Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species

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Incubation is an important component of parental care in birds, and species differ widely in their incubation rhythm. In this comparative study, we focused on factors responsible for those differences. As hypothesized by A. Skutch, increased parental activity at the nest increases the probability of nest depredation. High risk of nest predation should therefore lead to the evolution of lower frequency of parental activity at the nest. We thus expected to find a negative relationship between frequency of nest visits and the risk of nest depredation. Using a large dataset of 256 species of passerines breeding worldwide, we found that the frequency of nest visits decreased as the risk of nest depredation increased and that this effect was strongest in tropical species. Further, foraging bouts were longer in species experiencing warmer ambient temperatures during incubation and those with domed nests. Incubation bouts were longer and frequency of nest visits was lower in species with higher body mass. Our results support the view that natural selection favors lower frequency of nests visits in species under higher risk of nest predation and demonstrate the importance of other factors (temperature, geographic space, nest type, and body mass) in shaping the evolution of incubation rhythm.

KEY WORDS: Comparative study, incubation, parental care, songbirds.

Parental care differs widely in its form and intensity between species (Clutton-Brock 1991; Royle et al. 2012), and understanding those differences is a major focus of evolutionary behavioral studies (Lack 1968; Clutton-Brock 1991). It can range from oviposition site selection in some insects and fish to care of mature offspring in chimpanzees and humans (Smiseth et al. 2012). In birds and some other egg-laying species, incubation of eggs is a very important component of parental care with strong ramifications for offspring performance (Deeming and Ferguson 1991; Hepp et al. 2015). Even within this one type of care species differ widely in the overall length of incubation, whether and how the sexes share incubation duty, and whether and how often males feed incubating females (e.g., Bulla et al. 2017). Similarly, species differ strongly in nest attentiveness, that is, the percentage of daytime eggs are incubated (Conway and Martin 2000b; Deeming 2002; Matysioková et al. 2011; Matysioková and Remeš 2014).

Nest attentiveness is the most widely studied characteristic of incubation in birds (e.g., Deeming 2002; Matysioková and Remeš 2014; Martin et al. 2015). However, given the same nest attentiveness, species can differ in the length and frequency of incubation and foraging bouts (incubation rhythm), and the time on eggs can be divided between many short or a few long incubation bouts (Bulla et al. 2016). As hypothesized by Alexander Skutch (1949), increased parental activity at the nest increases the risk of nest depredation (Martin et al. 2000), which is the single main cause of breeding losses in birds (Ricklefs 1969), being responsible for 70–90% of nest failures in passerines globally (Remeš et al. 2012).

Considerable nest predation takes place during daytime and is caused by visually oriented predators (Libsch et al. 2008; Weidinger 2010; deGregorio et al. 2016; Schaaf et al. 2018). Because frequent bouts of incubation could increase nest visibility,

a high risk of nest predation should therefore lead to prolongation of the length of either incubation or foraging bouts. However, prolonging incubation bouts could be energetically costly for the incubating parent. Similarly, in uniparental incubators, prolonging foraging bouts alone would lead to lower overall nest attentiveness and could thus increase the overall incubation period (Lyon and Montgomerie 1985; Martin et al. 2007; Auer and Martin 2017), resulting in longer exposure of the nest to predators (Bosque and Bosque 1995). Moreover, egg temperatures would drop to lower levels during longer foraging bouts, with negative consequences for embryo development (Olson et al. 2006; Ospina et al. 2018). These costs of longer incubation or foraging need to be contrasted with the benefits of lower risk of nest depredation due to lower activity at the nest, and these trade-offs should be especially prominent in uniparental incubators.

In a pioneering study, Martin and Ghalambor (1999) studied the evolution of male incubation feeding in birds and showed that incubation feeding rate was negatively related to the risk of nest depredation. Their results supported the view that species under higher risk of nest predation decreased their activity around the nest (but see Matysioková et al. 2011). Subsequently, Conway and Martin (2000b) studied nest predation effects on the female's incubation rhythm in uniparental incubators and found that the number of nest visits decreased with increasing nest predation risk. However, this study was restricted to a limited number of passerine species breeding in North America. At the same time, tropical and southern hemisphere species show strongly contrasting and a broader range of incubation behaviors compared with northern temperate species (Martin et al. 2007, 2015; Martin 2015). Thus, extending the analyses to examine relationships across geographic space is important. To account for geographic variation in incubation behavior, in this study we analyze data on incubation rhythms of passerine species breeding all over the world.

Ambient temperature is also important in shaping avian incubation behavior (Conway and Martin 2000a; Londoño et al. 2008; AlRashidi et al. 2011; Amininasab et al. 2016). Optimal temperature for the development of bird embryo is between 36 and 40.5°C, with development being slowed down if the temperature falls below 26°C (Lundy 1969). Low temperature should thus select females to shorten their foraging bouts to secure optimal embryo development. On the other hand, the intensity of metabolism increases with decreasing ambient temperature, which is also true for incubating birds (Tinbergen and Williams 2002; De Heij et al. 2008). Consequently, as the ambient temperature declines, female energy reserves would be depleted faster and she would be forced to shorten the length of her incubation bouts. Taken together, the lengths of both foraging and incubation bouts should decrease with decreasing ambient temperature and this has been repeatedly observed, but more frequently so in foraging bouts (Conway and Martin 2000a). Hence, we

also studied whether and how parental behavior correlates with ambient temperature experienced by birds during incubation.

