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Elevation and latitude interact to drive life-history variation in precocial birds: a comparative analysis using galliformes

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Summary

1. Elevational gradients provide a powerful laboratory for understanding the environmental and ecological drivers of geographic variation in avian life-history strategies. Environmental variation across elevational gradients is hypothesized to select for a trade-off of reduced fecundity (lower clutch size and/or fewer broods) for higher offspring quality (larger eggs and/or increased parental care) in higher elevation species and populations. In birds, a focus on altricial species from north temperate latitudes has prevented an evaluation of the generality of this trade-off, and how it is affected by latitude and intrinsic factors (development mode).

2. We performed a comparative analysis controlling for body size and phylogenetic relationships on a global data set of 135 galliform species to test (i) whether higher elevation precocial species have lower fecundity (smaller clutch and/or fewer broods) and invest more in offspring quality (greater egg mass) and (ii) whether latitude influences the traits involved and/or the trade-off, and (iii) to identify ecological and environmental drivers of life-history variation along elevational gradients.

3. Life-history traits showed significant interaction effects across elevation and latitude: temperate higher elevation species had smaller clutches and clutch mass, larger eggs and shorter incubation periods, whereas more tropical species had larger clutches, eggs and clutch mass, and longer incubation periods as elevation increased. Number of broods and body mass did not vary with elevation or latitude. Latitudinal gradient in clutch size was observed only for low-elevation species.

4. Significantly, an overlooked latitude-by-elevation interaction confounds our traditional view of clutch size variation across a tropical-to-temperate gradient. Across all latitudes, higher elevation species invested in offspring quality via larger eggs but support for reduced fecundity resulting from smaller clutches was found only along temperate elevational gradients; contrary to expectations, tropical high-elevation species showed increased fecundity. Variation in nest predation risk could explain differences between temperate and tropical elevational gradients, but we lack a consistent mechanism to explain why predation risk should vary in this manner. Alternatively, a resource availability hypothesis based on physical attributes that globally differ between elevation and latitude (seasonality in day length and temperature) seems more plausible.

Key-words: altitude, clutch size, egg mass, elevation, fecundity vs. offspring quality galliformes, interspecific variation, life-history trade-off, phylogenetic comparative methods

Introduction

A central goal of evolutionary ecology is to understand the patterns and drivers of variation in life-history

strategies (Martin 1996). A powerful means of generating this understanding is to examine how species' traits vary along environmental gradients. Comparative studies of avian life-history strategies have furthered our understanding of the ultimate reasons for trait variation by elucidating trade-offs within and across regions, as well as the proximate environmental factors associated with those

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patterns. One of the most frequently examined traits has been variation in avian clutch size along a latitudinal gradient (Lack 1947); typically, tropical species lay smaller clutches than birds in north temperate climates, both within and among species (Böhning-Gaese *et al.* 2000; Jetz, Sekercioglu & Böhning-Gaese 2008). Comparing environmental conditions along an elevational gradient ranging from low to high altitudes produces many patterns similar to that of a tropical–temperate gradient: lower temperatures, greater seasonality, higher environmental stochasticity and, for birds, a shorter breeding season (Martin 2001). These similarities led to the expectation that life-history traits at high elevations should mirror those at high latitudes; that is, avian clutch sizes should increase with elevation as well (Cody 1966). However, high altitudes differ from high latitudes in several important respects: increased solar insolation, lower atmospheric pressure (including partial pressure of oxygen), but, compared to warmer lowlands below, the same photoperiod (Körner 2007). As it happens, in most studies reported to date avian clutch size actually declines with increasing elevation (Boyle, Sandercock & Martin 2016; Hille & Cooper 2015).

Recent studies of avian life-history variation along elevational gradients have revealed that distinct suites of traits covary among populations and species. Individuals and species breeding at higher elevations have smaller clutches and/or fewer broods, longer developmental periods, increased parental care via higher nestling provisioning rates, and increased post-fledging care, higher offspring condition and survival and increased adult survival (Badyaev 1997; Badyaev & Ghalambor 2001; Bears, Martin & White 2009; Boyce *et al.* 2015; Boyle, Sandercock & Martin 2016). Taken together, these studies suggest a trade-off between declining fecundity versus increasing adult survival and/or higher offspring quality (e.g. increased juvenile survival through increase in parental care) at higher elevations (Badyaev & Ghalambor 2001; Bears, Martin & White 2009).

Latitude (degrees north or south of the equator) and elevation (metres above sea level) are geographical surrogates for the physical environmental attributes that vary along these gradients. Thus, there is a decline in average temperature coupled with increased seasonality in day length and temperature with increasing latitude. Likewise, as elevation increases temperature declines, as does air pressure and the amount of oxygen available, whereas solar irradiation increases. Each of these can affect life-history traits directly and indirectly by influencing other ecological attributes. Studies of the environmental and ecological correlates of life-history variation along these geographical gradients have typically focused on four factors: the physical environment (temperature, atmospheric pressure, precipitation, seasonality), breeding season length (dependent on temperature and seasonality), food availability (a function of temperature, seasonality and precipitation) and age-specific mortality risk (nest

predation and adult mortality risk). We review several previously proposed hypotheses to explain avian life-history variation relevant to elevational patterns. Note that only the first two of these vary globally with elevation.

