Reproductive correlates of plumage coloration of female Mountain Bluebirds

Ashley Morrison, Nancy J. Flood, and Matthew W. Reudink¹

Department of Biological Sciences, Thompson Rivers University, Kamloops, British Columbia V2C 0C8, Canada

Received 24 July 2013; accepted 12 February 2014

ABSTRACT. Many studies have shown that the plumage coloration of male birds can act as an honest signal of quality, indicating benefits that a female could gain from pairing with a specific male. In some species, females also display ornamental plumage, but less is known about the function and potential adaptive significance of female coloration because most research has focused on male coloration. Male Mountain Bluebirds (*Sialia currucoides*) display full body, ultraviolet (UV)-blue plumage, whereas female plumage is more subdued, with blue color focused on the rump, wing, and tail. During the 2011 and 2012 breeding seasons (May–July) near Kamloops, BC, Canada, we examined coloration of the rump and tail of female Mountain Bluebirds to determine if their plumage could act as an indicator of direct reproductive benefits (e.g., enhanced parental care or reproductive success) to potential mates. We found no relationship between female plumage coloration and either provisioning rate or fledging success. However, female coloration varied with age, with after-second-year (ASY) females having brighter, more UV-blue tail feathers than second-year (SY) females. In addition, ASY females with brighter, more UV-blue tails had larger clutches. We also observed positive assortative mating by tarsus length. Because previous work with other species suggests that female body size may be a good predictor of breeding success, males could potentially benefit from pairing with larger females. However, reproductive success did not vary with female size in our study. Although our evidence that structural plumage coloration of female Mountain Bluebirds is a signal of direct reproductive benefits for males (e.g., higher reproductive success) is limited, our results (i.e., ASY females with brighter tails than SY females, and ASY females with brighter tails having larger clutches) do suggest the potential for sexual selection to act on female coloration.

RESUMEN. Asociación entre la reproducción y la coloración en hembras de Sialia currucoides

Muchos estudios han mostrado que la coloración del plumaje en machos puede actuar como una señal honesta sobre la calidad, indicando los beneficios que pueden ganar las hembras al apearse con un macho específico. En algunas especies, las hembras también despliegan plumajes ornamentales, pero su función y la capacidad adaptativa potencial de la coloración en las hembras es menos conocída, en gran parte porque la mayoría de las investigaciones se han enfocado en la coloración de los machos. Machos de Sialia currucoides despliegan en todo el cuerpo un plumaje azul ultravioleta (UV), mientras que el plumaje de la hembra es más suave, en donde el color azul se concentra en la rabadilla, alas y cola. Durante la temporada reproductiva del 2011 y 2012 (May-Jul) cerca de Kamloops, BC, Canadá, examinamos la coloración de la rabadilla y la cola en hembras de S. currucoides para determinar si su plumaje puede servir como un indicador de beneficios directos en la reproducción (e.g., aumenta el cuidado parental y el éxito reproductivo) a potenciales parejas. No encontramos ninguna relación entre la coloración del plumaje de la hembra y la tasa de alimentación o el éxito reproductivo. Sin embargo, la coloración de las hembras vario con la edad, en donde después del segundo año (DSA) las hembras tienen plumas de la cola UV-azules mas brillantes que las hembras de segundo año (SA). Adicionalmente, DSA hembras con plumas de la cola UV-azules mas brillantes tuvieron nidadas más grandes. También observamos una apareamiento dirigido y asociado positivamente con el largo del tarso. Debido a que estudios previos en otras especies sugiere que el tamaño corporal de las hembras puede ser un buen predictor de el éxito reproductivo, los macho se podrían beneficiar al aparearse con hembras más grandes. Sin embargo, el éxito reproductivo no vario con el tamaño de las hembras en nuestro estudio. Aunque nuestra evidencia muestra que la coloración estructural de las hembras de S. currucoides es una señal directa para el beneficio de los machos (e.g., mas alto éxito reproductivo) los datos son limitados. Pero, nuestros resultados (i.e., DSA hembras con colas mas brillantes que SA hembras, y DSA hembras con colas mas brillantes teniendo nidadas más grandes) sugieren que potencialmente la selección sexual podría actuar sobre la coloración de las hembras.

