

CHANGES IN EGG SIZE AND CLUTCH SIZE WITH ELEVATION IN A WYOMING POPULATION OF MOUNTAIN BLUEBIRDS

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Abstract. Few studies have examined how avian life-history traits vary within populations as elevation increases and climate becomes more severe. We compared egg and clutch sizes of Mountain Bluebirds (*Sialia currucoides*) nesting at two elevations (1500 m and 2500 m above sea level) in the Bighorn Mountains of Wyoming over two years. Eggs laid by females at the high-elevation site were, on average, significantly (6%) smaller in volume than eggs laid by their lower-elevation counterparts. Across elevations, egg size showed a significant positive correlation with female body condition (weight relative to size), and high-elevation females had significantly lower indices of condition than low-elevation females. Temperatures during clutch formation were colder at the high-elevation site, and egg size was negatively related to temperature after controlling for the effects of female condition. Clutches of females at high elevations were, on average, marginally smaller (by 5%, ~0.3 eggs) than clutches of low-elevation females. Unlike egg size, clutch size was unrelated to either female condition or temperature during clutch formation. This suggests that, when under energetic or nutritional stress at high elevations, females sacrifice egg size before sacrificing clutch size.

Key words: clutch size, egg size, elevation, female condition, Mountain Bluebird, *Sialia currucoides*, temperature.

Cambios con la Elevación en el Tamaño de los Huevos y de la Nidada en una Población de *Sialia currucoides* en Wyoming

Resumen. Pocos estudios han examinado cómo los caracteres de historia de vida cambian dentro de poblaciones a medida que la elevación aumenta y el clima se torna más severo. Comparamos el tamaño de los huevos y de la nidada de individuos de *Sialia currucoides* que se encontraban nidificando a dos altitudes (1500 m y 2500 m sobre el nivel del mar) en las Montañas Bighorn de Wyoming durante dos años. Los huevos puestos por hembras del sitio a mayor altitud fueron, en promedio, significativamente (6%) menores en volumen que los huevos puestos por hembras en los sitios de baja altitud. A través del rango de elevación, el tamaño de los huevos mostró una relación positiva y significativa con la condición corporal (peso en relación con el tamaño). Las hembras del sitio de mayor altitud tuvieron índices de condición significativamente menores que las hembras del sitio de baja altitud. Las temperaturas durante la formación de la nidada en el sitio de mayor altitud fueron, en promedio, marginalmente menores (en un 5%, ~0.3 huevos) que las nidadas de las hembras del sitio de menor elevación. De modo contrario al tamaño del huevo, el tamaño de la nidada no se relacionó con la condición de las hembras ni con la temperatura durante la formación de la nidada. Esto sugiere que cuando las hembras se encuentran bajo estrés energético o nutricional a altitudes altas, éstas sacrifican el tamaño del huevo antes de sacrificar el tamaño de la nidada.

INTRODUCTION

Most birds that occupy mountainous regions restrict breeding to a limited range of elevations. Some species, however, breed across steep elevational gradients and confront rapid changes in ecological conditions over short geographical distances. Compared to lower

elevation sites, higher elevation sites have persistently colder, cloudier, and windier weather, greater frequency and depth of snow cover, and, overall, a less predictable climate. Birds breeding at high elevations also face a shorter seasonal period during which reproduction is possible (Johnston 1954, Stewart et al. 1977, Milinkovich 1993).

At present, we know little about how avian life-history traits change within populations across elevational gradients. However, selection

Manuscript received 19 October 2005; accepted 21 April 2006.

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should favor larger eggs at higher elevations for several reasons. Larger eggs have a lower surface area-to-volume ratio and hence lose heat less rapidly during incubation recesses (Rhymer 1988). Larger eggs produce larger hatchlings (Williams 1994, Christians 2002), which would also benefit from greater thermal inertia in a cold, windy environment (Hamman et al. 1989). Some evidence suggests that larger eggs are more likely to confer a survival advantage to nestlings in harsher or otherwise lower-quality environments (Smith and Bruun 1998, Styrsky et al. 1999).