Another factor that can affect the thermal environment of the clutch and thus incubation behavior is nest type (Deeming 2011, Martin et al. 2017). Previous study showed that nest attentiveness is reduced and nestling growth enhanced in species with domed nests. This would suggest that in domed nests cooling rate is slowed and thermoregulatory costs reduced (Martin et al. 2017). Thus, we also studied whether incubation behavior differs between different types of nests.

To test these hypotheses, we studied incubation rhythms of 256 passerine species (based on 416 population-level estimates) distributed globally (Fig. 1A). Based on the reasoning above, if higher risk of nest depredation favors the evolution of lower parental activity at the nest, we would predict (1) lower frequency of incubation and foraging visits and (2) longer foraging or incubation bouts with higher risk of nest depredation. Considering the role of ambient temperature and nest type, we would also predict (3) shorter foraging and incubation bouts with decreasing temperature and (4) longer foraging bouts in species nesting in either domed nests or cavities.

Materials and Methods
DATA COLLECTION
We collected data for this study from the literature. For details of the search protocol, see Supporting Information 1. Because the evolutionary importance of energy and time constraints during incubation should be greatest for species with uniparental incubation, we included only articles with data on species with female-only incubation (male-only incubation is absent in passerines) and excluded all species in which two or more birds shared incubation duties (Conway and Martin 2000b). From resulting articles, we extracted data on the length of incubation and foraging bouts. We calculated the frequency of nest visits per hour as: $2 \times [60/(\text{mean incubation bout duration} + \text{mean foraging bout duration})]$ (Conway and Martin 2000b). In all species, we excluded data on incubation during the night, laying period, and hatching day.

From the original studies, we extracted information on the location of the study site. We used this information to obtain the geographic latitude and longitude where the study was conducted using Google Earth. We also extracted months during which the eggs were incubated in a given population (incubation season). Preferably, we used the exact months in which the incubation rhythm was measured in a given population. Alternatively, if there were only information about the months during which birds incubated in a given population, we used this as an estimate of the incubation season. If data on incubation season were missing in the original articles, we used information provided in ornithological
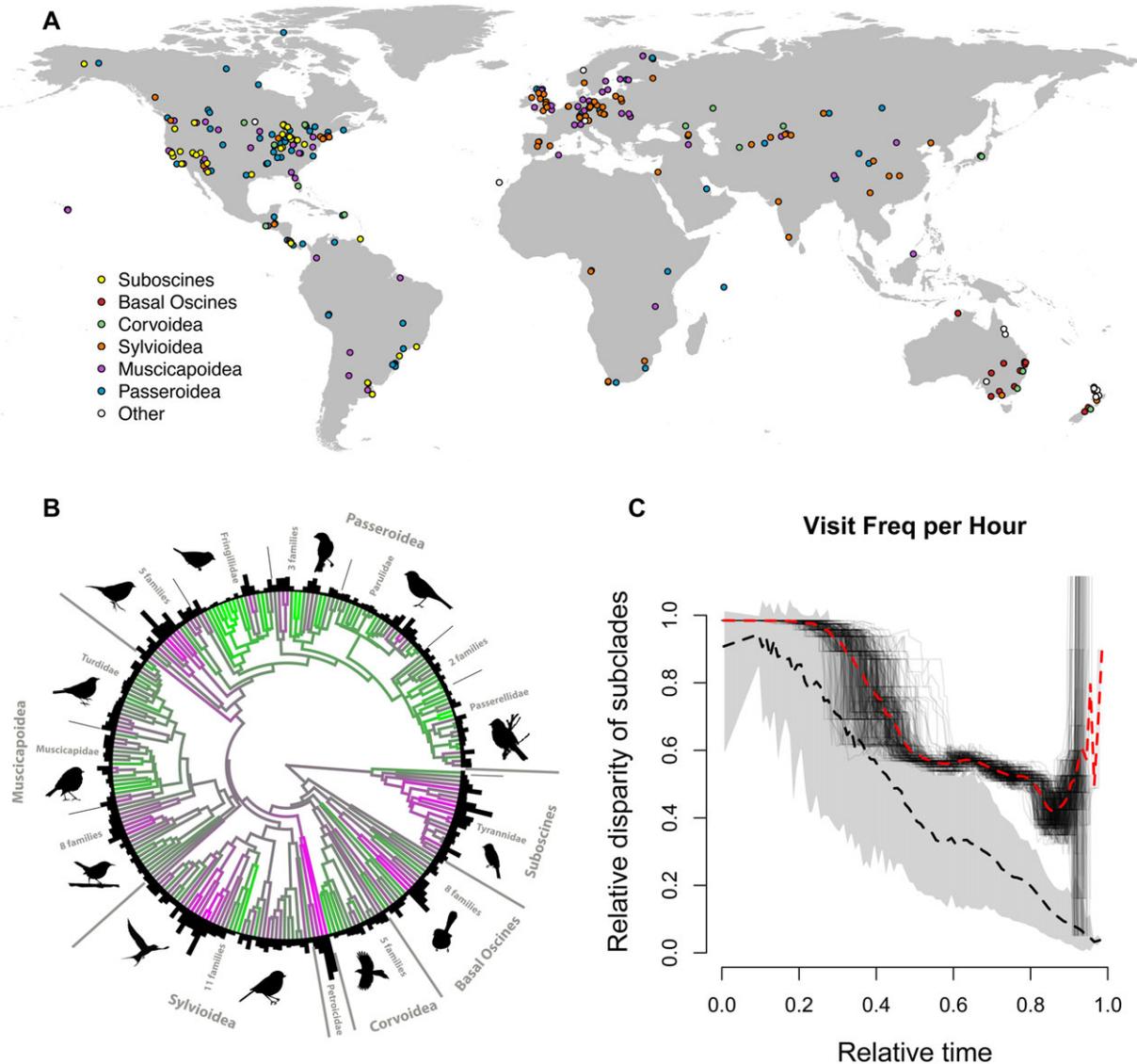
Figure 1. (A) Geographic distribution of 416 populations from which we had estimates of incubation behavior in passerines. Note that some of the points are not visible because of their overlap. (B) Phylogeny of 256 passerine species with frequency of nest visits depicted by the height of black bars (the higher the bar, the higher the frequency of nest visits) and reconstructed by maximum likelihood along the edges from low (green) to medium (gray) to high frequency (magenta). (C) Disparity through time plot for the frequency of nest visits analyzed on 200 sampled phylogenies (black lines; average by red hatched line) compared to expectations based on the Brownian motion model of trait evolution (black hatched line; 95% envelope depicted by gray area).