- 1 *Physical environment* – (i) Colder temperatures and/or reduced oxygen availability at higher elevations can increase metabolic and thermoregulatory costs of adults, thereby potentially limiting reproductive effort through reductions in clutch size, egg size and/or clutch mass and lengthen developmental periods (Conway & Martin 2000; Martin 2001). (ii) Lower atmospheric pressure with increasing elevation leads to greater water loss from eggs and more hypoxic conditions that may be mitigated by increasing the initial water content of eggs leading to larger eggs (Rahn & Ar 1974).
- 2 *Breeding season length* – Increased seasonality in temperature and/or precipitation towards higher elevations implies that conditions suitable for breeding may be constrained to a shorter period at higher elevations, thus limiting components of fecundity such as number of broods (Martin 2001; Hardesty 2008)
- 3 *Food availability* – Food resources can influence egg size, clutch size, incubation duration and fledging success, as well as adult and juvenile survivorship (Martin 1987). Food availability as indexed by net primary productivity declines with declining temperature and therefore with elevation (Sundqvist, Sanders & Wardle 2013), but this may be offset by changes in precipitation regimes that may not vary linearly with altitude. However, food limitation may increase foraging requirements of breeding females (Chalfoun & Martin 2007) in colder and hypoxic situations, thereby limiting reproductive effort (smaller clutches, eggs and/or clutch mass) and lengthening developmental periods (Jia, Sun & Swenson 2010).
- 4 *Predation risk* – Increased adult mortality risk selects for increased reproductive effort (Williams 1966; Ghalambor & Martin 2001) Higher nest predation risk, on the other hand, selects for smaller clutch sizes, repeated nesting attempts, lower attentiveness and shorter developmental periods (Martin 1995; Martin & Briskie 2009). Patterns of variation in nest predation risk across elevational gradients are unclear with studies reporting increasing (Sandercock, Martin & Hannon 2005) and decreasing nest predation risk at higher elevations (Badyaev 1997; Bears, Martin & White 2009).

Although predictions from some or a combination of these hypotheses have been tested repeatedly across latitudinal gradients such that the latitudinal increase in clutch size is now a well-recognized pattern, support for the generality of trade-offs across elevational gradients is inconsistent and there are few tests of mechanistic hypotheses that may influence these patterns. In a recent meta-analysis of intraspecific variation, Boyle, Sandercock & Martin

(2016) reported that a reduction in fecundity was observed at higher elevations, but consistent increases in survival or traits related to investment in offspring were not observed across all studies. Their results were most consistent with food availability driving life-history variation, and they suggested that temperature-driven reductions in primary productivity were responsible for reductions in number and size of clutches at higher elevations. Alternatively, their results were also consistent with the possibility that colder temperatures at higher elevations in low latitudes magnified temporal constraints imposed by other sources of climatic seasonality.

Two factors preclude assessing the generality of elevation–trait associations or trade-offs. First, previous studies have focused almost exclusively on passerine songbirds with altricial young (but see Sandercock, Martin & Hannon 2005); thus, we do not know how variation in intrinsic factors (such as species' developmental mode) influences the trade-off or traits involved. Precocial and altricial birds form two ends of a developmental continuum. Precocial species generally are larger bodied, lay larger eggs and clutches, have fewer broods annually, longer developmental periods and lack the intensive parental care associated with nestling and fledgling provisioning that occurs in altricial species (Starck & Ricklefs 1998). Thus, it is reasonable to expect that intrinsic differences between altricial and precocial species may affect the type of life-history trade-offs or the traits involved therein. For example, egg size has a significant effect on chicks and positively influences chick mass, survival and condition (Krist 2011). The lack of intensive parental care is thought to free up resources facilitating larger clutches (Winkler & Walters 1983; Martin 1987; Jetz, Sekercioglu & Böhning-Gaese 2008), and therefore, parental investment in precocial species may primarily be through investment in egg mass. Thus, high-elevation precocial species investing in offspring quality must do so primarily through laying larger eggs. Additionally, selection for larger and more developmentally advanced chicks at hatch should be greater for precocial than altricial species and this advancement should take longer to achieve (Starck & Ricklefs 1998). At higher elevations, the additional factor of colder temperatures should also favour longer developmental periods (Martin 2001). The need for longer developmental periods may magnify temporal constraints at higher elevations for precocial species, thus limiting fecundity through fewer broods. Additionally, we might also expect that if intensive parental provisioning of young is a constraint in altricial species that limits clutch size at higher elevations, then precocial species that do not feed young should not vary in clutch size across elevations or should have larger clutch sizes, again suggesting reduction in fecundity at higher elevations resulting from fewer broods.

Secondly, there exists a latitudinal bias in our understanding of elevation–trait trade-offs as most studies on elevational gradients have focused on temperate (Badyaev

1997; Badyaev & Ghalambor 2001) rather than tropical altitudinal gradients (Boyce *et al.* 2015). Although some environmental factors such as temperature and atmospheric pressure vary the same globally with elevation, tropical and temperate elevational gradients differ in some key respects: oxygen availability and irradiance vary with elevation but not latitude, whereas day length varies with latitude but not elevation. Temperature seasonality increases strongly with increasing latitude, but much less so with increasing elevation. The extent to which these features affect life-history traits suggests a potential for an interaction between the two geophysical gradients. For example, latitudinal variation in seasonality may lead to a difference in the expression of the temperature difference between low vs. high elevations in tropical vs. temperate regions. Janzen (1967) showed that in tropical latitudes, where the annual range in temperature is low, temperatures expressed at low elevations may never overlap those at nearby high elevations. In more strongly seasonal high latitudes, within-year temperatures are more variable, and ranges expressed at high and low elevations may overlap considerably. This differential expression of overlap led Janzen (1967) to conclude that from a biological perspective, 'mountain passes are higher in the tropics'. Furthermore, seasonality in the tropics is primarily driven by precipitation rather than temperature, and at a given site, temperatures tend to be less variable within the year than in temperate regions (Janzen 1967; Sarmiento 1986). These differences in climatic patterns across tropical and temperate elevational gradients suggest that trait variation along any particular elevational gradient may be determined by its latitudinal location. Strengthening this expectation of an interaction are studies that show that tropical and temperate birds behave differently across elevational gradients. For example, reproductive synchrony, expected to increase with latitude and elevation due to a shorter breeding season length, varies as expected across temperate elevational gradients but does not vary across tropical elevational gradients (Class *et al.* 2011). However, few tests of this potential interaction have been performed, principally due to a lack of a sufficient number of published studies of avian demography from the tropics (Boyle, Sandercock & Martin 2016; Hille & Cooper 2015).

