

# Patterns and drivers of intraspecific variation in avian life history along elevational gradients: a meta-analysis

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## ABSTRACT

Elevational gradients provide powerful natural systems for testing hypotheses regarding the role of environmental variation in the evolution of life-history strategies. Case studies have revealed shifts towards slower life histories in organisms living at high elevations yet no synthetic analyses exist of elevational variation in life-history traits for major vertebrate clades. We examined (i) how life-history traits change with elevation in paired populations of bird species worldwide, and (ii) which biotic and abiotic factors drive elevational shifts in life history. Using three analytical methods, we found that fecundity declined at higher elevations due to smaller clutches and fewer reproductive attempts per year. By contrast, elevational differences in traits associated with parental investment or survival varied among studies. High-elevation populations had shorter and later breeding seasons, but longer developmental periods implying that temporal constraints contribute to reduced fecundity. Analyses of clutch size data, the trait for which we had the largest number of population comparisons, indicated no evidence that phylogenetic history constrained species-level plasticity in trait variation associated with elevational gradients. The magnitude of elevational shifts in life-history traits were largely unrelated to geographic (altitude, latitude), intrinsic (body mass, migratory status), or habitat covariates. Meta-population structure, methodological issues associated with estimating survival, or processes shaping range boundaries could potentially explain the nature of elevational shifts in life-history traits evident in this data set. We identify a new risk factor for montane populations in changing climates: low fecundity will result in lower reproductive potential to recover from perturbations, especially as fewer than half of the species experienced higher survival at higher elevations.

*Key words:* alpine, climate change, demography, fecundity, Hedge's *d*, interspecific competition, Lack's hypothesis, montane, productivity, species range limits.

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## I. INTRODUCTION

Vertebrates exhibit a diversity of life-history strategies that can be arrayed along a fast–slow continuum. At one extreme, fast life histories are characterized by high reproductive rates, low parental investment per offspring, early maturation, and short life spans. At the other end, species with slow life histories have low reproductive rates, delayed maturity, repeated opportunities for reproduction over their long lives, and high *per capita* investment in offspring (Saether, 1987; Promislow & Harvey, 1990). Deviations from the fast–slow continuum can result from constraints or be imposed by behavioural traits and ecological associations (Sibly *et al.*, 2012), including bet-hedging strategies exhibited by animals living in stochastic environments (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003). Life-history theory is based on the premise of trade-offs where increases in reproductive effort impose energetic costs or behavioural changes that manifest as increases in intrinsic mortality risk. Thus, the fitness costs and benefits of variation in any one life-history trait may only become apparent *via* studies of suites of life-history traits. Identifying the key biotic and abiotic factors that drive variation in traits along environmental gradients is crucial to our understanding of life-history evolution (Martin, 2004). From an applied perspective, understanding how environmental variables shape life histories informs predictions of species-level responses to environmental change (Sekercioglu *et al.*, 2008; Buckley, 2010).

Avian comparative studies have played a central role in elucidating patterns of variation in life-history traits. For example, increases in body mass are related to both longer lifespans and shifts towards slower life-history strategies (Western & Ssemakula, 1982; Saether, 1987). Birds have also served as models for understanding environmental correlates of life-history strategies (Martin, 2004), revealing biogeographic patterns such as shifts toward faster life histories in north temperate breeding birds relative to their tropical and south temperate counterparts (Ricklefs, 1997; Sandercock *et al.*, 2000; Martin *et al.*, 2006; Jetz, Sekercioglu & Bohning-Gaese, 2008). The gradients in abiotic and biotic processes proposed to explain latitudinal life-history patterns are ultimately driven by climatic gradients. Mean annual

temperature is a key factor that declines with both increasing elevation and latitude (Barry, 2008). By contrast, day length varies with latitude but not with elevation, whereas partial pressure of atmospheric gases varies with altitude but not with latitude. Thus, determining whether or not animals exhibit similar changes in life history along elevational gradients as they do along latitudinal gradients, and determining the geographical and ecological correlates of life-history variation, can elucidate which selective pressures are most important in shaping the evolution of life-history strategies.

Empirical studies have documented consistent differences in life-history traits among bird populations living at different elevations (Stewart, Henderson & Darling, 1977; Lu, 2005; Bears, Martin & White, 2009; Martin, Camfield & Martin, 2009). The emerging pattern suggests a shift to slower life-history strategies at higher elevations, opposite to the predicted pattern for increases in latitude (Sandercock, Martin & Hannon, 2005; Novoa *et al.*, 2008; Wilson & Martin, 2011). Shifts in life history influence both behavioural ecology and morphology; comparative studies of Eurasian songbirds concluded that species living at higher elevations have higher levels of parental care and are less ornamented than their lowland counterparts (Badyaev, 1997*a,b*; Badyaev & Ghalambor, 2001). Life-history shifts with elevation have also been observed in some amphibians (Zhang & Lu, 2012), reptiles (Bronikowski & Arnold, 1999), and mammals (Bronson, 1979; McGuire & Boyle, 2013). Slower life histories at high elevations have been attributed to four major environmental factors; (i) colder temperatures, (ii) shorter breeding seasons, (iii) lower food availability, and (iv) higher predation risk (Badyaev, 1997*a*; Sandercock *et al.*, 2005; Turbill, Bieber & Ruf, 2011).

Our knowledge of avian life history along elevational gradients is incomplete with respect to taxonomy and geography. Our current understanding is based on (i) detailed intraspecific comparisons of demography for a few north temperate species of grouse and songbirds (Bears, Drever & Martin, 2008; Camfield, Pearson & Martin, 2010; Wilson & Martin, 2011; Evans Ogden, Martin & Martin, 2012), (ii) comparative studies restricted to eastern European taxa, primarily finches (Badyaev, 1997*a*; Badyaev & Ghalambor, 2001), and (iii) a review of clutch size and elevation (Krementz &

Handford, 1984). The above studies have made valuable contributions, but single-species studies lack generality whereas single-trait studies may overlook important drivers of variation in life-history strategies. In a comparative analysis, Badyaev (1997a) reported only the subset of taxon comparisons for which trait values increased or decreased, excluding comparisons for traits that did not differ between pairs of taxa, a method that might lead to inflated estimates of trait divergence. Moreover, Krementz & Handford (1984) used simple vote-counting methods such as tallies of studies reporting positive or negative relationships to investigate clutch size variation rather than formal meta-analyses. A recent review of avian life history provides a thorough discussion of potential drivers of trait differences along elevational gradients, but did not test hypothesized relationships using any of the available analytical methods (Hille & Cooper, 2015). None of the previous studies have formally analysed the geographic or ecological correlates of trait divergence that could provide insights into the underlying drivers of life-history differences. We first review the factors potentially shaping variation in strategies of montane and alpine birds worldwide, and then test hypotheses based on environmental factors and their effects on key demographic parameters.

### (1) Abiotic and biotic factors that vary along elevational gradients

Few abiotic factors covary globally with altitude, defined as absolute height in meters above sea level (masl; Körner, 2007). Factors relevant to avian life histories include decreases in temperature (on average  $-5.5^{\circ}\text{C}$  per km above sea level), increases in solar radiation, and reductions in the partial pressures of atmospheric gases including an  $\sim 11\%$  reduction in oxygen partial pressure per km above sea level. Colder temperatures could exert direct selective pressures on birds *via* thermoregulatory costs or direct mortality under extreme conditions. Increased solar radiation leads to greater diurnal variation in temperature which increases thermoregulatory costs and weather-related mortality risk in endotherms. Decreases in the partial pressure of oxygen with increasing altitude can increase the metabolic costs of reproduction and survival, especially affecting embryonic development and other physiological processes at altitudes above  $\sim 3800$  m (Carey *et al.*, 1982).