compendia (Supporting Information 1) and the Handbook of the Birds of the World (HBW; del Hoyo et al. 2018). We used the information on geographic coordinates and incubation season to extract average ambient temperature during incubation from the Climate Research Unit CRU.CL.2.0 dataset (New et al. 2002).

To examine relationships across geographic space, we assigned every population in our dataset into one of three latitudinal bands based on their geographic latitude (northern temperate—above 23.5°N, tropical—between 23.5°N and 23.5°S, and southern temperate—below 23.5°S). Furthermore, clutch size might influence incubation behavior. Thus, we also intended to add clutch

size as a covariate into our analyses. We extracted data on clutch size in a given population from original articles ($n = 319$). If those data were not available ($n = 97$), we used information provided in ornithological compendia (Supporting Information 1). In those cases, if possible we chose clutch size from the same geographic region (state) rather than more distant parts of the species range. However, clutch size was highly correlated with latitude (Table S1 and Fig. S1) and thus we did not include it into our final analyses. However, to make sure that its exclusion did not bias our results, we ran a series of models with clutch size included; results were the same as without it (and it was never statistically significant).

Although ambient temperature was also correlated with latitude, we retained it in our models, because it is one of the main factors shaping incubation behavior and its correlation with latitude was smaller than in clutch size (Table S1).

Body mass is a common correlate of life history traits and behavior (Schmidt-Nielsen 1984; Dial et al. 2008). Therefore, we used it as one of the predictors in our analyses. Adult body mass (g) was obtained from compendia listed in Supporting Information 1 and from Dunning (2008). Data on nest type (open, cavity, or domed) were obtained from HBW (del Hoyo et al. 2018). From the sources listed above, we also extracted data on nest predation (number of nests studied and number of nests destroyed by predators) for species for which data on incubation behavior were available. We included only populations where 10 nests had a known outcome. To transform the proportion of nests lost to predators to daily predation rates, we used the method proposed by Ricklefs (1969). For more information, see Remeš et al. (2012). In our final dataset, we included only species for which all variables of interest were available.

STATISTICAL ANALYSES AND PHYLOGENY

We used phylogeny-based comparative methods to test our hypotheses. We downloaded 500 phylogenetic trees for our species from a publicly available archive at birdtree.org using Hackett constraint, all species, and version 2 (V2) of the archive. We calculated one Bayesian maximum credibility tree using TreeAnnotator (Drummond et al. 2012) and used this tree in all subsequent analyses (Fig. S2).

Many variables were skewed and thus we used $\log_{10}$ transformations to improve their distribution (Fig. S3). We used $\log_{10}$(incubation bout length), $\log_{10}$(foraging bout length), and $\log_{10}$(frequency of visits on nest) as our response variables. We used $\log_{10}$(body mass), $\log_{10}$(daily nest predation rate + 0.001), ambient temperature, nest type, and latitudinal band as our predictors, and we checked that these variables were not highly correlated (Fig. S4). Because the effects of nest predation and ambient temperature might differ across latitude and nest type (Remeš et al. 2012; Bulla et al. 2016; Martin et al. 2017), we also fitted their interactions with latitudinal band and nest type, and also the interaction of nest type with latitudinal band itself (five two-way interactions altogether). We removed statistically nonsignificant interactions in a stepwise manner, starting with the least significant one, and retained only those significant at alpha = 0.05 in the final model.