Females may also produce larger eggs at higher elevations to provision eggs with proportionately more water. Because gases diffuse more rapidly under lower barometric pressures, all else being equal, eggs will lose water faster at higher elevations (Rahn 1977). To compensate, females have several options, including reducing the number of pores in the shell through which gases diffuse, increasing water vapor pressure within the nest, and increasing the initial water content of eggs and hence their size (Carey 1994). However, despite the potential benefits of laying larger eggs at higher elevations, eggs may nevertheless be smaller at such elevations because of greater climatically induced energetic demands on laying females.

Few studies have examined how egg size varies with elevation. An extensive review of factors affecting egg size variation in birds (Christians 2002) did not consider elevation. Some comparisons among different populations nesting in separate geographical areas have found larger eggs at higher elevations. However, results are confounded by the fact that females were structurally larger in the high-elevation populations (King and Hubbard 1981, Carey et al. 1983, Lu 2005). Within-population comparisons have produced mixed results. Milinkovich (1993) found that eggs of House Wrens (*Troglodytes aedon*) are ~12% larger at 3000 m above sea level (asl) than at 1130 m asl in Colorado. Likewise, eggs of Great Tits (*Parus major*) are larger at high-elevation sites along an approximately 775 m elevational gradient in Germany (Hamman et al. 1989). In contrast, there is no consistent change in egg size in Barn Swallows (*Hirundo rustica*), Cliff Swallows (*Petrochelidon pyrrhonota*), or Black-billed Magpies (*Pica pica*) nesting from ~1350 m to ~1800 m asl along the Colorado-

Wyoming border (Sotherland et al. 1980, Taigen et al. 1980), nor in Blackbirds (*Turdus merula*) nesting between 3800 m and 4500 m asl on the Tibetan plateau (Lu 2005). Finally, in northeast Algeria, Blue Tit (*Parus caeruleus*) females breeding at 500 m or 950 m asl produce smaller eggs than females breeding at 30 m asl (Chabi et al. 2000). Clearly, additional work is needed to determine how egg size varies with elevation in birds, and why.

Controversy exists as to whether and how clutch size varies with elevation. Cody (1966:182) stated that there was a "general trend for species nesting at higher altitudes to lay larger clutches," a conclusion that was challenged repeatedly (Slagsvold 1982, Krementz and Handford 1984). Most recently, Badyaev and Ghalambor (2001) compared clutch sizes in 24 pairs of closely related passerine taxa from Russia and nearby Eurasia, where members of taxonomic pairs breed at different elevations. Seven comparisons were between closely related species, 15 between subspecies, and the remaining two comparisons were between individuals in the same population along an elevational gradient. In 21 of the 24 comparisons, the higher-elevation representative produced smaller clutches. Badyaev and Ghalambor (2001) argued that laying a smaller clutch, which results in greater parental investment per nestling, is a strategy to increase offspring survival in response to harsher, less predictable abiotic conditions at higher elevations. However, smaller clutches at higher elevations could also result from greater energetic or nutritional constraints on females, especially if females are laying larger eggs. In addition, in species with altricial young, selection may favor maintenance of relatively large clutches at higher elevations because larger broods can thermoregulate both sooner and more effectively through shared body heat and mutual insulation (Dunn 1976, Clark 1982). Indeed, in contrast to the results of Badyaev and Ghalambor (2001), studies from North America have reported larger clutches in subspecies or populations nesting at higher elevations (Johnston 1954, Stewart 1973, Stewart et al. 1977, Weathers et al. 2002).

Badyaev and Ghalambor (2001) preferentially compared distinct taxa to provide some certainty that any differences in life-history strategy were genetically based. Also of interest,

TABLE 1. Results of studies that have examined changes in clutch size within populations of birds nesting along steep elevational gradients. Studies that involved elevational gradients of <500 m, or in which high-elevation sites were located \leq 500 m above sea level (e.g., Kremetz and Handford 1984, Zang 1980) were omitted. In cases where it was unclear whether comparisons were made within a single, contiguous population (e.g., Johnston 1954, Slagsvold 1982), the study was also omitted. 0 equals no significant change with elevation.

