ORIGINAL PAPER

Sexual selection in a socially monogamous bird: male color predicts paternity success in the mountain bluebird, *Sialia currucoides*

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Abstract Ornamental traits are thought to evolve because they give individuals an advantage in securing multiple mates. Thus, the presence of ornamentation among males in many monogamous bird species presents something of a conundrum. Under certain conditions, extra-pair paternity can increase the variance in reproductive success among males, thus increasing the potential for sexual selection to act. We addressed this possibility in the mountain bluebird (*Sialia currucoides*), a socially monogamous songbird in which males possess brilliant ultraviolet (UV)-blue plumage. Specifically, we asked whether a male's success at siring offspring within his own nest and within the nests of other males was related to his coloration. In pairwise comparisons, males that sired extra-pair offspring were not more colorful than the males that they cuckolded. However, males that sired at least one extra-pair offspring were, on average, brighter and more UV-blue than males that did not sire extra-pair offspring. Brighter, more UV-blue males sired more offspring both with their own mate and tended to sire more offspring with extra-pair mates and thus sired more offspring overall. Our results support the hypothesis that the brilliant UV-blue ornamental plumage of male mountain bluebirds evolved at least in part because it provides males with an advantage in fertilizing the eggs of multiple females.

Keywords Extra-pair paternity · Mountain bluebird · Sexual selection · *Sialia currucoides* · Structural plumage color

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Introduction

In many animal species, one or sometimes both sexes possess exaggerated, apparently costly traits that do not enhance, and may even detract from, survival. Darwin (1871) argued that such "ornamental" traits can evolve if they increase the number of matings that an individual obtains. More ornamented individuals may be preferred as mates for a variety of reasons; for example, ornamentation may signal an individual's quality or condition (Zahavi 1975; Kodric-Brown and Brown 1984; Andersson 1994; Griffith and Pryke 2006; Hill 2006; Senar 2006).

Male ornamentation is particularly common and dramatic in species that have polygamous or promiscuous mating systems. In such systems, there is ample opportunity for sexual selection to act on males due to the potential for large variation in male reproductive success. Curiously, males in a considerable number of monogamous species have also evolved ornamental traits, such as the elongated and colorful plumages seen in many species of birds. This suggests that there is greater variance in male reproductive success in some monogamous species than it would first appear. But what causes this variance? Darwin (1871) proposed two possible mechanisms. First, if males routinely outnumber females, then competition for mates increases and some males will fail to obtain mates (see also Kvarnemo and

Ahnesjö 1996; Dearborn et al. 2001). Second, some males may attract females that can produce more offspring (see also Fisher 1958; Kirkpatrick et al. 1990). Such females may, for example, be in better condition and hence more fecund. They may also be ready to breed earlier and thus can breed more times in a season than other females.

More recently, the discovery that some fraction of individuals in many monogamous animal species routinely mate outside the pairbond (Jones et al. 2001; Griffith et al. 2002; Leibgold et al. 2006; Mills et al. 2007) has promoted the idea that extra-pair (EP) mating substantially increases the variation in male mating success in "socially monogamous" species (Gowaty 1985; Westneat et al. 1990; Webster et al. 1995; Freeman-Gallant et al. 2005). Ornamentation could evolve if it increases a male's success at siring offspring, both in his own nest (i.e., by affecting the faithfulness of his own mate) and in the nests of other males.

Brilliantly colored plumage is one of the most common forms of ornamentation in birds. Several studies have found that more colorful males in sexually dichromatic, socially monogamous bird species experience either increased levels of EP mating success (Yezerinac and Weatherhead 1997; Sheldon and Ellegren 1999; Thusius et al. 2001; Bitton et al. 2007; Dehley et al. 2007), reduced levels of cuckoldry (Estep et al. 2005; Whittingham and Dunn 2005), or both (Møller and Tegelstrom 1997). Other studies, however, have failed to detect such relationships (Dunn et al. 1994; Stutchbury et al. 1997; Kraaijeveld et al. 2004; Westneat 2006).

We investigated the relationship between ornamentation and paternity success in the sexually dichromatic, socially monogamous mountain bluebird (*Sialia currucoides*). Males of this species are characterized by brilliant ultraviolet (UV)-blue plumage, which is produced exclusively through modification to feather nanostructure (Prum 2006; Shawkey et al. 2006). We have shown elsewhere that EP paternity increases the opportunity for sexual selection on males in our study population by increasing the variance in male reproductive success (Balenger et al. 2008). Our objective in this study was to determine whether male coloration is positively associated with male success at siring offspring both with his own mate and with females mated to other males in the population.