In this study, we use a globally distributed precocial group, the galliformes (grouse, quail, pheasants, megapodes, cracids and partridges), to perform an interspecific comparative analysis of patterns of life-history variation across elevational gradients. Galliforms are distributed across the world from tropical forests to tundra and from sea level to alpine areas, thus spanning long gradients in both latitude and elevation. They exhibit a wide range of variation in life-history traits and are thus an appropriate choice to study how elevation influences life-history variation in precocial species, while considering any confounding effects of latitude. We had three objectives:

- 1 We test the hypothesis that environmental variation with increasing elevation results in precocial species exhibiting a trade-off between reduced fecundity vs increased investment in offspring quality similar to that observed in altricial passerines. Specifically we predicted that
 - a. Environmental conditions at higher elevations limit fecundity, as they seem to in altricial species. There are two alternatives: (i) as with altricial species, reduced fecundity results from lower clutch sizes and/or fewer broods; (ii) alternatively, if environmental constraints on altricial species are magnified by the energetic costs of intensive parental provisioning, clutch sizes of precocial species should not vary, or even increase with elevation to compensate for shorter breeding seasons, and any reduction in fecundity should be through fewer broods.
 - b. In contrast to altricial species, where egg size does not systematically vary across elevation, we expect a significant positive association in galliforms as a means of increased parental investment in offspring.
- 2 We ask, is there an interaction between latitude and elevation in association with life-history patterns across elevational gradients? If so, we expect its explanation to lay with one or more of those physical attributes that differ between the two gradients, such as seasonality.
- 3 We then discuss potential mechanisms by which ecological and environmental correlates of elevational gradients known to influence avian life-history traits (e.g. food limitation, nest predation, seasonality, temperature, photoperiod and breeding season length) may shape patterns along elevational gradients by examining variation in multiple traits of galliformes: clutch size, egg mass, clutch mass and incubation period.

Materials and methods

ELEVATIONAL AND LATITUDINAL RANGES

We recorded upper and lower elevational distributional limits from the literature for 135 galliform species and used the mid-point in our analyses. We obtained data from world and regional handbooks and field guides, and online resources (data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.38s8g>). We used breeding elevations where available. We determined the latitudinal extent of breeding ranges using species distribution maps from (BirdLife International & NatureServe 2012) (<http://www.birdlife.org/datazone/info/spedownload>). We imported the shapefiles into ARCGIS 10.2.2 (ESRI 2013) and extracted data from the native range of species where it was extant or considered probably extant, and where it was a year-round resident or breeding visitor. We calculated the centroid latitude of the breeding range and used its absolute value in all analyses. For four species where data were not available from the above sources, we used species global range maps and distribution information from del Hoyo, Elliott & Sargatal (1994) and

visually estimated maximum and minimum latitudinal extent and calculated the latitudinal mid-point.

LIFE-HISTORY DATA

We collected data on clutch size, egg mass, incubation period and female body mass from the literature for the 135 galliform species for which such data have been published. Data on number of broods was available for a subset of 45 species (data available from Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.38s8g>). When data were available at the subspecies level, we averaged values across all subspecies to calculate species means. Only demographic data from a species' native range were used. Mean values of variables were used when available; otherwise, means were estimated as the mid-point of the range reported. If reported, we also used data from birds in captivity; we assumed that data from captivity fell within the range of variation observed for the trait in the wild. For nine species where data on egg mass were not available, we followed (Musvuugwa & Hockey 2011) and estimated egg mass from the equation provided by (Hoyt 1979): $W = K_w LB^2$, where W = egg mass(g), K_w = specific weight coefficient (g cm^{-3}), L = length of egg (cm) and B = breadth of egg (cm). K_w was calculated from congeners for which egg mass and dimensions were known and ranged from 0.526 to 0.726 g cm^{-3} . We ordinarily used female body mass, but in cases where sex-specific body mass was not given, we used the reported body mass. We calculated clutch mass as the product of egg mass and clutch size.

STATISTICAL ANALYSES

We \log_{10} -transformed all life-history traits except number of broods prior to analyses. To account for phylogenetic relatedness in interspecific comparisons (Felsenstein 1985), we used phylogenetic generalized least squares (PGLS) with simultaneous estimation of λ by maximum likelihood to analyse the relationships between life-history traits and elevation and latitude (Martins & Hansen 1997; Freckleton, Harvey & Pagel 2002). λ is an internal branch length transformation parameter that can range from 0 (no phylogenetic relationships; species can be treated as independent data points) to 1 (observed pattern of trait variation among species resemble those expected under a Brownian motion model of evolution). We built a majority rule consensus tree (data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.38s8g>) by sampling 4000 trees based on a Hackett backbone (Hackett *et al.* 2008) from www.birdtree.org (Jetz *et al.* 2012) using Mesquite software (Maddison & Maddison 2011). This tree was used in PGLS analyses. We implemented PGLS in R version 2.15.1 (R Core Team 2012) using the packages 'APE' (Paradis, Claude & Strimmer 2004) and 'NLME' (Pinheiro *et al.* 2012) after polytomies were arbitrarily resolved to zero length branches. As scaling variables by their standard deviations to obtain standardized regression estimates ignores their phylogenetic structure (D. Orme, pers. comm.), we standardized variables to have a phylogenetic mean of 0 and variance of 1 to fully account for this structure, and then subjected them to PGLS regression. This standardization allows us to obtain comparable effect sizes. Many life-history traits are highly correlated with body mass; therefore, we controlled for allometric effects by first conducting a PGLS regression of each life-history trait against body mass then using the resulting residuals in subsequent PGLS regressions against elevation and latitude. Analysis with number of broods as the dependent variable was carried out on a subset of 45 species. To assess how latitude may influence the

effect of elevation on life-history traits, trait residuals were regressed against elevation, latitude and an elevation \times latitude interaction term. If estimated λ values were indistinguishable from zero, then ordinary least squares (OLS) regression analysis was carried out using the same set of predictors as phylogenetic correction is not necessary. Since outliers can bias PGLS regression estimates, we excluded species with normalized residuals $>\pm 3$ standard deviations from the mean (Symonds & Blomberg 2014). Significance was considered as $P < 0.05$. To better interpret significant elevation \times latitude interaction terms (see below), for each trait with a significant interaction effect, we plotted values predicted from resulting regression equations using latitude fixed at observed high and low values while allowing elevation to vary, and with elevation fixed at observed high and low values while latitude varied. For illustrative purposes, we used a heuristic that classed species with mid-point elevation ≥ 2000 m as 'high' elevation (vs. 'low' elevation) species, and those with absolute value of centroid latitude $\geq |30|^\circ$ as 'temperate' (vs. 'tropical') species. Note that we did not perform any analyses based on this heuristic classification; all analyses treated latitude and elevation as continuously variable attributes.