Key words: mate choice, parental care, sexual selection, Sialia currucoides, structural coloration

Many studies have demonstrated that male plumage coloration may reflect various aspects of individual quality and condition (Hill 2006). Thus, male plumage traits may indicate both direct (e.g., parental care) and indirect (e.g., good genes) benefits that a female would gain from pairing with a particular male (Hill 2006). In many species, females also exhibit ornamental

¹Corresponding author. Email: mreudink@tru.ca

^{© 2014} Association of Field Ornithologists

plumage, and their color may similarly provide information about quality to potential mates (Amundsen 2000, Amundsen and Pärn 2006, Drobniak et al. 2013).

The mutual selection hypothesis states that female ornamentation may arise through mutual mate choice, with both sexes exercising choice (Kraaijeveld et al. 2007, Edward and Chapman 2011). Because both males and females benefit from choosing good mates, sexual selection may act on females (via mate choice by males) to increase their ornamentation (Clutton-Brock 2009). Additionally, females play a role in territory defense in some species (Whittingham et al. 1992, 1996, Bleiweiss 1997, Murphy et al. 2009, Midamegbe et al. 2011), and color may act as a signal of status and dominance when competing with other individuals (usually females) for limited resources; thus, this too could lead to selection for increased ornamentation (social selection; West-Eberhard 1979, Johnson 1988, Jones and Hunter 1999, LeBas 2006, Rosvall 2011). In either case, the highest-quality females are predicted to be the most colorful and be preferred as mates. Multiple studies have demonstrated condition-dependence of female plumage coloration (e.g., Siefferman and Hill 2005, Doutrelant et al. 2012) and there is also evidence of direct sexual selection on female plumage coloration through correlative studies, mate-choice trials, and manipulative experiments (Hill 1993, Amundsen et al. 1997, Griggio et al. 2005, 2009). One reason why males may prefer colorful females is that female color may signal reproductive benefits that potential mates would receive, such as parental care and reproductive capacity (Siefferman and Hill 2005, Amundsen and Pärn 2006, Doutrelant et al. 2008, Osmond et al. 2013).

Two main theories have been developed to explain the relationship between attractiveness and parental care in species that exhibit biparental care: the Good Parent Hypothesis and the Differential Allocation Hypothesis. The Good Parent Hypothesis suggests that there should be a positive association between parental care and individual attractiveness if plumage coloration is indicative of individual quality and higherquality individuals provide better resources to their offspring (Hoelzer 1989). On the other hand, the Differential Allocation Hypothesis states that an individual mated with a highquality partner will allocate more energy to parental investment than if it had a lower quality partner; in response, the high-quality partner can decrease its own investment, resulting in either a negative correlation between an individual's attractiveness and the amount of parental care it contributes, or a positive correlation between the attractiveness of an individual's mate and the level of parental care it provides (Burley 1988, Møller and Thornhill 1998). To date, few investigators have applied the Good Parent and Differential Allocation hypotheses to females to test whether plumage coloration is an indicator of the extent of parental care. Among studies that have been conducted, results are mixed and have revealed positive (Linville et al. 1998, Jawor et al. 2004, Siefferman and Hill 2005), negative (Badyaev and Hill 2002, Johnsen et al. 2005, Osmond et al. 2013), and no relationships (Rohde et al. 1999, Smiseth and Amundsen 2000, Balenger et al. 2007) between attractiveness and parental care.

Although most studies of the possible signaling function of plumage coloration have focused on species that display carotenoid-based coloration, some investigators have examined the role of structural coloration (e.g., blue, green, and iridescent colors) as an indicator of individual quality. Because structural color depends on feather microstructure (Prum 2006), nutritional health during molt may affect its expression (Keyser and Hill 1999, McGraw et al. 2002). Thus, structurally based plumage coloration may also function as an honest signal of individual quality, though the mechanisms of condition-dependence remain unclear (Keyser and Hill 2000, Peters et al. 2011).

Our objective was to examine the structural plumage coloration of female Mountain Bluebirds (Sialia currucoides) to determine if coloration in one or more body regions reflects individual quality in terms of parental care and reproductive success. Although socially monogamous, the rate of extra-pair paternity is high in this species (72% of broods; Balenger et al. 2009b), thus providing the opportunity for sexual selection. Because both sexes contribute to offspring provisioning and territory defense (Gibson and Moehrenschlage 2008), mutual mate choice is expected to be beneficial (Clutton-Brock 2009). Thus, Mountain Bluebirds are well suited for studying the role of structural plumage in mate choice and sexual selection. In closely related Eastern Bluebirds (Sialia sialis), female color appears to be correlated with condition, reproductive success, maternal care, and offspring quality (Siefferman and Hill 2005). However, in a Wyoming, USA, population of Mountain Bluebirds, no relationship between provisioning and female rump coloration was detected (Balenger et al. 2007). In the same Wyoming population, however, coloration of male Mountain Bluebirds did predict reproductive success (Balenger et al. 2009a). Thus, a second aim of our study was to determine if the relationships (or lack thereof) among plumage coloration, provisioning, and reproduction found in Wyoming (Balenger et al. 2007, 2009a) are also found in a British Columbia population facing different ecological and evolutionary pressures. In addition, we examined two plumage regions (tail and rump) that are grown under different conditions and may contain differing signal content.

