

# Effect of altitude on male parental expenditure in Mountain Bluebirds (*Sialia currucoides*): are higher-altitude males more attentive fathers?

L. Scott Johnson · Jessica L. Brubaker ·  
Emilene Ostlind · Susan L. Balenger

Received: 8 April 2006 / Revised: 5 May 2006 / Accepted: 24 May 2006 / Published online: 8 August 2006  
© Dt. Ornithologen-Gesellschaft e.V. 2006

**Abstract** Male investment of time and energy in caring for offspring varies substantially both between and within bird species. Explaining this variation is of long-standing interest to ornithologists. One factor that may affect male care is breeding site altitude, through its effects on climate. The harsher, less predictable abiotic conditions at higher altitudes are hypothesized to favour increased male investment of time and energy in offspring care. We tested this hypothesis by comparing male parental behaviour in Mountain Bluebirds (*Sialia currucoides*) nesting at 1500 and 2500 m a.s.l. in the Bighorn Mountains of Wyoming, USA. We compared rates of prey delivery to nestlings at these two altitudes at two times: 1–2 days after hatching, when females spend much of their time brooding young, and 12–13 days later, when brooding has ended and nestling energy demands are peaking. High-altitude males fed nestlings 18 and 28% more often than low-altitude males early and later in the nestling stage, respectively, but only the difference in late-stage feeding rates were significant. Like males, females at the high site also fed nestlings significantly more often than females at the low site later in the nestling stage (45% difference in feeding rates). Consequently, the proportion of all feeding trips made by males at the high site (40%) did not differ significantly from that at the low site (44%). Parents at the high

altitude may feed nestlings more often to compensate for their greater thermoregulatory costs. Parents may also be attempting to assist nestlings in storing fat and/or attaining a large size and effective homeothermy as quickly as possible to enhance nestling ability to survive bouts of severe weather which are common at high altitudes.

**Keywords** Altitude · Elevation · Mountain Bluebird · Parental care · *Sialia currucoides*

## Introduction

The widespread occurrence of paternal care is one trait that separates birds from all other major animal taxa. Within birds, however, the male's contribution to rearing offspring varies substantially both between and within species. Understanding the factors that affect male expenditure of time and energy caring for young is of long-standing interest in ornithology (e.g. Lack 1968; Bennett and Owens 2002).

Across the animal world, increased parental expenditure is repeatedly associated with more adverse climatic conditions (Clutton-Brock 1991). The breeding ranges of many species of birds lie within or extend into high latitudes and altitudes (Rahn 1977). These high latitudes and altitudes are characterized by persistently colder and windier conditions and increased depth and frequency of snow cover (Hodkinson 2005). High altitudes are further typified by the greater frequency and amounts of rainfall during the breeding season. At both high altitudes and latitudes, the weather is substantially more variable and less predictable than it is elsewhere.

---

Communicated by R. Holberton

---

L. S. Johnson (✉) · J. L. Brubaker · E. Ostlind ·  
S. L. Balenger  
Department of Biological Sciences, Towson University,  
Towson, MD 21252, USA  
e-mail: sjohnson@towson.edu

Various studies have documented patterns of paternal behaviour in birds breeding at high latitudes or altitudes (see Lyon et al. 1987; Badyaev 1993, 1994; Briskie 1995; Hemborg 1999; Hofstad et al. 2002). A substantial body of work has also examined proximate mechanisms (e.g. changes in hormone profiles and sensitivities) that allow individuals to care for offspring while they themselves are under significant stress brought on by difficult climatic conditions (Wingfield and Hunt 2002; Holberton and Wingfield 2003; Wilson and Holberton 2004, and references therein). Still other studies have measured the energetic costs of parental behaviour at high latitudes and altitudes (e.g. Weathers et al. 2002; Piersma et al. 2003).

In contrast, surprisingly few studies have made direct comparisons of paternal behaviour between or within species at different latitudes or altitudes. Such comparisons would show whether male parental expenditure does increase in harsher, less predictable climates and, if so, how (e.g. Briskie 1995; Summers and Nicoll 2004). Latitudinal comparisons may be somewhat difficult to interpret because differences in day length between latitudes could affect how males allocate parental effort across individual days when caring for offspring (Sanz et al. 1998, 2000). Comparisons between individuals at the same latitude but different altitudes avoid this problem.

