and because several species as well as site and year of the studies accounted for multiple records. Thus, when modeling nest predation, we included phylogeny, species, study sites, and year as random effects in the BPMMs, which proved to be the best random structure according to both the deviance information criterion and the widely applicable information criterion. The proportion of daily nest predation variance explained for each random factor was assessed by means of intraclass correlation coefficients (ICCs; Nakagawa and Schielzeth 2010). Variation in the mean square root of daily predation rates across species was illustrated with a phylogenetic reconstruction based on the function contMap from Phytools R package (Revell 2012), which allow visualization of continuous data on a phylogeny.

Daily nest predation rates and body size estimates were, respectively, square root and log transformed prior to analyses to improve normality. We explored the possible contributing effects of nest location, habitat type, nest structure, latitude, and elevation by including these variables as fixed effects (Z transformed) in the model. We analyzed interactions between fixed factors and also examined whether nest predation relationships with elevation and latitude were better described by a polynomial model than by a linear model. To assess which predictors better explained daily nest predation variation, we performed a model selection approach based on phylogenetically informed deviance information criterion, in which a set of models containing all combinations of traits were analyzed and compared. We also investigated the relationship between nest size and daily nest predation rates after accounting for body size effects. To avoid collinearity between nest size and body size, we estimated residual nest size as the residual from a BPMM of nest size (log transformed) against body size (log transformed). In complementary analyses modeling body size or residual nest size as response variables, random structures were adjusted using those structures that better accounted for the nonindependence of the data. Using noninformative priors, each model was run for 3,100,000 iterations with a 100,000 burn-in and a thinning interval of 2,000 to allow convergence. Model convergence was confirmed by ensuring that sample autocorrelation was <0.1 and that the number of iterations to obtain samples was at least 1,000.

To ensure that the results were not affected by heteroscedasticity, the models were reexamined through a quantile regression approach. Current approaches to conduct quantile regression assume phylogenetic independence in the data. However, this assumption proved to be false (see "Results"). To tackle this limitation, we split our response variable (daily nest predation) into different quantiles along the values of the explanatory variable of interest (body size), and we then fitted a different BPMM for each quantile.

We also used BPMMs within a path analysis framework to test how social organization, the ability to attack large predators, and nest size directly and/or indirectly influenced the relationship between body size and daily nest predation. Because the maximum predator size and the range of predator body sizes that species are able to attack were highly correlated, we used the former in this analysis to maximize sample size. The R package dSep (available at https://github.com/jmaspons/dSep) was used to test the fit of the causal models using the d-separation method (von Hardenberg and Gonzalez-Voyer 2013). This method predicts the minimal set of conditional probabilistic independence constraints that must all be true for the causal model to be correct (von Hardenberg and Gonzalez-Voyer 2013). All numerical variables were Z transformed (mean centered with $\mathrm{SD} = 1$) to allow assessment of the relative importance of each path. We used the Fisher's C statistic to test whether the predicted basis set of conditional independencies was fulfilled in the observational data (Shipley 2000, 2004; von Hardenberg and Gonzalez-Voyer 2013). The *C* statistic information criterion (CICc), an information criterion modified for small sample sizes and adapted to path analysis, was used to perform a model selection procedure (von Hardenberg and Gonzalez-Voyer 2013). The standardized path coefficients of the best-fit models (ΔCICc < 2) were averaged following the conditional average method, where path coefficients of those paths not occurring in all models were averaged only between the models including that path (von Hardenberg and Gonzalez-Voyer 2013).

Results

Daily nest predation rates showed variation across geographic locations (ICC mode = 0.26, confidence interval [CI] = 0.17–0.35). Predation rates increased toward the equator (fig. 1*A*; pMCMC latitude = 0.044; pMCMC latitude^2 = 0.013; table S1; tables S1–S19 are available online) at similar rates in both northern and southern hemispheres (pMCMC = 0.290; table S2) but did not vary with elevation even after accounting for latitude (pMCMC = 0.582; table S1). Daily nest predation rates also showed substantial variation across species (ICC species = 0.40). Much of this variation was explained by the phylogeny (ICC phylogeny = 0.33, CI = 0.20–0.52; fig. S2). This result indicates that daily nest predation rates are influenced not only by extrinsic factors but also by some intrinsic features shared by closely related species.

