RESEARCH ARTICLE

Clutch size declines with elevation in tropical birds

Andy J. Boyce,[1]#* Benjamin G. Freeman,[2,3]#* Adam E. Mitchell,[1] and Thomas E. Martin[4]

[1] Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA
[2] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, USA
[3] Cornell Laboratory of Ornithology, Ithaca, New York, USA
[4] U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA
# These authors contributed equally to the paper.
* Corresponding authors: Andy Boyce, andrew1.boyce@umontana.edu; Benjamin Freeman, bgf27@cornell.edu

ABSTRACT
Clutch size commonly decreases with increasing elevation among temperate-zone and subtropical songbird species. Tropical songbirds typically lay small clutches, thus the ability to evolve even smaller clutch sizes at higher elevations is unclear and untested. We conducted a comparative phylogenetic analysis using data gathered from the literature to test whether clutch size varied with elevation among forest passerines from three tropical biogeographic regions—the Venezuelan Andes and adjacent lowlands, Malaysian Borneo, and New Guinea. We found a significant negative effect of elevation on variation in clutch size among species. We found the same pattern using field data sampled across elevational gradients in Venezuela and Malaysian Borneo. Field data were not available for New Guinea. Both sets of results demonstrate that tropical montane species across disparate biogeographic realms lay smaller clutches than closely related low-elevation species. The environmental sources of selection underlying this pattern remain uncertain and merit further investigation.

Keywords: clutch size, elevation, life history, PGLS, tropics, Borneo, Venezuela, New Guinea

El tamaño de la nidada disminuye con la elevación en las aves tropicales

RESUMEN
El tamaño de la nidada normalmente disminuye al aumentar la elevación en las especies de aves canoras de zonas templadas y subtropicales. Las aves canoras tropicales poseen tamaños de nidada pequeños y, por ende, no está clara y no se ha evaluado su capacidad para evolucionar tamaños de nidada aún menores a elevaciones más altas. En este trabajo realizamos un análisis filogenético comparativo usando datos tomados de la literatura para evaluar si el tamaño de la nidada varía con la elevación entre las aves Paseriformes de las selvas de tres regiones tropicales de tres continentes diferentes— los Andes venezolanos y las tierras bajas adyacentes, Borneo malasio y Nueva Guinea. Encontramos un efecto negativo significativo de la elevación sobre la variación inter específica en el tamaño de la nidada. Encontramos el mismo patrón usando datos de campo registrados a lo largo de gradientes de elevación en Venezuela y Borneo malasio. No contamos con datos de campo de Nueva Guinea. Ambos juegos de resultados demuestran que las especies montanas tropicales provenientes de reinos biogeográficos distintos ponen nidadas más pequeñas que las especies cercanamente emparentadas de elevaciones bajas. Las fuentes ambientales de selección subyacentes a este patrón no están claras y merecen ser investigadas con más profundidad.

Palabras clave: Borneo, elevación, historia de vida, Nueva Guinea, PGLS, tamaño de la nidada, tópicos, Venezuela

INTRODUCTION

Avian clutch sizes vary tremendously, both among species at a single site and among related species inhabiting different regions (Cody 1966, Martin et al. 2000, Jetz et al. 2008). For example, clutch size predictably declines with latitude from the northern temperate zone to the tropics, with tropical species laying smaller clutches (Martin et al. 2000, Jetz et al. 2008). The change in clutch size with latitude has been extensively described, but investigations of clutch size variation across elevational gradients have

mostly been limited to temperate-zone analyses (e.g., Badyaev 1997, Sanz 1998, Badyaev and Ghalambor 2001, Johnson et al. 2006, Wilson and Martin 2011, but see Kleindorfer 2007). Elevational gradients in the tropics have been poorly studied.

In both temperate and subtropical latitudes, clutch size commonly decreases with increasing elevation, both within and among species (Krementz and Handford 1984, Badyaev 1997, Sanz 1998, Badyaev and Ghalambor 2001, Johnson et al. 2006, Lu et al. 2010, Wilson and Martin 2011, Yang et al. 2012). The mechanisms underlying this

pattern presumably arise from the different suite of abiotic (e.g., temperature) and biotic (e.g., predation rate, food availability, adult survival rate) conditions that are present at high elevations in the temperate zone (Badyaev 1997, Badyaev and Ghalambor 2001) and in the tropics (Kleindorfer 2007). Yet the tropics differ substantially from temperate environments in daily and seasonal climatic stability (Janzen 1967) and in avian life-history traits such as clutch size and adult survival (Martin et al. 2000, 2015, Martin 2002, Jetz et al. 2008). Specifically, climatic stability varies drastically along elevational gradients in the temperate zone, with high-elevation environments being more climatically variable on both daily and seasonal timescales than lower elevations. Climate is much more stable in the tropics, with smaller daily and seasonal temperature changes at all elevations and with less elevational variation in stability (Janzen 1967). Thus, if clutch-size variation is influenced by seasonality (Ashmole 1963), we might expect little or no elevational variation in clutch size in the tropics.