METHODS

Our study was conducted during the 2011 and 2012 breeding seasons (May-July) in the Knutsford area, near Kamloops, BC, Canada (803-953 m asl; 50°37′N, 120°19′W). Nest boxes were monitored every 1-3 d to determine first egg date, clutch size, hatch date, number of nestlings, and fledging success (nests empty at the putative fledge date were considered to have successfully fledged; number of fledglings was estimated as the number of nestlings present during the last visit prior to fledging). Five to 10 d after eggs hatched, adult males (N = 54) and females (N = 60) were captured at nests while provisioning young. Adults were banded with a single Canadian Wildlife Service aluminum band and a unique combination of three color bands. We classified adults as either second-year (SY) or after-second-year (ASY) by examining molt limits of the primary and greater coverts (Pyle 1997). We collected 10 rump feathers and a single tail feather (R3) from each individual. We measured mass, unflattened wing chord, tail length, and tarsus length to evaluate body size and condition.

Parental care. We measured the level of parental care provided by males and females during the early nestling stage (3–5 d after hatching) and a late stage (14–16 d after hatching), following Balenger et al. (2007). Nests were watched either by making recordings using video

cameras (Handycam DCR-SX45, Sony, Tokyo, Japan, and HD Hero2, GoPro, San Mateo, CA) or via focal observation periods lasting 2 h at each nest. All nest watches occurred between 06:20 and 11:15 (mean = $08:48 \pm 92$ [SD] min) during both the early and late stages (4 h/nest). When using video cameras, cameras were placed in a plywood box (to avoid theft) on a fencepost \sim 5–10 m from nests. Parental care was quantified as the number of trips to nests per hour per nestling (Smiseth et al. 2001). Similar to Balenger et al. (2007), we also recorded the time per hour that females spent at nests during the early phase, which we interpreted as time spent brooding. (Nest visits that lasted <30 s were not recorded as brooding.) We checked and recorded the number of nestlings each time we video-recorded nests. When analyzing videos, we began the 2 h of measurements after the first trip to a nest by either the male or female. We avoided capturing adults at nests within 48 h preceding measuring nestling provisioning rates.

We quantified plumage Color analysis. coloration by measuring reflectance across the avian visual range (300-700 nm) using a spectrometer (JAZ, Ocean Optics, Dunedin, FL) with a xenon light source. The fiber optic probe was housed in a non-reflective probe holder to consistently measure feathers at a 90° angle and 5.9 mm from feathers. We mounted rump feathers in an overlapping pattern on ebony paper (#142, Canson, Inc., South Hadley, MA). We took 10 readings for each plumage region (tail [R3] and rump) at haphazard locations along the feather. We calculated three different color variables (brightness, UV-blue chroma, and hue) using the R-based color analysis program RCLR v.28 (Montgomerie 2008) and averaged the value for each variable over the 10 measurements. Brightness was measured as the percent reflectance averaged across the avian visual spectrum (300–700 nm). Chroma was measured as the proportion of total reflectance within both the blue range (400–510 nm) and the ultraviolet (UV) range (300-400 nm) relative to total light reflected (300–700 nm). Hue was determined as the wavelength at maximum reflectance. Due to a high degree of colinearity among these color variables, the three were examined together using principal components analysis in JMP 10 (SAS Institute 2012). Because the first principle component (PC1) explained most

| | Eigenvalue | Proportion of variance | Color variable | Factor loading |
|-----------------|------------|------------------------|------------------|----------------|
| Male tail PC1 | 1.99 | 0.66 | Brightness | 0.82 |
| | | | UV + blue chroma | 0.87 |
| | | | Hue | -0.75 |
| Female tail PC1 | 1.97 | 0.66 | Brightness | 0.62 |
| | | | UV + blue chroma | 0.87 |
| | | | Hue | -0.91 |
| Male rump PC1 | 1.5 | 0.50 | Brightness | 0.29 |
| | | | UV + blue chroma | 0.90 |
| | | | Hue | -0.78 |
| Female rump PC1 | 1.87 | 0.62 | Brightness | 0.37 |
| | | | UV + blue chroma | 0.94 |
| | | | Hue | -0.92 |