Species	Elevational gradient (m asl)	Location	Trend in clutch size	Reference
Great Tit (<i>Parus major</i>)	120–900	Germany	0	Zang (1982)
Blue Tit (<i>Parus caeruleus</i>)	270–875	Germany	0	Hamman et al. (1989)
	30–900	Algeria	+	Chabi et al. (1995, 2000)
Eurasian Nuthatch (<i>Sitta europaea</i>)	100–650	Germany	–	Zang (1988)
House Wren (<i>Troglodytes aedon</i>)	1130–3000	Colorado, U.S.	+	Milinkovich (1993)
Pied Flycatcher (<i>Ficedula hypoleuca</i>)	130–900	Germany	–	Zang (1980)
Blackbird (<i>Turdus merula</i>)	3800–4500	Tibet	0	Lu (2005)
Meadow Pipit (<i>Anthus pratensis</i>)	0–1000	Great Britain	–	Coulson (1956)
White-winged Grosbeak (<i>Mycerobas carripes</i>)	2000–3500	Russia	–	Badyaev (1993) ^a
Gold-fronted Serin (<i>Serinus pusillus</i>)	2000–2700	Russia	–	Badyaev (1994) ^a

^a As described in Badyaev and Ghalambor (2001).

however, is how birds *within* populations respond to steep elevational gradients. Because short distances between high and low elevation sites can facilitate gene flow, differences between high and low elevations are more likely to be facultative responses to differing environmental conditions (but see Garant et al. 2005, Postma and van Noordwijk 2005). Few studies have examined intrapopulation variation in clutch size along elevational gradients and results are decidedly mixed (Table 1). Researchers found clutches to be smaller at higher elevations in fewer than half of the studies, in contrast to the comparisons of Badyaev and Ghalambor (2001). However, most intrapopulation studies have involved parids and only a few studies have involved birds breeding at more substantial elevations, i.e., at or above 2000 m. Thus, further research is necessary to determine how frequently, and under what conditions, females breeding at high elevations lay fewer, more, or about the same number of eggs as their counterparts breeding at lower elevations.

To further elucidate how avian reproduction varies in response to increased elevation, we examined the sizes of eggs and clutches within a population of Mountain Bluebirds (*Sialia currucoides*) nesting at two elevations in north-central Wyoming.

METHODS

STUDY SPECIES AND POPULATION

Mountain Bluebirds are medium-sized (~30 g), sexually dimorphic, socially monogamous passerines that breed at elevations up to ~3800 m in the high plains, deserts, shrubsteppe, and mountains of western North America (biology of the species is summarized in Power and Lombardo 1996). Mountain Bluebirds nest naturally in preformed cavities such as old woodpecker holes, but readily use human-made nest boxes. Eggs, which are subelliptical in shape, are usually laid at 24 hr intervals. Most clutches contain 4–7 eggs. Only females incubate eggs and brood the altricial, heterothermic hatchlings, but both parents deliver prey to young. Mountain Bluebirds feed almost exclusively on ground-dwelling insects (Power 1980). Foraging success can thus be strongly affected by even small amounts of snow cover. Young typically fledge 19–22 days after hatching, after which they are fed by one or both parents for 2–6 weeks. Pairs that fledge one brood relatively early in the season may attempt to produce a second brood.

We conducted this study using a large population of Mountain Bluebirds that is distributed continuously throughout the Big-horn Mountains and surrounding foothills in

north-central Wyoming. Data were gathered during the 2004 and 2005 breeding seasons. All individuals in this study used wooden nest boxes erected along fencelines in meadows and pastures. We obtained data only from clutches laid during the first round of breeding each season. We did not use data from pairs making a second nesting attempt after fledging young from their first attempt.