Additionally, clutch sizes of tropical songbird species in low-elevation forests are often quite small, with many species laying only 2 eggs (Lack 1948, Lack and Moreau 1965, Skutch 1985, Martin et al. 2006). Given these small clutch sizes, the potential to evolve even smaller clutch sizes in high-elevation environments is unclear. A decrease in clutch size by 1 egg represents a 50% decrease in potential fecundity for a tropical species with a 2-egg clutch, whereas it represents a much smaller proportional reduction for a temperate species with a larger clutch. Additionally, single-egg clutches eliminate the possibility of an "insurance offspring," which may carry a large cost if hatching rates are low or if rates of offspring mortality are high (Forbes 1990). Thus, these latitudinal differences raise the question of whether elevational patterns documented in the temperate zone should be expected to extend to the tropics.

We addressed this question by investigating interspecific clutch size variation across elevations in tropical passerines. We used comparative phylogenetic methods to examine interspecific patterns of clutch size across elevational gradients in the tropical avifaunas of three regions in which we have worked: Malaysian Borneo, New Guinea, and Venezuela. These three tropical regions span a latitudinal gradient from 10°N in northern Venezuela to 10°S in southeastern New Guinea. The avifaunas of these three regions have largely evolved independently (Supplemental Material Figure S1), which increases inference to the general pattern of clutch size variation across elevations in the tropics, as opposed to a description of a pattern that may be idiosyncratic to a single site or community of birds. We also compared our results to those of the most extensive north-temperate analysis in the literature (i.e. Badyaev and Ghalambor 2001), which found

a decrease in clutch size with increasing elevation, to determine if the elevational effects on clutch size reported were similar in directionality and effect size to our data from the tropics.

METHODS

Clutch Size and Elevation: Literature Data

To investigate interspecific variation in clutch size across elevations, we first compiled clutch size and elevational distribution information for tropical passerines from reference volumes. We limited our analysis to forest species, as broad habitat-type differences (e.g., forest vs. open-country) may influence clutch size patterns (Lack and Moreau 1965). The primary sources that we used were Handbook of the Birds of the World (HBW) volumes (e.g., Boles 2007, Higgins et al. 2008, Frith and Frith 2009) and, for Borneo, two texts specifically addressing the status and distribution of birds in Borneo (Smythies 1999, Sheldon et al. 2001). We supplemented reference volume data with field data collected in Borneo and Venezuela. For widely distributed species, we used clutch size estimates and elevational distributions explicitly measured within our regions of interest (i.e. New Guinea, Borneo, and Venezuela) whenever possible. We considered outlier elevation records (e.g., a lowland species with a single high-elevation record) unlikely to influence clutch size evolution within a species. Thus, when multiple elevational distributions for a single species were given in reference volumes, we used the midpoint of 'typical' elevational distributions to characterize a species' elevational distribution for analysis.

Clutch size estimates in the literature are typically presented as a range of the number of eggs laid, and infrequently reference specific nests. Therefore, to characterize clutch size for analysis, we used the midpoint of clutch size ranges, and mean values when clutch size data for two or more specific nests were available. Because allometric effects can influence clutch size (Sæther 1987), we also included adult body mass in our analyses. Body mass data were gathered primarily from the literature (Dunning 1993), and supplemented where possible with our field-collected data from the sites detailed above. When available, female body mass was used; however, given that many tropical species are not sexually dimorphic, the majority of body mass data represented non-sex-specific values. When body mass ranges were given, the midpoint was used as an estimate of mean body mass. For species with available field data, we took the mean body mass of all individuals aged as after-hatch-year via plumage or skull pneumatization.

Patterns of clutch size variation across elevations may also be affected by nest type. Slagsvold (1982) hypothesized that, because predator communities change across eleva-

tions, selection on clutch size by nest predation may lead to differing patterns of variation between species nesting on the ground vs. above ground. Thus, we included nest type in our analyses to examine its potential effect on clutch size. To characterize nest type, we assigned each species to one of two nest types, "above-ground" or "ground," based on nest descriptions in the literature resources outlined above.