Results

The average breeding latitudes for species in this study spanned 31.29°S to 65.39°N, and mid-point breeding elevations ranged from 150 to 4250 m. Out of 135 species, the absolute value of latitudinal centroid lay within 0–30° for 93 species and between 30 and 66° for 42 species. Most life-history traits showed substantial variation; for example,

mean clutch size ranged from 1 to 17.5 eggs per clutch, and adult mass varied over almost 2 orders of magnitude from 38.5 g to 3.6 kg (Table 1). A phylogenetic approach was justified as model residuals showed a significant phylogenetic signal (λ substantially >0) in all regressions except those with number of broods as the dependent variable (Table 2). As the λ value involving regressions with number of broods was indistinguishable from zero, we report results from ordinary least squares regressions.

RELATIONSHIPS BETWEEN LIFE-HISTORY TRAITS AND BODY MASS

After standardization accounting for phylogeny, egg mass ($\beta_{st} = 0.86$, $P \leq 0.001$), clutch mass ($\beta_{st} = 0.64$, $P \leq 0.001$) and incubation period ($\beta_{st} = 0.50$, $P \leq 0.001$) were highly positively related to adult body mass. Clutch size did not vary with body mass ($\beta_{st} = -0.01$, $P = 0.843$). Number of broods was significantly negatively related to body mass ($\beta_{st} = -0.32$, $P \leq 0.01$).

RELATIONSHIPS OF LIFE-HISTORY TRAITS TO ELEVATION AND LATITUDE

Most traits, when body size and phylogenetic relationships were taken into account, revealed significant covariation with at least one of the independent variables

Table 1. Mean, standard deviation and range of life-history attributes of 135 species of galliformes. Data available from the Dryad Digital Repository <http://dx.doi:10.5061/dryad.38s8g>

	Latitude (degrees)	Elevation (metres)	Clutch size	Egg mass (g)	Clutch mass (g)	Incubation (days)	Number of broods	Adult mass (g)
Mean	–	–	6.1	46.3	214.0	24.1	1.27	907.5
Std. Dev.	–	–	3.25	47.91	151.12	3.97	0.33	829.32
Maximum	65.39	4250	17.5	279.6	766.6	35	2.5	3685
Minimum	0.43	150	1	5	27.5	16	1	38.5

Table 2. Results of PGLS multiple regressions of phylogenetically standardized trait residuals against mean elevation, absolute value of centroid latitude and their interaction. λ is a measure of phylogenetic correlation (Freckleton, Harvey and Pagel 2002). 95% CI for λ across all regressions ranged from 0.66 to 1.01

Trait	λ	Intercept	Elevation			Latitude			Interaction			No. species
			$\beta_{st} \pm SE$	t	P	$\beta_{st} \pm SE$	t	P	$\beta_{st} \pm SE$	t	P	
Clutch size	0.96	0.16	0.31 \pm 0.15	2.01	0.047	0.35 \pm 0.08	4.63	<0.001	-0.10 \pm 0.04	-2.41	0.018	132
Egg mass (g)	0.99	0.05	0.42 \pm 0.08	5.15	<0.001	-0.17 \pm 0.04	-3.76	<0.001	-0.03 \pm 0.02	-1.54	0.126	129
Clutch mass (g)	0.83	0.13	0.36 \pm 0.13	2.71	0.008	0.12 \pm 0.06	2.00	0.048	-0.08 \pm 0.03	-2.35	0.020	131
Incubation period (days)	0.84	0.16	0.54 \pm 0.15	3.62	<0.001	-0.02 \pm 0.07	-0.22	0.824	-0.08 \pm 0.04	-2.08	0.039	130
Body mass (g)	1.00	0.02	0.0007 \pm 0.15	0.01	0.996	0.10 \pm 0.09	1.13	0.259	-0.01 \pm 0.04	-0.23	0.815	134
Broods ^a	–	0.06	-0.10 \pm 0.10	-0.97	0.338	-0.16 \pm 0.11	-1.47	0.149	-0.21 \pm 0.11	-1.86	0.070	43

^aNumber of broods coefficients are standardized estimates from ordinary least squares regression.

(Table 2). Clutch size was significantly positively related to elevation and latitude but negatively with the interaction term, increasing with elevation at tropical latitudes but decreasing with increasing elevation at temperate latitudes (Table 2, Fig. 1a). As for the well-documented latitudinal increase in clutch size, this pattern held only for lower elevation species in galliforms (Fig. 2a). Egg mass significantly increased with elevation and decreased with an increase in latitude, but with no significant interaction (Table 2, Figs 1b and 2b). Clutch mass was significantly

related to elevation, latitude and the interaction term; clutch mass increased with elevation at low latitudes but decreased with increasing elevation at high latitudes (Table 2, Figs 1c and 2c). Incubation period was significantly positively related to elevation, not related to latitude, and showed a significant interaction effect; incubation period increased with elevation at low latitudes but decreased with increasing elevation at high latitudes (Table 2, Figs 1d and 2d). Number of broods did not vary significantly with elevation, latitude or the