Badyaev and Ghalambor (2001) compared male provisioning of nestlings in 20 pairs of closely related passerine taxa from Eurasia (primarily subspecies and congeners), where the two members of each taxa pair bred at different altitudes (the breeding latitudes of the taxa compared were not reported). In 16 of the 20 pairwise comparisons, males at the higher-altitude location took on a greater share of the feeding trips to feed nestlings. This comparative analysis focussed on differences between related but genetically divergent taxa breeding at different altitudes. Also of interest, however, is how birds within single populations respond to an altitudinal gradient. Short distances between high and low altitude sites will facilitate gene flow and, thus, changes in behaviour with altitude within populations are most likely to represent facultative responses to differing environmental conditions. To our knowledge, a systematic examination of how parental care varies with altitude within individual populations has been made for only two species of birds. In montane populations of gold-fronted serins (*Serinus pusillus*) and white-winged grosbeaks (*Mycerobas carnipes*), males at higher altitudes both feed nestlings at a greater rate and take on a greater share of the feeding trips than their counterparts at lower altitudes (Badyaev 1993, 1994).

In the study reported here, we tested the hypothesis that, within populations nesting along steep altitudinal gradients, males respond to harsher, less predictable climatic conditions at higher altitudes with increased parental expenditure. Specifically, we compared male parental behaviour between Mountain Bluebirds (*Sialia currucoides*) nesting at a low altitude and their counterparts nesting at a high altitude in the Bighorn Mountains of Wyoming, USA.

### Study species

Mountain Bluebirds are medium-sized (approx. 30 g), socially monogamous passerines that breed at altitudes up to approximately 3800 m a.s.l. in the high plains, deserts, shrub-steppe and mountain meadows of western North America (Power and Lombardo 1996 summarize this species' biology). Mountain Bluebirds nest naturally in pre-formed cavities, such as old woodpecker holes, but readily use human-made nest boxes. Most clutches contain four to eight eggs (Johnson et al. 2006). Females alone incubate the eggs and brood the altricial, heterothermic hatchlings, but both parents provision nestlings with a diet made up almost exclusively of ground-dwelling insects (Power 1980). Parents typically deliver one prey item to the nest at a time. Fledging occurs 19–22 days after hatching, after which offspring are fed by one or both parents for 2–6 weeks. Polygyny is rare or non-existent, but extra-pair mating does occur (Monk 1999).

### Study site and methods

We documented parental behaviour at two sites in the Bighorn Mountains, Sheridan County, Wyoming, USA, during 2004 and 2005. All breeding pairs observed used wooden nest boxes mounted in meadows and pastures. Our low-altitude site was located in the eastern foothills of the mountains, near the town of Big Horn (44°38'N, 107°01'W). Boxes used at this site had a mean altitude of 1485 m a.s.l. (range: 1258–1620 m a.s.l.). Our high-altitude site was located 44 km to the northwest in rolling meadows on a high plateau in the central mountains, near the settlement of Burgess Junction (44°46'N, 107°32'W). Boxes used at this site had a mean altitude of 2507 m a.s.l. (range: 2443–2582 m a.s.l.).

Each box was checked every 1–5 days to determine the date that the first egg appeared and final clutch size. As the expected date of hatching approached, we checked the boxes daily to determine the date that

hatching began, which we termed nestling day 1. At some point between nestling days 5 and 10, we trapped adults in the boxes when they entered to feed nestlings either by tacking a transparent, flexible piece of plastic over the entrance hole on the inside of the nestbox (birds could push their way into the box but could not push their way out) or by using a trapdoor which we operated manually with fishing line. We marked each adult with a unique combination of coloured leg bands. We avoided trapping at a nest <48 h before recording parental behaviour at that nest.

We documented parental behaviour by videotaping nests at two different points during the nestling stage. The first taping session was on nestling day 2 or 3 (the 'Early' stage) when females typically spend much time in nests brooding young. We then taped again on nestling day 14, 15 or 16 ('Late' stage) when young are more feathered, little, if any, brooding occurs and nestling energy demand is likely at its maximum (Weathers 1992). Cameras were located 4–5 m from the nests on tripods. During each taping session, activity at the nests was taped continuously for 4 h, starting an average of 77 min after sunrise (SD: 33 min). Care was taken to maintain approximately the same mean start time for nests observed at the low and high altitudes. We recorded temperatures using a hand-held thermometer at the start and end of each taping session and used the mean of the two readings in subsequent analyses. The number of nestlings in the nest was counted after each taping session. We did not tape during continuous rain or snow.