Our analyses suggest that body size can be one of these intrinsic features. After accounting for regional, phylogenetic, and year effects, we found a consistent decrease in daily nest predation rates with increasing body size (fig. 1*B*; pMCMC = 0.002; table S1). This association remained strong even when including a number of potential confounding factors, such as latitude and elevation (table S1). Moreover, the relationship also held consistent when removing the effects of the possible presence of exotic predators in the study sites (pMCMC = 0.008; table S3). The lower daily nest predation rates in larger species were statistically robust, as indicated by a regression by quantiles (fig. S3), and in a model selection approach, body size and latitude emerged as the only predictors in the best model (pMCMC body size $<$ 0.001; pMCMC latitude = 0.056; pMCMC latitude^2 = 0.004; table S4). These results were not affected by collinearity, as our data on body size did not show latitudinal patterns (pMCMC latitude = 0.997; pMCMC latitude^2 = 0.995; table S5).

As expected, larger species typically built larger nests (fig. S4; pMCMC $<$ 0.001; table S6), which should be easier to detect by predators. Instead, we found a tendency of larger nests to suffer lower (rather than higher) daily predation rates than smaller nests (pMCMC = 0.037; table S7). However, nest size did not explain any additional variation in nest predation rates (pMCMC = 0.218) after accounting for body size and latitude (table S8).

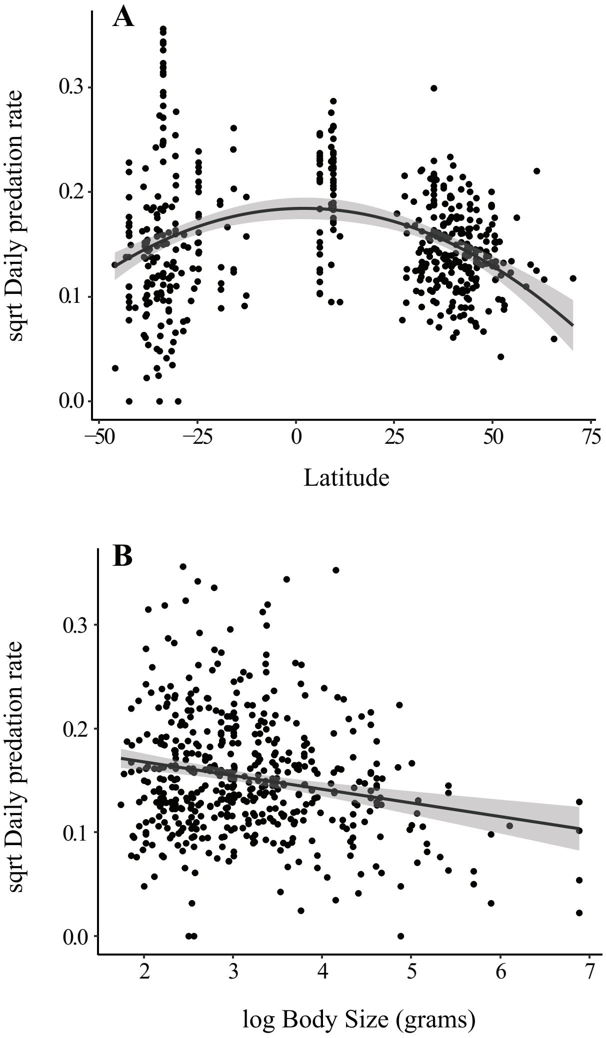

Figure 1: *A*, Relationship between daily nest predation and latitude (*N* species = 270; *N* populations = 495). *B*, Relationship between daily nest predation and body size across species (*N* species = 270; *N* populations = 422).

To clarify the reasons why larger birds experience lower daily predation rates despite building larger nests, we examined the potential of larger species to proactively reduce predation risk through behavioral responses. Although birds can reduce nest predation by selecting less exposed nest locations or by building more protected nests, we found no evidence that either of these scenarios explains the pattern (table S1). Moreover, body size was not associated with either the construction of more protected nests or the choice of more protected habitats and nest sites (table S9).