Clutch Size and Elevation: Field Data

To examine a potential relationship between interspecific clutch size variation and elevation at the local level and to test the veracity of results from our literature dataset, we conducted a fine-scale analysis. In particular, we quantified the relationship between clutch size and elevation using data measured directly in the field. These data were gathered primarily at two discrete sites: Kinabalu Park (6°N) in Malaysian Borneo, between 1,450 and 3,300 m; and Parque Nacional Yacambu (9°N) in the Venezuelan Andes, between 1,400 and 2,000 m. We defined clutch size as the final number of eggs laid and observed on two nonconsecutive days (Martin et al. 2006), and used all nests with measured clutch sizes to estimate the mean clutch size for that species. We used the lowest and highest elevations of nests found at our field sites to generate a midpoint elevation of the zone in which clutch size was measured for a given species. Elevations of each nest were measured using GPSMAP 64 handheld GPS units (Garmin International, Olathe, Kansas, USA), regularly calibrated at points of known elevation at Kinabalu Park. With such calibration, the published accuracy of the barometric altimeter in these units is ±3.05 m. We then used these measures of clutch size and elevation to analyze interspecific variation in clutch size. Body size estimates were generated following the same methodology described above for the literature data.

Seasonality

In an attempt to explain possible regional variation in clutch size, we examined environmental seasonality across our three study regions. To do so, we downloaded mean monthly temperature layers for the warmest and coldest months of the year (BIO5, BIO6), and mean monthly precipitation layers for the wettest and driest months of the year (BIO13, BIO14), from the WorldClim database (Hijmans et al. 2005), with 10-km resolution. We clipped the layers to match the areas from which our data were gathered based on ecoregion shape files from the World Wildlife Fund (Olson et al. 2001). Temperature units are (°C) times 100, and precipitation values are given in millimeters. We used mean values for the difference between hottest and coldest and wettest and driest months to characterize temperature and precipitation seasonality for each region. We used ANOVA to test for differences in

each seasonality variable among sites, and a Tukey post-hoc test to determine the significance of all pairwise comparisons of seasonality across sites.

Statistical Analysis

Literature data. Comparative analyses have to consider possible phylogenetic influences when analyzing relationships between traits (Felsenstein 1985). Therefore, we used a phylogenetic generalized least-squares (PGLS) modeling approach implemented in the 'ape' (Paradis et al. 2004) and 'nlme' (Pinheiro et al. 2013) packages within R (R Development Core Team 2014) to examine the relationship between elevation and clutch size.

Phylogenetic trees were obtained from a complete passerine phylogeny provided by Jetz et al. (2012). We used birdtree.org to prune this complete phylogeny to match our dataset and to sample 500 trees from the available distribution using the Hackett backbone (Hackett et al. 2008). Majority rules consensus trees were produced from these tree-blocks using program Mesquite (Maddison and Maddison 2011). These consensus trees were imported into R using the 'ape' package and were used for all phylogenetic analyses.

We were primarily interested in understanding the influence of elevation on clutch size across regions in the tropics. However, clutch size may vary among tropical regions (Freeman and Mason 2014) and may not change with elevation at the same rate among regions. We thus included region and region × elevation interaction terms in our full model. The interaction was not significant, however, and was dropped from the final model. Body mass was included due to its potential influence on clutch size. To test for the influence of nest type on elevational variation in clutch size, we included both nest type and its interaction with elevation in our full model. Both were insignificant and were dropped in the final model. Finally, both clutch size and body mass were $\log_{10}$-transformed to normalize their distributions. Numeric variables were standardized to facilitate comparison of effect sizes between mass and elevation, and to facilitate comparison with effect size estimates produced by Badyaev and Ghalambor (2001) for temperate elevational gradients. For reference, the full model is presented in Appendix Table 1.

To determine whether phylogenetic analyses were necessary for our data, we estimated Pagel's λ by maximum likelihood using phylogenetic generalized least-squares regression (PGLS; Pagel 1999), and then compared this model to an identical model in which λ was forced to remain fixed at 0. Pagel's λ approaches 0 if data are distributed independently of phylogeny, whereas λ approaches 1 as trait variation between species is proportional to their shared evolutionary history. PGLS is equivalent to phylogenetic independent contrasts (PIC;

TABLE 2. A general linear model table for phylogenetic (λ_{ML}) and nonphylogenetic (λ_0) models explaining clutch size variation in tropical passerines for our (**A**) literature-based and (**B**) field-based datasets. AIC is Akaike's Information Criterion, and ΔAIC is the difference in AIC from the top model. LogLik is the maximized log-likelihood function. The final two columns provide the likelihood ratio and P-value for a likelihood-ratio test between the two types of models.

A. Literature data

Model	df	λ	ΔAIC	logLik	L.Ratio	P
λ_{ML}	7	0.76	0.00 [a]	17.76		
λ_0	6	0.00	141.02	−53.75	143.02	<0.001

B. Field data

Model	df	λ	ΔAIC	logLik	L.Ratio	P
λ_{ML}	6	0.85	0.00 [b]	−2.49		
λ_0	5	0.00	0.30	−3.64	2.30	0.130

[a] AIC = −21.52.
[b] AIC = 16.99.