STUDY SITES

Our low-elevation site surrounded the town of Big Horn (44°38'N, 107°01'W). Boxes were in three clusters: 30 boxes were at elevations from 1240 m to 1287 m in the low foothills, 33 boxes were situated between 1400 m and 1550 m in the high foothills, and 18 boxes, which we used only in 2005, were situated between 1460 m and 1610 m on the eastern slope of the mountains. Only two of the 30 boxes in the lowest-elevation cluster were used by bluebirds. These two boxes were the two highest in this cluster (at 1256 m and 1287 m), which confirms anecdotal observations that Mountain Bluebirds rarely nest below 1350 m in this part of Wyoming. Over the two years of our study, the mean elevation of nests at lower-elevation sites was 1482 m (range: 1256–1610 m).

Our high-elevation site was located 44 km northwest of our main low-elevation site in rolling meadows on a high plateau in the central Bighorn Mountains, near the settlement of Burgess Junction (44°46'N, 107°32'W). Sixty-eight and 112 boxes were available to bluebirds in 2004 and 2005, respectively. Over the two years of our study, the mean elevation of nests at this location was 2504 m (range: 2443–2582 m).

Breeding pairs occurred at lower density at the low-elevation site than the high-elevation site. At the low-elevation site, the mean distance (\pm SD, n) between a pair's nest and the nearest active nest (within 500 m) was 221 m (\pm 73, 33), compared to 180 m (\pm 81, 103) at the high-elevation site.

Most boxes at the lower elevation had internal dimensions (length, width, and entrance-to-floor distance) of 12.7, 9.5, and 12.7 cm, whereas most boxes at the higher elevation had dimensions of 12.7, 12.7, and 14 cm. High rates of nest predation at the lower-elevation site (exceeding 25% in some years) caused us to mount boxes on thin poles

equipped with metal cones to prevent predator access. Predation is rare at the high-elevation site (<2% of nests) and boxes were mounted on wooden fence posts or trees and left unprotected.

FIELD METHODS

We checked boxes every 1–5 days to determine the date that the first egg was laid (egg-1 date) and final clutch size. Midway through the incubation stage, we selected two eggs from each nest at random and, using digital calipers, measured each egg's length and width to the nearest 0.01 mm. To increase the accuracy of measurements, we measured length and width twice, rotating the egg between measurements. We used the mean of the two measurements in all analyses. We estimated each egg's volume (cm^3) using Hoyt's (1979) formula: $0.51 * \text{length} * \text{width}^2$. We then calculated the grand mean volume of the two eggs from each clutch and used this value in analyses.

We trapped adults in boxes when they entered to feed nestlings. We marked each adult with a unique combination of colored leg bands, and measured its weight and the length of its right wing cord as an index of body size. As an index of female body condition, we used the residuals from a regression of weight against wing length. We captured and weighed females on different days of the nestling stage and females steadily lose weight as they care for nestlings (0.24 g day^{-1} , on average; see also Merkle and Barclay 1996). Thus, we included the number of days elapsed between the start of a female's clutch hatching and her capture as a variable in the regression.

We obtained egg or clutch size data for some individual females in both years of the study. We only included data from one year, chosen at random, in analyses. Some females that were captured in 2004 and returned to breed in 2005 were not recaptured in 2005 due to trap-shyness or time constraints. Thus, in some cases we randomly chose a returning female's 2005 egg or clutch data to be included in analyses but had no morphometric data for the female that year. Because we required morphometric data for the year in which egg and clutch size data were obtained, we instead used egg and clutch data from 2004. As a result, sample sizes involving comparisons of female morphometrics differ from those for some egg and

clutch size comparisons. Sample sizes for egg and clutch size comparisons differ because we did not obtain both egg size and final clutch size at some nests.

We obtained weather data from stations that were located 3 km south of the lower-elevation site, and in the center of the higher-elevation site. To determine whether egg and clutch sizes were related to ambient temperature during clutch formation, we followed Hargitai et al. (2005) and calculated the mean daily temperature (where daily temperature equaled the mean of the daily high and low temperatures) for a nine-day "clutch formation period." This period extended from four days prior to until four days after the laying of the first egg.