Table 1. Results from a principle components analysis of measures of plumage coloration (brightness, hue, and chroma) for rump and tail coloration of male and female Mountain Bluebirds. Because the first principle component (PC1) explained most of the variation, we used PC1 to represent overall color variation.

of the variation for each plumage area (Table 1), we used variation in PC1 to represent overall color variation. PC1 scores loaded positively on brightness and UV-blue chroma and negatively on hue (lower hue values indicate a shift toward UV); (Table 1). No color variables differed between years (male tail PC1: $t_{53} = 0.8$, P = 0.41, male rump PC1: $t_{53} = 0.4$, P = 0.67, female tail PC1: $t_{59} = -1.7$, P = 0.09, female rump PC1: $t_{59} = 0.2$, P = 0.86) so data for 2011 and 2012 were combined for subsequent analyses.

Statistical analyses. Statistical analysis was performed using JMP 10 (SAS Institute 2012). All analyses were performed separately for males and females. Linear mixed models with individual as a random effect (because six males and six females were present in both years) were used to determine relationships between color and (1) body size and condition, (2) clutch size, (3) number of young fledged, (4) provisioning rates during the early nestling period (3–5 d after hatching), and (5) provisioning rates during the late nestling period (14–16 d after hatching). Differences in sample sizes between early and late stages were due to nest failures that occurred between stages. We used analysis of covariance with year as a fixed effect to examine whether the time or Julian date of a nest watch predicted provisioning rates. Because there was a relationship between early female provisioning and nest watch date (see Results), we included date as a covariate in subsequent analyses examining factors predicting early female provisioning.

When age classes were separated for analyses using tail PC1 (due to differences in tail PC1 between ASY and SY females), linear mixed models were used with ASY females, whereas linear regression was used with SY females because repeated samples with SY females were not possible. Mixed models were also used to determine if there were differences between ASY and SY individuals in plumage coloration, body size, clutch size, fledging success, and parental care. Prior to analysis, we conducted a square root transformation on clutch size, but nontransformed data are shown in Figure 1. Values are presented as means \pm SD.

RESULTS

Differences between age classes. ASY females (0.26 ± 0.21) had higher tail PC1 scores than SY females $(-0.66 \pm 0.33; F_{1,38.2} = 9.4, P = 0.004;$ Fig. 2), but the rump coloration of ASY and SY females did not differ $(F_{1,56.5} = 0.4, P = 0.55;$ Fig. 2). ASY (N = 41) and SY (N = 13) males did not differ in either rump (PC1: $F_{1,51.0} = 2.4, P = 0.13$) or tail (PC1: $F_{1,51.8} = 0.9, P = 0.36$) coloration (Fig. 2). In addition, ASY and SY females did not differ in size (wing chord, tarsus, and tail length; all $P \ge 0.12$), first egg date, clutch size, number of young fledged, early or late provisioning rates, or duration of brooding during the early period (all $P \ge 0.22$).

ASY males (N = 46; mean = 116.6 \pm 2.1 mm) had longer wing chords than SY males (N = 13; mean = 114.8 \pm 3.0 mm)



Fig. 1. Female Mountain Bluebirds with brighter, more UV-blue tail coloration had larger clutches, but this relationship remained significant only for ASY females after separating by age class (black circles: second-year [SY] females, white circles: after-second-year [ASY] females). Best fit lines are shown for SY (black) and ASY (gray) females.

 $(F_{1,46.8} = 8.9, P = 0.005)$, but did not differ in tarsus or tail length $(P \ge 0.26)$, first egg date, clutch size, number of young fledged, or early provisioning rates (all $P \ge 0.16$). However, SY males provisioned at higher rates (N = 11;mean = 3.5 ± 2.6 trips/h/chick) than ASY males (N = 25; mean = 2.2 ± 1.4 trips/h/chick) during the late nestling period $(F_{1,6.4} = 8.1, P = 0.03)$.

