

Parental Effort in Relation to Structural Plumage Coloration in the Mountain Bluebird (*Sialia currucoides*)

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Abstract

Indicator models of sexual selection suggest that costly ornaments signal reliable information regarding an individual's quality to potential mates. In species that produce altricial offspring, the amount of parental care provided by both males and females can impact reproductive success. The Good Parent Hypothesis proposes that ornamentation in biparental species can act as an honest signal of parental ability to potential mates. We tested this hypothesis using the mountain bluebird (*Sialia currucoides*), a sexually dichromatic, socially monogamous species in which both sexes have structurally based ornamental plumage coloration. A male's plumage color predicted neither the rate at which it provisioned nestlings nor brood growth rate. The same was true for females. We also found no indication of assortative mating by color or body condition. Feeding rates within pairs were positively correlated, which we suggest may be due to pairs responding similarly to the perceived needs of nestlings or to local area prey availability. In sum, our results do not support the Good Parent Hypothesis as an explanation for the evolution of ornamental plumage color in mountain bluebirds. We suggest alternative hypotheses for the evolution of ornamental plumage color in this species.

Introduction

Indicator models of sexual selection propose that costly ornaments evolve to reliably signal an individual's quality to potential mates (Zahavi 1975; Andersson 1994). In socially monogamous species with biparental care, it has been argued that both males and females should benefit from discriminating between potential mates (Burley 1977; Ligon 1999; Amundsen 2000; Amundsen & Pärn 2006). In particular, males and females in such species should benefit by evaluating ornamental traits that signal parental quality (the Good Parent Hypothesis: Heywood 1989; Hoelzer 1989).

Ornamental plumage color is common among the many species of birds that are both socially monogamous and biparental. Male plumage color, however,

has been found to be significantly and positively correlated with the rate of nestling provisioning in just two species of monogamous, biparental birds: the house finch (*Carpodacus mexicanus*; Hill 1991, 2002) and the cattle egret (*Bubulcus ibis*; Krebs et al. 2004). Although a few other studies have reported a trend toward more colorful males provisioning nestlings at higher rates (Palokangas et al. 1994; Sætre et al. 1995; Keyser & Hill 2000; Siefferman & Hill 2003), most studies have reported no relationship between color and provisioning effort (Sundberg & Larsson 1994; Wiehn 1997; Smiseth et al. 2001; Perrier et al. 2002), or a negative relationship (Badyaev & Hill 2002; Jawor & Breitwisch 2004, but see Linville et al. 1998).

Few studies have tested for a relationship between *female* plumage coloration and parental effort. Female rump color is weakly, but significantly,

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associated with maternal provisioning rate in eastern bluebirds (*Sialia sialis*; Siefferman & Hill 2005a). In northern cardinals (*Cardinalis cardinalis*), provisioning rate correlates with female underwing color (Linville et al. 1998) as well as the size and darkness of the face mask (Jawor et al. 2004). Studies of blue-throats (*Luscinia svecica*) and European starlings, (*Sturnus vulgaris*) found no correlation between female color and provisioning rate (Rohde et al. 1999; Smiseth & Amundsen 2000; Komdeur et al. 2005).

Much work is still needed to establish to what extent and under what conditions male and female ornaments signal individual quality in socially monogamous bird species. To this end, we studied the function of ornamental plumage color in a socially monogamous, biparental passerine bird, the mountain bluebird (*Sialia currucoides*). Males, and to a lesser extent females, of this species are characterized by striking structural UV-blue plumage (Shawkey et al. 2006). Our primary focus for the current study was to determine whether color predicts rates at which individuals provision nestlings. We also looked for relationships between color and age and assortative mating by color as potential ways sexual selection could be acting on plumage color in this species (Andersson 1994).

Methods

Study Species

Mountain bluebirds are medium-sized (approx. 30 g) thrushes that breed at elevations up to 3800 m above sea level (a.s.l.) in western North America (biology summarized by Power & Lombardo 1996). This species nests naturally in pre-formed tree cavities but readily uses human-made nest boxes. Clutches typically contain four to eight eggs. Only females incubate eggs and brood the altricial, heterothermic hatchlings. Both parents, however, feed nestlings a diet composed primarily of ground-dwelling insects (Power 1980). Young fledge 19–22 days after hatching, and are fed by parents for 2–6 more weeks.