High elevations are commonly described as differing from lower elevations in other abiotic factors such as decreased precipitation, increased wind velocity, greater climatic seasonality, and shorter seasons suitable for reproduction (Martin, 2001). These factors do not vary consistently with altitude globally, however. Precipitation can increase or decrease with altitude, and is frequently greatest at mid-elevations (Sanders, Moss & Wagner, 2003; Kluge, Kessler & Dunn, 2006). Exposed alpine ridges at temperate latitudes can be subject to

high winds, but the topographic complexity of mountains creates friction that slows air flow, generating unpredictable patterns of elevational variation in wind speed (Barry, 2008).

The paradigm that montane birds experience greater temporal constraints on reproduction than birds living at low elevations depends on assumptions of climatic seasonality and thresholds of climatically suitable conditions. Elevational gradients in duration of growing seasons are well established at temperate latitudes, but seasonal variation in temperature is small in the tropics. Birds can modulate climatic tolerances *via* metabolic, morphological, and behavioural mechanisms (Andreev, 1991; Cooper, 2002; Symonds & Tattersall, 2010), but the seasonal duration of temperatures suitable for breeding generally increases towards low latitudes. At low, tropical latitudes, cold temperatures are unlikely to constrain the timing of breeding directly, but seasonality in precipitation replaces temperature in imposing temporal constraints (Lloyd *et al.*, 2001; Boyle, Norris & Guglielmo, 2010). Elevational variation in precipitation shows no clear latitudinal pattern, because patterns of seasonality and total precipitation along elevational gradients differ among and within regions (Barry, 2008). We lack a mechanistic understanding of how precipitation affects animal physiology and behaviour and cannot make general predictions regarding elevational patterns of seasonal constraints due to precipitation comparable to those made elsewhere for temperature (Janzen, 1967; Ghalambor *et al.*, 2006; Tingley *et al.*, 2012). Elevational climatic gradients influence biotic factors that indirectly affect life histories. Colder temperatures depress primary productivity and reduce food availability at higher trophic levels. However, elevational variation in precipitation can equalize or invert relationships between elevation and plant productivity. Climatic conditions set limits on vegetation structure, determining the location of the tree line and concealment for vertebrates. Treeless alpine areas are often hypothesized to be riskier environments because prey have fewer ways to hide or escape from predators. However, because high altitudes tend to have low species diversity, montane populations may resemble arctic populations with fewer species of predators, and perhaps lower predation risk (Skutch, 1985; Boyle, 2008; McKinnon *et al.*, 2010). Of the four major ecological factors proposed to explain elevational shifts in life-history strategy, only temperature gradients apply globally. Temporal constraints may apply only in temperate regions, lower food availability would occur only where precipitation gradients do not equalize or invert productivity gradients, and higher predation risk may only apply where high-elevation populations inhabit open environments with little concealment.

The direct and indirect consequences of climatic variation along elevational gradients could affect selection on components of fecundity or mortality through a

variety of mechanisms. (i) Colder temperatures may result in elevated mortality risk, especially to dependent young during the breeding season or during winter months when climates are harshest with the greatest predicted effects among small-bodied species (Calder, 1974). (ii) Colder temperatures (and lower partial pressures of oxygen) at higher elevations may increase the physiological costs of basal metabolism, growth, and reproduction, potentially limiting reproductive effort. (iii) Colder temperatures at high elevations may result in longer development times at embryonic and nestling stages, which could increase the exposure to predation risk (Conway & Martin, 2000b). (iv) Lower primary productivity may result in lower *per capita* food availability at high elevations. Even if population densities are low at higher elevations, lower primary productivity should result in increased foraging costs which could result in fewer or smaller offspring and increased development times. (v) Shorter periods of suitable environmental conditions could impose temporal constraints on reproduction for birds breeding at high elevations, especially at temperate latitudes. (vi) Harsh climatic conditions that shape vegetation of open alpine habitats could result in increased predation risk particularly for eggs and nestlings, the avian life stages most vulnerable to predation. These six non-exclusive hypotheses provide testable predictions regarding patterns of trait and phenological variation, and the geographical and ecological correlates of intraspecific shifts in life history between matched pairs of populations that breed over elevational gradients.

The goals of this study were twofold. First, we evaluated the evidence for shifts in life histories of avian populations living at high elevations over wide taxonomic and geographic scales, analysing multiple life-history traits reported in the literature. Our response variables are equivalent to species-pair comparisons employed in many comparative studies (e.g. Møller & Birkhead, 1994; Zhang & Lu, 2012) because they consist of contrasts between matched pairs of populations differing in elevation. Thus, our experimental design explicitly incorporated paired-taxon (i.e. population-level) comparisons to control for phylogenetic effects (Ackerly, 2000; Maddison, 2000). By contrasting population-level trait values, we focused on the tips of the phylogeny because our research objectives were to assess recent divergence in response to environmental conditions associated with high-elevation habitats. We analysed trait responses separately because our sources varied in the trait differences reported. Second, we tested predictions of the above hypotheses by examining the elevational patterns of reproductive phenology and the ecological covariates of elevational trait differences. We employed three analytical approaches that balanced sample size and statistical power *versus* analytical rigour as published estimates of life-history trait data varied in quality.

## II. MATERIALS AND METHODS

### (1) Life-history data

We conducted a literature search for empirical field studies reporting life-history parameters for two or more breeding populations of the same bird species at different elevations. We used the *Web of Knowledge* database, entering all pair-wise combinations of the following search terms: (i) either *altitud\** or *elevation\**, plus one of (ii) life history, age, body mass, body size, breeding, clutch, demograph\*, egg, fecundity, juvenile, mortality, nest success, offspring, reproduction, and survival. These searches resulted in over 600 records. We read abstracts of all records, narrowing the list of articles potentially containing relevant data to over 200. We obtained full-text versions of these articles and reviewed the content for numerical data from two populations separated by elevation for the life-history traits listed above. We included all studies that presented population comparisons for one or more of the life-history traits that we considered. We expanded our search to include older articles and recent publications linked by citations from articles discovered during initial searches. To control for variation due to latitude, we restricted our sample to pairs of breeding populations located within 5° of latitude. When data from sites at multiple elevations were presented in a single publication, we used data from the highest and lowest sites, or if sample sizes from individual sites were small, we pooled multiple low- and high-elevation sites. A majority of comparisons were derived from two sites using the same methods reported in a single article, but in six cases we paired studies reporting life-history data from single populations with another from a different elevation. Few of the studies from which we obtained data were designed to answer questions about elevational differences in life-history traits. Thus, risk of publication bias and under-reporting of non-significant results should be lower than in meta-analyses of observational or experimental studies testing similar hypotheses.