Felsenstein 1985) in this latter case (Blomberg et al. 2012).

Field data. We followed the same procedure for generating and importing phylogenetic trees as with our literature data. Our model was parameterized similarly to the final model for our literature data.

RESULTS

Literature Data

We compiled clutch size and elevation estimates for 572 species of forest passerine: 344 from Venezuela, 127 from Borneo, and 101 from New Guinea. Mean and standard deviation for clutch size across all sites was 2.12 ± 0.66,

with clutch sizes ranging from 1 to 5 eggs. Based on a likelihood ratio test, the model in which λ was allowed to vary was significantly better than that in which it was fixed at 0 (Table 2A), demonstrating a strong phylogenetic signal in the clutch size data ($\lambda = 0.75$). The elevation term was significantly negative, indicating that clutch size declined with increasing elevation, even after controlling for phylogenetic effects (Table 3A, Figure 1A). The coefficients translated to a decrease in mean clutch size of ∼10% per 1,000 m, all else being equal.

Based on standardized regression coefficients, elevation had a larger effect on clutch size than did adult body mass (Table 3A). This result matched that of Badyaev and Ghalambor (2001, table 4), who also found a larger effect

TABLE 3. Parameter estimates, standard errors, t-values, and P-values for our final models explaining variation in Log$_{10}$-transformed clutch size in tropical passerines in the (**A**) literature dataset and (**B**) field-based dataset based on phylogenetic least-squares regression models. Clutch size in Malaysian Borneo is subsumed into the intercept in both models; thus, coefficients and P-values represent comparisons with that region. All data are standardized to provide comparable partial-regression coefficients for numeric variables.

A. Literature data

	Coefficient	SE	t-value	P
Intercept	−0.30	0.33	0.89	0.37
Elevation	−0.24	0.03	−7.58	<0.001
Log$_{10}$ mass	−0.15	0.05	−2.99	0.003
Region (New Guinea)	−0.66	0.18	−3.79	<0.001
Region (Venezuela)	0.54	0.20	2.72	0.007

B. Field data

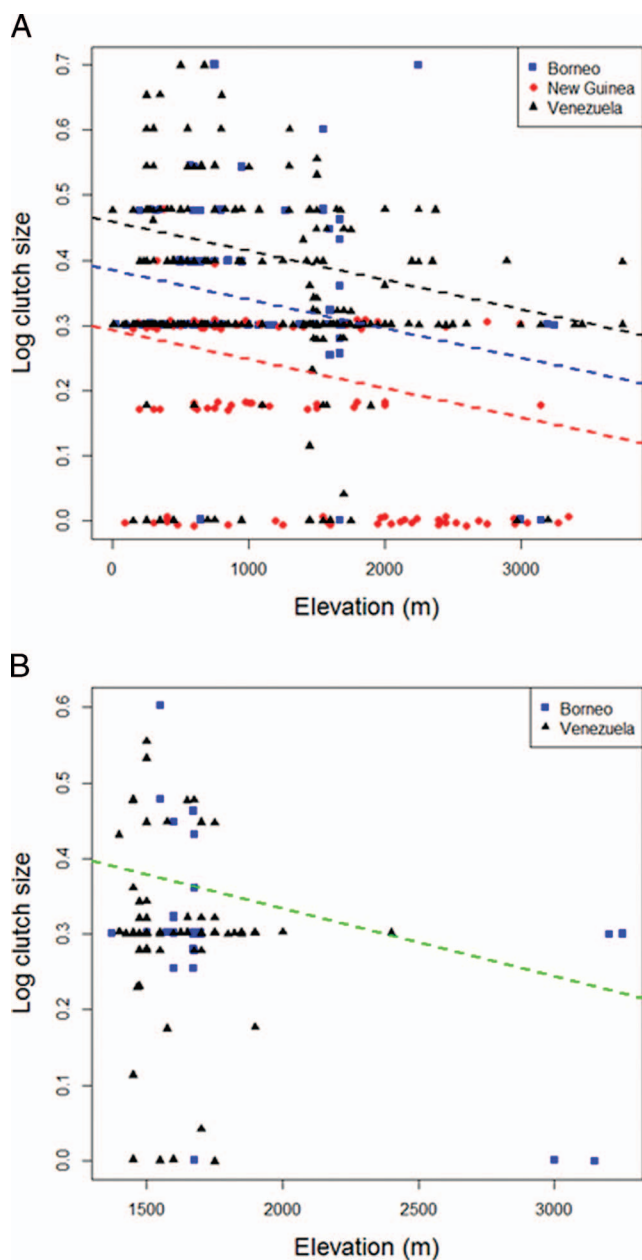|	Estimate	SE	t-value	P
Intercept	−0.12	0.54	−0.22	0.82
Elevation	−0.25	0.09	−2.86	0.005
Log$_{10}$ mass	−0.17	0.11	−1.63	0.11
Region (Venezuela)	0.02	0.35	0.06	0.96