Materials and methods

Study species

Mountain bluebirds are medium-sized (~30 g) passerines that breed in western North America at elevations up to 3,800 m above sea level (a.s.l.; biology summarized by Power and Lombardo 1996). Males exhibit structural UV-

blue plumage coloration over their entire dorsal side, with the rump being the brightest and most spectrally pure region of the body. Male wing, tail, and breast feathers are also UV-blue. In females, rump, tail, and primary wing feathers are a pale, dull blue, while head, back, and breast feathers are rusty-brown and gray. Mountain bluebirds are short-distance migrants, typically wintering at lower elevations in the southern part of the breeding range and returning in late winter or very early spring to the breeding grounds. This species nests naturally in pre-formed cavities but readily uses human-made nest boxes. Clutches typically contain four to eight eggs. Only females incubate eggs and brood hatchlings, but both sexes feed offspring. Polygyny has not been reported in this species and was not observed in this study.

Mountain bluebirds not only form season-long monogamous pairbonds but also engage in EP mating (Monk 1999). In a previous study of this population, we found that 72% of broods contained ≥1 EP offspring, and 36% of all offspring were sired by EP males (Balenger et al. 2008).

Study site and field methods

We conducted this study during the 2004 and 2005 breeding seasons on a population of bluebirds living near and in the Bighorn Mountains of north-central Wyoming, USA. We observed birds at two sites, a low-elevation site (1,258–1,620 m a.s.l.) in the eastern foothills of the mountains (44°38′ N, 107°01′ W) and a high-elevation site (2,443–2,582 m a.s.l.) 44 km away on a mountain plateau (44°46′ N, 107°32′ W; see Johnson et al. 2006 for a detailed description of the two sites). All observed pairs used nest boxes. In both years, data were obtained for first broods only; we did not document the occurrence or fate of second breeding attempts. In addition, because time constraints prevented us from working with every available nest, we excluded from this study those nests in which two or fewer nestlings survived to bleeding age. At such nests, we typically only trapped, bled, and marked males.

We checked boxes every 1–5 days to determine the date that eggs began hatching in each nest. We marked nestlings with a numbered aluminum leg band and collected a small blood sample (~50 uL) from them between 4 and 7 days after hatching began. Blood samples were stored at room temperature in Queen's lysis buffer (Seutin et al. 1991) until DNA extraction. We trapped adults as they entered boxes to feed nestlings 4–9 days after hatching began. Upon capture, we marked adults with a unique combination of colored leg bands (excluding blue and purple) and a numbered aluminum band, collected a blood sample, and collected 12–15 feathers from the center of their rump. Feathers were stored in opaque envelopes at room temperature. We also weighed each adult (nearest 0.1 g) and measured the length

of their right wing cord (nearest 1 mm). As an index of body condition, we used the residuals from a regression of weight against wing length.

Color analysis

We measured reflectance spectra for rump feathers across the avian visual range (300–700 nm) 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 (Cuthill et al. 1999; Montgomerie 2006; Fig. 1). Following the protocol of Siefferman and Hill (2003) (see also Perrier et al. 2002; Quesada and Senar 2006), we taped each individual's rump feathers to non-reflective black paper in an overlapping manner that mimics the bird's natural plumage. 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 extracted the following three indices of color using ColoR v. 1.7 (Montgomerie 2008): (1) hue, the wavelength at which the greatest amount of light was reflected, (2) UV-blue chroma, the proportion of the total reflectance (300–700 nm) contained within the ultraviolet and blue regions combined (300–512 nm), and (3) total brightness, the total amount of light being reflected relative to a white standard. The three measures of male rump color showed extensive colinearity (Balenger et al. 2007). We therefore performed a principal components analysis that generated a color score summarizing the variance in our three color variables (Montgomerie 2006). The first principal component score (PC1) explained 66% of the overall variance in male rump color (factor loadings: total brightness=0.679, UV-blue chroma=0.953, hue=−0.790; see also Balenger et al. 2007), and we use PC1 scores as a measure of rump color

in all analyses. Males with high PC1 scores had hues shifted more toward UV, had more of their color concentrated within the UV-blue range (greater UV-blue chroma), and were generally brighter.