To control for variation in hesitancy to return to nests after our presence, we began extracting data from each video recording from the time of the male's first feeding visit to the nest (females were usually less hesitant to return than were males). We noted the time that each adult entered the nest and whether it carried a prey item, but we did not record the size or type of prey. All periods that females were in nests for  $\geq 2$  min were designated as time spent brooding.

Females often entered boxes so quickly, especially during the Early stage, that we could not determine whether or not they carried food. It was clear, however, based on instances when we did observe females just before entry, that females sometimes returned to nests without food during the Early stage but very rarely or never (depending on the female) did so during the Late stage. We therefore did not calculate or compare number of female feeding trips or the proportion of feeding trips made by females during the Early stage. In the Late stage, we assumed that females returned to nests with food during each trip unless we saw otherwise. Observations suggested

that males almost never enter nest boxes without food early or late in the nestling stage and so all trips into boxes by males were scored as feeding trips unless we saw otherwise.

The Early stage feeding behaviour of 56 different males was documented: 18 males in 2004 only, 32 males in 2005 only and six males in both years. The Late stage feeding behaviour of 60 males was documented: 19 males in 2004 only, 37 males in 2005 only and four males in both years. For males observed in both years of study, we chose to include data from both years in the analyses. The 2 years of the study differed substantially in climate and apparent food supply. Moreover, most repeat males were living on different territories each year, were always feeding different numbers of nestlings and, with one exception, were paired with different females. The inclusion of only one, randomly chosen year for each repeat male in the analyses did not result in changes in the major conclusions drawn from the complete data set.

#### Measures of parental behaviour and analyses

We first compared the rate at which individuals at the two altitudes visited nests to feed nestlings and used this as an index of the overall time and energy spent gathering prey for nestlings. However, because brood sizes differed among nests, rate of feedings *per nestling* was eventually chosen as our primary index of parental effort. We also compared the proportion of the pair's total feeding trips that were made by the male. Finally, for Early stage observations, we compared the proportion of time that females spent brooding at each altitude and the duration of the brooding bouts (using mean bout duration for individual females in the analyses).

Feeding rates and brooding bout durations were compared using analysis of variance (ANOVA) with year and altitude as the main factors. We calculated and reported least-squares means for each factor adjusted for the effects of the other factor: for example, feeding rate at each altitude adjusted for the effects of year. We compared these least-squares means using *t*-tests (results are equivalent to the *F* test from the ANOVA). The proportion of time that females spent brooding and the proportion of feeding trips made by males were compared using generalized linear models with binomial errors and logit links. In the analysis of the male proportion of feeding effort in the Late period, the number of male feeding trips was used as the dependent (response) variable and the total number of trips (male + female) was used as the binomial denominator. In the analysis of the proportion of time

females spent brooding in the Early period, we used total minutes that the female spent brooding as the dependent variable and total minutes of observation as the binomial denominator. We tested the significance of predictor variables by the change in deviance of the model with and without the predictors, using a chi-square approximation. In all analyses, interactions are reported only when significant. All means, adjusted and otherwise, are reported  $\pm 1$  SE unless noted. All analyses were conducted using SAS, ver. 8.1 (SAS Institute 1999).

## Results

### Early stage

We observed nine and 16 pairs during the Early stage at the low-altitude site in 2004 and 2005, respectively, compared to 15 and 22 pairs at the high-altitude site. In 2004, the temperature during the Early stage observations averaged 14°C at the low site ( $\pm 4^\circ$  SD; range: 6–20°C) and 8.5°C ( $\pm 3^\circ$ ; 5–16°C) at the high site. In 2005, temperatures were, by chance, cooler than normal when most low-altitude nests had Early stage nestlings, but they were unseasonably warm when most high-altitude nests had such nestlings, several weeks later. As a result, mean temperatures during observations at the low and high sites were nearly equivalent, specifically 12°C ( $\pm 4^\circ$ ; 9–26°C) at the low site and 13°C ( $\pm 2^\circ$ ; 9–18°C) at the high site.