We tabulated data from all comparisons that reported one or more of the following variables: (i) clutch size or size of first clutches in multi-brooded species; (ii) mean number of reproductive attempts each year following successful fledging of first broods; (iii) breeding propensity or the proportion of adult females breeding each year; (iv) age of maturity for females at first breeding; (v) body size of adults; (vi) egg size; (vii) nestling size; (viii) nest survival; (ix) juvenile survival; (x) adult survival; and (xi) stable age distribution. Estimates of breeding propensity, age of maturity, stable age distribution, and juvenile survival were each reported in five or fewer studies, precluding analyses of these variables. Measurements and metrics reported for a given trait frequently differed among studies and were sometimes based on methods known to be biased such as length *versus* mass for size metrics, or apparent nest survival

versus daily nest survival rates that controlled for losses before discovery. Nevertheless, our comparisons should be robust because the same methods were used within each pair of populations, and all estimates of differences depended upon the magnitude of differences between populations where methods were identical. Our complete data set is archived at the Dryad Digital Repository (<http://doi.org/10.5061/dryad.h13vg>).

**(2) Vote-counting, contrasts, and meta-analytical methods**

We used three analytical approaches to examine elevational patterns in life history by analysing all trait variables represented by six or more studies. We used ‘vote-counting’ methods to tabulate the number of studies reporting a significant positive or negative difference or no difference between population trait values when numerical details were not reported by the original authors. We tested the proportion of studies reporting a positive, negative, or no difference against a null expectation of an equal probability of these three outcomes among studies. Some studies reporting population means did not report the results of tests comparing those means, and were not included in vote-counting analyses. We included 30 records in vote-counting analyses derived from analyses in which elevation was treated as a continuous variable. Vote-counting was the least informative of the methods that we employed and is weakest as a stand-alone method because all studies are weighted equally, regardless of study precision and magnitude of effect sizes (Koricheva & Gurevich, 2013). Nevertheless, vote-counting allowed analyses of the largest possible subset of the data and permitted comparison with earlier reviews of elevational variation in life-history traits (Klomp, 1970; Thomson, Monaghan & Furness, 1998). Thus, we report results of vote-counting methods in addition to improved methods of data synthesis.

A majority of published studies reported mean trait values permitting us to calculate contrasts of the magnitude of trait differences between matched pairs of populations. We did not compare absolute differences in means, instead contrasting population means ( $\bar{x}$ ) based on the per cent relative difference (%RD) between high (H) and low-elevation (L) populations:

$$\%RD = \frac{(\bar{x}_H - \bar{x}_L)}{(\bar{x}_H + \bar{x}_L) / 2} \times 100 \quad (1)$$

The %RD is similar to the *ln*-response ratio (Hedges, Gurevitch & Curtis, 1999), but expresses differences between populations in units that are easier to interpret. We tested the distribution of contrasts for each trait against a null hypothesis of a mean of 0 using one-sample tests. We used *t*-tests when Goodness-of-Fit tests confirmed that the distribution of responses approximated a normal distribution, and non-parametric

Wilcoxon signed-rank tests if responses deviated significantly from a normal distribution. We identified outliers (values  $\pm 3$  S.D. of the mean), and re-ran analyses excluding outliers, reporting the results from a censored sample if outliers affected significance tests.

Contrasts were based on differences in means only and did not account for variance in parameter estimates among studies. If authors provided means, variance, and sample sizes, we calculated effect sizes and conducted formal meta-analyses, based on weighted population means. For population-level binomial responses such as nest success that are frequently reported as a single proportion, we calculated variance from the binomial distribution. Meta-analyses were based on the most restricted subset of our data because many published studies failed to report all three descriptive statistics. We used the *metafor* package in R to calculate effect sizes based on Hedges’ *d* as follows (Viechtbauer, 2010; R Core Team, 2014):

$$d = \frac{(\bar{x}_H - \bar{x}_L)}{S} \left( 1 - \frac{3}{4(N_H + N_L - 2) - 1} \right), \quad (2)$$

where

$$S = \sqrt{\frac{(N_H - 1)(s_H)^2 + (N_L - 1)(s_L)^2}{N_H + N_L - 2}} \quad (3)$$

and  $\bar{x}_i$ ,  $s_i$ , and  $N_i$  are the mean, standard deviation, and sample size for the high ( $H$ ) and low elevation ( $L$ ) populations. We chose *d* as our measure of effect size because the majority of our data consisted of comparisons of pairs of mean trait values from high- and low-elevation populations, not regression coefficients based on estimates from multiple elevations across a gradient (Harrison, 2011). For each trait comparison, we calculated the overall mean effect size  $\pm 95\%$  bias-corrected confidence interval (CI) using the *rma.uni* function in the *metafor* package. We assessed the evidence for consistent shifts toward lower fecundity and higher survival at higher elevations based on the magnitude of the cumulative effect size and whether the 95% CI overlapped 0. Effect sizes of  $d < 0.2$ ,  $d = 0.2-0.8$ , and  $d > 0.8$ , are considered ‘small’, ‘medium’, and ‘large’, respectively (Cohen, 1969).

We used our data set for clutch size to explore potential publication biases and phylogenetic constraints in species-level plasticity to environmental drivers because we had the largest sample size available for this trait, and thus the greatest statistical power to detect biases that may affect interpretation of other traits (Chamberlain *et al.*, 2012). We inspected funnel plots, normal quantile plots, and tested for publication bias using rank correlation tests. We report the metric of heterogeneity *Q* and results of associated  $\chi^2$  tests to assess the degree of heterogeneity among effect sizes attributable

to random variation among studies *versus* biologically attributable variation related to covariates. We used the low-elevation population as the reference population for all three analytical methods. Thus, negative values represent reductions in trait values at higher elevations whereas positive values represent increases in trait values at higher elevations.

We assessed whether overall trends in elevational shifts in life-history traits were influenced by phylogenetic history. Detecting a phylogenetic signal would imply that responses of a closely related subset of species were responsible for the overall patterns in our data, and that plasticity in life-history traits is phylogenetically conserved. We downloaded 500 phylogenetic trees from [www.birdtree.org](http://www.birdtree.org) for the species included in our clutch size comparisons (Jetz *et al.*, 2012). We chose a selection of trees from the global set based on the Hackett *et al.* (2008) higher-level framework. We tested whether the data exhibited a significant phylogenetic signal by calculating Pagel's  $\lambda$  (Pagel, 1999) on all 500 trees using the `phylosig` function in the `phytools` package in R (Revell, 2012).

We explored another potential source of bias in our analyses; we compiled data from one or more pairs of populations for some trait/species combinations. Because multiple estimates of population-level responses were derived from different latitudes, spanning different elevational gradients, and in some cases, associated with different sub-species, we were reluctant to discard data that may prove biologically informative. To verify that our results were not affected by duplicate comparisons, we re-analysed our data based on a restricted data set that included a single comparison per species. We retained the comparison represented by the most complete data (i.e. means and S.D.) and the largest sample size for each species. In cases where duplicate comparisons were comparable in data quality, we selected the population comparison spanning the largest elevational gradient. Results from a single comparison per species were qualitatively identical to the full data set, and we report results from the full data set.