Plumage color and body size. Tail PC1 was positively associated with rump PC1 in females ($F_{1,57,8} = 4.4$, P < 0.0001, N = 60), but not males ($F_{1,51,7} = 0.4$, P = 0.54, N = 54). We found a significant positive correlation between female tail PC1 and tail length for SY females: ($r_{16} = 0.33$, P = 0.015), but not ASY females: $F_{1,35,5} = 0.5$, P = 0.48). No other relationships between color and body size were significant (Table 2).

Plumage color and reproduction. ASY females with higher tail PC1 scores had larger clutches ($F_{1,37.1} = 4.4$, P = 0.04, N = 43), but the relationship was marginal and non-significant for SY females ($r^2 = 0.21$, P = 0.07, N = 17). There was a non-significant trend toward higher rump PC1 scores for ASY females with larger clutches ($F_{1,39.9} = 4.4$, P = 0.06, N = 43), but no such trend existed for SY females ($r^2 = 0.01$, P = 0.71, N = 17). We found no relationship between female plumage coloration (tail or rump) and either first egg date or number

of young fledged (all $P \ge 0.11$). For males (N = 54), we found no relationship between either tail or rump coloration and clutch size, first egg date, or number of young fledged (all $P \ge 0.24$).

Parental care. We found no effect of time of day on provisioning rates of males and females during the early or late periods (all $P \ge 0.42$). Similarly, date had no effect on provisioning rates of males during the early period, and both males and females during the late period (all $P \ge 0.35$). However, during the early period, females had higher provisioning rates later in the season ($F_{1,52} = 11.9$, P = 0.001). Thus, for subsequent analyses of female provisioning during the early period, we also include models with date as a covariate.

Provisioning rates of mated pairs were positively correlated during the early nestling stage (male mean = 1.4 ± 0.8 trips/h/chick, female mean = 1.3 ± 0.7 trips/h/chick; $r_{52} = 0.41$, P = 0.002), but not the late nestling stage (male mean = 2.6 ± 1.9 trips/h/chick, female mean = 2.8 ± 1.6 trips/h/chick; $r_{35} = 0.11$, P = 0.52). Provisioning rates of males and females did not differ during either the early ($t_{52} = -0.5$, P =0.59) or late ($t_{35} = 0.7$, P = 0.52) nestling stages. We found no relationship between fledging success and provisioning rates for either males or females (including model with date) during the early nestling stage (all $P \ge 0.43$) or for females during the late nestling stage ($F_{1,34.0} = 3.6$,



Fig. 2. (A) Older, after-second-year (ASY) female Mountain Bluebirds (N = 43) had brighter, more UV-blue tail coloration than second-year (SY) females (N = 17), but (C) rump coloration did not differ with female age. Neither tail (B) nor rump (D) coloration differed with male age. Brightness, chroma, and hue were examined together using principal components analysis and, because the first principle component (PC1) explained most of the variation, we used PC1 to represent overall color variation. Boxes illustrate median (thick line) and quartiles (box), whiskers are defined as the upper quartile plus 1.5 times the interquartile distance (IQD) and lower quartile minus 1.5 times the IQD, and open circles represent individuals that fell outside this range.

Table 2. Relationships between plumage coloration and body size of male and female Mountain Bluebirds. Correlation coefficients are shown with sample sizes in parentheses.

| | Mass | Wing chord | Tarsus length | Tail length |
|-------------------|------------|------------|---------------|-------------|
| Male tail color | -0.07 (30) | -0.04 (56) | -0.03 (55) | -0.14 (56) |
| Male rump color | 0.03 (30) | -0.02 (56) | -0.01(55) | -0.19 (56) |
| Female tail color | -0.04(30) | 0.00 (60) | -0.04(59) | 0.28 (59)ª |
| Female rump color | 0.29 (30) | -0.02 (60) | 0.10 (59) | 0.16 (59) |

^aSignificant at $\alpha = 0.05$.

P = 0.06, N = 36). However, fledging success was negatively related to male provisioning rate during the late nestling stage ($F_{1,31.9} = 6.9$, P = 0.01, N = 36). Provisioning rates

during early and late periods were correlated for males ($F_{1,26.0} = 14.9$, P = 0.0007, N = 36), but not females ($F_{1,28.3} = 1.4$, P = 0.24, N = 36).



Fig. 3. Male Mountain Bluebirds with brighter, more UV-blue rump coloration mated with females with less bright, UV-blue tail color, but, analyzing by age class (dark circles: second-year [SY] females, white circles: after-second-year [ASY] females), this relationship remained significant only for SY females. Best fit lines are shown for reference (black: SY females, gray: ASY females).