We analyzed our data on the species level using mean values of response variables calculated for each species across populations available for that particular species. To obtain mean values across populations, we first calculated point estimates of a given variable (e.g., foraging bout length) for individual populations and then averaged these point estimates across all available populations for a given species. This approach was justified, because repeatabilities of incubation behavior were reasonably high: 0.64 for incubation bouts, 0.80 for foraging bouts, and 0.65 for frequency of nest visits. We used phylogenetic generalized least squares (Symonds and Blomberg 2014) to fit our multiple regression models on species means in the ape package (Paradis et al. 2004) of R 3.2.1 software. We checked that residuals from these models were normally distributed and homoscedastic and that there were no nonlinearities (Mundry 2014).

We conducted several checks that our results were robust. First, although we did not use *P*-values to select main effects in our models, we did use them to exclude nonsignificant interactions (see above). Thus, we validated our model selection using an information theoretic approach (Anderson 2008). We did model selection using MuMIn package for R (Bartoń 2018) starting with the full model with all main effects and five two-way interactions (see above) and calculated Akaike weights for all submodels to judge their relative support (Anderson 2008). Second, within species variation in traits and phylogenetic uncertainty could affect parameter estimates. Thus, we also fitted our models on population level data across several phylogenies using phylogenetic mixed models implemented in MCMCglmm package (Hadfield 2010).

We scaled all continuous variables (subtracted mean and divided by 1 SD) to obtain parameter estimates comparable across variables and models. Parameter estimates for the factors nest type and latitudinal band are not comparable to other estimates (Schielzeth 2010). We also reconstructed ancestral states of frequency of nest visits using maximum likelihood in function plotBranchbyTrait of the *phytools* package (Revell 2012). We further calculated disparity through time plots (Harmon et al. 2003) for both dependent variables and predictors (Figs. S5 and S6). We calculated them on a sample of 200 phylogenies from birdtree.org (see above) using a custom R code.

Results

The length of incubation and foraging bouts increased as the risk of nest depredation increased, so both factors contributed to an overall decrease in nest visitation (Table 1 and Fig. S7), but this effect was strongest in tropical species, weaker in northern temperate species, and virtually absent in southern temperate species (Table 1, Fig. 2, and Supporting Information 3). Foraging bouts were longer in species experiencing warmer ambient temperatures during incubation (Fig. 3) and in species with domed nests (Fig. 4) but the effect of ambient temperature was not statistically significant when latitudinal bands were in the model (Table 1). However, because ambient temperature was correlated with latitude (Table S1 and Fig. S1), we also fitted our models without latitudinal bands. They revealed that foraging bouts

Table 1. Phylogenetic generalized least squares models of incubation behavior in passerines in relation to major hypothesized selective factors and covariates.

Response	Foraging bout length [$\log_{10}$] ($R^2 = 0.19$, $\lambda = 0.62$)				Incubation bout length [$\log_{10}$] ($R^2 = 0.16$, $\lambda = 0.87$)				Frequency of visits [$\log_{10}$] ($R^2 = 0.17$, $\lambda = 0.81$)			
Predictors	df	F	P	Estimate (SE)	df	F	P	Estimate (SE)	df	F	P	Estimate (SE)
Intercept	1	0.51	0.476	−0.30 (0.42)	1	1.06	0.304	−0.55 (0.54)	1	1.04	0.309	0.51 (0.50)
Body mass [$\log_{10}$]	1	2.36	0.126	0.12 (0.08)	1	10.78	**0.001**	0.27 (0.08)	1	11.50	**<0.001**	−0.27 (0.08)
Temperature	1	1.81	0.180	0.10 (0.07)	1	0.06	0.808	0.02 (0.07)	1	0.19	0.659	−0.03 (0.07)
Nest type (Open)	2	7.89	**<0.001**	Domed: 0.74 (0.19) Cavity: 0.31 (0.19)	2	0.64	0.526	Domed: 0.21 (0.19) Cavity: 0.03 (0.18)	2	2.39	0.093	Domed: −0.41 (0.19) Cavity: −0.10 (0.18)
Daily predation rate [$\log_{10}$]	1	17.48	**<0.001**	0.65 (0.15)	1	15.64	**<0.001**	0.58 (0.15)	1	19.46	**<0.001**	−0.65 (0.15)
Latitudinal band (Tropical)	2	0.17	0.844	N Temp: −0.02 (0.21) S Temp: −0.13 (0.24)	2	9.31	**<0.001**	N Temp: 0.48 (0.19) S Temp: −0.34 (0.22)	2	5.57	**0.004**	N Temp: −0.36 (0.20) S Temp: 0.29 (0.23)
Daily predation rate [$\log_{10}$] * Latitudinal band (Tropical)	2	4.88	**0.008**	N Temp: −0.53 (0.17) S Temp: −0.52 (0.21)	2	5.58	**0.004**	N Temp: −0.44 (0.16) S Temp: −0.65 (0.20)	2	6.18	**0.002**	N Temp: 0.53 (0.16) S Temp: 0.64 (0.20)