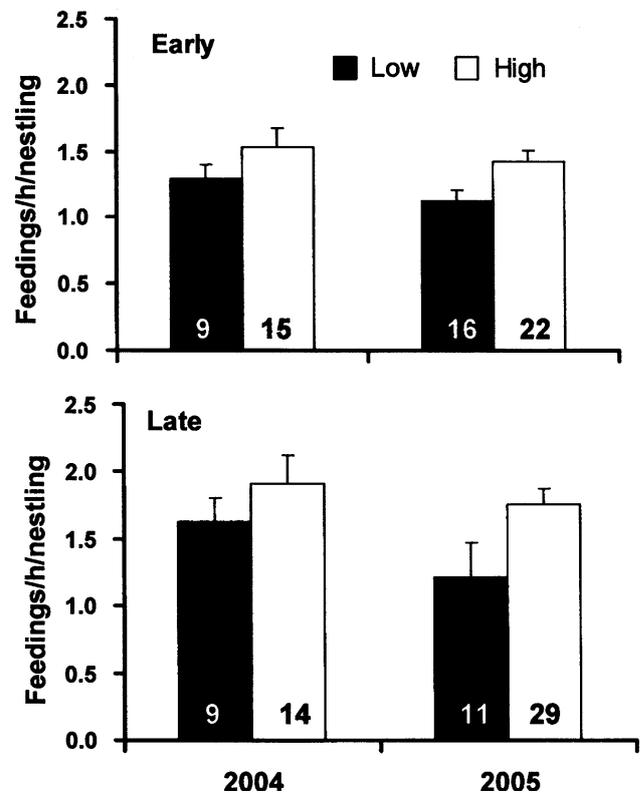
Across years and altitudes, the percentage of time that females spent brooding was negatively related to the temperature during observations ( $r = -0.38$ ,  $n = 62$ ,  $P = 0.002$ ); however, the mean duration of brooding bouts was not ( $r = -0.07$ ,  $n = 62$ ,  $P = 0.56$ ). Because temperature during the Early stage differed between altitudes in 1 year but not the other (see above), we compared brooding time at the two altitudes in each year separately. In 2004, when temperatures during the Early stage were colder at the high site than at the low site, females spent a greater proportion of their time brooding, on average, at the high site than at the low site (low:  $60 \pm 4\%$ ,  $n = 9$ ; high:  $66 \pm 3\%$ ,  $n = 15$ ). However, the difference equated to only 3.6 min per hour and was not significant ( $\chi^2 = 1.34$ ,  $df = 1$ ,  $P = 0.25$ ). The mean duration of brooding bouts did not differ between altitudes (low:  $843 \pm 156$  min; high:  $750 \pm 67$  min;  $t_{10,9} = 0.54$ ,  $P = 0.60$ ). In 2005, when temperatures during the Early stage were similar at the two altitudes, the percentage of time that females spent brooding at the two altitudes was also similar (low:  $64 \pm 3\%$ ,  $n = 16$ ; high:  $62 \pm 3\%$ ,  $n = 22$ ;  $\chi^2 = 0.29$ ,  $df = 1$ ,

$P = 0.29$ ), as was the mean duration of brooding bouts (low:  $725 \pm 85$  min; high:  $703 \pm 67$ ;  $t_{36} = 0.23$ ,  $P = 0.82$ ).

On average, males at the high site visited nests more often to feed young than did males at the low site but the difference was not significant (low:  $6.6 \pm 0.5$  feedings/h; high:  $7.2 \pm 0.4$ ;  $t_{58} = -1.07$ ,  $P = 0.29$ ). However, brood sizes of pairs observed at the high site were, on average, smaller than those at the low site (low:  $\bar{x} = 5.4$ , range: 3–7, SD: 0.91; high: 5.1, 3–6, 0.92), and there was a strong tendency for males at the high site to provision more on a per-nestling basis than did males at the low site (Fig. 1; low:  $1.24 \pm 0.09$  feedings/h per nestling; high:  $1.48 \pm 0.07$ ;  $t_{58} = -1.96$ ,  $P = 0.055$ ). The per-nestling rate at which males visited nests to feed young during the Early stage did not differ significantly between years (2004:  $1.4 \pm 0.1$  feedings/nestling per hour; 2005:  $1.3 \pm 0.1$ ;  $t_{58} = 0.85$ ,  $P = 0.40$ ).

### Late stage

We observed nine and 14 pairs during the Late stage at the low-altitude site in 2004 and 2005, respectively,



**Fig. 1** Per nestling feeding rates of male Mountain Bluebirds breeding at a low and a high altitude in Wyoming's Bighorn Mountains. Data are from observations made both early (*upper panel*) and late (*lower panel*) in the nestling stage. Shown are means ( $\pm$ SE) with the number of nests observed embedded in the bars. For statistical comparisons, see text

compared to 11 and 29 pairs at the high-altitude site. The temperature during the observations at the low site averaged 17 and 22°C in 2004 and 2005, respectively, compared to 9° and 12°C at the high site.