STATISTICAL ANALYSES

We compared egg sizes at the low and high elevation sites with an analysis of variance that included elevation (low or high) and year (2004 or 2005) as factors. We calculated and report least-squares means for each factor adjusted for the effects of the other factor, e.g., mean egg size at each elevation adjusted for the effects of year. Unlike egg size, clutch size showed variation with time of season. Therefore, we compared clutch sizes using an analysis of covariance with elevation and year as factors and egg-1 date as a covariate. Because the timing of the breeding season differed with elevation, we used "local egg-1 day" as our covariate. Local egg-1 day for a nest was the number of days that laying began in that nest after the day that the first egg was laid at that elevation. We report least-squares mean clutch size for each elevation adjusted for the effect of year and time of season. To test for linear associations between egg or clutch size and different variables we used simple linear correlation, generating Pearson product-moment correlations coefficients (r).

All means, adjusted and unadjusted, are reported \pm SE unless otherwise noted. All analyses were done using SAS version 8.1 (SAS Institute 1999).

RESULTS

TIMING OF BREEDING SEASONS

In 2004, egg-laying began on 19 April and 1 May at the low and high elevations, respectively. In 2005, laying began several weeks later at

both elevations, on 2 May and 19 May, respectively. The later start in 2005 probably resulted from colder temperatures and greater snow cover during weeks that most individuals were on location and preparing to breed at each elevation, specifically the month of April at the low-elevation site and late April–early May at the high-elevation site. At the low-elevation site, mean daily temperature from 1 to 30 April was $9.1 \pm 4.1^\circ\text{C}$ (SD) in 2004 and $7.4 \pm 3.9^\circ\text{C}$ in 2005. During this period, 15.3 cm of snow fell in 2004 compared to 40.1 cm in 2005. At the high-elevation site, mean daily temperature from 15 April to 14 May was $2.8 \pm 5.6^\circ\text{C}$ in 2004 and $-0.7 \pm 5.0^\circ\text{C}$ in 2005. During this 30-day period, 27.9 cm of snow fell in 2004 compared to 63.5 cm in 2005.

EGG SIZE

During the two years of our study we measured 310 eggs from 158 clutches. The volume of the largest egg, 3.73 cm^3 , was 81% greater than that of the smallest egg, 2.06 cm^3 (mean volume \pm SD: $2.96 \pm 0.29 \text{ cm}^3$). Egg length averaged 21.39 mm, ranging from 18.30 mm to 25.33 mm, a 38% difference. Egg width varied less than length, averaging 16.47 mm and ranging from 14.48 mm to 17.77 mm, a 23% difference.

Egg size did not change significantly with time of season (i.e., no correlation with local egg-1 day) at either elevation in either year (r range: -0.24 to 0.09 , all $P > 0.50$). The effect of elevation on egg volume also did not differ between years (Fig. 1; no elevation * year interaction: $F_{1,122} = 0.1$, $P > 0.77$). Egg volume was, on average, 6% greater in 2004 than in 2005 (least-squares means adjusted for the effect of elevation: $3.09 \pm 0.05 \text{ cm}^3$, $n = 50$ vs. $2.93 \pm 0.03 \text{ cm}^3$, $n = 76$, respectively), a significant difference ($F_{1,122} = 8.3$, $P < 0.01$). After adjusting for the effect of year, we found that eggs were 6% smaller in volume at the high-elevation site than at the low-elevation site ($2.92 \pm 0.03 \text{ cm}^3$, $n = 91$ vs. $3.09 \pm 0.05 \text{ cm}^3$, $n = 35$, respectively), also a significant difference ($F_{1,122} = 10.6$, $P < 0.01$).