Males exhibit brilliant structural UV-blue plumage over their entire dorsal side, with the rump being the bluest and brightest region of the body. Male wing and tail feathers are also blue. The male upper breast is a pale blue, fading downwards into mixtures of bluish-gray and white feathers. In females, rump, tail, and primary wing feathers are pale blue, while head, back and breast feathers are rusty-brown and gray.

Study Site and General Methods

We conducted this study on a population of bluebirds occupying the Bighorn Mountains of north-central Wyoming, USA. We observed birds in 2004 and 2005 at two sites, a low-elevation site (1258–1620 m a.s.l.) in the eastern foothills of the mountains (44°38'N, 107°01'W) and a high-elevation site (2443–2582 m a.s.l.) on a mountain plateau (44°46'N, 107°32'W; see Johnson et al. 2006 for a more detailed description of the two sites). All observed pairs used nest boxes. Some pairs attempt to raise two broods in a season; however, we collected data during first complete breeding attempts only. We checked boxes every 1–5 days to determine the date that egg-laying began, clutch size, and hatching date (nestling day 1).

We trapped adults as they entered boxes to feed nestlings 5–10 days after hatching began. We avoided trapping birds <48 h before documenting parental behavior at a particular nest. Upon capture, we marked individuals with a unique combination of colored leg bands (excluding blue and purple), and a numbered aluminum band. We collected 10–15 rump feathers from males and females for color analysis, and then weighed individuals to the nearest 0.1 g and measured the length of their right wing cord to the nearest 1 mm. As an index of body condition, we used the residuals from a regression of weight against wing length. Female mountain bluebirds steadily lose weight throughout the nestling stage (0.24 g/d, on average in our study; see also Merkle & Barclay 1996). Therefore, for females, we included number of days after hatching that the female was captured as a variable in the regression. We weighed each nestling on day 2 and again on day 14 when nestlings are at or near their peak weight. As an index of nestling growth rate, we used mean daily increase in weight from day 2 to day 14 (g/d), a period during which weight gain is approximately linear (Herlugson 1983). We used brood mean growth rate in analyses to avoid pseudoreplication. Mean nestling weight on day 14 was closely correlated with brood growth rate ($r = 0.91$, $p < 0.001$, $n = 65$); thus we analyze and report only growth rates.

Parental Care

We documented rates at which adults provisioned nestlings by videotaping nests at two points during the nestling stage. We taped first on nestling day 2 or 3, which we term the 'Early' stage, when

females typically spend >50% of their time brooding young. We taped again on nestling day 14, 15 or 16, which we term the 'Late' stage, when young are more feathered, little to no brooding occurs, and nestling energy demand is highest (Weathers 1992). We did not tape during continuous rain or snow. Cameras were located 4–5 m from nests on tripods. We taped activity at nests continuously for 4 h, starting an average of 77 min after sunrise (SD: 33 min). We counted the number of nestlings in the nest after each taping session. Nests included in analyses contained between three and seven nestlings.

To control for variation in hesitancy to return to nests after our presence, we began extracting data from each video recording with the male's first feeding visit to the nest (females were usually less hesitant to return than were males). Direct observations of parents foraging for nestlings, and images of parents on videotapes indicated that parents usually deliver only one prey item per visit. On occasion, however, we did observe birds with an unusually large beakful of food suggesting that two or more items were being delivered. We did not attempt quantify the number or type of prey delivered.

Females often entered boxes so quickly, especially during the Early stage, that we could not determine whether 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 Early stage observations but very rarely or never did so (depending on the female) during the Late stage observations. We therefore did not quantify female provisioning 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 at any time during the nestling stage, so all male trips were scored as feeding trips unless we saw otherwise. All periods that females remained in nests for ≥ 2 min were designated as time spent brooding.

Color Analysis

We measured reflectance spectra across the avian visual range (300–700 nm) for rump feathers using an Ocean Optics S2000 spectrometer (Dunedin, FL, USA). Spectrometer readings produce a spectral curve that represents percent reflectance for each color wavelength relative to a white standard

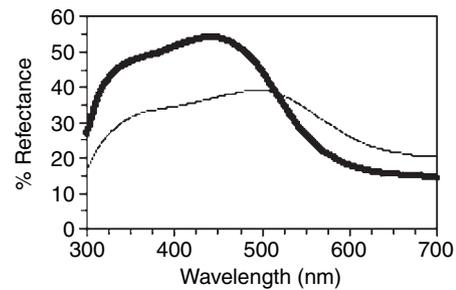


Fig. 1: Average reflectance curves for male rump (—) and female (---) rump feathers. Results are from 120 males and 111 females.