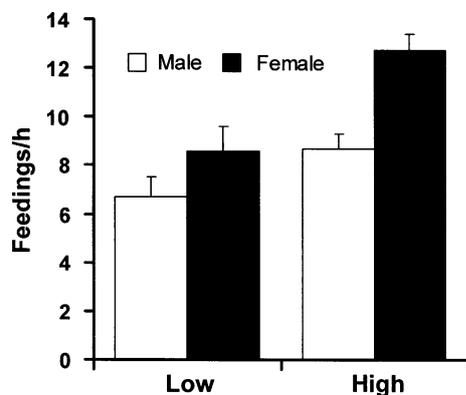
Males at the high site visited nests significantly more often to feed young than did males at the low site (Fig. 1; low:  $6.7 \pm 0.8$ ; high:  $8.6 \pm 0.6$ ;  $t_{59} = -2.01$ ,  $P = 0.049$ ). Mean brood sizes of pairs that we observed at the two altitudes were similar (low  $\bar{x}$ : 4.9, range: 3–6, SD: 0.91; high: 5.0, 3–6, 0.92), and males at the high site also provisioned significantly more on a per-nestling basis than did males at the low site (Fig. 1; low:  $1.43 \pm 0.16$  feedings/h per nestling; high:  $1.83 \pm 0.12$ ;  $t_{59} = -2.06$ ,  $P = 0.04$ ). The per-nestling rate at which males fed broods during the Late state did not differ significantly between years (2004:  $1.8 \pm 0.2$  feedings/nestling per hour; 2005:  $1.5 \pm 0.1$ ;  $t_{59} = 1.44$ ,  $P = 0.15$ ).

Like males, females at the high site visited nests to feed young at a significantly greater rate than did females at the low site (low:  $8.7 \pm 1.0$  feedings/h; high:  $12.7 \pm 0.7$ ;  $t_{59} = -3.18$ ,  $P = 0.002$ ). Female feeding effort per nestling was also significantly greater at the high site (low:  $1.82 \pm 0.18$  feedings/h per nestling; high:  $2.63 \pm 0.13$ ;  $t_{59} = -3.55$ ,  $P < 0.001$ ).

The male's feeding effort relative to that of his mate, as measured by the percentage of all feeding trips made by the male, did not differ significantly between altitudes (means: low:  $44 \pm 3\%$ ; 2005:  $40 \pm 2\%$ ;  $\chi^2 = 0.71$ ,  $df = 1$ ,  $P = 0.39$ ; see also Fig. 2).

## Discussion

Late in the nestling stage, when nestling energy demands are the highest, male Mountain Bluebirds fed nestlings 28% more often at 2500 m a.s.l. on a high



**Fig. 2** The rate at which male and female Mountain Bluebirds delivered food to broods late in the nestling stage at a low- and a high-altitude site over 2 years. Shown are least-squares means (+SE) adjusted for effects of year

mountain plateau than they did at an altitude 1000 m lower in the warmer foothills. High-altitude males also fed nestlings more often than their low-altitude counterparts shortly after hatching, but the difference in feeding rates was less (18%) and marginally insignificant.

We suggest two reasons for a smaller difference in male feeding rates shortly after hatching than later in the nestling stage. First, as in all passerines, hatchling bluebirds are quite small and hence will be satiated more quickly than larger, later-stage nestlings. This may limit the degree to which males can increase the rate at which they feed recently hatched nestlings. Second, contrary to expectations, females at the high site did not spend significantly more time brooding nestlings than females at the low site. In part, this was the result of unusual weather patterns in 2005 that caused temperatures to be nearly equivalent at the two altitudes on the days that most nests had newly hatched young. Not surprisingly, females at the two altitudes spent nearly equal amounts of time brooding in 2005. However, even in 2004, when temperatures during observations averaged 5°C colder at the high-altitude site, females at this site spent an average of only 3.6 more minutes brooding each hour than low-altitude females. In other words, females at the high site had about as much time to help males gather food for nestlings as did their counterparts at low altitudes (although we could not confirm that they did so).