Egg size was not significantly related to clutch size at either elevation in either year (r range: -0.14 to 0.05 , all $P > 0.30$) suggesting that females were not trading smaller eggs for larger clutches at the higher elevation. More-

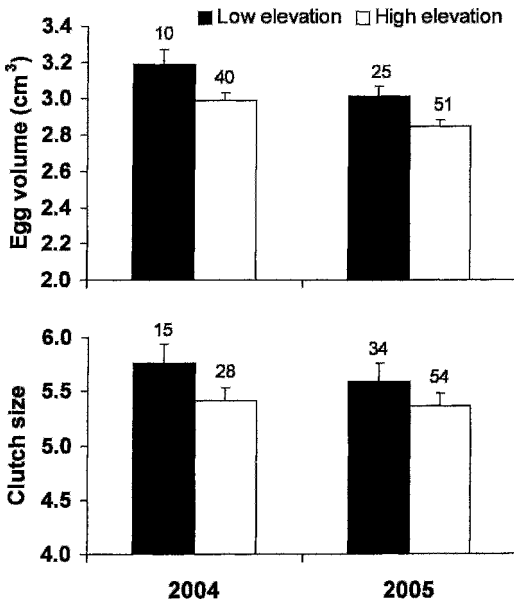


FIGURE 1. The mean (+ SE) volume of eggs (upper panel) and size of clutches (lower panel) produced by female Mountain Bluebirds at a low-elevation and a high-elevation site in the Bighorn Mountains, Wyoming, 2004–2005. Clutch sizes are least-squares means adjusted for seasonal effects. Sample sizes are given above bars.

over, clutches also tended to be smaller at the higher elevation (see below).

Females did not produce smaller eggs at the high-elevation site because they themselves were smaller in structural size. As measured by wing length, females were larger, although not significantly so, at the high-elevation site (low-elevation: 110.5 ± 0.50 mm, $n = 31$; high-elevation: 111.5 ± 0.37 mm, $n = 68$; $t_{97} = -1.5$, $P = 0.14$). Moreover, across elevations and years, egg volume was unrelated to female wing length ($r = 0.12$, $n = 90$, $P = 0.27$).

Females at our high-elevation site had significantly lower indices of body condition when captured during the nestling stage than females at lower elevations (comparison of residual weights: $t_{90} = 2.8$, $P = 0.01$). Across elevations and years, there was a highly significant positive correlation between female condition and egg volume ($r = 0.41$, $n = 85$, $P < 0.001$; Fig. 2).

Mean temperature during nine-day clutch-formation periods of females at the low-elevation site during 2004 and 2005 averaged

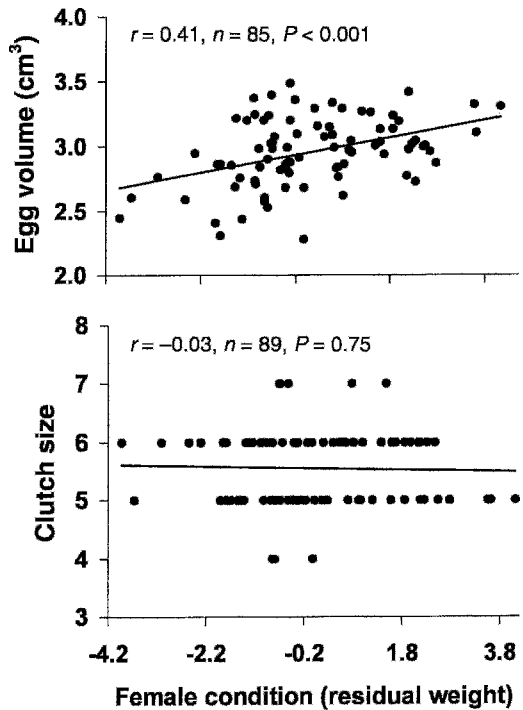


FIGURE 2. Relationship between the body condition of female Mountain Bluebirds (the residual from a regression of weight against structural size, measured by wing length) and egg volume (upper panel) and clutch size (lower panel) in the Bighorn Mountains, Wyoming, 2004–2005.