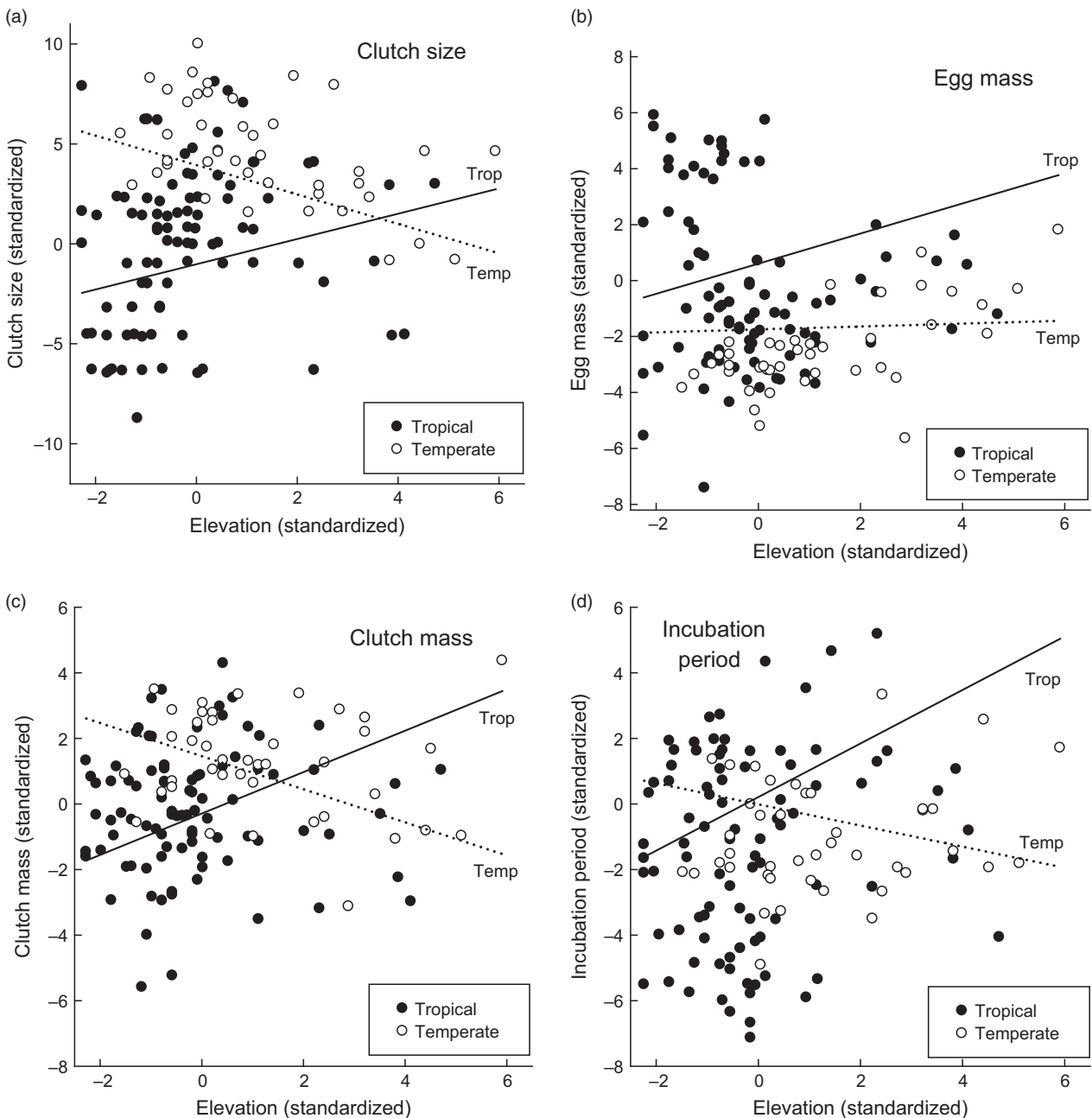


Fig. 1. Effects of increasing elevation on life-history traits (phylogenetically standardized) at different latitudes. Filled circles denote species with absolute value of centroid $<|30^\circ|$ latitude ('Tropical'); open circles denote species with centroid values $\geq|30^\circ|$ latitude ('Temperate'). Lines fitted based on regression coefficients in Table 2, at constant values of 0° and 61° for tropical ('Trop' solid line) and temperate ('Temp' dotted line) species, respectively.