(Cuthill et al. 1999; Montgomerie 2006; Fig. 1). We taped each individual's rump feathers to non-reflective black paper in an overlapping manner that mimics the bird's natural plumage (following Siefferman & Hill 2003, 2005a; see also Perrier et al. 2002; Quesada & Senar 2006). We then recorded feather spectral reflectance from five randomly chosen locations using a bifurcated micron fiber optic probe mounted at a 90° angle in a metal sheath. We used average values from the five readings to produce an individual's spectral curve.

We focused on three measures of color: (1) *hue*, the wavelength at which the greatest amount of light was reflected, which corresponded to the highest peak in the spectral curve, (2) *chroma*, a measure of spectral purity, which we define as the proportion of the total reflectance contained within the ultraviolet (300–400 nm) and blue (401–512 nm) regions combined, and (3) *total brightness*, which is the total area of light being reflected relative to a white standard (a measure of brightness that is independent of hue).

Our three measures of rump color showed extensive colinearity both in males and in females (Table 1). We therefore used principal components analysis to generate color scores that summarize the variance in our color measures (Montgomerie 2006). For males, the first principal component explained 66% of the overall variance in rump coloration (Table 2). Males with high PC1 scores were brighter, had a hue shifted more toward UV, and had more of their color concentrated within the UV-blue range (greater UV-blue chroma). For females, the first principal component explained 74% of the variance in coloration (Table 2). As with males, females with high PC1 scores were brighter, had a more UV-shifted hue, and had a greater concentration of color in the UV-blue range.

Table 1: Associations between different measures of the color of rump feathers of male and female mountain bluebirds. Shown are Pearson's correlation coefficients (*r*) with *p* values in italics below

	Male rump color (<i>n</i> = 120)		Female rump color (<i>n</i> = 111)	
	Total brightness	UV + blue chroma	Total brightness	UV + blue chroma
UV + blue chroma	0.57 <i><0.0001</i>		0.59 <i><0.0001</i>	
Hue	-0.16 <i>-0.07</i>	-0.71 <i><0.0001</i>	-0.39 <i><0.0001</i>	-0.84 <i><0.0001</i>

Table 2: Results of principal components analyses on measures of male and female rump feather coloration. Shown are eigenvalues, the proportion of the variance in coloration explained, and factor loadings for each of the three color variables for the first principal component (PC1) for each sex

	Eigenvalue	Proportion of variance	Color measure	Factor loading
Male PC1	1.99	0.66	Total brightness	0.679
			UV + blue chroma	0.953
			Hue	-0.790
Female PC1	2.23	0.74	Total brightness	0.737
			UV + blue chroma	0.954
			Hue	-0.883

Statistical Analyses

As described in detail elsewhere (Johnson et al. 2007), we found differences in provisioning rates and nestling growth rates between years and/or elevations. We also found differences in plumage color characteristics for both males and females between years and/or elevations (data not shown for brevity). We therefore standardized each of these parameters to a mean of 0 and a standard deviation of 1 at each elevation and within each year. Thus our analyses ask whether, within a particular environmental and social regime, more colorful individuals provisioned nestlings at a greater rate than less colorful individuals.

We used Pearson's correlations to test for relationships between color scores and: (1) individual size and condition, (2) Early and Late nestling stage provisioning rates (feedings per nestling per hour), (3) share of the pair's total provisioning effort (percent of total feedings) during the Late stage, and (4) brood growth rate. We also tested for relationships between color scores and feeding rates unadjusted for the number of nestlings in the nest (i.e. feedings

per hour). Measures of the absolute number of feedings per hour and feedings per nestling per hour were strongly and positively correlated (males Early: $r = 0.81$, $p < 0.0001$, $n = 62$; males Late: $r = 0.85$, $p < 0.0001$, $n = 64$; females Late: $r = 0.74$, $p < 0.0001$, $n = 64$). Furthermore, results from analyses using feedings per nestling per hour were qualitatively identical to results from analyses using feedings per hour. Thus we report only the latter for brevity. In the analysis of brood growth rate, we used residuals from a regression of nestling growth against brood size on nestling day 2 to control for the effects of brood size on growth rate.