11.2°C and 13.8°C, respectively, compared to 5.4°C and 5.6°C for females at the high-elevation site. Across years and elevations, egg volume showed a significant positive correlation with temperature during the clutch-formation period ($r = 0.24$, $n = 124$, $P = 0.01$; Fig. 3). Colder temperatures during and prior to the clutch-formation period probably affected egg size by lowering female condition. However, a temperature effect remained after controlling for the effect of female condition (partial r for temperature: 0.26 , $n = 85$, $P = 0.02$). The effect of condition also remained after controlling for the effect of temperature (partial r for temperature: 0.38 , $n = 85$, $P < 0.001$).

CLUTCH SIZE

Clutch size showed a marginally significant decline with local egg-1 date in 2004 at the high-elevation site (correlation with local egg-1 date:

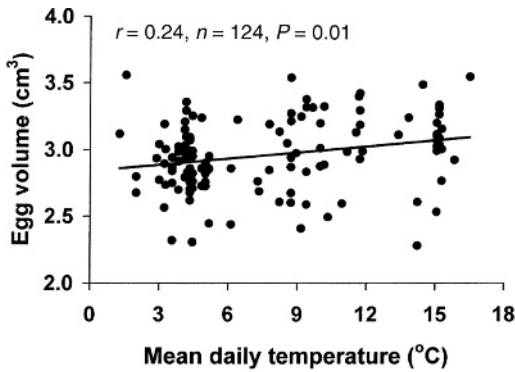


FIGURE 3. Relationship between mean daily temperature ($^{\circ}\text{C}$) during the nine-day clutch formation period and egg size of Mountain Bluebirds in the Bighorn Mountains, Wyoming, 2004–2005.

$r = -0.36$, $n = 33$, $P = 0.04$) and showed a similar trend at the low-elevation site ($r = -0.48$, $n = 15$, $P = 0.07$). The negative relationship between clutch size and time of season was weaker and insignificant at both elevations in 2005 (low-elevation: $r = -0.21$, $n = 28$, $P = 0.28$; high-elevation: $r = -0.08$, $n = 54$, $P = 0.58$). After adjusting for both seasonal and elevation effects, we found clutches to be 4% or ~ 0.2 eggs larger on average in 2004 than in 2005, an insignificant difference (least-squares means: 2004 = 5.7 ± 0.1 eggs, $n = 49$; 2005 = 5.4 ± 0.1 eggs, $n = 82$; $F_{1,126} = 2.1$, $P = 0.16$). After adjusting for both seasonal and year effects, clutches were 5% or ~ 0.3 eggs smaller on average at the high-elevation site compared to the low-elevation site (least-squares means: high-elevation site = 5.4 ± 0.1 eggs, $n = 88$; low-elevation site = 5.7 ± 0.1 eggs, $n = 43$), a difference that was marginally insignificant ($F_{1,126} = 3.5$, $P = 0.06$). There were no significant interactions between year, elevation, and egg-1 date. The strong tendency for clutches to be smaller at the higher-elevation site was evident only when we included data from both years in the analysis (comparison of least-squares means for 2004 alone: $F_{1,45} = 2.4$, $P = 0.13$; for 2005 alone: $F_{1,79} = 1.1$, $P = 0.29$; Fig. 1).

Across elevations and years, we detected no relationship between clutch size and either female wing length ($r < 0.01$, $n = 94$, $P = 0.98$) or female condition ($r = -0.03$, $n = 89$, $P = 0.75$; Fig. 2). We also attempted to determine whether smaller clutches at higher elevations

might partly result from colder temperatures at those elevations. Complicating any analysis is the fact that clutch size tends to decline as the season progresses, while ambient temperatures are rising. We therefore asked whether, at a given point in the season, females laid larger clutches when temperatures were relatively warm. At each elevation we calculated residuals from a regression of clutch size against local egg-1 date and then determined whether the residuals were positively correlated with mean temperature during the clutch-formation period. We found no correlation at either elevation (low-elevation: $r = 0$, $n = 43$, $P = 0.99$; high-elevation: $r = 0.13$, $n = 86$, $P = 0.23$), suggesting that clutch size was unaffected by temperature.