Instead, our results suggest that body size effects on nest predation rates could be influenced in part by nest defense behaviors. We found that adults in larger species can attack larger predators (fig. 2*A*; pMCMC = 0.001; table S10) and a wider range of predator body sizes (fig. 2*B*; pMCMC = 0.005; table S10) than adults of smaller species. These enhanced antipredatory abilities were in turn associated with lower daily nest predation rates (fig. 2*C*, 2*D*; pMCMC < 0.002; table S11).

Species with abilities to respond to larger and more diverse body sizes of predators often built nests that were larger than expected for their body size (pMCMC < 0.006; table S12). However, these disproportionally larger nests did not suffer higher daily predation rates (pMCMC = 0.230; table S13). This suggests that the conspicuity of larger nests to predators may be compensated in part by a greater ability of large birds to respond to a wider array of predators.

The range of predators that a species can defend against was also influenced by sociality. In particular, the maximum size of attacked predators was bigger in social breeders than in solitary breeders (pMCMC = 0.001; table S14). Social breeders also exhibited a marginally significant tendency to be able to attack a broader range of predators (pMCMC = 0.057; table S15). Daily predation rates were

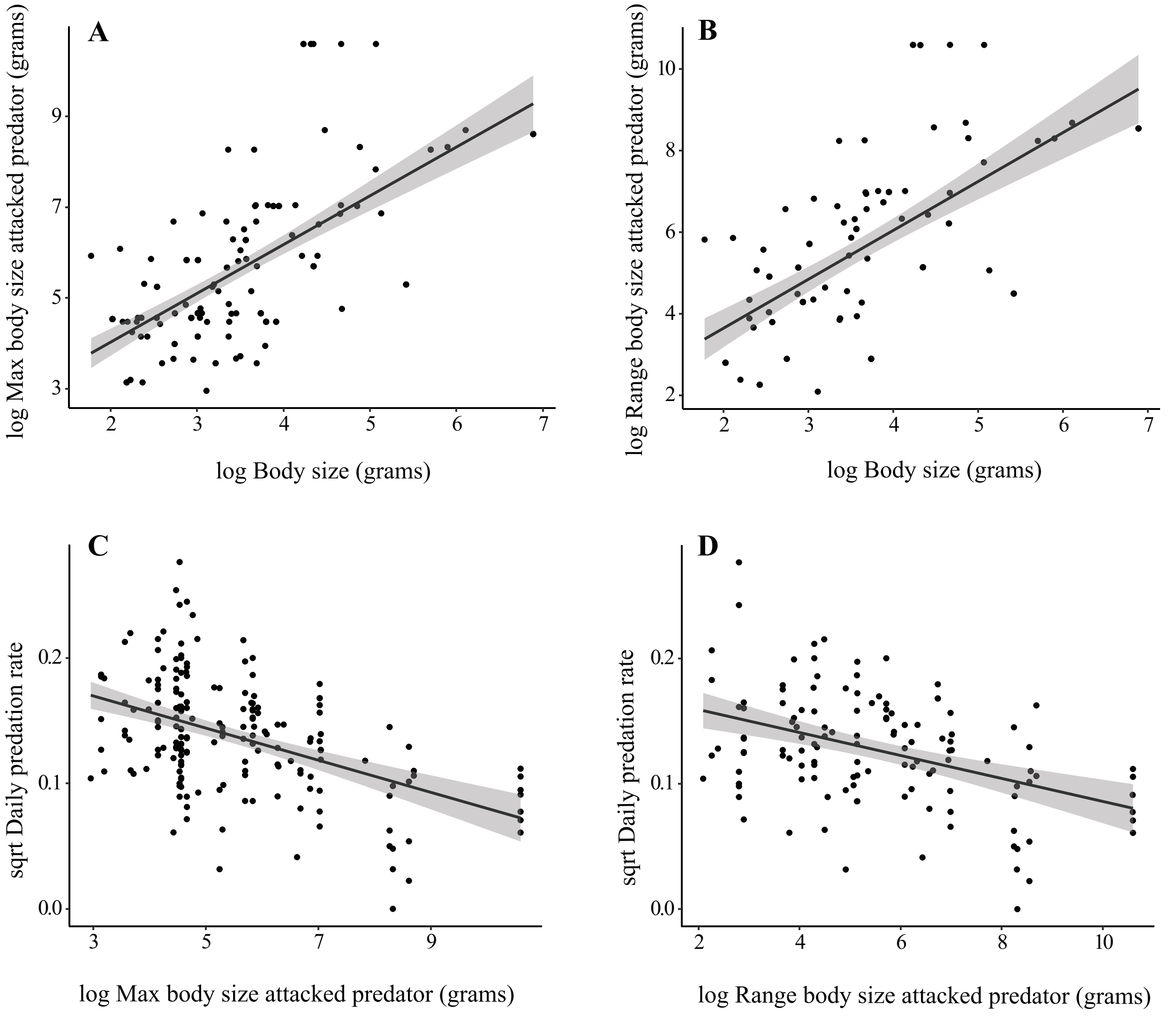

Figure 2: The ability of species to respond to bird and mammal predators is related to body size and daily nest predation rates. Larger species were able to attack a larger (*A*; *N* species = 96) and wider (*B*; *N* species = 65) range of predator body sizes. Daily nest predation rates decreased with the ability to attack a larger (*C*; *N* species = 79; *N* populations = 152) and wider (*D*; *N* species = 52; *N* populations = 98) range of predator body sizes.

also reduced in social species (pMCMC = 0.005; table S16), suggesting that a number of mechanisms allowed by group breeding may contribute to the reduced nest predation pressure. However, sociality was not related to body size and hence did not explain the link between body size and daily predation rates (pMCMC = 0.688; table S17).