Male color scores differed between elevations and between years at each elevation (Balenger et al. 2007). We therefore standardized color scores to a mean of 0 and a standard deviation of 1 at each elevation and within each year.

Microsatellite genotyping and paternity assignment

Microsatellite genotyping and paternity assignment methods are presented in detail elsewhere (Balenger et al. 2008). Briefly, we determined genotypes at between three and five highly polymorphic microsatellite loci for 99 adult males, 86 adult females, and 465 nestlings. We used M13-tailed microsatellite primers designed for use in mountain bluebirds (*Mobl87b* and *Mobl49*; Balenger et al., 2008) and in eastern bluebirds (*Sialia37*; Faircloth et al. 2006, *Eabl129* and *Eabl007b*; Balenger et al. 2008). Of 650 individuals, 526 (81%) were genotyped at four loci. We were unable to amplify by polymerase chain reaction and/or confidently determine the length of one microsatellite locus for 77 (12%) individuals. These individuals, therefore, were genotyped at only three loci. In some cases, individuals were genotyped at a fifth locus (*n*=47; 7%) to clarify paternity. Only one nestling matched more than one EP male at all loci genotyped. In this instance, one matched male had a nest nearly 6 km away, while the other male was at the nearest neighboring nest, 225 m away. We assigned paternity to the neighboring male. We had two broods in which one and six nestlings mismatched the within-pair (WP) female at one locus. Both families with mother-nestling mismatches were excluded from further analyses. All nestlings in all other broods matched the attending female at 100% of loci genotyped.

Sample sizes and statistical analyses

Fourteen males and 11 females were present during both years of the study. In three cases, the same pair returned to breed at the same location as the previous year. In these cases, we randomly selected the data from 1 year to include in analyses. In other cases, individuals either returned to breed the second year with a different mate at a new location (seven males and four females), returned to the same nest site but paired with a different mate (three males and three females), or formed the same mated pair but nested at a new location and had new neighbors (one pair). In these cases, we treated each year's breeding attempt as independent and included both in analyses. Ultimately, we had for analyses 92 families (29 in 2004 and 63 in 2005)
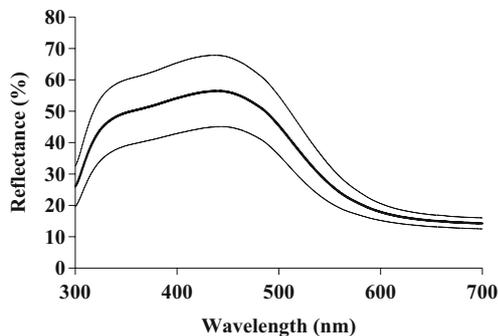

Fig. 1 Reflectance spectra of the rump feathers of male mountain bluebirds. The *bold line* shows the reflectance curve from the rump feathers of a hypothetical male with an average PC score (based on a sample of 120 males). The *dotted lines* show ±1 SD

containing three to seven nestlings each (mean, 5.1). Sample sizes vary slightly between analyses, however, because, in 2005, we did not obtain feathers from two males, wing length from one male, and mass from another male.

We used binomial logistic regression to test whether color score and two other measures of male morphology, wing length, and condition were related to the probability of a male either: (1) being cuckolded himself or (2) cuckolding one or more other males (i.e., siring ≥ 1 EP offspring). We also directly compared the morphology of cuckolded males to their cuckolders using paired t tests. In nests where the identity of more than one EP male was determined ($n=4$), we used the mean value of identified EP males weighted by the number of offspring sired for this analysis.

We used logistic regression to test whether male morphology was related to the *number* of WP, EP, and total offspring sired (i.e., the number that reached the age at which we drew blood, 5–8 days). More specifically, we used bivariate ordinal logistic regression to examine the relationship between color and number of offspring sired. Multivariate logistic regression models were used to calculate both maximum likelihood estimates of the individual regression parameters (i.e., color, wing length, and body condition) within the full model and that of the cumulative logit model including all predictors. Models were evaluated based on Wald χ^2 values.