During the early nestling stage, there was no relationship between the tail PC1 scores and nestling provisioning rates of females (SY: $r_{16} = 0.29, P = 0.25; \text{ ASY: } F_{1,17.1} = 1.3, P =$ 0.26). We found no relationship between female tail PC1 scores and either male provisioning rates during the early and late nestling stages or female provisioning rates during the late nestling stage (all $P \ge 0.17$). In addition, there was no relationship between female rump PC1 and the provisioning rates of males and females during either nestling stage (all $P \ge 0.08$). Similarly, we found no relationship between either male tail or rump PC1 scores and the provisioning rates of males and females during either nestling stage (all $P \ge 0.38$), or between time spent brooding during the early nestling phase and either female tail PC1 or female rump PC1 (both $P \ge 0.37$).

Assortative mating. We found a significant negative correlation between SY female tail PC1 scores and male rump PC1 scores $(r_{16} = -0.61, P = 0.01)$, although this relationship was not observed with ASY females (ASY: $r_{31} = -0.29, P = 0.11$; Fig. 3). There was no evidence of assortative mating for any other color variables, including female tail PC1 and male tail PC1, female rump PC1 and male tail PC1, and female rump PC1 and male rump PC1 (all $P \ge 0.08$). We found a positive correlation between male and female tarsus length ($r_{50} =$

0.52, P < 0.0001), but not mass ($r_{23} = 0.33$, P = 0.12), wing chord ($r_{52} = 0.13$, P = 0.37), or tail length ($r_{51} = -0.05$, P = 0.74). We also found no evidence of assortative mating by age ($\chi^2 = 2.3$, P = 0.13, N = 53).

DISCUSSION

The Mutual Selection Hypothesis predicts that more highly ornamented females should provide more care (e.g., Linville et al. 1998, Siefferman and Hill 2005, but see Smiseth and Amundsen 2000), mate assortatively with highly ornamented males (MacDougall and Montgomerie 2003, Jawor et al. 2004, Griggio et al. 2005), and generally have higher reproductive success (Doutrelant et al. 2008, Henderson et al. 2013). Our results were mixed with respect to the Mutual Selection Hypothesis; we found no relationship between female color and provisioning rate, and evidence of negative assortative mating by SY females. Similarly, Balenger et al. (2007) found no relationship between parental care and plumage coloration for either male or female Mountain Bluebirds. We did find that ASY female Mountain Bluebirds exhibited brighter, more UV-blue (higher PC1 scores) tail feathers than SY females. In addition, tail coloration of SY females was positively correlated with body size, and ASY female Mountain Bluebirds with higher tail PC1 scores produced larger clutches. Thus, although our evidence that structural plumage coloration of female Mountain Bluebirds is a signal of direct reproductive benefits for males (e.g., higher reproductive success) is limited, our results (i.e., ASY females with brighter tails than SY females, tail color of SY females correlated with size, and ASY females with brighter tails had larger clutches) do suggest the potential for sexual selection to act on female coloration.

ASY female Mountain Bluebirds in our study had brighter, more UV-blue tail coloration than SY females, but we observed no age-specific differences in males. Age-related differences in female plumage have been reported in several songbird species (Flood 2002, Morales et al. 2007, del Val et al. 2010, Winkler et al. 2011, Osmond et al. 2013). Among bluebirds, Siefferman and Hill (2005) found no significant differences between age classes in plumage coloration of female Eastern Bluebirds, but the UV-blue coloration of male Eastern and Western (Sialia mexicana) bluebirds was found to increase in brightness with age (Siefferman et al. 2005, Budden and Dickinson 2009). In addition, Balenger et al. (2007) found that older female Mountain Bluebirds had marginally higher rump PC1 scores (P = 0.08). Variation among bluebird species and populations with respect to the presence or absence of age-specific variation in plumage coloration of males and females could be caused by a variety of proximate, ecological (e.g., nutrient limitation and molt constraints), or ultimate, evolutionary (e.g., mate choice and age-related dominance) factors. Differences in tail coloration of SY and ASY female Mountain Bluebirds in our study could be due to differences in how food is obtained during molt (i.e., older birds would have been foraging independently, whereas SY birds would have been fed by their parents), and the time when feathers are grown. For example, because nestling tail feathers are grown several months prior to adult tail feathers (Power and Lombardo 1996, Pyle 1997), the feathers of SY birds would likely experience more wear.