### (3) Reproductive phenology and explanatory variables

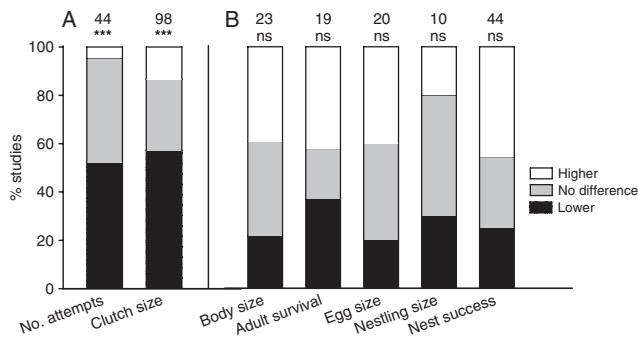
We explored potential drivers of life-history shifts over elevational gradients by examining differences in four components of reproductive phenology and by analysing the covariates of life-history differences. We converted phenological data reported in source publications to units of ordinal day: date of onset of breeding season, duration of incubation periods, duration of nestling periods, and duration of the breeding season. We tested for shifts in reproductive phenology with elevation using similar methods as the contrast and meta-analyses of life-history traits. In our analyses of onset of breeding, we used the absolute difference in number of days between high- and low-elevation

populations because %RD has no biological meaning for calendar dates.

Using contrasts as our response variable, we examined how the magnitude of life-history trait differences varied as a function of the (i) absolute altitude of the higher elevation population, and (ii) mean latitude of the paired populations. We also analysed associations between the magnitude of elevational trait differences and (iii) mean adult body mass compiled from Dunning (1993, 2008), using natural logarithms to transform body masses prior to analysis to improve normality of residuals. We did not evaluate the relationship between mean species-level body mass and contrasts in body size between elevations. We then examined associations between trait differences and (iv) the migratory status of the high-elevation population, classifying populations as either resident, or latitudinal or altitudinal migrants. When migratory status was not clear from source publications, we located this information in individual species accounts (del Hoyo, Elliot & Christie, 1992–2013; Poole, 2005). Last, we included a simple binary classification of (v) vegetation structure; whether or not the high-elevation site was located above the tree line or in another non-forested vegetation type potentially leading to differences in predation pressure. If the authors did not include habitat information in site descriptions, we located study sites using *Google Earth* (Google Inc., 2011) and examined aerial and terrestrial images to determine if the high-elevation site was in an area without tree cover. We analysed relationships between contrasts and explanatory variables using multiple linear regression (for continuous explanatory variables) and analysis of covariance (ANCOVA) (for categorical explanatory variables) in models that accounted for the difference in elevation between population pairs using JMP statistical software (SAS Institute Inc., 2009). We repeated the above analyses examining how the magnitude of life-history trait differences varied as a function of absolute altitude of the higher elevation population, and mean latitude of the two populations in a formal meta-analysis context using the `rma.uni` function in the `metafor` package of R. Unless otherwise noted, means are presented  $\pm 1$  S.E.M.

## III. RESULTS

Our sample included 104 studies that reported comparisons of one or more life-history traits between high- and low-elevation populations in 101 species of birds, resulting in a total data set of 441 trait comparisons. Of these records, we were able to include 423 comparisons in vote-counting analyses, 391 comparisons in contrast analyses, and 131 effect sizes in our meta-analysis. Clutch size was the most frequently reported life-history trait and accounted for 102 comparisons. We compiled data for birds living in mountains



**Fig. 1.** Results of vote-counting analyses for traits related to fecundity (A), and traits related to parental investment and survival (B). Each bar indicates the percentage of comparisons reporting significantly lower (black) or higher (white) trait values at higher elevations relative to lower elevations, or no significant difference (grey) between populations. We indicate sample sizes ( $N$  comparisons) and results of likelihood ratio  $\chi^2$  tests above each bar (\*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; ns,  $P > 0.05$ ).

around the world including South America, Africa, and New Zealand. Most records came from sites in Europe, the Himalayas, and North America. Few data were available from tropical latitudes; only seven studies were conducted at sites within the tropics. The difference in elevation between pairs of populations ranged from 175 to 4708 m (median 1000 m) with the highest elevation populations reaching 4728 masl. Eighty-six of the bird species belonged to Order Passeriformes, with the remaining species in the orders Struthioniformes (one species), Anseriformes (two species), Galliformes (three species), Pelecaniformes (one species), Accipitriformes (one species), Falconiformes (two species), Gruiformes (three species), Charadriiformes (one species), and Strigiformes (one species).

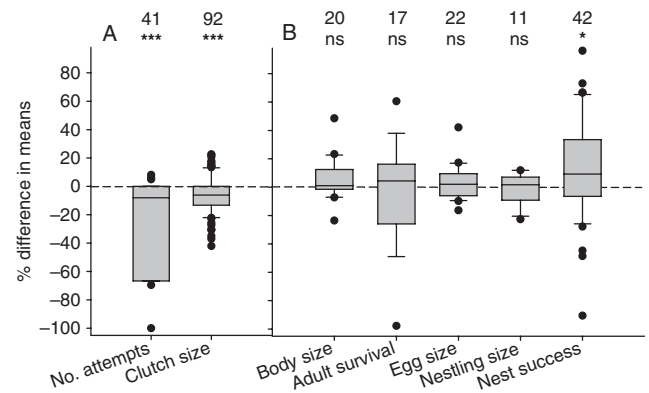
### (1) Patterns of life-history variation over elevational gradients

#### (a) Vote-counting

The mean number of nesting attempts was lower at high elevations in 52% of 44 comparisons (likelihood ratio  $\chi^2 = 22.6$ , d.f. = 2,  $P < 0.001$ ; greater in 5% and no difference in 43% of comparisons). Clutch sizes were significantly smaller at high elevations in 57% of 98 comparisons with 13% reporting larger clutches and 30% reporting no difference in clutch size at high elevations (likelihood ratio  $\chi^2 = 29.5$ , d.f. = 2,  $P < 0.001$ ). None of the traits related to survival or reproductive effort differed consistently between populations at low and high elevations (Fig. 1).

#### (b) Contrasts

Analyses of the per cent relative difference in mean trait values yielded similar results to vote-counting analyses,

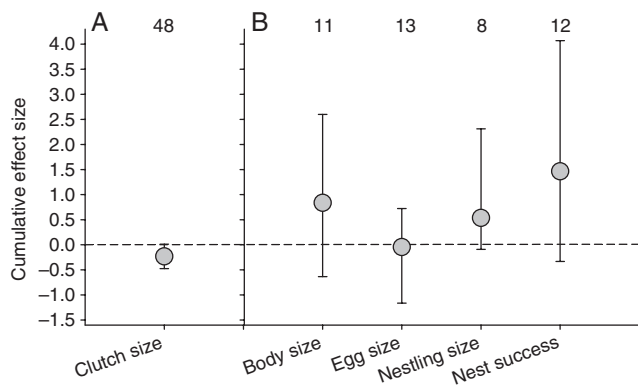


**Fig. 2.** Results of contrast analyses for traits related to fecundity (A) and traits related to parental investment and survival (B). Boxes indicate the responses spanning the 25th to 75th percentile with the median response indicated by the line within each bar. Error bars represent the 10th and 90th percentiles and outliers are denoted by filled circles. Negative values below the dashed reference line indicate that trait values of the higher elevation population were lower than those of the lower elevation population. Above each bar, we indicate sample sizes ( $N$  comparisons) and results of  $t$ -tests or Wilcoxon signed rank tests (\*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; ns,  $P > 0.05$ ).

with the exception that the probability of nest survival was significantly greater at higher elevations (Fig. 2). The mean number of nesting attempts decreased by 0.4 attempts per season or 25.8% ( $\pm 4.9\%$ ) at high elevations ( $t = -155.5$ ,  $P < 0.001$ ). Similarly, mean clutch size was on average 6.6% ( $\pm 1.4\%$ ) smaller at high elevations ( $t = -4.9$ ,  $P < 0.001$ ). Comparison of raw differences in clutch size indicated that on average, higher-elevation populations lay 0.38 ( $\pm 0.08$ ) fewer eggs per nest than lower-elevation conspecifics. Nest success averaged 8.4% ( $\pm 6.7\%$ ) higher in high-elevation than low-elevation populations ( $W = 164.0$ ,  $P = 0.019$ ). High- and low-elevation populations did not differ consistently in adult body size, adult survival, egg size, or nestling size. Last, we tested for phylogenetic signal in contrasts of clutch size, but found no evidence that population-level plasticity in clutch size was constrained by evolutionary history at deeper nodes in the avian phylogeny ( $P = 1$  for Pagel's  $\lambda$  test for all 500 trees).