Finally, we used a generalized linear model with binomial errors and logit links to determine whether male morphology was related to the proportion of offspring that a male sired in his nest. Number of offspring sired was the dependent variable, and total number of offspring in the nest was the binomial denominator. Deviance for this model was scaled to one for each degree of freedom, and significance was determined using a type III analysis.

We identified the sires of 47% of the EP offspring in the 92 nests under study. Not identifying the sires of a large proportion of EP offspring would obviously reduce the validity of results generated for several of the analyses described above, specifically those that examine male success at siring EP offspring. Therefore, prior to conducting these analyses, we excluded data from several clusters of nests in which, collectively, we identified relatively few of the sires of EP offspring. These clusters were adjacent to areas where there were pairs of mountain bluebirds (and hence many potential EP sires and mates) nesting either in natural cavities or in nest boxes that were not under our surveillance. Ultimately, we retained for analyses 59 nests in which we identified the sires of 70% of EP offspring. In one case, we obtained paternity but not color measurements of the social male; thus, analyses using the reduced data set contain 58 families. Mean distance between a pair's nest

and the nearest active nest for the full and reduced data sets were similar (full, 185 m; range, 98–457; reduced, 182 m; range, 98–415). We repeated our analyses with the complete data set and report results that were not qualitatively similar to those produced with the reduced data set.

All statistical analyses were performed using SAS v. 9.1 (SAS Institute 2007). Mean values are given ±1 standard error.

Results

Correlations among measures of male morphology

As we found in previous analyses (Balenger et al. 2007), across the study population, there was a significant correlation between a male's color score and his size as measured by wing length ($r=0.24$, $n=119$, $P=0.01$) but not by weight ($r=0.06$, $n=116$, $P=0.49$). Color score was unrelated to condition (i.e., weight relative to size; $r=0.01$, $n=109$, $P=0.86$).

Male morphology vs. the probability of being cuckolded or siring EP offspring

Males that were and were not cuckolded did not differ in color score (logistic regression: $\chi^2=1.74$, $df=1$, $P=0.19$; Fig. 2) or size as measured by wing length ($\chi^2=0.002$, $df=1$, $P=0.96$). However, males not cuckolded were in better condition ($\chi^2=4.04$, $df=1$, $P=0.04$).
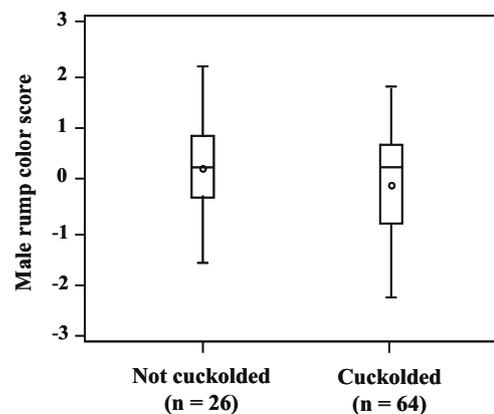

Fig. 2 Comparison of rump color scores (from principle components analysis; see "Materials and methods") of male mountain bluebirds that sired all the offspring within their nest ('Not cuckolded') and males that failed to sire ≥ 1 offspring within their nest ('Cuckolded'). *Boxplots* show means (*open circles*), medians (*horizontal lines within boxes*), 25th and 75th percentiles (*lower and upper bounds of boxes*, respectively), and minimum and maximum values (*extreme lower and upper bars*, respectively). For statistical analyses, see text

In the reduced data set (see "Materials and methods"), males that sired at least one EP offspring had higher color scores than males that did not sire EP offspring ($\chi^2=4.12$, $df=1$, $P=0.04$; Fig. 3; full data set, $\chi^2=0.15$, $df=1$, $P=0.70$). Males that did and did not sire at least one EP offspring did not differ in size ($\chi^2=1.01$, $df=1$, $P=0.32$; full data set, $\chi^2=4.08$, $df=1$, $P=0.04$) or condition ($\chi^2=0.35$, $df=1$, $P=0.55$).

In pairwise comparisons, males that sired EP offspring had neither higher color scores nor were in better condition than the males that they cuckolded (color: $t=-0.18$, $df=28$, $P=0.86$; condition: $t=0.35$, $df=29$, $P=0.73$). However, they were larger in terms of wing length ($t=2.14$, $df=24$, $P=0.04$).