The apparent increase in parental expenditure by males at high altitudes may have an interesting ramification: it may restrict male ability to pursue extra-pair matings, thereby affecting the intensity of sexual selection (Badyaev 1997; Badyaev and Ghalambor 2001). This assumes, however, that the rate at which a male provisions a brood correlates closely with the total time and energy that he spends foraging for the brood. If prey are more readily available at the high elevation, this would reduce search times and shorten foraging trips (e.g. Tremblay et al. 2005), possibly allowing high-altitude males to increase feeding rates without increasing the time and energy they devote to feeding nestlings.

Based on a comparison of phylogenetically paired taxa (primarily subspecies and congeners) nesting at different altitudes, Badyaev and Ghalambor (2001) concluded that male participation in nestling provisioning is greater at higher altitudes. Our within-population comparison using Mountain Bluebirds supports this contention. However, in their analysis, Badyaev and Ghalambor (2001) used the *proportion* of feeding trips made by the male as their primary indicator of

male parental expenditure rather than male feeding rate. Our results show that the proportion of feeding trips made by males will sometimes be a poor indicator of the male's actual parental investment. In our study, males at the higher altitude fed nestlings more often late in the nestling stage, but females did so as well. Consequently, the mean proportion of feeding trips made by males at the low and the high site were, on average, quite similar (44 and 40% of trips, respectively). A lack of an altitudinal effect on male share of the feeding effort is also evident from two previous studies on Mountain Bluebirds: males reportedly make about 40% of the feeding trips in both a low-altitude (approx. 1600 m a.s.l.) population in Montana and a high-altitude (approx. 3000 m a.s.l.) population in Colorado (Power 1980; Monk 1999). Moreover, the males of the high-altitude subspecies of water pipits (*Anthus spinoletta*) and pied wagtails (*Motacilla alba*) that Badyaev and Ghalambor (2001) included in their comparative analysis also appear to feed young more often, but not proportionately more often, than males of the low-altitude subspecies (see their Table 2).

The use of the proportion of feeding trips made as an index of male parental investment at low and high altitudes can be problematic in a second way. For instance, one can imagine a scenario in which males and females make an average of six and seven trips to nests per hour, respectively, at low altitudes but five and four trips, respectively, at high altitudes. Here, the proportion of feeding trips made by males is greater at the high altitude (56 vs. 46%), but the male's rate of feeding, and hence possibly his overall parental expenditure, is actually less (six vs. five feeding trips per hour). This appears to be the case in the high-altitude populations of grey wagtails (*M. cinerea*), brown accentors (*Prunella fulvescens*) and goldcrests (*Regulus regulus*) included in Badyaev and Ghalambor's analysis (2001). In sum, we suggest that male parental response to the high-altitude environment may be more variable than Badyaev and Ghalambor (2001) asserted.

Further work is necessary to understand why parent Mountain Bluebirds at our high-altitude site feed nestlings at higher rates than those at the low-altitude site, especially later in the nestling stage. While the direct effect of climate on the birds, especially nestlings, likely plays a role, other factors could also have an impact. For example, high-altitude parents may feed young more often simply because prey are more abundant or accessible at higher altitudes. Alternatively, prey at high altitudes may be of lower quality than prey at high altitudes prompting high-altitude parents to feed nestlings more prey to compensate.

That nestlings at our higher altitude site grow at a rate equal to, but not faster than, nestlings at our low site (Johnson et al., unpublished data) is consistent with this suggestion. However, it is also possible that high-altitude prey are of the same or greater quality than low-altitude prey but that the extra energy that high-altitude nestlings get as a result of being fed more and/or better prey is channeled not into growth but rather into thermoregulation (Weathers 1992; Hoset et al. 2004).

In addition to meeting the greater thermoregulatory costs of nestlings, increased provisioning of offspring at high altitudes may be linked to the harsher, less predictable abiotic conditions at those altitudes in other ways. For example, individuals at the high-altitude site can experience bouts of harsh weather at almost any point in the breeding season, with freezing temperatures, high winds and snowfall (see Hendricks and Norment 1992 and references therein). Such weather is expected to both increase nestling thermoregulatory costs while simultaneously reducing parental foraging success as a result of reduced exposure and activity levels of ground-dwelling insects (Avery and Krebs 1984; Hodkinson 2005). Perhaps to maximize nestling ability to survive unpredictable, stressful, lean periods, high-altitude parents feed nestlings at a high rate when conditions are favourable to assist nestlings in storing fat, growing feathers and/or attaining a large size and hence effective homeothermy as quickly as possible (Clark 1982).