#### (c) Meta-analyses

Analyses of effect sizes based on Hedge's  $d$  were possible for five life-history traits: clutch size, adult body size, egg and nestling size, and nest success (Fig. 3). Inspection of the funnel plot for clutch size provided no indication that effect sizes were dependent upon variance. The distribution of points in the normal quantile plot fell close to the  $x = y$  line and the values for only one study fell outside of the 95% CI interval. We found no evidence of a correlation between effect size and publication (Spearman rank correlation coefficient

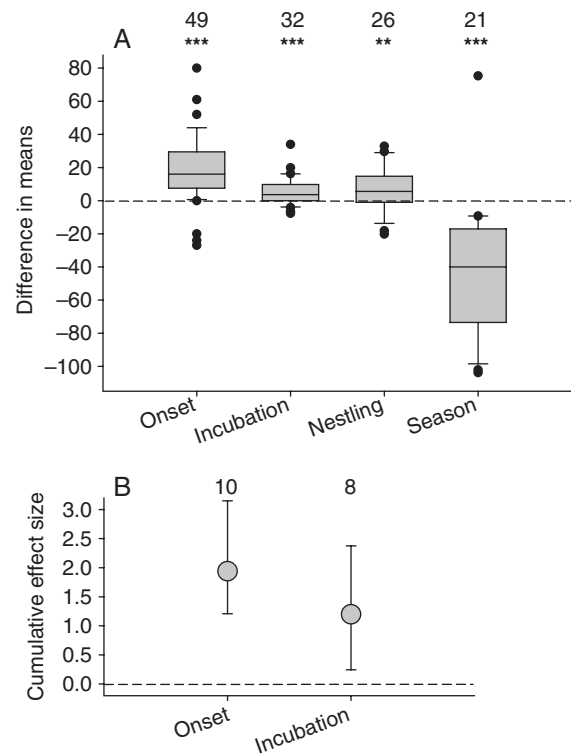


**Fig. 3.** Cumulative mean effect sizes of Hedge's  $d \pm 95\%$  bias-corrected confidence interval (CI) for traits related to fecundity (A), and traits related to parental investment and survival (B). Means with CIs that do not overlap 0 were considered statistically significant. Values at the top of the figure indicate  $N$  comparisons upon which the analyses were based.

$R_s = 0.06$ ,  $P = 0.708$ ). Rosenthal's fail-safe number was 274.5 indicating that five times as many non-significant unpublished studies would have to exist to result in a non-significant effect size for this trait. The cumulative effect size of clutch size comparisons was  $-0.23$  (95% CI  $-0.48$  to  $+0.01$ ;  $Q_{47} = 44.8$ ,  $P = 0.564$ ), indicating a trend towards a moderate but consistent reduction in clutch size at higher elevations (although the 95% CI just overlaps 0). We found trends toward positive effect sizes in adult body size, nestling size, and nest success, but the 95% CIs associated with these cumulative effect sizes were large and overlapped 0 (Fig. 3). Associated metrics of heterogeneity indicated considerable unexplained variation in elevational differences in these traits (body size  $Q_{10} = 17.9$ ,  $P = 0.056$ ; egg size,  $Q_{12} = 21.4$ ,  $P = 0.045$ ; nestling size,  $Q_7 = 49.3$ ,  $P < 0.001$ ; nest success,  $Q_{14} = 69.2$ ,  $P < 0.001$ ).

## (2) Tests of hypotheses explaining elevational patterns: reproductive phenology

All metrics of reproductive phenology differed between high- and low-elevation populations in both contrasts and meta-analyses (Fig. 4). Results of contrast analyses indicated that high-elevation populations initiated breeding  $18.3 \pm 2.8$  days later than low-elevation counterparts. Incubation lasted 5.6% ( $\pm 1.5\%$ ) longer and nestling periods were 5.7% ( $\pm 2.6\%$ ) longer in higher-elevation populations. However, high-elevation populations had breeding seasons that were 41.6% ( $\pm 8.8\%$ ) shorter than lower-elevation populations. Meta-analyses were consistent with contrast analyses in revealing widespread shifts toward increases in incubation duration (effect size 1.20, 95% CI 0.24–2.37) with no evidence for considerable unexplained heterogeneity in responses ( $Q_7 = 9.0$ ,  $P = 0.253$ ). Likewise, high-elevation populations exhibited later onsets of the



**Fig. 4.** Shifts in avian reproductive phenology with elevation. (A) Differences in onset of breeding, duration of incubation, nestling period, and breeding season at higher relative to lower elevations (raw difference in days for onset of breeding, and contrasts for other variables). Boxes indicate responses spanning the 25th to 75th percentile with the median response indicated by the line in the middle of each bar. Negative values below the dashed reference line indicate that trait values of the higher elevation population were lower than those of the lower elevation population. Error bars indicate the 10th and 90th percentiles and outliers are denoted by filled circles. Above each bar, we indicate  $N$  comparisons and results of statistical tests (\*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ). (B) Results of meta-analyses. Dots represent cumulative mean effect sizes and error bars are bias-corrected 95% CIs. Means with 95% CIs that do not overlap 0 are statistically significant.

breeding season (effect size 1.94, 95% CI 1.21–3.15), although we found considerable unexplained heterogeneity among studies in effect sizes for timing of onset ( $Q_9 = 34.4$ ,  $P < 0.001$ ).

## (3) Tests of hypotheses explaining elevational patterns: geographical and ecological covariates

We found no evidence for a relationship between the magnitude of the contrasts for life-history traits and either the absolute altitude of the high-elevation population or latitude of the study (Table 1). Meta-analyses of effect sizes indicated that after accounting for elevational differences between sites, the magnitude of population differences in clutch size, adult body size, egg



Table 1. Results of analytical models examining the relationship between contrasts in life-history traits (rows; see text) predicted by key explanatory variables of the environment and bird ecology (columns). The response variables are contrasts between trait values of higher- relative to lower-elevation populations. For each model, *b* is the coefficient for the magnitude and direction of the main effects per 100 m in models accounting for variation in the elevational difference between sites, *N* is the number of comparisons (by group for categorical variables), and *P* is a test of parameter estimates (*b* = 0). Individually significant coefficients are highlighted in bold. The number of studies differs by analysis due to missing explanatory variable data. We did not run models if the error d.f. was <6, which we denote by ellipses: (‘...’)