DISCUSSION

Despite several potential benefits to laying larger eggs at higher elevations, female Mountain Bluebirds in our study laid significantly smaller eggs at 2500 m on a mountain plateau than they did at elevations about 1000 m lower in the foothills. To our knowledge, this is only the second report of female passerines laying smaller eggs at higher elevations (see also Chabi et al. 2000). However, too few studies of this kind have been done to declare our results as unusual.

The production of smaller eggs by females at higher elevations in our study was not the result of females being structurally smaller at that elevation (they were not), nor did it result from females trading smaller eggs for larger clutches at higher elevations (egg and clutch size were unrelated). Rather, the most likely explanation for this result is that colder, windier conditions, along with greater and more frequent snow cover at the high-elevation site, caused greater energetic or nutritional stress in laying females and hence the allocation of fewer resources to individual eggs. Females at our high-elevation site had lower indices of physical condition, i.e., they weighed less for their size, and presumably carried fewer reserves than females at lower elevations. Numerous other studies on passerines have reported smaller eggs among females with lower condition indices (reviewed by Christians 2002).

Persistently colder temperatures at our higher-elevation site presumably affected egg size indirectly by lowering female condition.

However, a significant negative relationship between temperature during the clutch-formation period and egg size still existed after we controlled for the effects of female condition on egg size, suggesting that temperature had additional, indirect effects on egg size. Colder temperatures may have lowered female foraging success by delaying the emergence or reducing the mobility of insects, thereby making them more difficult to detect in ground vegetation.

Distances between breeding pairs were significantly shorter at the higher-elevation site than the lower-elevation site, raising the possibility that increased intraspecific competition for food may also have contributed to the production of smaller eggs at higher elevations. However, the fact that parents feed nestlings more often at the high-elevation site (LSJ et al., unpubl. data) argues against this.

Over the two years of our study, clutches produced by females at high elevations were, on average, smaller than those at low elevations. This difference was insignificant, although only marginally. Further work is thus needed to determine whether, or under what conditions, female Mountain Bluebirds at higher elevations do lay smaller clutches.

Unlike the size of her eggs, the size of a female's clutch was unrelated to her physical condition. This suggests that when females at higher elevations are under energetic or nutritional stress, they tend to sacrifice egg size before sacrificing egg number. This may partly explain why clutch size appears to be, at best, only weakly affected by elevation. Sacrificing egg size before clutch size would make sense if egg number affects fitness more strongly than egg size. In most studies of passerines, egg size has not had strong, lasting effects on offspring survival, size, or condition (Christians 2002), although few studies have been conducted under relatively harsh environmental conditions (Smith and Bruun 1998). One could further test for a link between female condition and egg size (and the lack of a link to clutch size) experimentally, by providing supplemental food to females (Arcese and Smith 1988, Källander and Karlsson 1993, Ramsay and Houston 1997) or by warming nest boxes (Nager and van Noordwijk 1992) or, conversely, by increasing energetic or thermoregulatory demands on females. These experiments and additional explorations of how elevation af-

fects egg and clutch size in birds await further study.

ACKNOWLEDGMENTS

Beatrice Beuf, Robert Berry, and the Garber family granted permission to work on their properties. Beatrice Beuf provided living accommodations at the low-elevation site and much moral support. Roberta Young and the staff of Bear Lodge Resort provided accommodations at the high-elevation site. Jerry Eastman built many of the nest boxes used in this study. Dick Newman and the Powderhorn Bluebird Club allowed us access to their nest boxes. Alex Badyaev shared insights and data on the biology of passerines breeding at high elevations. Anne Balogh, Robin Rauch, Tom Risch, and an anonymous reviewer provided comments on the manuscript. Financial support came through grants from Towson University's Faculty Development and Research Committee and Undergraduate Research Committee, and from the National Science Foundation (grants DBI-9732442 and IBN-0316541). To all we are grateful. This paper is dedicated to Mrs. Beatrice Beuf on the advent of her 100th birthday for her ardent, intelligent, and generous support of research on, and conservation of, Wyoming wildlife.

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