P-values of statistically significant factors are highlighted in bold. Reference values for nest type and latitudinal band are given in the table. Reference values for nest type and latitudinal band are given in parentheses. Transformation functions of a particular variable, if any, are given in square brackets. Numerator df are listed in the table; denominator df are always 250. All continuous variables were scaled (subtracted mean and divided by 1 SD) and so their effect size estimates are comparable, whereas effect sizes for nest type and latitudinal band are not comparable. Reference categories were chosen so that they agree with the typical passerine (tropical open nester). Latitudinal bands were delimited by 23.5° north and south, where Southern temperate (S Temp) is south of 23.5S, tropical is between 23.5S and 23.5N, and northern temperate (N Temp) is north of 23.5N. Sample size is 256 species in all analyses.
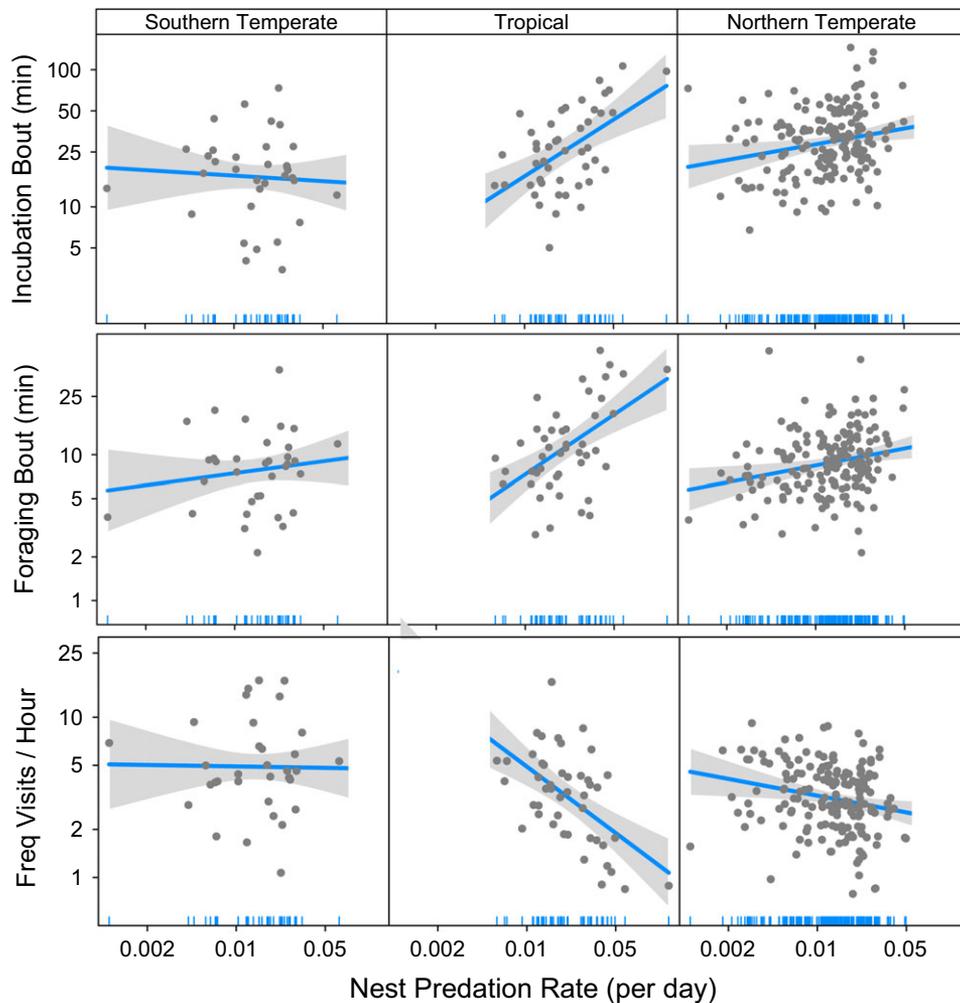
Figure 2. Incubation behavior of 256 species of passerines in relation to nest predation rate across latitudinal bands delimited by 23.5° north and south. Southern temperate is south of 23.5S, tropical is between 23.5S and 23.5N, and northern temperate is north of 23.5N.

were significantly longer in species experiencing warmer ambient temperatures during incubation (Table S2, Fig. 3, and Fig. S7). Incubation bouts were longer and frequency of nest visits was lower in species with higher body mass (Table 1 and Fig. 4). These results were generally well supported by inference based on information theoretic criteria (Table S3) and phylogenetic mixed modeling taking into account within-species variation and phylogenetic uncertainty (Supporting Information 4).

Across all major phylogenetic lineages of passerines (Fig. 1B), the phylogenetic signal λ of incubation behavior ranged from 0.62 to 0.87 (Fig. 1B, Table 1, and Fig. S8). We found particularly high frequency of nest visits in some tyrant flycatchers (Tyrannidae), honeyeaters (Meliphagidae), Australasian robins (Petroicidae), reed-warblers (Acrocephalidae), and weavers (Ploceidae), whereas low frequency was found in some finches (Fringillidae), tanagers (Thraupidae), and New World sparrows (Passerellidae, Fig. 1B and Fig. S2). Relative disparity of subclades in all aspects of incubation behavior was consistently high compared to Brow-

nian motion expectations across most of evolutionary time (Fig. 1C and Fig. S5). The situation was the same for nest predation rate and ambient temperature, in contrast to body mass that followed Brownian motion expectations for the same set of species (Fig. S6).