When testing for correlations between color and feeding rate, sample sizes ranged from 56 to 64, depending on sex and time of the nestling stage. This gave us a 62–68% chance of detecting a 'medium' effect size (Cohen 1988), i.e. finding that at least 9% of the variation in feeding effort could be attributed to color ($r = 0.3$). Likewise, when testing for a correlation between parent color and nestling growth rate, our sample sizes of 41 for females and 47 for males gave us a 49% and a 55% chance, respectively, of detecting the same effect size. We report the exact power of tests where *p* was between 0.05 and 0.20.

We captured some individuals in both years of study. We used paired *t*-tests to determine whether an individual's color scores changed consistently with age.

All analyses were made using SAS v. 9.1. All means are reported ± 1 SE unless noted.

Results

Coloration and Individual Size, Condition, and Age

We found a weak but significant correlation between male wing length and color score. No other measure of male or female size or condition was correlated with color (results summarized in Table 3).

For the 16 males captured in both years of this study, the mean change in rump color score from 2004 to 2005 did not differ significantly from 0 (\bar{x} change in color score: $+0.14 \pm 0.27$, $t_{15} = 0.53$, $p = 0.60$). For the 10 females captured in both years, rump color score showed a tendency to increase from 2004 to 2005 (\bar{x} change in color score: $+0.81 \pm 0.40$, $t_9 = 1.99$, $p = 0.08$).

Mating was random with respect to plumage coloration and body condition, i.e. we found no evidence of assortative mating. Neither the color ($r = -0.09$, $p = 0.34$, $n = 105$) nor the body condition of

Table 3: Associations between rump color score (first principal component from a principal components analysis on three measures of color) and measures of size and condition in male and female mountain bluebirds. Shown are Pearson's correlation coefficients (*r*) with sample sizes (*n*) provided below in parentheses

	Weight	Wing length	Body condition
Male color	0.06 (116)	0.24* (119)	0.01 (109)
Female color	0.14 (102)	0.11 (110)	0.11 (101)

**p* < 0.01

mates (*r* = 0.11, *p* = 0.27, *n* = 94) were significantly related.

Parental Provisioning – Early Nestling Stage

Male rump color was unrelated to nestling provisioning rate shortly after nestlings hatched (*r* = 0.09, *p* = 0.49, *n* = 60; Fig. 2). Male provisioning rate showed a moderately strong, negative association with the color score of its mate (*r* = -0.48, *p* = 0.003, *n* = 54), i.e. males mated to more colorful females fed nestlings less often. Females with higher color scores tended to spend a smaller percentage of their time brooding nestlings (*r* = -0.22, *p* = 0.10, *n* = 54, power: 21%). Males that provisioned more often tended to be mated to females that spent a greater percentage of their time brooding nestlings (*r* = 0.20, *p* = 0.11, *n* = 62, power: 20%).

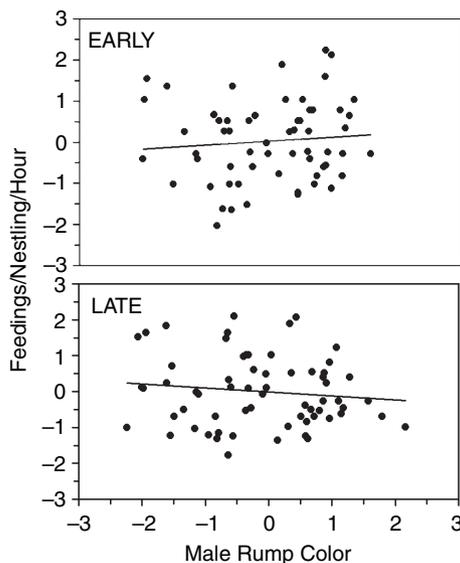


Fig. 2: Relationship between male rump color score and nestling provisioning rate both early and late in the nestling stage. Color scores and feeding rates were standardized to control for year and elevational effects (see Methods).

Parental Provisioning – Late Nestling Stage

Male provisioning rates early and late in the nestling stage were positively but not significantly correlated (*r* = 0.19, *p* = 0.25, *n* = 38). Male rump color was unrelated to nestling provisioning rate in the Late stage (*r* = -0.12, *p* = 0.34, *n* = 64; Fig. 2). Unlike in the Early part of the nestling stage, male provisioning rate in the Late stage was unrelated to mate color score (*r* = 0.18, *p* = 0.18, *n* = 56, power: 15%).

On average, the male was responsible for 41% of the parental provisionings to offspring (SD: 12%; range 10–73%). The proportion of all feeding trips made by the male was unrelated to its color (*r* = 0.01, *p* = 0.95, *n* = 64).