Male morphology vs. number of offspring sired

In bivariate analyses (Fig. 4), male color score predicted number of WP offspring sired ($\chi^2=5.15$, $r=0.31$, $n=90$, $df=1$, $P=0.003$), number of EP offspring sired ($\chi^2=3.82$, $r=0.25$, $n=64$, $df=1$, $P=0.05$), and total number of offspring sired ($\chi^2=7.93$, $r=0.34$, $n=58$, $df=1$, $P=0.005$). Male color score also predicted the proportion of offspring a male sired in his own nest ($F=4.39$, $n=90$, $df=1$, $P=0.04$).

In multivariate models that included male rump color score, wing length, and condition, male color score remained a significant, positive predictor of both the number of WP offspring sired and the total number of offspring sired (Table 1). The relationship between male color score and number of EP offspring sired remained positive but was non-significant ($P=0.10$). Males with higher color scores sired, though not significantly, a greater proportion of offspring their own nests ($P=0.07$; Table 2).

Male wing length and body condition did not predict number of offspring sired in any analysis.

Fig. 4 Relationship between the rump color of male mountain bluebirds and: (*top*) the number of within-pair offspring sired ($n=90$ males), (*middle*) the number of extra-pair offspring sired ($n=64$ males), and (*bottom*) the total number of offspring sired ($n=58$ males). Total number of offspring sired is the sum of within-pair and extra-pair offspring sired. For statistical analyses, see text
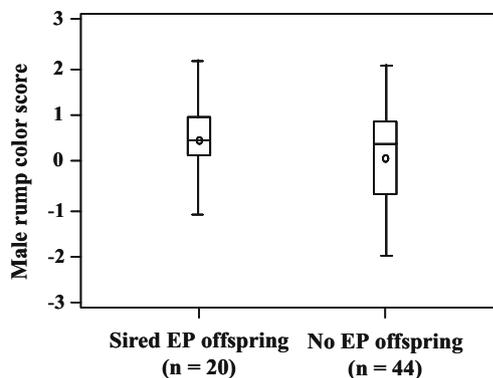

Fig. 3 Comparison of rump color scores of male mountain bluebirds that sired extra-pair offspring and those that did not. *Boxplots* are as described in Fig. 2. For statistical analyses, see text
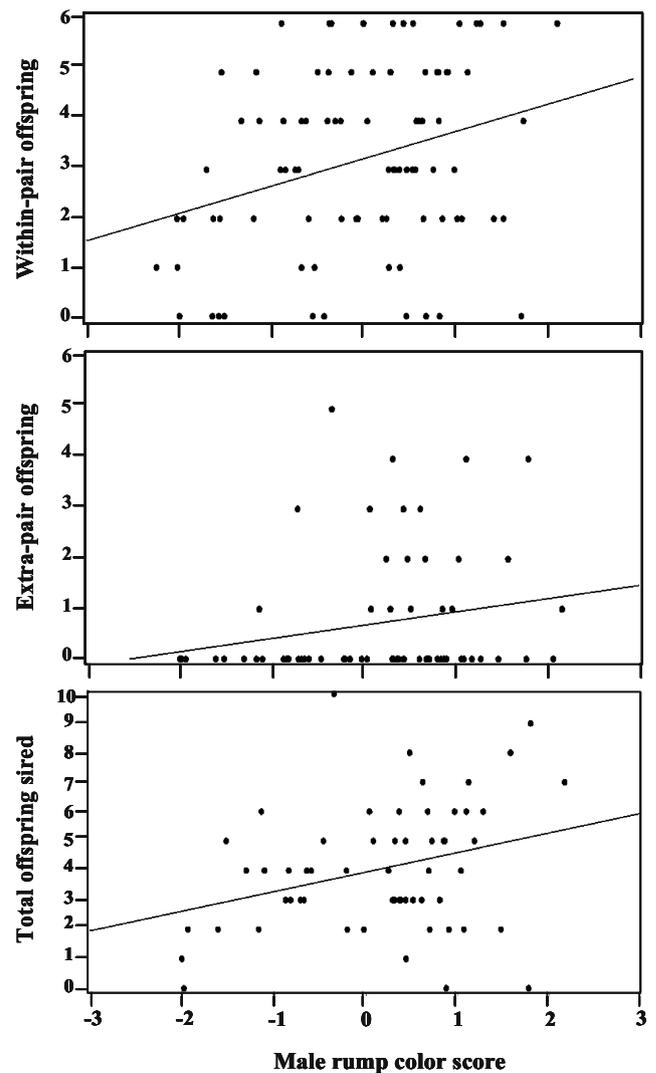
Discussion