FIGURE 1. Mean clutch size ($\log_{10}$ transformed) declines with increasing mean elevation in tropical passerine birds. Scatter-plots illustrate phylogenetic least-squares regressions of mean elevation on mean clutch size using (**A**) literature data collected from three geographic regions or (**B**) field data from local elevational gradients. The trend lines for both plots are based on phylogenetic least-squares models (Table 2). Region-specific trend lines are not shown for our field-based dataset because clutch size did not differ between these two sites (Table 3B). Untransformed clutch size values that contribute to the log-transformed scale on the *y* axis range from 1 to 5 in (**A**) and from 1 to 4 in (**B**). Points are jittered for ease of viewing.

of elevation compared with mass. The reduction in clutch size with increasing elevation, estimated by the standard-ized partial regression coefficients (Schielzeth 2010), was greater in the temperate-zone study ($\beta_{st} = -0.75$, SE $= 0.18$) than in our tropical analysis ($\beta_{st} = -0.24$, SE $= 0.03$).

In addition, species in different regions differed in their clutch sizes. New Guinean passerines laid smaller clutches and Venezuelan passerines laid significantly larger clutches than passerines in Borneo (Table 3A, Figure 1A).

Field Data

Our field-based dataset consisted of data from Venezuela (2,374 nests of 80 species sampled from March to July in 2002–2008) and Malaysian Borneo (1,559 nests of 38 species sampled from February to June in 2009–2013). Mean clutch size for these data was 2.07 ± 0.52, with clutch size ranging from 1 to 4 eggs. Likelihood ratio tests indicated that there was no significant difference in the fit of our phylogenetic and nonphylogenetic models of clutch size variation (Table 2B), and that the effect of elevation remained significant and negative in the nonphylogenetic model. We chose to use the phylogenetic model, based on the fact that a significant phylogenetic signal was detected in our larger literature dataset as well as in previous studies (Badyaev and Ghalambor 2001). Clutch size again declined with increasing elevation (Figure 1B). Contrary to our analysis of the literature data, no difference was detected in clutch size between Bornean and Venezuelan species using field data. The decreasing trend in clutch size with elevation became nonsignificant when the four high-elevation species in Borneo were removed from the analysis. However, these species represented the entirety of the high-elevation bird community in Borneo, sample sizes for these species were robust, and the resulting pattern in clutch-size variation agreed with the larger analysis, suggesting that the trend was not an artifact of four anomalous species.

Seasonality

The climate in Venezuela was significantly more seasonal than the climate of both New Guinea and Borneo, in terms of monthly temperature and precipitation variations (Table 4, $P < 0.001$). New Guinea was less seasonal than Borneo in terms of precipitation (Table 4, $P < 0.001$), and was significantly more seasonal than Borneo in temperature fluctuations (Table 4, $P < 0.001$).

DISCUSSION

Our study extends elevational clutch-size patterns to tropical regions. We found that high-elevation tropical songbird species laid smaller clutches than their low-elevation relatives (Figure 2). This result held when analyzing literature-derived data on the largely indepen-

TABLE 4. Mean values and standard deviations for indices of seasonality in temperature (°C) and precipitation (mm) for our three study regions based on the WorldClim database (Hijmans et al. 2005). Sample size values are the number of 10 arc-minute raster blocks from which these mean values were derived. Sites differ significantly in both their temperature and precipitation seasonality (ANOVA, $P < 0.001$). All pairwise comparisons are also significantly different based on Tukey post-hoc tests ($P < 0.001$).

	Temperature seasonality	Precipitation seasonality	n
Venezuela	12.49 ± 1.15	286.32 ± 117.00	1,626
Borneo	8.77 ± 0.78	185.22 ± 80.40	577
New Guinea	10.14 ± 1.58	153.58 ± 55.10	1,356

dently evolved avifaunas (Supplemental Material Figure S1) of three discrete biogeographical regions, and also when using field data collected along elevational gradients in the northern Andes (Venezuela) and Southeast Asia (Borneo). Our results based on field data are admittedly limited in inference by the absence of a significant relationship between elevation and clutch size when the four high-elevation species from Borneo were removed from analyses. Our study sites in Borneo and Venezuela were designed for intensive studies of breeding biology and demographics, and thus did not cover broad elevational ranges. Based on our literature data model, we would expect a difference in clutch size of only ~5% across the 500 m elevational span of these sites. Given the large

FIGURE 2. The previously undescribed nest and egg of Pale-faced Bulbul (*Pycnonotus leucops*), an endemic resident of high-elevation forests in Borneo. On Mt. Kinabalu, this species is restricted to an elevational range of 2,000–3,600 m. As with several other high-elevation tropical passerines, Pale-faced Bulbuls lay only a single egg. Their closest relative at this site, Ochraceous Bulbul (*Alophoixus ochraceous*), occupies an elevational range of 1,450–2,000 m and lays a 2-egg clutch.

interspecific variation in clutch size and the small expected change across the constrained elevational range, detection of an effect of elevation likely will require a particularly large sample. Nonetheless, the four high-elevation species in our study represented the entirety of the high-elevation bird community in Borneo, had robust sample sizes, and had clutch sizes consistent with what we would expect based on the pattern shown in our literature dataset.