Discussion

In accordance with our expectations, species where nest predation was high visited their nests less frequently than species in which the risk of nest predation was comparatively lower, with the exception of southern temperate birds. This global result echoes previous studies that showed that across bird populations or communities, visitation rates on nests reflected the risk of nest predation. In several species nest visitation rate was lower in populations living in habitats experiencing stronger predation pressure (Massaro et al. 2008; Pretelli et al. 2016). In addition, experimental manipulation of perceived predation risk resulted in
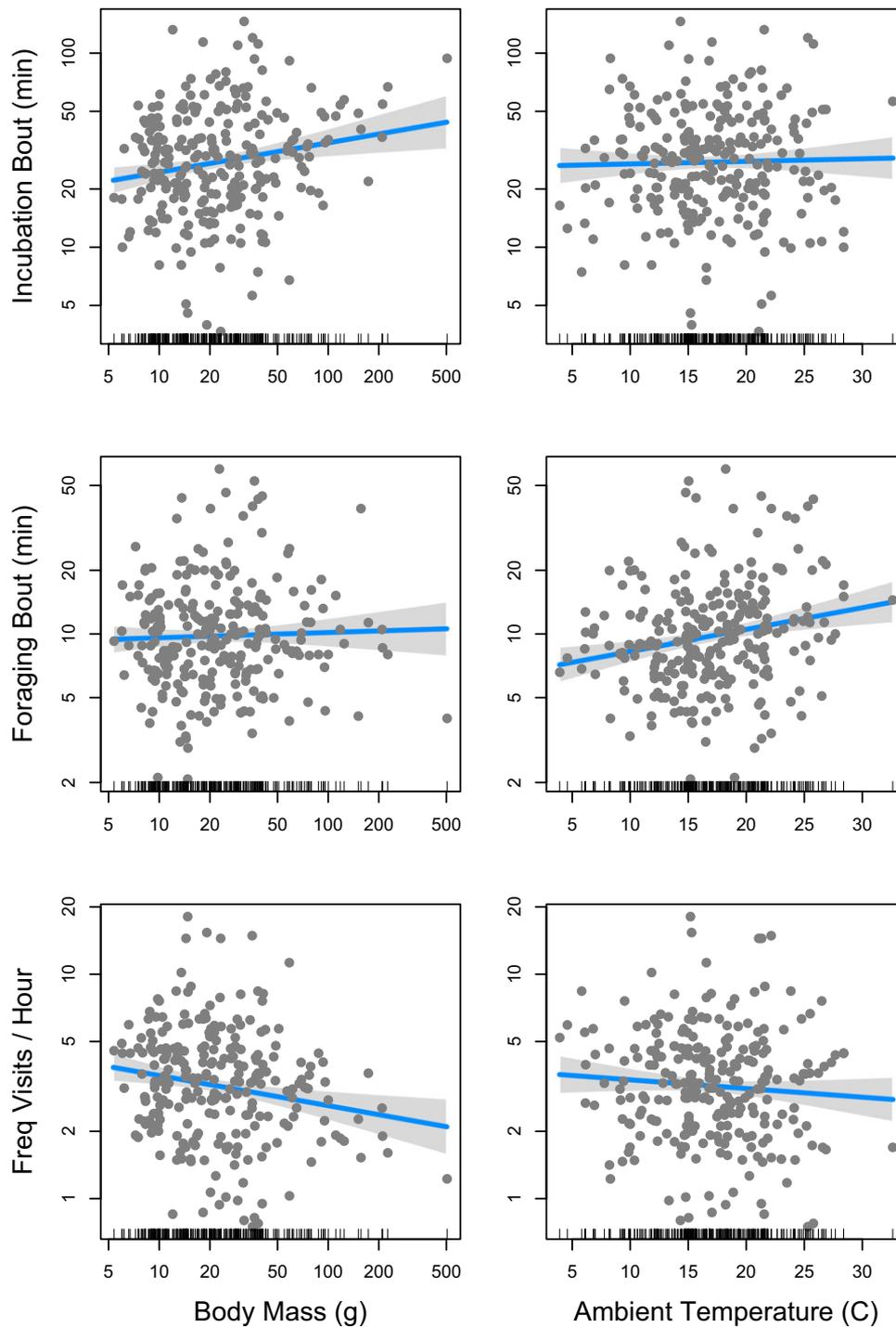
Figure 3. Incubation behavior of 256 species of passerines in relation to body mass and ambient temperature.