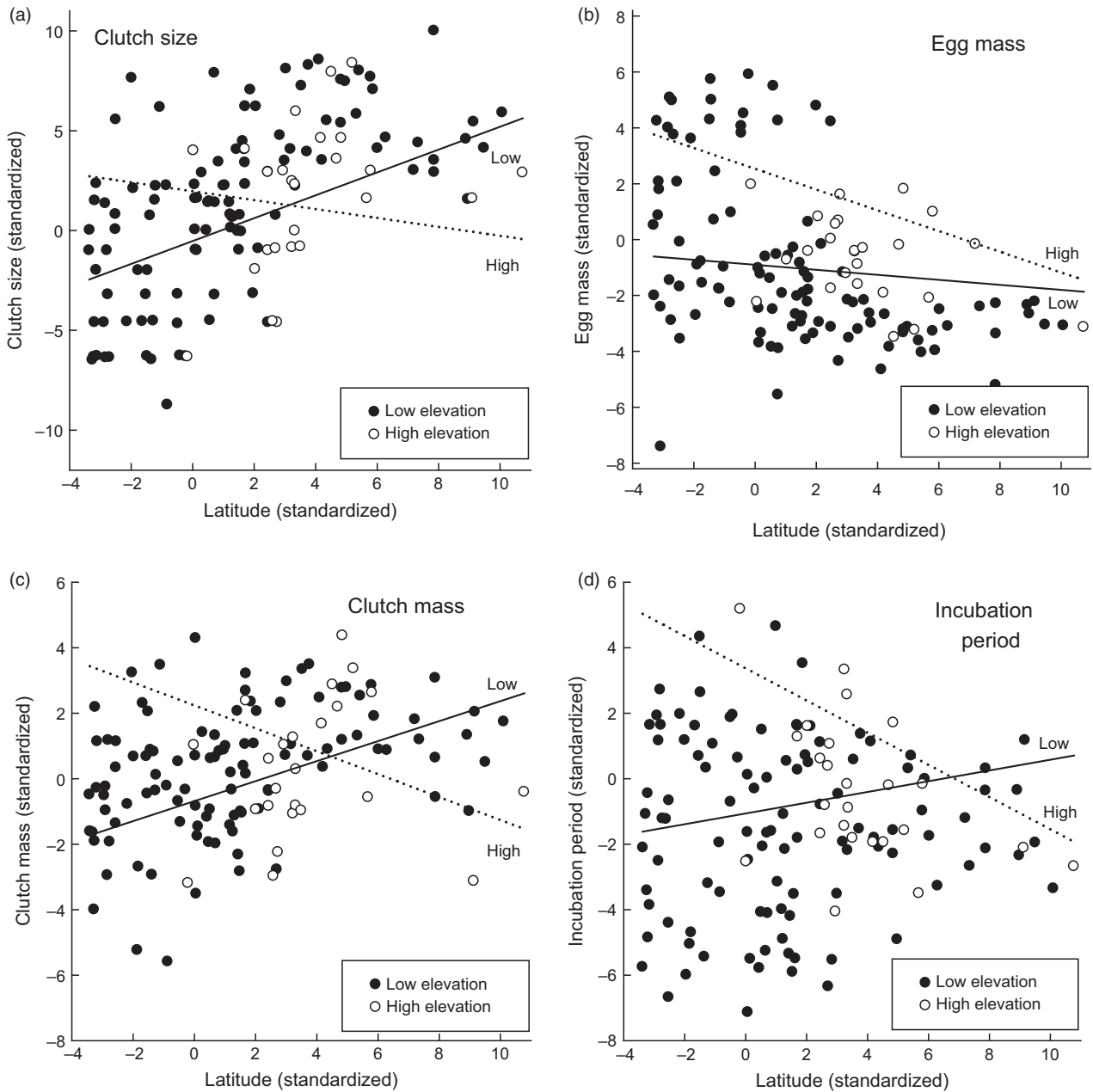


Fig. 2. Effects of increasing latitude on life-history traits (phylogenetically standardized) at different elevations. Filled circles denote species with mean elevation <2000 m ('Low elevation'); open circles denote species with mean elevation \geq 2000 m ('High elevation'). Lines fitted based on regression coefficients in Table 2, at constant values of 150 m and 4000 m for low-elevation ('Low' solid line) and high-elevation ('High' dotted line) species, respectively.

interaction term (Table 2). Body mass also did not vary with elevation, latitude or the interaction term (Table 2).

TRADE-OFFS ALONG ELEVATIONAL GRADIENTS

Clutch size and egg mass varied in opposite directions along elevational gradients at high latitudes but not low. With increasing elevation, clutch size decreased but egg mass increased towards temperate latitudes whereas at tropical latitudes, both clutch size and egg mass increased with increasing elevation (Fig. 3).

Discussion

After controlling for phylogeny and body mass, using a globally distributed data set of 135 galliform species we demonstrated that several life-history traits varied significantly along elevational gradients. However, expression of that variation differed depending on latitude. Compared to low-elevation counterparts, higher elevation species in the tropics had larger clutches and eggs, larger clutch mass and longer incubation periods, whereas at temperate latitudes species had smaller clutches, smaller clutch mass,

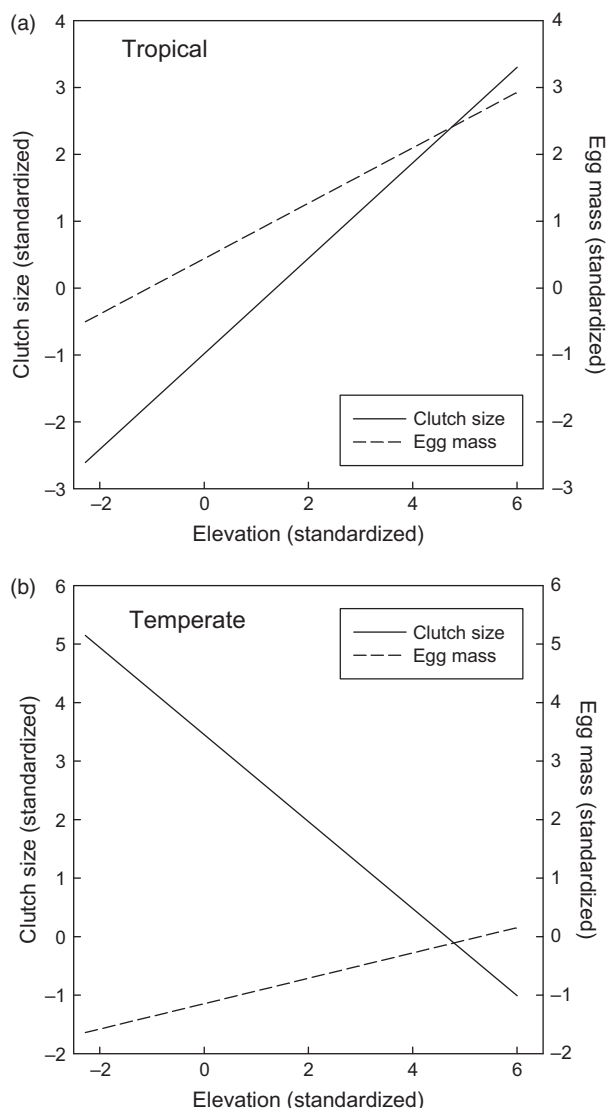


Fig. 3. Variation in clutch size (solid line) and egg mass (dashed line) with increasing elevation for tropical ($<30^\circ$; (a)) and temperate ($\geq 30^\circ$; (b)) latitude species. Lines are taken from Fig. 1.

shorter incubation periods and larger eggs at higher elevations. This previously overlooked elevation-by-latitude interaction confounds our traditional view of avian reproductive variation across a tropical–temperate gradient.