A phylogenetic path analysis further clarified direct and indirect effects of antipredatory behavior, nest size, and group breeding on the relationship between body size and nest predation (fig. S5). The best-supported models (fig. 3) indicated that social factors contribute to reduce daily nest predation rates indirectly by favoring antipredatory behavior (path coefficient = 1.02, pMCMC = 0.002). However, group breeding was only slightly related to body size (path coefficient = 0.12, pMCMC = 0.042) and hence did not explain the relationship between body size and daily nest predation. Instead, the relationship was better explained by the larger and more diverse array of predators that parents of larger species were able to deter. Thus, our results suggested that larger species show enhanced antipredator behaviors (path coefficient = 0.67, pMCMC < 0.001) that are associated with reduced daily nest predation rates (path coefficient = −0.45, pMCMC < 0.001) despite having larger, more conspicuous nests (path coefficient = 0.90, pMCMC < 0.001) that did not contribute to nest predation rates.

Because the duration of the development period tends to increase with body size (fig. 4*A*; pMCMC < 0.001; table S18), daily predation rates may underestimate the fitness costs of predation in larger species. However, we found that larger species exhibited slightly reduced nest predation rates over the entire development period compared with smaller species (fig. 4*B*; pMCMC = 0.024; table S19). This latter result indicates that the reduction in daily nest predation rates is sufficient to compensate for the extended development time of larger species.

Discussion

We found that larger species had lower predation rates despite their longer development periods and more conspicuous nests compared with smaller species. This finding is remarkable considering that predation pressures are expected to vary geographically as a function of the diversity and abundance of local predators (Fischer 1960), and it challenges the notion that higher exposure to nest predators is a major cost of being larger.

Nest predation has long been argued to be greater in the tropics than north-temperate zones (Skutch 1949; Ricklefs 1969; Snow 1978; but see Kubelka et al. 2018), whereas the change with latitude in the southern hemisphere has been less clear (Martin 1996). Our extended data set confirmed the existence of substantial geographic variation in daily nest predation rates, with clear latitudinal patterns in both the northern and southern hemispheres. However, the existence of latitudinal variation was not strong enough to obfuscate the association between body size and nest predation risk.