Trait	Altitude high site			Latitude			<i>ln</i> -mean body mass			Migrants versus residents			High site alpine versus with trees		
	<i>b</i>	<i>N</i>	<i>P</i>	<i>b</i>	<i>N</i>	<i>P</i>	<i>b</i>	<i>N</i>	<i>P</i>	<i>b</i>	<i>N</i> <sub>MIG, RES</sub>	<i>P</i>	<i>b</i>	<i>N</i> <sub>ALP, NOT</sub>	<i>P</i>
<i>Fecundity-related response variables</i>															
Clutch size	-0.2	92	0.17	0.2	71	0.15	0.2	91	0.85	<b>3.8</b>	<b>48, 41</b>	<b>0.01</b>	-0.1	31, 61	0.96
<i>N</i> attempts	-0.1	41	0.93	-0.8	24	0.21	3.5	41	0.51	-6.5	22, 17	0.21	-13.3	13, 28	0.19
<i>Reproductive effort and survival-related response variables</i>															
Body size	-0.2	20	0.73	-0.3	16	0.28	...	...	...	2.0	12, 7	0.47	0.6	8, 11	0.91
Egg size	-0.1	22	0.51	-0.1	22	0.81	-2.3	21	0.10	-0.9	8, 13	0.59	-1.1	15, 7	0.85
Nestling size	0.2	9	0.53	0.2	8	0.49	0.0	9	0.99	0.8	4, 5	0.81	...	...	...
Nest success	0.2	42	0.77	0.2	43	0.70	-8.0	42	0.13	8.0	23, 19	0.13	30.7	15, 28	0.06
Adult survival	-0.3	17	0.82	...	...	...	5.3	17	0.55	-2.8	13, 4	0.80	9.3	6, 11	0.62

Table 2. Results of meta-analytical models based on estimates of effect size calculated with the *metafor* package (Viechtbauer, 2010) implemented in R (R Core Team, 2014). We tested five explanatory factors (columns) of life-history traits (rows) under alternative hypotheses explaining life-history differences between elevations. For each analysis, *b* is the coefficient of the magnitude and direction of the main predictor variables in models accounting for variation in the elevational difference between sites, *N* is the number of comparisons (by group for categorical variables), and *P* is a test of parameter estimates. Individually significant coefficients are highlighted in bold. We did not run models for which the error d.f. was <6, which we denote by ellipses: (‘...’)

Trait	Altitude of high site			Latitude			<i>ln</i> -mean body size			Migrants versus residents			High site alpine versus with trees		
	<i>b</i>	<i>N</i>	<i>P</i>	<i>b</i>	<i>N</i>	<i>P</i>	<i>b</i>	<i>N</i>	<i>P</i>	<i>b</i>	<i>N</i> <sub>MIG, RES</sub>	<i>P</i>	<i>b</i>	<i>N</i> <sub>ALP, NOT</sub>	<i>P</i>
<i>Fecundity-related response variables</i>															
Clutch size	0.01	47	0.61	-0.01	47	0.85	0.05	46	0.53	0.19	23, 25	0.47	0.20	15, 33	0.48
<i>Investment and survival-related response variables</i>															
Body size	-0.01	10	0.79	0.11	10	0.17	...	...	...	-1.01	6, 5	0.54	1.48	3, 7	0.40
Egg size	0.01	12	0.22	0.02	12	0.68	0.05	12	0.54	-0.27	5, 8	0.79	<b>2.24</b>	<b>7, 6</b>	<b>0.02</b>
Nest success	-0.01	11	0.65	0.03	11	0.63	-1.08	11	0.10	-0.23	9, 3	0.91	6.48	2, 10	0.09

size, and nest success were unrelated to the absolute altitude of the higher site or latitude of the study (Table 2). Population-level differences in body size tended to be less pronounced at high latitudes in contrast analyses, but not meta-analyses. Similarly, we found no evidence for the magnitude of elevational differences in life-history traits to be greater in smaller-bodied species in either contrast analyses (Table 1) or meta-analyses (Table 2).

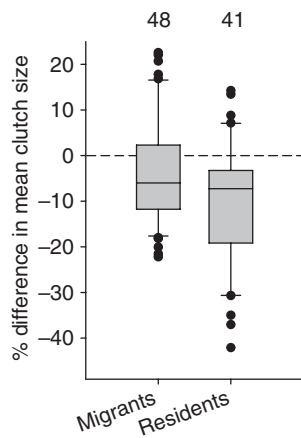
The magnitude of clutch size differences between populations was related to migratory status. Migrants laid slightly smaller clutches at high elevations (-2.8 ± 1.6%) than lower-elevation conspecifics, but residents laid substantially smaller clutches at high elevations than lower-elevation conspecifics (-10.4 ± 2.1%; Fig. 5). However, these trends were not detected in the smaller dataset used in the meta-analyses (Table 2).

High-elevation populations inhabiting alpine areas experienced on average 32.0% (±8.9%) higher nest success than their lower-elevation counterparts, whereas high-elevation populations inhabiting other vegetation types differed little in nest success relative to lower elevation populations (-4.3 ± 8.9%; Table 1). In meta-analyses, only egg size was larger at high elevations in populations breeding above tree line (Table 2).

#### IV. DISCUSSION

##### (1) Do high-elevation populations of birds exhibit shifts in life history?

Our results revealed consistent reductions in fecundity of montane and alpine birds worldwide compared to



**Fig. 5.** Reductions in clutch size among higher-elevation populations of migrant *versus* resident birds relative to their low-elevation counterparts ( $t = -2.8$ ,  $P = 0.007$ ). Negative values below the dashed reference line indicate that trait values of the higher elevation population were lower than those of the lower elevation population. We indicate sample sizes ( $N$  comparisons) for the two groups above the figure.

lower-elevation conspecifics. All analytical approaches revealed that populations living at higher elevations generally had fewer nesting attempts per year and laid smaller clutches. Phylogenetic tests indicated that the magnitude of these population-level differences was not constrained by evolutionary history. Clutch size variation has been the focus of theoretical and empirical studies for over half a century (Lack, 1947; Klomp, 1970; Ricklefs, 1980), but reductions in the number of breeding attempts at high elevation likely have a greater effect on seasonal productivity (Gillis *et al.*, 2008; Camfield *et al.*, 2010). Together, fewer nesting attempts with fewer offspring per attempt can result in large reductions in fecundity between high- and low-elevation populations. For example, dark-eyed juncos (*Junco hyemalis*) have 55% lower annual fecundity per km elevational difference in breeding range (Bears *et al.*, 2009). In our analyses, elevational differences in traits related to *per capita* investment in offspring and survival were inconsistent, varying among species and analytical approaches. The probability of nest survival increased at higher elevations in contrast analyses with similar trends observed in the meta-analyses. Greater nest success may compensate to some extent for the reductions in fecundity experienced by high-elevation populations, but we did not find consistent evidence of parents investing more in each offspring at higher elevations. Overall, we failed to detect a general shift toward slower life histories at higher elevations because reductions in reproductive output were not consistently associated with increases in adult survival (42% of comparisons showed increases in survival, 21% showed no change, and 37% showed decreases).