changes in the activity at the nest in several species (Kovařík and Pavel 2011; Ibáñez-Álamo and Soler 2012; Basso and Richner 2015). Similarly to this phenotypic plasticity, higher nest predation risk might cause an evolutionary response in terms of lower nest visit frequency as we found here across passerines worldwide and also as Conway and Martin (2000b) found previously in North American passerines. All these results support the original hypothesis by Skutch (1949) claiming that nest predation risk is a critical factor molding parental activity at the nest. Additionally, the disparity of visitation rates was consistently higher than expected under a neutral Brownian model, exemplified by comparison to body mass. This is in line with the idea that species within daughter clades were under diversifying selection of nest predation that led to higher than expected disparity of
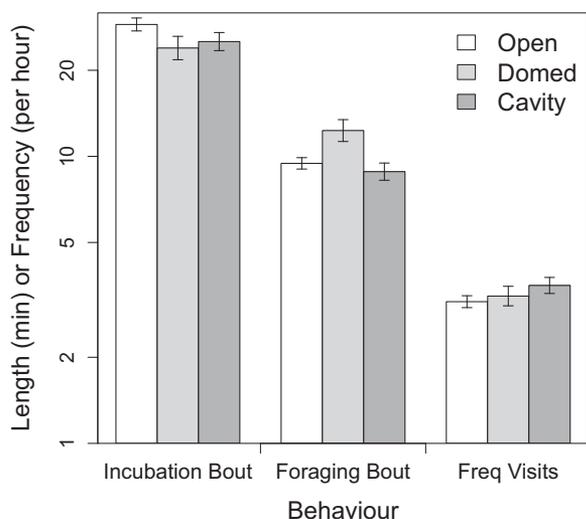
Figure 4. Incubation behavior of 256 species of passerines in relation to nest type. Error bars are 1 SE.

visitation rate. This is consistent with empirical observation that community-level nest predation rates have usually quite wide distribution of values across species (e.g., Remeš et al. 2012).

Visitation rate decreased with increasing nest predation risk most strongly in the tropics, followed by northern temperate species, whereas that relationship was absent in southern temperate species. Why should tropical species respond more strongly to the risk of nest predation than those breeding in temperate regions? Tropical species live longer and have lower fecundity, which selects them to minimize harm to adults rather than to their clutch (Ghalambor and Martin 2001). Accordingly, high nest predation risk might select them to avoid being detected during incubation and thus revealing nest location, which could substantially reduce the risk of the depredation of the incubating adult. However, this would make sense only if the value of one adult life was higher for tropical species than the value of one clutch for northern temperate species, because northern temperate species are in turn selected to minimize harm to their clutches. This may easily be the case, because from the perspective of the individual it is relatively easy to replace a lost clutch (that brings potential future fitness benefits) but a lost adult is gone forever (and its future fitness drops instantly to zero). Alternatively, absence of nest predation effect in southern temperate species might have been caused by lower sample of species ($n = 34$) compared to the tropics ($n = 46$) and northern temperate regions ($n = 176$).

To decrease the frequency of nest visits, it is necessary to prolong either incubation or foraging bouts. Hence, a lower frequency of nest visits under high nest predation risk must be necessarily mirrored by lengthening of one or both bouts. However, we did not anticipate whether the resulting costs would be paid by the female (in the case of longer incubation bouts) or embryo (in the

case of longer foraging bouts). It turned out that both incubation and foraging bouts were longer in species with higher risk of nest predation as was previously found in North American species (Conway and Martin 2000b). Benefits of this evolutionary change are clear (lower conspicuousness to predators), but what are the costs and can they be mitigated?

One clear cost of longer incubation bouts is a possible negative impact on female condition. However, females might be able to reduce the cost of prolonged incubation bouts by obtaining more energy during their foraging bouts. They could do this either by foraging more intensely per unit of time (without changing the length of the foraging bout) or for a longer period (with the same intensity; Fedy and Martin 2009). Both possibilities assume that females can adjust their gastrointestinal tract to higher rate of short-term intake (Karasov 1996). This assumption seems justified, because in food supplementation studies, females were able to prolong their incubation bouts due to higher energy intake (Rastogi et al. 2006; Lothery et al. 2014). Out of the two possibilities outlined above (intensity vs. length of foraging), our data speak only to the length of foraging bouts and indeed show that foraging bouts are longer in species suffering higher risk of nest predation and consequently longer incubation bouts. Acquisition of more energy during prolonged foraging bouts could thus enable females to stay longer on the nest without paying any additional cost of increased starvation during prolonged incubation bouts. It is important to note that these effects are independent of body mass and thus are not confused by allometry of metabolic rate, food intake, and starvation resistance (Sibly et al. 2012).

On the other hand, relatively longer foraging bouts might have a negative effect on the developing embryo. Longer recess duration exposes eggs to lower ambient temperatures due to extended clutch cooling. This brings costs of delayed embryonic development and longer incubation periods (Martin et al. 2015; Auer and Martin 2017), reduced hatching rate (MacDonald et al. 2013; Hasegawa and Arai 2016), and lower survival of hatchlings (Ospina et al. 2018). Similarly, experimental periodic egg cooling decreased embryo mass and efficiency of growth in Zebra finches (*Taeniopygia guttata*; Olson et al. 2006), and inefficient growth under low temperatures might even require increased investment into eggs in species with clutches exposed to extensive periods of cooling (Martin 2008). Nevertheless, species experiencing higher risk of nest depredation may "accept" these costs if they are outweighed by benefits of resulting lower activity at the nest.

In our study, species breeding in domed nests had longer foraging bouts compared to species breeding in open nests and cavities. Previous experimental studies showed that nest type can affect egg cooling rate. Adding cover to the top of an open nest slowed egg cooling rate (Lamprecht and Schmolz 2004), whereas removing a roof of an originally domed nest had the opposite effect (Kendeigh et al. 1977). Our data are in concordance with a novel

view that domed nests provide thermal benefits to incubating parents (Martin et al. 2017) by slowing egg cooling rate and thus enabling them to spend longer time outside the nest. Surprisingly, the length of foraging bouts was not prolonged in species breeding in cavities suggesting that insulation provided by cavities might be poorer than that of domed nests. Unfortunately, we found no studies comparing thermal properties of cavities versus domed nests and thus this possibility remains to be rigorously tested in the field.