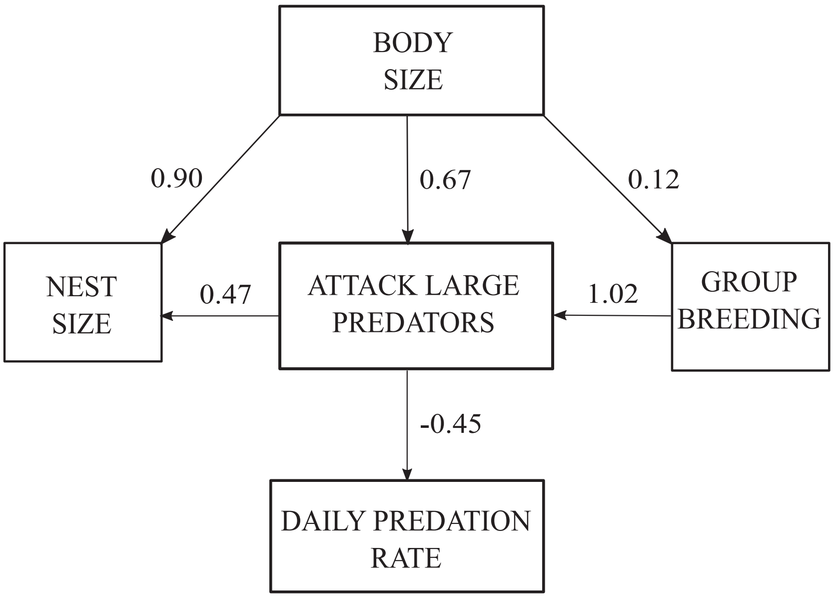

Figure 3: Path coefficients averaged among the best-fit models (*C* statistic information criterion, ΔCICc < 2) of a phylogenetic path analysis approach to test direct and indirect effects influencing the body size and daily nest predation relationship (*N* species = 62; *N* populations = 116).

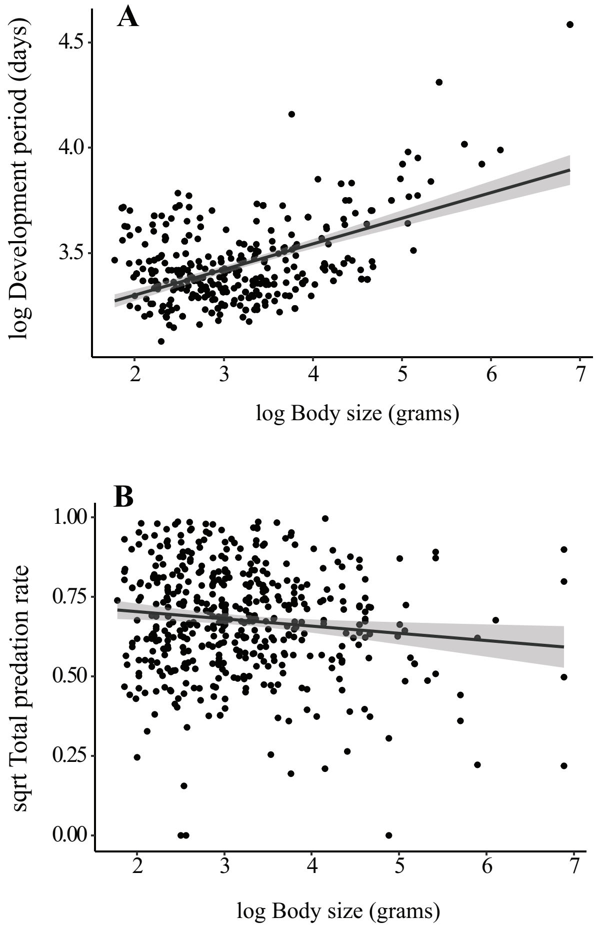

Figure 4: *A*, Relationship between development period and body size (*N* species = 288). *B*, Relationship between total nest predation and body size across species (*N* species = 240; *N* populations = 391).

Our results of reduced predation in larger species are counter to long-standing arguments that their larger nests should cause higher nest predation (Snow 1978; Murphy and Fleischer 1986; Slagsvold 1989; Møller 1990; Biancucci and Martin 2010; Mouton and Martin 2019). The reasons of such reductions are unclear, but our results suggest a role for antipredator behavioral mechanisms. A larger body size provides physical advantages when confronting a wide array of predators (Rensch 1959; Borgmann and Conway 2015), which may reduce exposure risks (Montgomerie and Weatherhead 1988), allowing larger species to defend the nest against a larger number of potential predators (Werner and Gilliam 1984). Our results suggest that a larger body allows adults of songbird species to attack a wider array of large and small predators (Werner and Gilliam 1984). These results align with previous studies reporting more aggressive nest defense behaviors in larger species (Larsen et al. 1996) and a variety of evidence that shows that active defense can reduce predation risk (reviewed in Martin 1992*b*).