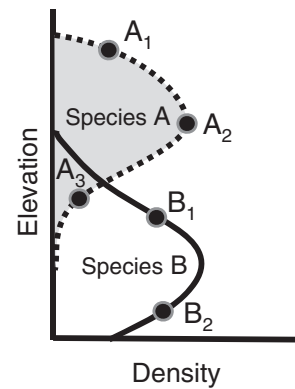
Why do so many birds choose to nest at high elevations where most species experience lower annual fecundity but where the majority do not appear to have higher survival than their low-elevation counterparts (58% of studies)? This pattern begs the question: how do high-elevation populations persist? We considered three possible explanations for these demographic results. First, meta-population structure may explain the difference if high elevations are marginal habitats occupied by sink populations, but maintained by immigration from lower elevations (Pulliam, 1988; Martin, Stacey & Braun, 2000; Evans Ogden *et al.*, 2012). Yet some high-elevation populations have been the focus of long-term research and demographic models indicate that fecundity and survival are sufficient for them to be self-sustaining (Sandercock *et al.*, 2005; Sasvari & Hegyi, 2011). Rescue by immigration implies there is no local adaptation to high elevations, with smaller clutches resulting from phenotypic plasticity. The relative importance of genes *versus* environment for life-history differences can be tested by common garden or reciprocal transplant experiments, but such experiments are challenging to conduct with free-living birds (James, 1983; Rhymmer, 1992; Bears *et al.*, 2008).

A second possible explanation for our results is that birds deploy a variety of compensatory mechanisms that act to increase survival, but such trade-offs may go undetected for one or more of the following reasons. (i) Small differences in annual survival can have large effects on longevity and lifetime fitness of long-lived organisms, but detecting survival differences can be difficult if the duration of a study is relatively short (Calder, 1984), especially when demographic rates vary annually and sample sizes of marked birds are small. (ii) Disentangling emigration from mortality in survival analyses based on live encounter data is challenging and rarely possible (Sandercock, 2006). (iii) Juvenile survival is widely considered to be especially important in balancing life-history equations (Badyaev & Ghalambor, 2001), but is rarely estimated because strong natal dispersal is common in vertebrates. We found five studies reporting comparisons of juvenile survival at different elevations. Only two studies reported higher juvenile survival at higher elevations (Bears *et al.*, 2009; Martin *et al.*, 2009), a trend inconsistent with this parameter being the demographic factor that rescues high-elevation populations. (iv) The compensatory mechanisms balancing reduced fecundity may differ among bird species. Our compilation of trait comparisons did not permit testing for trade-offs or integrated shifts in life-history strategies within bird populations. Thus it is possible that the problem of lower fecundity resulting from a common set of selective pressures is solved by different life-history trade-offs by different species, with the result that comparative studies of any one trait would be too variable to reveal consistent increases across species. For example, high-elevation populations of common kestrels (*Falco*

*tinnunculus*) in Tenerife, common blackbirds (*Turdus merula*) in Tibet, and willow ptarmigan (*Lagopus lagopus*) in Canada all lay smaller clutches than do their lowland counterparts. However, high-elevation kestrels have higher nest success (Carrillo & Gonzalez-Davila, 2005), blackbirds lay larger eggs (Lu, 2005), and ptarmigan have higher adult survival (Sandercock *et al.*, 2005).

A last explanation for our results challenges the expectation that reductions in fecundity must always be accompanied by increased survival in elevational population-level comparisons. Terborgh (1971) argued that upper distributional limits of species ranges are often shaped by abiotic constraints and physiological tolerances, whereas lower distributional limits are often shaped by interspecific competition. Although the relative role of biotic and abiotic factors is still debated, recent work has supported this hypothesis. For example, in simulated territory intrusions at species range boundaries, lower-elevation *Catharus* thrushes respond more strongly to higher-elevation congeners than *vice versa* (Jankowski, Robinson & Levey, 2010). When the upper distributional limits of species ranges are constrained by abiotic factors but their lower limits constrained by competition, different demographic rates and life-history trait values are expected near the upper and lower limits. We expect the density of individuals to decline near both the upper and lower range boundaries as limiting factors act to reduce fitness near range margins. In the two hypothetical species illustrated in Fig. 6, individuals breeding near the upper distributional limit at  $A_1$  would be expected to have lower *per capita* fecundity and/or longevity than those breeding at  $A_2$  due to approaching the limits of their fundamental niche. Near the upper limits where densities are low ( $A_1$ ), most individuals should attempt to reproduce every year because they will be able to acquire a territory successfully, even though environmental conditions may lead to high variance and lower overall reproductive success. However, if lower distributional limits are determined by competition for food and space (between A and B at  $A_3/B_1$ ), competitively superior individuals capable of breeding near their lower distributional limit ( $A_3$ ) may have similar *per capita* fecundity and longevity as individuals breeding at  $A_2$ . Near the lower limits, we expect delayed onset of reproduction, resulting in more 'floaters' and a lower proportion of individuals reproducing each year at the population level.

The different predictions resulting from a comparison of hypothetical populations  $A_1$  *versus*  $A_2$  relative to  $A_2$  *versus*  $A_3$  highlights a shortcoming of attempting to combine individual-level metrics such as clutch size or nest success (which are only measured on breeding individuals) and population-level metrics such as annual survival (which are based on all individuals in the population). The hypothesized trade-offs underlying life-history theory operate at the level of the individual. Yet we often lack the data to link individual- and population-level



**Fig. 6.** Distributions of hypothetical species A and B over an elevational gradient. Points along these distributions (e.g.  $A_1$ ,  $B_2$ ) represent populations breeding at different elevations. If upper elevational limits are constrained by abiotic factors and physiological tolerances whereas lower limits result from interspecific competition (e.g. A limited by B), these different sources of selection could result in the fecundity differences we observed, and predict both a reduction in the proportion of individuals breeding, and increased age of maturity near lower ( $A_3$ ) *versus* upper ( $A_1$ ) distributional limits.

estimates, and parameterize population models to understand how variation in individual-level fecundity translates into population-level metrics. The apparent paradox presented by our results could be resolved if higher fecundity at low elevations is realized by a proportionally smaller fraction of the reproductively mature individuals.

Comparisons of populations near the upper or lower portions of their range with those nearer the centre of their range may also help interpret individual results inconsistent with the general patterns evident in our results. For example, 21–50% of studies reported no difference between populations in the traits we examined (Fig. 1). If the elevation of populations chosen for study were distributed similarly to the hypothetical case of  $B_1$  and  $B_2$  (Fig. 6), we might find few demographic differences, even if the elevational difference between sites is large relative to the elevational distribution of the species.

## (2) Why do birds have lower fecundity at high elevations?

Regardless of questions about survival at high elevations, our results strongly suggest that environmental conditions at high elevations act to limit fecundity, and our analyses of reproductive phenology and associations between ecological variables and life-history traits shed light on the mechanisms limiting populations near their upper limits. Our results, combined with evidence of reduced extra-pair paternity among high-elevation birds (Bonier *et al.*, 2014), suggest strong differences in selective pressures on reproductive tactics at high elevations.

Our results are not consistent with hypotheses relying on increased predation risk driving observed life-history variation; egg and nestling development were slowed at high elevations, but nest success was variable, and tended to be higher at high elevations in contrast and meta-analyses.

We found little support for hypotheses relying on temperature effects to explain life-history variation, either *via* increased physiological costs or direct mortality. Hypotheses based on temperature predict larger population differences among smaller-bodied species, and in populations living at the highest latitudes and altitudes. Unexpectedly, the magnitude of elevational differences in traits was largely unrelated to biogeographical or intrinsic factors. Climate-related mortality risk to young would be expected to select for parental investment in larger, more thermally efficient offspring. However, we found that egg size and nestling size did not differ consistently between high- and low-elevation populations; only 40 and 20% of studies reported larger eggs or nestlings at higher elevations respectively. Last, if increased winter mortality drives life-history variation, then we expect larger differences in trait values among populations of residents than migrants. However, only clutch size differed between residents and migrants (of the six traits we evaluated). Migrants typically lay smaller clutches than resident species at north temperate latitudes (Martin, 1995); thus, migrants may have more limited potential for clutch size reductions at high elevations.