We found a significant, positive correlation between male and female provisioning rates within pairs (*r* = 0.32, *p* = 0.01, *n* = 64; Fig. 3). Thus, as with males, the rate at which the female provisioned nestlings was unrelated to its color score (*r* = -0.03, *p* = 0.83, *n* = 56; Fig. 4). Likewise, the proportion

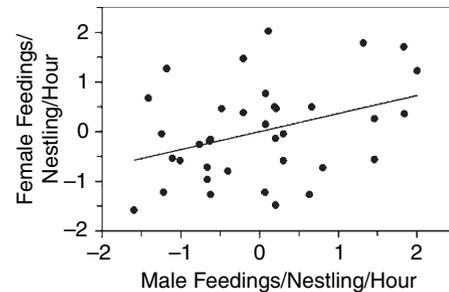


Fig. 3: Relationship between male and female provisioning effort late in the nestling stage. Feeding rates were standardized to control for year and elevational effects (see Methods).

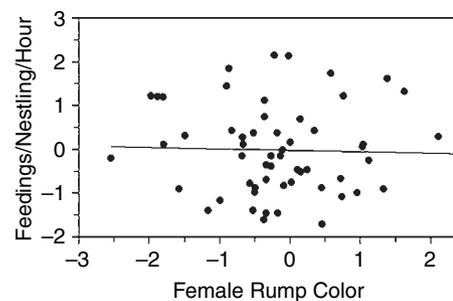


Fig. 4: Relationship between female rump color score and nestling provisioning rate late in the nestling stage. Color scores and feeding rates were standardized to control for year and elevational effects (see Methods).

of all feeding trips made by the female was unrelated to its color ($r = -0.09$, $p = 0.50$, $n = 56$). Male share of the provisioning effort remained unrelated to male coloration after controlling for the effect of female color on share of feeding effort (partial $r = -0.03$, $p = 0.84$, $n = 56$). Female feeding rate was not significantly related to its mate's color ($r = -0.10$, $p = 0.45$, $n = 64$). A female's share of the total feeding effort was unrelated to its mate's color ($r = -0.01$, $p = 0.95$, $n = 64$).

Color and Brood Growth

Brood growth rate was unrelated to the color score of both the male ($r = 0.07$, $p = 0.65$, $n = 47$) and the female parent ($r = -0.02$, $p = 0.90$, $n = 41$). These results held true when using partial correlation to hold constant the effects of mate's color (males: partial $r = 0.03$, $p = 0.88$, $n = 41$; females: partial $r = -0.02$, $p = 0.93$, $n = 41$) or the effects of provisioning effort on brood growth rate (males: partial $r = 0.04$, $p = 0.81$, $n = 47$; females: partial $r = -0.02$, $p = 0.90$, $n = 41$).

Discussion

In our study population of mountain bluebirds, a male's plumage coloration showed no tendency to predict the rate at which it provisioned nestlings, or its share of the feedings relative to its mate. This was true both early in the nestling stage when the female was spending most of its time brooding and later in the nestling stage when brooding had ended and nestling energetic demands were peaking. As was the case for males, a female's coloration also showed no tendency to predict its absolute provisioning effort or its effort relative to that of its mate.

We documented provisioning effort for 4 h both early and late in the nestling stage. We recorded only the number of prey delivered during those periods and not the size or quality of prey. Some have argued that, with only a snapshot of the total provisioning effort across the nestling stage and no information on the quality of food delivered, nestling growth rate (or size at fledging) may be a better indicator of parental effort than provisioning rate (Norris 1990; Sundberg & Larsson 1994; Senar et al. 2002; but see Velando et al. 2005). However, in our study, nestling growth was also not predicted by the coloration of either parent.

In sum, we found no direct support for the hypothesis that structurally based plumage coloration signals parental quality in either male or female

mountain bluebirds. Our findings, therefore, suggest that this ornamentation either serves some other function in each sex or, in the case of females, coloration is merely the result of a genetic correlation (discussion in Amundsen & Pärn 2006; LeBas 2006).

One alternative possibility is that color in one or both sexes is used intrasexually to signal fighting ability during competition for critical resources such as nest cavities, which may naturally be in short supply. That more colorful males in our population are larger, as measured by wing length, lends some support to this suggestion. In the congeneric eastern bluebird, UV-chroma (i.e. amount of reflectance in the UV range) predicted success in staged contests for nest cavities (Siefferman & Hill 2005b). An investigation of whether and how color affects competition for resources in mountain bluebirds thus seems warranted.