The importance of defense as a potential mechanism to reduce nest predation rates was further suggested by the effect of group breeding on increasing the ability to deter predators (Hoogland and Sherman 1976; Wiklund and Andersson 1994; Krams et al. 2009). Thus, nest defense may add to additional mechanisms of group breeders to reduce nest predation risk, such as increased vigilance or dilution effects (Hamilton 1971; Kenward 1978; Martin 1992*b*; Caro 2005). Nonetheless, group breeding effects did not obscure the role of antipredatory behavioral responses in mediating the relationship between body size and nest predation. Thus, our broad results from across the world are consistent with previous suggestions that enhanced antipredatory defense capabilities of larger birds can reduce the risk of nest predation (Ricklefs 1977; Weidinger 2002).

The alternative that the reduced daily predation reflects a higher tendency of larger species to use more protected nests or less exposed nest locations was less supported by our data. Our geographically broader analyses did not detect systematic differences in daily nest predation rates across habitats or nest locations, in contrast to previous studies within North America (Martin 1993). Enclosed structures have been proposed to confer protection benefits against predators (Nice 1957; Snow 1978; Oniki 1985), but not all studies support this expectation (Martin et al. 2017; Mouton and Martin 2019; this study). Moreover, enclosed nests were not more common in large species (Martin et al. 2017; this study), demonstrating that they cannot contribute to the lower predation rates observed for larger species. Additional conditions such as landscape configuration, predator assemblage, or vegetation structure can have greater effects on nest predation than the habitat or nest site (Donovan et al. 1997; Martin and Joron 2003; Renfrew and Ribic 2003; Colombelli-Négrel and Kleindorfer 2009). Given the lack of support for differences in nest predation pressures across habitats and nest locations, nest structure and site choice do not seem to be an explanation for lower nest predation pressures in larger species.

While our results highlight the importance of antipredatory responses in explaining why larger birds suffer lower nest mortality despite more conspicuous nests, the existence of substantial unexplained variation suggests that other mechanisms can also play a role. Additional parental behaviors, such as nest attentiveness or visitation rates (Fontaine and Martin 2006; LaManna and Martin 2016), parental investment (Larsen 1991), and the role of learning aimed at improving selection for safer nest sites (Burhans and Thompson 1998; Chalfoun and Martin 2010), deserve particular attention in the future (Cresswell 1997; Weidinger 2002). For example, a reproductive failure can cause parents to modify nest site choices and parental behaviors in subsequent breeding attempts (Chalfoun and Martin 2010). These responses are expected to be linked to life history—and hence to body size—because a slow strategy increases the probability of future reproduction and provides more opportunities to learn and benefit from learned behaviors (LaManna and Martin 2016; Sol et al. 2016; Maspons et al. 2019). Interestingly, our findings show how behavioral responses of slow-lived species can have a positive feedback on selection of slow-lived strategies. Understanding how behavior varies as a function of life-history strategies seems a crucial next step to further understand the mechanisms behind the selective forces driving the evolution of body size.

Regardless of the exact behavioral mechanism, our analyses indicate that the declines in daily nest predation rates observed in larger passerines are sufficiently reduced so as to yield lower predation rates over the entire nesting cycle. If extending the development period does not increase offspring exposure to predation, it follows that the fitness costs may be less important than generally believed. The existence of substantial phylogenetic signal in daily nest predation rates is consistent with this interpretation, as it suggests that inheriting a larger body from ancestors may contribute to buffer species against nest predation. Given the importance of reduced offspring predation to fitness (Ricklefs 1969; Martin 1992*a*; Thompson 2007; Remeš et al. 2012*b*), our findings suggest that the reduction in nest predation may have been an important contributor to the evolution of larger body size, providing an additional mechanism for Cope's rule. Because changes in offspring mortality are expected to shape selection on delayed maturity and decreased reproductive effort (Reznick et al. 2002), the possibility that a large body facilitates behavioral responses that reduce nest predation is also expected to have important implications for life-history evolution.

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Statement of Authorship

M.U., T.E.M., and D.S. contributed to the conception and conceptualization of the study. T.E.M. and M.U. gathered data; M.U. ran the analyses and wrote the first draft of the manuscript; and T.E.M. and D.S. critically reviewed, made direct intellectual contributions, and approved its publication.