LIFE-HISTORY TRADE-OFFS IN PRECOCCIAL GALLIFORMS WITH INCREASING ELEVATION

We observed support for the hypothesis that with increasing elevation, species have reduced fecundity (indexed by clutch size) and increase investment in offspring quality (indexed by egg mass), but only at temperate latitudes. That temperate precocial species follow similar patterns seen in temperate altricial passerines supports the premise that high-elevation environments, at least in temperate areas, select for such trade-offs despite variation in intrinsic factors such as development mode. Although our

results are in contrast to the decline in clutch size towards higher elevations found in altricial passerines across tropical elevational gradients (Boyce *et al.* 2015), they can be reconciled by considering the influence of differences in developmental mode. Nestling provisioning, the primary mode of parental care in altricial species, is energetically expensive (Drent & Daan 1980) and is known to influence clutch size through a cost of reproduction (Dijkstra *et al.* 1990). If the energy costs of nestling provisioning are magnified by environmental constraints prevalent at higher elevations that may limit clutch size in altricial passerines, then it is reasonable to expect that precocial species freed from such constraints may have larger clutch sizes at higher elevations. However, this begs the question, why is a similar increase in clutch size not observed in temperate high-elevation galliforms? In many temperate bird species, there is a seasonal decline in clutch size, chick growth rate and reproductive success (Winkler & Walters 1983; Lepage, Desrochers & Gauthier 1999). We hypothesize that at temperate high elevation, clutch sizes may represent a trade-off between offspring number and delay in laying resulting from the need to acquire enough resources to lay additional eggs (Lepage, Gauthier & Desrochers 1998). This trade-off may be exacerbated by both the energetic costs of breeding at high elevations and shorter breeding seasons. Alternatively, within the limits of the constraints mentioned above, it is perhaps easier for higher elevation species to effect an increase relative to the smallest clutches (tropical low elevation) than the largest clutches (temperate low elevation).

Contrary to expectations, number of broods did not vary with latitude or elevation, although our inference is limited by a smaller sample of 45 species. Two potential scenarios present themselves: (i) as more demographic data become available for galliforms, we may observe a pattern of fewer broods raised at higher elevations due to shorter breeding seasons. This expectation is bolstered by the observation that most studies to date have reported a decrease in number of broods attempted at higher elevations (Boyle, Sandercock & Martin 2016; Hille & Cooper 2015), and shorter breeding seasons even at tropical high elevations are implied by greater breeding seasonality observed in tropical montane birds (Hardesty 2008; Peh *et al.* 2012). In our study, only one of the 21 multi-brooded species occurred at high elevation. (ii) If brood number indeed does not vary across elevations in the tropics, then tropical high-elevation species that lay larger clutches and eggs are opposite of the trend of declining fecundity with increasing elevation in altricial species. Life-history theory posits that increased fecundity involves a cost of reproduction through reduced adult survival (Roff 1992), and tropical passerines have been shown to have increased adult survival and lower fecundity compared to temperate species (Ghalambor & Martin 2001). Thus, increased fecundity in tropical high-elevation galliforms suggests a potential trade-off with reduced adult

survival. Tests of this trade-off are precluded by the lack of adult survival estimates for many galliform species.

As predicted, independent of latitude higher elevation species had larger egg mass. Egg mass is a form of parental investment analogous to post-hatching parental care that influences offspring quality and survival. In general, larger eggs are associated with increased hatching success, and result in larger and heavier chicks that have increased growth and survival (Krist 2011). Larger eggs also result in increased nutrient reserves available to the chick at hatch (Martin 1987; Pelayo & Clark 2003) and a larger size at hatch helps increase thermoregulatory efficiency, a significant advantage given the lower temperatures at higher elevations (Rhymmer 1988). In altricial species, although egg mass can have similar benefits, parental care can override the effects of egg quality (Krist 2011). Therefore, investment in egg mass is a viable strategy for precocial species. Although we do not have data on offspring survival or condition in high-elevation species, increased investment in eggs with elevation has been reported across a wide variety of taxa lacking post-hatching parental care; for example, frogs and snails breeding at high elevations lay larger eggs relative to body size and have increased reproductive investment per egg, respectively (Berven 1982; Baur & Raboud 1988; Chen *et al.* 2013).

ECOLOGICAL AND ENVIRONMENTAL FACTORS SHAPING ELEVATIONAL PATTERNS OF LIFE-HISTORY TRAITS

As noted in the Introduction, avian life-history variation along elevational gradients may be influenced by a variety of factors and their interactions; principal among them are seasonality (the magnitude of within-year variation in ambient conditions), temperature, food limitation and nest predation.

Increasing seasonality and cooler temperatures as elevation increases may serve to limit the length of time suitable for breeding. The primary effect of shorter breeding seasons is the reduction in number of broods raised. Unexpectedly, our data showed no variation in this critical component of fecundity across latitude or elevation, indicating a limited role for breeding season length. We view this result cautiously as our inferences are limited by a comparatively smaller sample size.

Direct effects of cold temperatures and hypoxia include increased metabolic and thermoregulatory demands on adults that may lower reproductive effort at higher elevations, particularly when they interact with any food limitation with increasing elevation. Increasing elevation is also associated with decrease in net primary productivity signifying decreasing food availability compared to lowland areas (Sundqvist, Sanders & Wardle 2013). In precocial birds, clutch size is considered to be limited by food availability to the laying female (Winkler & Walters 1983). Thus, decreased food availability may magnify the energetic costs of breeding at higher elevations and may

explain the lower clutch sizes and clutch masses observed at temperate higher elevations. A meta-analysis by Boyle, Sandercock & Martin (2016) also found results consistent with food limitation at high elevations as a driver of reduced fecundity using predominantly temperate comparisons. However, food limitation does not explain larger egg mass and shorter incubation periods observed at temperate higher elevations. Alternately, for a given level of food limitation, selection may favour a strategy of reduction in offspring number vs. increased offspring quality (Badyaev & Ghalambor 2001). Energetic constraints at temperate higher elevations are still indicated by lower clutch mass. On the contrary, the increased clutch size, egg mass and clutch mass observed for tropical high-elevation species suggests that food limitation and/or energetic constraints may be less limiting at tropical high elevations. The longer incubation periods, however, indicate a potential role for food limitation. Alternately, precocial species may benefit from longer incubation periods as it may result in developmentally more advanced chicks, thereby increasing their post-hatching survival (Starck & Ricklefs 1998). However, a more parsimonious explanation suggests that patterns of variation in incubation periods may be reconciled by the positive correlation between clutch size and developmental periods (Smith 1989). Thus, variation in incubation periods may be a by-product of selection on components of fecundity.