The fact that few differences in vital rates between populations varied with latitude was surprising. Few trait comparisons were available from study sites at tropical latitudes, but the latitudes of 28–60°N were well represented in our data set, a ~3500 km span which ought to be sufficient to detect gradients in seasonality related to latitude. Indeed, smaller latitudinal spans were sufficient to reveal latitudinal trends in other recent comparative studies (Bonier *et al.*, 2014). Thus, our results are most consistent with food availability and/or temporal constraints driving life-history variation because alternative drivers of elevational differences in life histories resulting from direct mortality, slower development, or reduced fecundity at high elevation should act more strongly on birds living at high latitudes than low latitudes.

One of two hypotheses consistent with our results is that temperature-driven reductions in primary productivity and consequent reductions in food explains reductions in the number and size of clutches at higher elevations. Lower food availability can result in incubating parents leaving nests more frequently or for longer durations to meet the energy requirements of the parents or their nestlings (Moreno, 1989), a factor that may extend developmental periods and select for increased biparental care among high-elevation species (Badyaev & Ghalambor, 2001). Smaller clutches of eggs

and broods re-warm faster, reducing parental energetic costs during incubation (Biebach, 1981; Conway & Martin, 2000a). Thus, reductions in clutch size may also function to minimize the costs of lower food availability while coping with higher metabolic costs and colder temperatures (Camfield & Martin, 2009).

An alternative hypothesis consistent with our results is that colder temperatures at higher elevations on low-latitude mountains magnify temporal constraints imposed by precipitation or other sources of climatic seasonality (Class *et al.*, 2011). We found that birds initiated breeding later at high elevations, and their breeding seasons were of shorter duration. However, the duration of each developmental stage was not shorter, implying that selection for shorter breeding periods is likely constrained by factors limiting developmental rates. It is curious that the magnitude of delays in the onset and reductions in the duration of breeding seasons at high elevations were unrelated to latitude. Nevertheless, our results are consistent with a study from tropical Asia reporting greater reproductive seasonality in montane bird taxa relative to lower elevations (Peh *et al.*, 2012). We interpret our results for reproductive phenology as evidence that precipitation or other climatic variables may interact with relatively aseasonal but colder high-elevation temperatures to impose temporal constraints on the breeding seasons of tropical montane birds (Tye, 1992; Woodworth, 1997). The limited data available are consistent with this idea; a high-elevation population of tropical house wrens (*Troglodytes aedon intermedius*) in Costa Rica began nesting at the beginning of the dry season, and nest-initiation attempts declined sharply once the rainy season resumed, whereas lowland wrens initiated nesting attempts in 10 out of 12 months, including the wettest month of the year (Young, 1994).

Despite a comprehensive literature search, we found few tropical studies to include in our analysis and our sample may not accurately represent responses to elevational gradients for the diversity of tropical birds. While tropical avifaunas have received far less research attention than temperate avifaunas generally (Sandercock *et al.*, 2000), it seems that studies of montane taxa, and elevational comparisons of tropical birds are especially under-represented. The conservation implications of this knowledge gap are worrisome. Climate change is an increasing threat to highland taxa that have been historically less affected by anthropogenic habitat loss and direct exploitation (Sekercioglu *et al.*, 2008). We emphasize an urgent need for detailed studies of life-history variation of tropical montane birds.

## V. CONCLUSIONS

(1) Our results indicate that well-established latitudinal gradients in avian life histories are not mirrored

by comparable patterns along elevational gradients. In fact, we present evidence for patterns apparently opposite to those predicted by latitudinal variation. Early explanations of shifts toward lower fecundity and slower life histories at lower latitudes relied on food limitation and/or high nest predation selecting for small clutches and reduced parental activity at the nest (Lack, 1947; Skutch, 1949; Tarwater, Kelley & Brawn, 2009).

(2) Martin (2002) argued that reductions in extrinsic sources of adult mortality at low latitudes due to more benign climatic conditions select for reduced reproductive effort through a cost of reproduction. Similar explanations cannot explain patterns of fecundity along elevational gradients. Risk-averse strategies minimize intrinsic sources of mortality risk to levels not exceeding extrinsic risks (Martin, 1996; Martin *et al.*, 2000). Martin's (2002) view rests upon continental-scale variation in seasonality due to the configuration and geography of land masses and ocean currents. However, high elevations are not less seasonal than adjacent lowlands. Instead, high elevations likely challenge animals with greater diurnal and seasonal fluctuations in environmental conditions that could result in increased extrinsic mortality risk.

(3) Our analyses suggest that shifts toward lower fecundity at high elevations may be shaped by temperature-driven differences in productivity mediated by temporal constraints, and possibly by other temperature-related metabolic costs. High altitudes and high latitudes share similar temporal constraints, but at high northern latitudes, birds can exploit one of the most productive environments on the planet with long day lengths during a short growing season (Huston & Wolverson, 2009; Rose & Lyon, 2013). By contrast, high altitudes are rarely as productive as nearby lower elevations. Studies from regions where elevational patterns of productivity are inverted due to precipitation gradients provide the opportunity to test productivity-based hypotheses directly; small ground finches (*Geospiza fuliginosa*) in the Galapagos and black-throated sparrows (*Amphispiza bilineata*) in California both lay smaller clutches at higher elevations despite increases in food availability (Kleindorfer, 2007) and reductions in drought-induced nest failure (Hargrove & Rotenberry, 2011). Thus, primary productivity alone cannot explain elevational differences in avian fecundity.

(4) High-elevation habitats impose a distinct set of selective pressures that often result in behavioural, physiological, and morphological differences between high- and low-elevation populations (Martin, 2001). High-elevation taxa are threatened by range contractions as a consequence of climate change because upward range shifts result in reduced land area towards the tops of mountains (Franzén & Molander, 2011). Given naturally fragmented ranges and low population densities, conservation of montane taxa will be

extremely challenging. The paucity of demographic data from tropical montane taxa is especially worrisome given the diversity and endemism of montane tropical avifaunas and their susceptibility to climate change (Freeman & Class Freeman, 2014).

(5) The results of our study identify the demographic mechanisms underlying the lower reproductive potential of high-elevation taxa. If only ~40% of high-elevation populations have increased adult survival to potentially offset the fecundity disadvantages of breeding at high elevation, the remaining 60% of taxa will require even more aggressive conservation efforts because populations will be more susceptible to extirpation due to stochastic environmental or disturbance events. Given that 25% of the global landmass is classified as mountainous with a relatively under-studied fauna, understanding the factors influencing the demography of high-elevation taxa should be a conservation priority (Martin, 2012).

(6) We expect that the selective pressures resulting in reduced avian fecundity at high elevations may also influence life-history strategies among other terrestrial vertebrates. However, it is possible that different taxa have solved the same set of evolutionary challenges in different ways. Degree of mobility, endo- and ectothermy, climatic escape or avoidance mechanisms, and developmental modes could all affect the nature and strength of climate-driven selection on life-history traits. Adaptation to high elevations has shaped the life histories of species exploiting mountainous environments around the globe in ways that differ markedly from the constraints of living at high latitudes.

## VI. ACKNOWLEDGEMENTS

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