Data and Code Availability

Supplemental data can be found in the Dryad Digital Repository (https://doi.org/10.5061/dryad.4f4qrfj8z; Unzeta et al. 2020).

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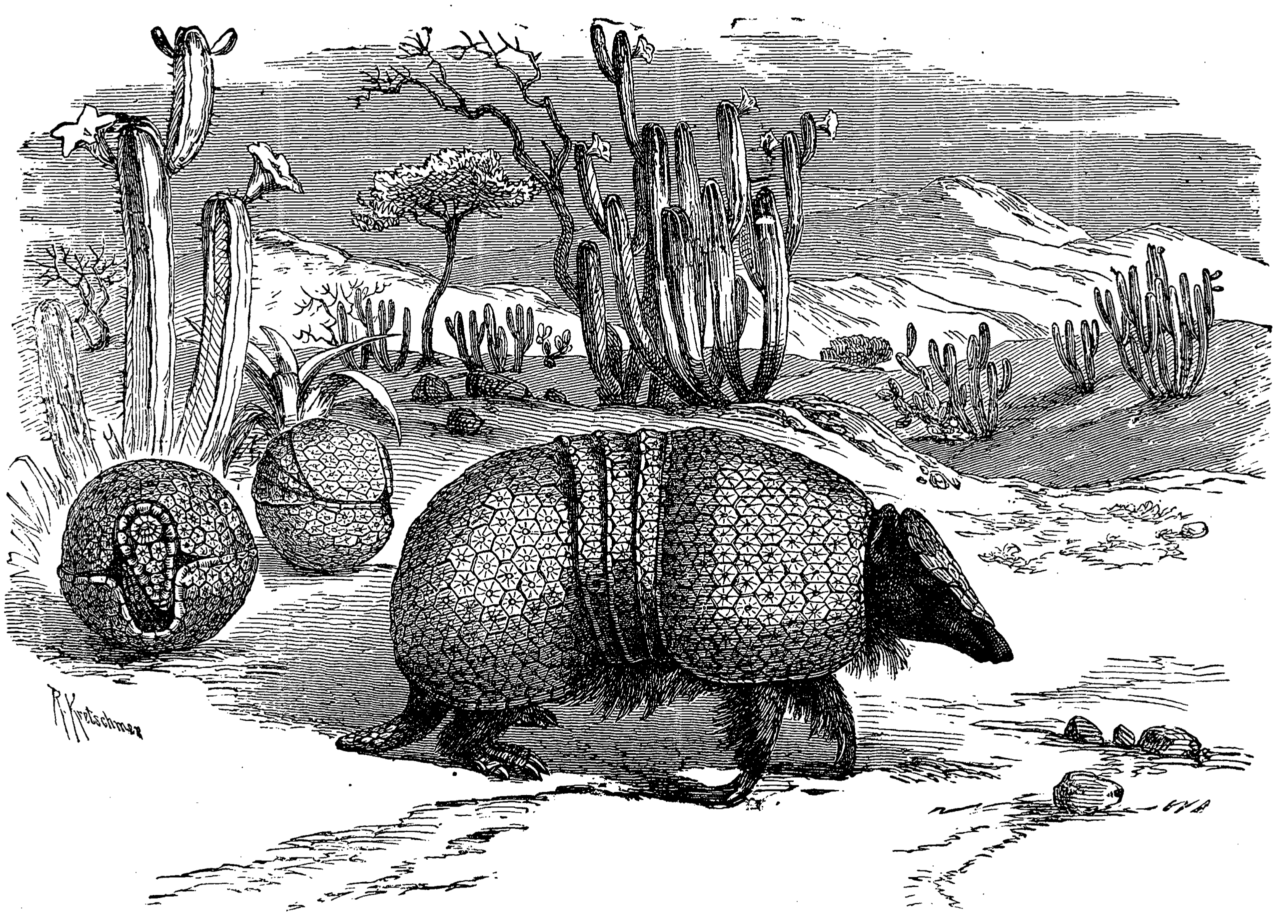

"*Polypeutes tricinctus*, three-banded Armadillo." From the review of *The Standard Natural History* (*The American Naturalist*, 1884, 18:166–168).