Increased reproductive effort (clutch size, egg and clutch mass) at higher elevations along tropical elevational gradients is consistent with reduced nest predation risk with increasing elevation. Lower nest predation risk is associated with increased reproductive effort including larger clutches, eggs and clutch mass and longer developmental periods (Martin 1995; Martin & Briskie 2009). Although nest predation risk increases towards tropical latitudes (Martin 1996), the few studies that have examined patterns of nest predation risk across tropical elevational gradients indicate that nest predation risk is lower at higher elevations (Skutch 1985; Boyle 2008). However, across temperate elevational gradients, nest predation risk may not fully explain patterns, as the lower clutch masses, clutch size and shorter developmental periods that imply increased nest predation risk contrast with larger egg masses that imply lower nest predation risk. Alternately, higher nest predation risk along with food limitation at temperate higher elevations may have selected for investment in fewer but better quality offspring given temporal constraints. The lower clutch mass at temperate higher elevations indicates a lower reproductive investment expected under higher predation risk (Martin *et al.* 2006). Although patterns of variation in nest predation risk along temperate elevational gradients are not yet fully understood, studies on white-tailed ptarmigan (*Lagopus leucura*) have shown that alpine ptarmigan suffer higher nest predation and have the smallest clutch size compared to subalpine and arctic ptarmigan (Sandercock, Martin & Hannon 2005).

Declining atmospheric pressure leads to greater water and carbon dioxide loss from eggs and more hypoxic developmental conditions (Rahn & Ar 1974). Water loss from eggs may be mitigated by increasing the initial water content of eggs, leading to larger eggs at higher elevations (Rahn & Ar 1974). Although this mechanism may explain the increase in egg mass, it implies that increase in egg mass is the result of a physical constraint and is required to achieve a base level of offspring viability, and thus may not correlate with offspring quality. As a caveat, this has been examined only in a few species to date (Carey 1994). Because the eggs of precocial species have lower relative water content than altricial species due to their greater yolk/albumen ratio (Carey, Rahn & Parisi 1980), hypoxia-induced water limitation may be a greater constraint on the former.

In summary, whereas patterns observed across tropical elevational gradients conform to hypotheses involving variation in nest predation risk, life-history variation across temperate elevational gradients suggests a role for food limitation as well as nest predation risk. We add that due to limited data, we do not rule out a role for temporal constraints resulting from shorter breeding seasons.

RETHINKING LATITUDINAL PATTERNS OF CLUTCH SIZE VARIATION

It is clear that at least in precocial galliforms, latitudinal variation in several life-history traits is significantly influenced by elevation. Latitudinal gradients in life-history patterns are often observed along the tropical-to-north-temperate axis (Martin 1996). Because of the availability of published data, our results similarly reflect a north-temperate bias. Thus, although we observed a latitudinal increase in clutch size, a pattern commonly seen in passerines (Jetz, Sekercioglu & Böhning-Gaese 2008) and previously reported for galliforms (Lack 1947; Musvuugwa & Hockey 2011), this pattern was only evident across species occurring at lower elevations; at higher elevations, the trend was reversed. Thus, long-standing generalized latitudinal patterns of variation in avian clutch size may need to be reinterpreted in the light of the potential additional effects of elevational variation on life-history traits; elevation confounds some of our basic temperate–tropical comparisons, at least in galliforms.

The significant interaction between elevation and latitude in explaining variation in clutch size and other traits must be associated with one of the variables that differs between the two. Among the physical variables, the candidates are seasonality (within-year day-length and temperature variation), atmospheric pressure/oxygen concentration and solar irradiation. The first of these has both empirical and theoretical support and is related to food limitation. The ‘day length hypothesis’ proposes that longer days at high latitudes during the breeding season allow greater foraging hours, resulting in a greater total amount of food delivered to nestlings, resulting in more

offspring (Lack 1947; Rose & Lyon 2013). This differs from the ‘food resource hypothesis’ (also known as Ashmole’s hypothesis; Ashmole 1963), which posits that increased seasonality in temperate latitudes results in greater mortality during winter resulting in higher per capita food resources in the subsequent spring facilitating larger clutches. Examining mid- and high-latitude Tree Swallow (*Tachycineta bicolor*) populations, Rose & Lyon (2013) provide clear evidence for the day length hypothesis, but little support for the alternative. Although tested in an altricial species, the same principle applies to precocial species as well. McNamara *et al.* (2008) used dynamic programming to arrive at the evolutionary stable strategy that maximized fitness given variation in seasonality of food supply and time available for foraging (daylight). Birds in less seasonal environments were ultimately constrained by low food during breeding seasons, whereas birds in more seasonal environments died during the period of resource scarcity. Increasing food seasonality selected for larger clutch sizes, shorter parental care times, younger age at first breeding and lower juvenile survival. The upshot is that while both food resource-based hypotheses explain a positive clutch size–latitude association, the driver is a physical attribute (seasonality in day length) that does not vary with elevation. Thus, we should not necessarily expect to see a parallel clutch size–elevation association. Currently, it is not known whether interactive effects of latitude and elevation produce similar patterns of trait variation in altricial bird species because (i) latitudinal and elevational patterns to this point have largely been studied in separate contexts, and (ii) the comparative scarcity of avian life-history data from the tropics seriously limits our ability to detect such patterns (Boyle, Sandercock & Martin 2016). The increased representation of tropical species in our data set may have influenced our ability to detect this pattern.

CONCLUSION

We demonstrated for the first time that elevation and latitude interact to influence life-history variation in avian reproductive traits. At higher latitudes, reduced fecundity at higher elevations was due to smaller clutches as number of broods did not vary with elevation or latitude. However, fecundity increased with elevation in the tropics as tropical species’ clutch sizes increase with elevation, suggesting a potential trade-off with adult survival. Across all latitudes, higher elevation galliform species had larger egg mass as a means to invest in offspring quality. A latitudinal gradient in clutch size, commonly reported for altricial species, was observed only in low-elevation species; it remains to be determined whether altricial species’ traits demonstrate similar latitude-by-elevation interactions manifest in precocial galliforms. Variation in nest predation risk could explain differences between temperate and tropical elevational gradients, but we lack a consistent mechanism to explain why predation risk should

vary in this manner. Alternatively, a resource availability hypothesis based on physical attributes that globally differ between elevation and latitude seems more plausible. Ultimately, elevational gradients offer a valuable laboratory to understand the drivers of geographic variation in avian life histories.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.38s8g> (Balasubramaniam & Rotenberry 2016).

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