We are aware of only two other comparisons of parental provisioning within populations nesting along steep altitudinal gradients. Badyaev (1993, 1994) compared the parental behaviour of gold-fronted serins nesting at 2000 and 2700 m a.s.l. and white-winged grosbeaks nesting at 2700 and 3500 m a.s.l. in Russia's Phansky Mountains. In both species, males at the higher altitude not only fed nestlings at a higher rate but also took on a greater share of the feedings. Why males at higher altitudes increase their parental expenditure relative to females in these two species but not in Mountain Bluebirds is unclear. The serins and grosbeaks do, however, differ from the bluebirds in several potentially influential respects. For example, both the serins and grosbeaks build open-cup nests, and thus their nestlings are more exposed to cold and wind. Also, nestling diets in both of these species consist primarily of plant material (e.g. berries, seeds, leaves), not insect prey. A clear understanding of whether or how these and other traits affect parental response to increased altitude within populations will require additional studies on a variety of species.

## Zusammenfassung

Der Einfluss von Meereshöhe und Männchenaufwand beim Berghüttensänger (*Sialia currucoides*): Sind Männchen in größerer Höhe aufmerksamere Väter?

Die Beteiligung des Männchens am Brutgeschäft variiert innerhalb und zwischen verschiedenen Vogelarten sehr stark und ist seit langem im Blickpunkt der Ornithologen. Ein Einfluss kann, über das Klima, die Meereshöhe sein. Die rauerer und unvorhersehbareren abiotischen Faktoren in größerer Meereshöhe könnten die Brutbeteiligung der Männchen erhöhen. Wir untersuchten dies am Berghüttensänger (*Sialia currucoides*), der in den

Bighorn Mountains von Wyoming, USA, bei 1,500 und 2,500 mNN brütet. Wir verglichen die Nestlingsnahrung auf beiden Höhenstufen im Nestlingsalter von 1–2 Tage, wenn die Weibchen die meiste Zeit mit Hudern verbringen, und im Alter von 12–13 Tagen, wenn nicht mehr gehudert wird und der Nahrungsbedarf für die Nestlinge maximal ist. Die Männchen in großer Meereshöhe fütterten 18% bzw. 28% häufiger als Männchen in tieferen Lagen, wobei aber nur der Unterschied bei den späten Nestlingen signifikant ist. Auch die Weibchen fütterten in größerer Meereshöhe häufiger (um 45% mehr) als in tieferen Lagen. Daraus ergibt sich, dass der Anteil der Männchen in beiden Meereshöhen nicht verschieden war (40% in großer Meereshöhe gegenüber 44% geringerer Meereshöhe). Ursachen für die in höheren Lagen häufigeren Fütterungen dürften sein, dass die höheren thermoregulatorischen Kosten der Nestlinge erfüllt werden und dass die Nestlinge bei der Anlage von Fettreserven, beim Erreichen einer größeren Körpergröße und einer effektiven Homöothermie unterstützt werden, um so rasch wie möglich Witterungseinbrüchen, wie sie in großer Meereshöhe häufig sind, überleben zu können.

**Acknowledgments** Beatrice Beuf, Robert Berry and the Garber family granted permission to work on their property. Dick Newman, the Powderhorn Bluebird Club and Bob Berry allowed us access to their nest boxes at the low-elevation site. Harald Golden of the U.S. Forest Service allowed us access to nest boxes at our high-elevation site and provided logistical support. Beatrice Beuf provided living accommodations at the low-altitude site and much moral support. Roberta Young and the staff of Bear Lodge Resort provided accommodations at the high-altitude site. Jerry Eastman built many of the nest boxes used in this study. Bonnie Johnson and Nell MacCarty assisted in the field. We benefited from extensive discussions with Alex Badyaev regarding his work in Russia. Anne Balogh, Clint Otto, Don Forester, Quent Lupton and two anonymous reviewers provided comments, which improved the manuscript considerably. 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 research complies with the laws of the United States of America.