While birds of tropical lowland forests have small clutch sizes (Lack 1948, Lack and Moreau 1965, Skutch 1985), and the mean clutch sizes among species in our literaure-based and field-based samples were 2.12 and 2.07, respectively, we conclude that selection imposed by high-elevation tropical environments is sufficiently strong to drive further reductions in clutch size in tropical montane birds. However, we found that the magnitude of the decrease in clutch size across elevations was smaller in our study of tropical species than in Badyaev and Ghalambor's (2001) study of temperate-zone birds. While this result provides some support for the idea that, because clutch sizes in the tropics are already small, the ability to further decrease clutch size at high elevations in the tropics may be constrained, it should be treated with caution given that much of the data from the temperate-zone study represents intraspecific variation, which may represent plasticity in clutch size as opposed to evolved differences as described with our strictly interspecific approach.

Ecological mechanisms, such as predation and food limitation, have been hypothesized to underlie the reduction in clutch size of high-elevation bird species (Slagsvold 1982, Badyaev and Ghalambor 2001), but their importance in tropical environments is unexplored and unclear. For example, high nest predation rates might favor reduced clutch sizes to facilitate reduced parental activity at the nest (Skutch 1949, 1985, Slagsvold 1982, Martin et al. 2000), or to allow energy savings for future breeding attempts (Slagsvold 1984, Martin 1995). Yet the only studies examining nest predation across elevational gradients in the tropics have found nest predation to be lower, not higher, at high elevations (Skutch 1985, Boyle 2008). This predation pattern, if it applies generally to tropical species, would predict larger clutches at high elevations rather than the smaller ones that we observed.

Alternatively, high-elevation birds may be sufficiently food-limited that selection favors small clutch sizes (Badyaev 1997). This hypothesis assumes a decline in food availability relative to energy requirements with increasing elevation. Few such studies have been completed, with some showing declines in insect abundance with increasing elevation (Ferger et al. 2014), but others finding the highest arthropod abundance at middle elevations (Janzen 1973, Ghosh-Harihar 2013). Finally, Ashmole's seasonality hypothesis (Ashmole 1963) seems to hold little promise because seasonality does not necessarily increase with elevation in the tropics (Janzen 1967, Stevens 1992), although seasonality does vary among regions in the tropics, which may help to explain regional variation in clutch size (Jetz et al. 2008).

Clutch-size reductions in high-elevation tropical birds may also reflect life-history tradeoffs favored by environmental variation. For example, decreased investment in reproduction via small clutch sizes has been hypothesized to be an adaptive slow life-history strategy associated with high adult survival (Martin 2002, 2004). In particular, the small clutch sizes of high-elevation species have been argued to reflect adaptive slow life-histories (Sæther et al. 1996, Camfield et al. 2010, Lu et al. 2010), yet this assumes that high-elevation species are particularly long-lived, which remains untested. The decrease in nest predation with increasing elevation (Skutch 1985, Boyle 2008) may reflect a decreasing overall predation risk that applies to adults as well as to nests. Increased adult survival at higher elevations has been described for birds from temperate mountains (Bears et al. 2009, Camfield et al. 2010, Wilson and Martin 2010, 2011), as well as for other taxa including anurans (Morrison et al. 2004) and small mammals (Zammuto and Millar 1985). An increase in adult survival among high-elevation tropical birds is, to the best of our knowledge, unexamined.

We detected geographic, in addition to elevational, variation in clutch size in the tropics. The three clades responsible for the largest clutches in our literature dataset (swallows, jays, and finches) were not represented in the New Guinea dataset, and their absence may partly explain the smaller clutch size found in New Guinea. However, clutches in New Guinea remained significantly smaller than those in the other two regions, even with these clades removed from analysis ($P < 0.001$). Clutch size is known to increase in more seasonal environments (Jetz et al. 2008), and higher seasonality in Venezuela may have been linked to the higher clutch size that we described there. However, it is unclear how seasonality relates to the small clutch sizes observed in New Guinea, given that, while it was the least seasonal region in terms of precipitation, Borneo had significantly less seasonal temperature variation and larger clutches.