Ambient temperature is among the strongest drivers of avian incubation behavior (Conway and Martin 2000a, 2000b; Deeming 2002). Accordingly, our broad-scale comparative study revealed that passerines breeding in higher ambient temperatures had longer foraging bouts compared to those living in colder environments (after removing the confounding effect of latitude). The same result was also previously found in North American passerines (Conway and Martin 2000b). In general, egg cooling rate is slower and egg temperature does not drop so much under higher ambient temperatures compared to colder environments (Szentirmai et al. 2005; McClintock et al. 2014). This enables females breeding in warmer environments to stay outside the nest longer (Conway and Martin 2000a). Females could use this extra time to acquire more energy or spend more time on self-maintenance activities (Londoño et al. 2008). Our study shows that unlike the length of foraging bouts, the length of incubation bouts does not change with changing ambient temperature. This suggests that females may take the advantage of breeding under higher temperatures and invest extra time gained due to slower egg cooling into themselves rather than into their offspring.

We showed that females of bigger species spent more time on their nests without spending more time foraging, which is in line with a previous finding that nest attentiveness increases with body mass (Martin et al. 2007). First, bigger species have relatively larger fat reserves than smaller species (Calder 1974), which makes them more resistant to starvation (Kendeigh 1945) and thus should enable them to endure longer incubation bouts (Skutch 1962). Second, bigger species have lower mass-specific metabolic rate (Kleiber 1947) while having relatively same gizzard mass as smaller species (Herrera 2007). Moreover, bigger species might be more efficient in foraging and thus able to acquire relatively more energy than smaller species during the same time period (Pawar et al. 2012), which would again enable them to endure longer incubation bouts. It is interesting to note that estimates of allometric slopes of incubation bout duration and frequency of nest visits (Table 1) almost exactly agree with values predicted by metabolic theory of ecology, namely 0.25 for durations and -0.25 for biological rates (Sibly et al. 2012).

In sum, we showed that the strongest driver of incubation behavior in passerines breeding worldwide was nest predation risk, and that its effect was largest in the tropics. This is a novel and particularly interesting result, because tropical species typically have high adult survival rates, which might predispose them to be exceptionally sensitive to the risk of depredation of the incubating adult (Ghalambor and Martin 2001). We also for the first time showed that foraging bouts were longer in species with domed nests, which surprisingly well agrees with a novel hypothesis proposing the superior insulation function of such nests (Martin et al. 2017). We also confirmed previous findings that show that incubation behavior was correlated with ambient temperature and adult body mass.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Relationships of geographic latitude with clutch size, ambient temperature, and daily predation rate in 256 species of passerines breeding worldwide.

Figure S2. Phylogeny of 256 passerine species used in this study with nest type (inner circle) and latitudinal band (outer circle) depicted by color.

Figure S3. (this and preceding page) Distributions of raw and log10-transformed values of both response and predictor continuous variables, and of categories of discrete variables (i.e., nest type and latitudinal band).

Figure S4. Scatterplots of continuous variables at the species level (n = 256 species) showing also their distribution (histograms along the diagonal) and linear correlation coefficients (lower triangular part).

Figure S5. Disparity through time plots for incubation behavior analyzed on 200 phylogenies sampled from birdtree.org (black lines; average by red hatched line) compared to expectations based on the Brownian motion model of trait evolution (black hatched line; 95% envelope depicted by grey area).

Figure S6. Disparity through time plots for predictor variables analyzed on 200 phylogenies sampled from birdtree.org (black lines; average by red hatched line) compared to expectations based on the Brownian motion model of trait evolution (black hatched line; 95% envelope depicted by grey area).

Figure S7. Incubation behavior of 256 species of passerines breeding worldwide in relation to body mass, nest predation rate, and ambient temperature.

Figure S8. (preceding page) Distribution of incubation traits on the phylogeny of 256 species of passerines breeding worldwide, including incubation bout length (min, left), foraging bout length (min, center), and frequency of nest visits per hour (right).

Table S1. Summary of linear models relating clutch size, ambient temperature, and daily predation rate (DPR) to latitude, which is treated either as a continuous trait or as latitudinal bands cut at 23.5 degrees North and South.

Table S2. Phylogenetic generalized least squares models of incubation behavior in passerines in relation to major hypothesized selective factors and covariates.

Table S3. Results of multimodel inference based on AICc and run in MuMIn package for R.

Figure S1. Estimates of standardized regression coefficients from phylogenetic generalized least squares analyses between incubation bouts (left column), foraging bouts (middle column), and frequency of nest visits (right column) and daily nest predation rate, shown separately for middle species (top row), north species (middle row), and south species (bottom row).

Figure S1. Relationship between parameter estimates from phylogenetic generalized least squares models (PGLS estimate) and Bayesian phylogenetic mixed models (PMM estimate).

Table S1. Parameter estimates from PMM with their 95% highest posterior density intervals (HPDinterval, package coda).