## References

- Avery MI, Krebs JR (1984) Temperature and foraging success of great tits *Parus major* hunting for spiders. *Ibis* 126:33–38
- Badyaev AV (1993) Breeding biology of the gold-fronted Serin (*Serinus pusillus*) in a subalpine zone of Pamir Mountains. *Biol Sci (Biol Nauk)* 348:89–99
- Badyaev AV (1994) Breeding biology of White-winged Grosbeak (*Mycerobas carripes*) in the Pamir Mountains. *Bull MOIP (Biol Div)* 99:20–28
- Badyaev AV (1997) Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oecologia* 111:357–364
- Badyaev AV, Ghalambor CK (2001) Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology* 82:2948–2960
- Bennett PM, Owens IPF (2002) Evolutionary ecology of birds: life histories, mating systems, and extinction. Oxford University Press, Oxford
- Briskie JV (1995) Nesting biology of the yellow warbler at the northern limit of its range. *J Field Ornithol* 66:531–543
- Clark L (1982) The development of effective homeothermy and endothermy by nestling starlings. *Comp Biochem Physiol* 73A:253–260
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Hemborg C (1999) Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. *J Anim Ecol* 68:429–436
- Hendricks P, Norment CJ (1992) Effects of a severe snowstorm on subalpine and alpine populations of nesting American pipits. *J Field Ornithol* 63:331–338
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol Rev* 80:489–513
- Hofstad E, Espmark Y, Moksnes A, Haugen T, Ingebrigtsen M (2002) The relationship between song performance and male quality in snow buntings (*Plectrophenax nivalis*). *Can J Zool* 80:524–531
- Holberton RL, Wingfield JC (2003) Modulating the corticosterone stress response: a mechanism for balancing individual risk and reproductive success in arctic-breeding sparrows? *Auk* 120:1140–1150
- Hoset KS, Espmark Y, Moksnes A, Haugen T, Ingebrigtsen M, Lier M (2004) Effect of ambient temperature on food provisioning and reproductive success in snow buntings *Plectrophenax nivalis* in the high arctic. *Ardea* 92:239–246
- Johnson LS, Ostlind E, Brubaker JL, Balenger SL (2006) Changes in egg size and clutch size with elevation in a Wyoming population of mountain bluebirds. *Condor* 108: (in press)
- Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London
- Lyon BE, Montgomerie RD, Hamilton LD (1987) Male parental care and monogamy in snow buntings. *Behav Ecol Sociobiol* 20:377–382
- Monk DS (1999) Differential allocation of parental care in free-ranging Mountain Bluebirds. PhD thesis, Indiana University, Bloomington, Ind.

- Piersma T, Lindstrom A, Drent RH, Tulp I, Jukema J, Morrison ROG, Reneerkens J, Schekkerman H, Visser GH (2003) High daily energy expenditure of incubating shorebirds on high arctic tundra: a circumpolar study. *Funct Ecol* 17:356–362
- Power HW (1980) The foraging behaviour of Mountain Bluebirds, with emphasis on sexual foraging differences. *Ornithol Monogr* 28
- Power HW, Lombardo MP (1996) Mountain Bluebird (*Sialia currucoides*). In: Poole A, Gill F (eds) The birds of North America, No. 222. The Birds of North America, Philadelphia, Pa.
- Rahn H (1977) Adaptation of the avian embryo to altitude. In: Paintal AS, Gill-Kumar P (eds) Respiratory adaptations, capillary exchange and reflex mechanisms. Vallabhbhai Patel Chest Institute, University of Delhi, pp 94–105
- Sanz JJ, Tinbergen JM, Orell M, Rytönen S (1998) Daily energy expenditure during brood rearing of great tits *Parus major* in northern Finland. *Ardea* 86:101–107
- Sanz JJ, Tinbergen JM, Moreno J, Orell M, Verhulst S (2000) Latitudinal variation in parental energy expenditure during brood rearing in the great tit. *Oecologia* 122:149–154
- SAS Institute (1999) SAS/STAT user's guide, Release 8.1. SAS Institute, Cary, N.C.
- Summers RW, Nicoll M (2004) Geographical variation in the breeding biology of the purple sandpiper *Calidris maritima*. *Ibis* 146:303–313
- Tremblay I, Thomas D, Blondel J, Perret P, Lambrechts MM (2005) The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. *Ibis* 147:17–24
- Weathers WW (1992) Scaling nestling energy requirements. *Ibis* 134:142–153
- Weathers WW, Davidson CL, Olson CR, Morton ML, Nur N, Famula TR (2002) Altitudinal variation in parental energy expenditure by white-crowned sparrows. *J Exp Biol* 205:2915–2924
- Wilson CM, Holberton RL (2004) Individual risk versus immediate reproductive success: a basis for latitudinal differences in the adrenocortical response to stress in yellow warblers (*Dendroica petechia*). *Auk* 121:1238–1249
- Wingfield JC, Hunt KE (2002) Arctic spring: hormone-behavior interactions in a severe environment. *Comp Biochem Physiol B* 132:275–286