Many questions regarding the influence of elevation on the evolution of clutch size in tropical and temperate birds remain unanswered. While environmental causes of clutch-size evolution are typically considered in a latitudinal framework, here we show that elevation has an added effect on clutch size independent of latitude. Elevational gradients provide an independent geographical arena within which it is more locally tractable to test hypotheses that may explain clutch-size evolution. Additional field studies are necessary to assess patterns of clutch size along tropical elevational gradients (e.g., at the intraspecific level), and to test hypotheses that may explain the causes of these broad, geographically replicated patterns.

ACKNOWLEDGMENTS

LITERATURE CITED

Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

Badyaev, A. V. (1997). Avian life history variation along altitudinal gradients: An example with cardueline finches. Oecologia 111:365–374.

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

Bears, H., K. Martin, and G. White (2009). Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. Journal of Animal Ecology 78:365–375.

Blomberg, S. P., J. G. Lefevre, J. A. Wells, and M. Waterhouse (2012). Independent contrasts and PGLS regression estimators are equivalent. Systematic Biology 61:382–391.

Boles, W. E. (2007). Family Petroicidae (Australasian robins). In Handbook of the Birds of the World, Volume 12: Picathartes

to Tits and Chickadees (J. del Hoyo, A. Elliott, and D. A. Christie, Editors), Lynx Edicions, Barcelona, pp. 12438–12489.

Boyle, W. A. (2008). Can variation in risk of nest predation explain altitudinal migration in tropical birds? Oecologia 155:397–403.

Camfield, A. F., S. F. Pearson, and K. Martin (2010). Life history variation between high and low elevation subspecies of Horned Larks Eremophila spp. Journal of Avian Biology 41:273–281.

Cody, M. L. (1966). A general theory of clutch size. Evolution 20:174–184.

Dunning, J. B. (1993). CRC handbook of avian body masses. CRC Press, Boca Raton, FL, USA.

Felsenstein, J. (1985). Phylogenies and the comparative method. American Naturalist 125:1–15.

Ferger, S. W., M. Schleuning, A. Hemp, K. M. Howell, and K. Böhning-Gaese (2014). Food resources and vegetation structure mediate climatic effects on species richness of birds. Global Ecology and Biogeography 23:541–549.

Forbes, L. S. (1990). Insurance offspring and the evolution of avian clutch size. Journal of Theoretical Biology 147:345–359.

Freeman, B. G., and N. A. Mason (2014) New Guinean passerines have globally small clutch sizes. Emu 114:304–308.

Frith, C., and D. Frith (2009). Family Paradisaeidae (birds of paradise). In Handbook of the Birds of the World, Volume 14: Bush-Shrikes to Old World Sparrows (J. del Hoyo, A. Elliott, and D. A. Christie, Editors), Lynx Edicions, Barcelona, pp. 14404–14493.

Ghosh-Harihar, M. (2013). Distribution and abundance of foliage-arthropods across elevational gradients in the east and west Himalayas. Ecological Research 28:125–130.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K.-L. Han, J. Harshman, C. J. Huddleston, et al. (2008). A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

Higgins, P. J., L. Christidis, and H. A. Ford (2008). Family Meliphagidae (honeyeaters). In Handbook of the Birds of the World, Volume 13: Penduline-Tits to Shrikes (J. del Hoyo, A. Elliott, and D. A. Christie, Editors), Lynx Edicions, Barcelona, pp. 13498–13691.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. American Naturalist 101:233–249.

Janzen, D. H. (1973). Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese (2008). The worldwide variation in avian clutch size across species and space. PLOS Biology 6:2650–2657.

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

Johnson, L. S., E. Ostlind, J. L. Brubaker, S. L. Balenger, B. G. Johnson, and H. Golden (2006). Changes in egg size and clutch size with elevation in a Wyoming population of Mountain Bluebirds. The Condor 108:591–600.

Kleindorfer, S. (2007). The ecology of clutch size variation in Darwin's Small Ground Finch Geospiza fuliginosa: Comparison between lowland and highland habitats. Ibis 149:730–741.

Krementz, D. G., and P. Handford (1984). Does avian clutch size increase with elevation? Oikos 43:256–259.

Lack, D. (1948). The significance of clutch-size. Part III—Some interspecific comparisons. Ibis 90:25–45.

Lack, D., and R. E. Moreau (1965). Clutch-size in tropical passerine birds of forest and savanna. Oiseau 35:76–89.

Lu, X., T. Yu, W. Liang, and C. Yang (2010). Comparative breeding ecology of two White-bellied Redstart populations at different altitudes. Journal of Field Ornithology 81:167–175.

Maddison, W. P., and D. R. Maddison (2011). Mesquite: A modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

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

Martin, T. E. (2004). Avian life-history evolution has an eminent past: Does it have a bright future? The Auk 21:289–301.