A further possibility is that plumage coloration in mountain bluebirds may signal an individual's genetic quality. Kokko (1998) noted that ornamentation can signal both a male's genetic quality and parental quality simultaneously. However, it was argued that if the genetic quality signal is relatively strong, then more ornamented males may benefit from investing time and energy in securing second mates or extra-pair fertilizations rather than investing in offspring care. Such a strategy could result in either no relationship between ornamentation and parental effort or a negative relationship. Although polygyny is rare in mountain bluebirds (Power & Lombardo 1996), extra-pair paternity is relatively common (Monk 1999; Balenger et al. unpubl. data). Thus, more ornamented males in our population may gain fitness benefits through a greater number of extra-pair fertilizations (and greater paternity in their own nests).

Siefferman & Hill (2003, 2005a,b) have explored the relationship between plumage color and parental behavior in a population of the congeneric eastern bluebird in southern Alabama. Like mountain bluebirds, eastern bluebirds have UV-blue dorsa, wings, and tails; however, both sexes have an additional melanin-based, chestnut-colored patch on their breast. Siefferman & Hill (2003) found a strong tendency for more colorful male eastern bluebirds to provision nestlings more frequently during 4-h observation sessions conducted on nestling day 8. More colorful males also produced significantly heavier offspring. However, in their study, Siefferman & Hill combined various measures of structural UV-blue and melanin chestnut coloration into a single color score. Males with high scores had brighter and

more purely colored (i.e. greater chroma) UV-blue feathers but also had larger, brighter, more purely colored chestnut breast patches. Thus it is unclear whether one or both types of coloration, or some specific relationship between the two types, potentially provides information on male parental quality (discussed further by Siefferman & Hill 2005b). In a later study, Siefferman & Hill (2005a) used multiple linear regression to show that a *female's* rump coloration, in combination with its age, condition, and its mate's rump coloration predicted female provisioning rate. However, the amount of variation in provisioning rate explained by these four variables was small (8%), suggesting that the association between female rump coloration and provisioning effort in eastern bluebirds is weak.

A potential problem of all correlational tests of the Good Parent Hypothesis, such as our own, is that the provisioning effort of one sex may be affected by the effort of the other sex (Linville et al. 1998; Griffith & Pryke 2006; Johnstone & Hinde 2006 and references therein). For example, females may benefit from investing more heavily in offspring of highly ornamented males, allowing such males to feed less (Burley 1986, 1988). In our study, a female's provisioning effort was unrelated to its mate's coloration. Nevertheless, to control for the potentially confounding effect of mate provisioning effort, one approach is to remove the mate and then observe the effort of the remaining parent and/or monitor the weight gain of offspring (e.g. Sætre et al. 1995). We recommend this experimental design to confirm observational results in our study and similar studies.

Male provisioning rate early in the nestling stage showed a moderately strong, negative association with female color. In addition, more colorful females tended to spend a smaller percentage of their time brooding. More colorful females may have used the extra time outside the nest to gather food, thereby relaxing some pressures on their mates to feed. We could not confirm this, however, because we were unable to document female feeding rates early in the nestling stage. However, the fact that we found no relationship between male provisioning effort and mate color late in the nestling stage, when females no longer brood, is consistent with our suggestion.

Individuals that provisioned nestlings at a relatively higher rate later in the nestling stage had mates that did the same. We suggest several possible explanations for this relationship. First, both members of the pair may be attempting to provision nest-

lings at as high a rate as possible, but may each be constrained to the same degree by the availability/accessibility of prey on their territory. Second, individuals that are of higher quality in terms of provisioning ability may acquire mates that also have exceptional provisioning ability. This could result, for example, if high-quality males and females arrive on breeding grounds and pair before lower-quality individuals. Third, recent theoretical work suggests that, under certain conditions, individuals in biparental species may use their mate's provisioning rate as one index of the brood's need for food, and hence may match their mate's provisioning effort (Hinde 2006; Johnstone & Hinde 2006).

In conclusion, we found no evidence that UV-blue plumage coloration in either male or female mountain bluebirds signals nestling provisioning effort. Thus, there remains no strong or unequivocal evidence that structurally based plumage coloration reliably signals parental quality in any species of bird (see also: Smiseth et al. 2001; Perrier et al. 2002; Komdeur et al. 2005). However, work in this area has just begun and many more species must be examined before any firm conclusions are drawn.

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