Previously, we showed that, in our study population of mountain bluebirds, the number of offspring that a male sires increases significantly with the number of females with whom he sires offspring (Balenger et al. 2008). One would therefore expect persistent directional selection for any trait that increases male mating success (Arnold and Wade 1984; Jones et al. 2002; Mills et al. 2007). In the current study, we asked whether males with brighter, more purely UV-blue plumage had an advantage in competition for matings, both with their own mates and with females

Table 1 Results of multivariate logistic regression asking whether three measures of the morphology of male mountain bluebirds (rump color, size as measured by wing length, and body condition) were related to: (1) the number of within-pair offspring sired, (2) the number of extra-pair offspring sired, and (3) the total number of offspring sired (within- and extra-pair combined)

	χ^2	p value	n	Model χ^2	Model r	Model p
Within-pair offspring sired						
Rump color	8.07	**0.003**	88	10.20	0.32	**0.02**
Wing length	0.10	0.75				
Body condition	1.66	0.20				
Extra-pair offspring sired						
Rump color	2.67	0.10	63	4.64	0.28	0.20
Wing length	0.92	0.34				
Body condition	0.07	0.79				
Total offspring sired						
Rump color	7.74	**0.005**	58	8.26	0.34	**0.04**
Wing length	0.01	0.99				
Body condition	0.13	0.71				

Models are based on maximum likelihood estimates

paired to other males. We found that brighter, more UV-blue males tended to sire a greater proportion of their social mate's offspring and, hence, produced more WP offspring than did duller, less UV-blue males. In bivariate analyses, brighter, more UV-blue males also sired more EP offspring than did duller, less UV-blue males, although color score was no longer a significant predictor when entered into a multivariate model. In total, brighter, more UV-blue males sired more offspring overall than did duller, less UV-blue males.

We caution that we only examined the relationship between a male's coloration and WP and EP paternity during a single breeding attempt. In all cases, this was the first successful breeding attempt of the season made by males in our study. To better assess the degree to which coloration affects fitness through WP and EP paternity success, ideally, one should tally paternity for males across the entire breeding season or, if possible, across multiple seasons. For logistic reasons, we were unable to stay on site and follow second breeding attempts to their conclusion. However, it was clear that, as in other populations of this species (Power 1966), only a fraction of pairs attempted second broods. If females that were paired with duller, less UV-blue males were more likely to produce second broods, this could have negated some of the paternity advantage gained by brighter, more UV-blue males during first breeding attempts. However, we have no reason to suspect that duller, less UV-blue males typically have more breeding episodes per season. For example, males could reserve energy or cause their mates to be more faithful by adjusting their share of parental care during first breeding

attempts (see Kvarnemo 2006); however, in a previous study, we did not find a relationship between a male's color and his share of the feeding of offspring (Balenger et al. 2007). As regards tracking individuals across multiple seasons, it will be critical to confirm that males that are both relatively colorful and reproductively successful in 1 year remain so in subsequent years. Work on the congeneric eastern bluebird (*Sialia sialis*) suggests that color is condition dependent (Siefferman and Hill 2005a) and can be plastic from year to year (Siefferman and Hill 2005b). We expect future studies to address such questions and to examine whether male color is related to survival and longevity.

Potential causal links between male color and mating success

Although our study suggests an association between male coloration and WP and EP mating success in mountain bluebirds, we cannot determine the underlying cause(s) of such relationships. One possibility is that color is an honest indicator of male genetic quality. If true, then females should prefer to have eggs fertilized by brighter, more UV-blue males so as to produce offspring that are more fit. Several experimental studies suggest that structurally derived coloration of feathers can reflect physical condition (McGraw et al. 2002; Hill et al. 2005; Peters et al. 2007). Most notably, female eastern bluebirds that were subjected to food deprivation grew duller, less UV-blue rump feathers during molt than did females fed ad libitum (Siefferman and Hill 2005b). In a previous study (Balenger et al. 2007), we did not find that males become more colorful with age (cf. Johnstone 1995; Siefferman et al. 2005) nor did we find that brighter, more UV-blue males carried more weight relative to their size (i.e., were in better condition) when captured early in the nestling stage. Brighter, more UV-blue