Martin, T. E., R. Bassar, S. Bassar, J. Fontaine, P. Lloyd, H. Mathewson, A. Niklison, and A. Chalfoun (2006). Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. Evolution 60:390–398.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine (2000). Parental care and clutch sizes in North and South American birds. Science 287:1482–1485.

Martin, T. E., J. C. Oteyza, A. J. Boyce, P. Lloyd, and R. Ton (2015). Adult mortality probability and nest predation rates explain parental growth effort in warming eggs with consequences for embryonic development time. American Naturalist. In press.

Morrison, C., J. Hero, and J. Browning (2004). Altitudinal variation in the age at maturity, longevity, and reproductive lifespan of anurans in subtropical Queensland. Herpetologica 60:34–44.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, et al. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. BioScience 51:933–938.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. Nature 401:877–884.

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

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and the R Development Core Team (2013). nlme: Linear and nonlinear mixed effects models. R package version 3.1–111. http://www.inside-r.org/packages/nlme/versions/3-1-111

R Development Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.r-project.org/

Sanz, J. J. (1998). Effects of geographic location and habitat on breeding parameters of Great Tits. The Auk 115:1034–1051.

Sæther, B. E. (1987). The influence of body weight on the covariation between reproductive traits in European birds. Oikos 48:79–88.

Sæther, B. E., R. Andersen, O. Hjeljord, and M. Heim (1996). Ecological correlates of regional variation in life history of the moose *Alces alces*. Ecology 77:1493–1500.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish? Ibis 91:430–458.

Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithological Monographs 36:575–594.

Sheldon, F. H., R. G. Moyle, and J. Kennard (2001). Ornithology of Sabah: History, Gazetteer, Annotated Checklist and Bibliography. Ornithological Monographs 52.

Slagsvold, T. (1982). Clutch size, nest size, and hatching asynchrony in birds: Experiments with the Fieldfare (*Turdus pilaris*). Ecology 63:1389–1399.

Slagsvold, T. (1984). Clutch size variation of birds in relation to nest predation: On the cost of reproduction. Journal of Animal Ecology 53:945–953.

Smythies, B. E. (1999). The Birds of Borneo, 4th edition (revised by G. W. H. Davison). Natural History Publications, Borneo, in association with The Sabah Society.

Stevens, G. C. (1992). The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. American Naturalist 140:893–911.

Wilson, S., and K. Martin (2010). Variable reproductive effort for two ptarmigan species in response to spring weather in a northern alpine ecosystem. Journal of Avian Biology 41:319–326.

Wilson, S., and K. Martin (2011). Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range. Population Ecology 53:459–471.

Yang, C., W. Liang, Y. Cai, J. Wu, S. Shi, and A. Antonov (2012). Variation in Russet Sparrow (*Passer cinnamomeus*) breeding biology in relation to small-scale altitudinal differences in China. Zoological Science 29:419–422.

Zammuto, R. M., and J. S. Millar (1985). Environmental predictability, variability, and *Spermophilus columbianus* life history over an elevational gradient. Ecology 66:1784–1794.

APPENDIX TABLE 1. Parameter estimates, standard errors, *t*-values, and *P*-values for our full phylogenetic generalized least-squares (PGLS) model explaining variation in Log_{10}-transformed clutch size in tropical passerines in the literature dataset. Clutch size in Malaysian Borneo is subsumed into the intercept; thus, coefficients and *P*-values represent comparisons with that region. The effects of ground-nesting, its interaction with elevation, and the interaction between elevation and region were all nonsignificant and were dropped from the final model.

	Estimate	SE	*t*-value	*P*
(Intercept)	0.38	0.06	6.96	0.00
Elevation	−4.20E−05	1.43E−05	−2.93	0.004
Log_{10} mass	−0.05	0.02	−2.91	0.004
Region (New Guinea)	−0.06	0.03	−1.82	0.07
Region (Venezuela)	0.07	0.03	2.16	0.03
Ground nest	−0.02	0.03	−0.54	0.59
Elevation * Ground nest	2.24E−05	2.07E−05	1.08	0.28
Elevation * Region (NG)	−2.70E−05	1.86E−05	−1.45	0.15
Elevation * Region (VZ)	2.50E−06	1.59E−05	0.16	0.88

SUPPLEMENTAL MATERIAL FIGURE S1. Majority-rules consensus tree describing phylogenetic relationships among all species of tropical passerines in our literature-based dataset with branches and taxa colored by region. The consensus tree was constructed in program Mesquite, from 500 trees obtained from birdtree.org (Jetz et al. 2012), based on the Hackett backbone (Hackett et al. 2008). Black = Venezuela, Blue = Borneo, and Red = New Guinea.