Table 2 Results of a generalized linear model testing whether color, size (as measured by wing length) and/or body condition predict the proportion of offspring within a nest sired by the social male in a population of mountain bluebirds

Proportion of within-pair offspring sired

	Estimate	df	F	p value
Rump color	0.34	1	3.34	*0.07*
Wing length	0.03	1	0.24	*0.62*
Body condition	−0.10	1	0.40	*0.40*

Estimates are partial coefficients used to evaluate the effect of each variable when all others were held constant. Analysis includes data for 88 males

males were, however, larger in size as measured by wing length. Such males may have experienced better nutrition during development or molt (cf. Siefferman and Hill 2007).

If females do prefer to have their eggs fertilized by brighter, more UV-blue males, the critical prediction is that females will permit EP fertilizations only by males that are brighter and more UV-blue than their WP mates. In contrast, we found that EP sires were not brighter and more UV-blue, on average, than the males that they cuckolded. EP sires were, however, larger than their cuckolds, as measured by wing length, a variable significantly correlated with male color score. One possibility is that longer-winged males may be able to physically dominate shorter-winged males, perhaps driving them away from their mates and thereby increasing the opportunity for EP copulations. Longer winged males may also be better able to traverse broad swaths of habitat in search of EP partners. Previously, we showed that EP sires are not typically neighbors of the females whose eggs they fertilize; EP sires often come from territories 0.5 to >1 km away (Balenger et al. 2008). Detailed observations of both interactions between males and male movement patterns will be needed to test these proposals.

Other potential influences on male color

That male coloration appears to affect mating success does not rule out other factors favoring ornamentation in males. For instance, the good parent hypothesis proposes that ornamentation evolves as an honest signal of an individual's ability or willingness to provide parental care (Heywood 1989; Hoelzer 1989). However, in this population, previous research showed no relationship between male coloration and the rate at which they provision offspring (Balenger et al. 2007). In addition, females also do not lay more or larger eggs or work harder to feed offspring when paired with a more colorful male (Balenger et al. 2007 and unpublished data).

Darwin hypothesized (1871) (see also Fisher 1958; O'Donald 1972) that selection favors ornamentation among males of monogamous bird species because more ornamented males mate with more fecund females. In mountain bluebirds, the most fecund females may be those that arrive earliest to the breeding grounds, given that individuals begin returning to their high-altitude/high-latitude breeding grounds while it is still winter (as early as February: Criddle 1927; Bent 1949; Lane and Pearman 2003). Only females in superior condition may be able to risk the harsh environmental conditions that exist at this time. Such females may lay larger clutches and/or provide their eggs and young with more resources, ultimately producing more offspring. Furthermore, those females that

arrive and begin breeding early are most likely to be among the fraction of females that produce two broods in a year. If more ornamented males arrive on the breeding grounds first, such that they typically acquire early arriving, more fecund mates, this could contribute to the evolution of male ornamentation (Cotton et al. 2006).

Male coloration may also influence male success in competition for nest sites. If nest sites are scarce under natural conditions, then male coloration may play a role in intra-sexual competition for nest sites. A male's ability to compete for and obtain such a naturally limited resource (i.e., a pre-formed nest cavity) would directly affect his reproductive success, which would in turn favor traits that signal such ability. Indeed, in eastern bluebirds, more purely UV-blue males are more likely to acquire nest boxes than are less chromatic males when boxes are in limited supply (Siefferman and Hill 2005c).

Finally, as in many studies of this type, the effect of providing an abundance of artificial nest boxes likely has an effect on the density of breeding pairs and thus the frequency of EP paternity. Indeed, as we argue in more detail elsewhere (see Balenger et al. 2008), EP mating may be less common and hence have less impact on the evolution of traits such as plumage color in secondary cavity nesting species under natural conditions. Future studies that assess the impact of nest boxes on rates of EP paternity in secondary cavity nesters will be important for the interpretation of studies such as the current one.

In conclusion, our results support the hypothesis that the brilliant UV-blue ornamental plumage of male mountain bluebirds evolved at least in part because it provides males with an advantage in fertilizing the eggs of multiple females. It remains to be shown why such a mating advantage exists and whether other mechanisms also select for ornamental plumage color in this species.

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