Age-related plumage variation and delayed plumage maturation (DPM) is relatively common among male songbirds, but less so for females (Hawkins et al. 2012). However, female Tree Swallows exhibit pronounced DPM, whereas males exhibit more moderate changes in plumage coloration (Bitton and Dawson 2008); the duller coloration of young female swallows appears to reduce conspecific aggression during the breeding season (Coady and Dawson 2013). Although female Mountain Bluebirds do not exhibit DPM, reduced ornamentation of SY female Mountain Bluebirds could also function to reduce intrasexual aggression from older females. Importantly, we observed no difference between rump PC1 scores of ASY and SY males or females. In contrast to tail feathers, contour feathers of SY bluebirds, such as those on the rump, are grown at about the same time as those of ASY bluebirds (late summer) and are thus subject to the same constraints for both age classes (Pyle 1997). Thus, if molt timing is a critical component of plumage expression, this could explain why we observed age-specific differences in tail, but not rump, coloration. Regardless of the mechanism(s) underlying plumage differences between ASY and SY females, males that could differentiate female age by color could potentially benefit because older, more experienced individuals tend to have higher reproductive success than first-time breeders in other species (Forslund and Pärt 1995, Martin 1995, Fowler 1995), including Eastern Bluebirds (Siefferman and Hill 2005). We did not, however, observe age-specific variation in reproductive success in our study. Other than tail coloration, we found no other significant differences between female age classes in either individual characteristics or reproductive variables. It is possible that age effects only manifest under more extreme conditions, such as drought or food limitation. In addition, the presence and use of nest boxes may artificially increase mating opportunities for young females, thus masking potential age effects on reproduction (Robertson and Rendell 1990).

We found no relationship between female plumage coloration and either first egg dates or fledging success, but observed a positive relationship between female tail color and clutch size (though this relationship was marginal for SY females, P = 0.07), suggesting a potential benefit for males that mate with more colorful females. These results are consistent with those of previous studies, suggesting that relationships between female plumage coloration and reproductive variables, such as first egg date (Siefferman and Hill 2005, Osmond et al. 2013), may provide evidence of selection on female plumage coloration (but see Amundsen and Pärn 2006).

The only relationship we observed between body size and plumage coloration was between SY female tail color and tail length, which could indicate that SY female coloration is dependent on nesting conditions the previous year and the parental care they received while developing tail feathers. Balenger et al. (2007) found no relationship between color and body size of female Mountain Bluebirds, but did observe a significant positive relationship between plumage coloration and wing length in males. One possible explanation for the difference between these studies could be nutrient limitation; ecological conditions in the Wyoming population studied at low and high elevation sites in the Bighorn Mountains may be variable and contribute to differences in the ability of individuals to produce longer, more colorful wing feathers. Positive relationships between body size and plumage coloration in either sex may indicate better nutritional condition during molt or development and condition-dependence of plumage coloration. For example, male Eastern Bluebird nestlings in experimentally reduced broods were in better condition (i.e., greater mass) and grew brighter UV-blue flight feathers (Siefferman and Hill 2007). If the plumage of female Mountain Bluebirds is similarly conditiondependent, the opportunity exists for sexual selection to occur.

Our provisioning rate data did not support the Good Parent Hypothesis, which suggests that more colorful females should provision offspring at higher rates. Balenger et al. (2007) also found no relationship between female plumage coloration and provisioning rates in Mountain Bluebirds. The lack of a relationship between plumage coloration and provisioning may be interpreted as indicating little or no sexual selection on female color. However, we did observe a positive relationship between ASY female color and clutch size.

We also observed negative assortative mating by plumage coloration (for SY females) and positive assortative mating by tarsus length. In previous studies, positive assortative mating by body size (Delestrade 2001) and color (MacDougall and Montgomerie 2003, Jawor et al. 2004, Griggio et al. 2005) has been proposed as providing indirect evidence of sexual selection acting on females, with brighter color and larger body size potentially functioning as signals either during female-female competition or male mate choice (Kraaijeveld et al. 2007). Surprisingly, rather than positive assortative mating, which could provide further evidence of positive selection on female coloration, we found evidence of negative assortative mating, i.e., SY females with lower PC1 scores paired with males with higher rump PC1 scores. Few examples of negative assortative mating have been reported (Houtman and Falls 1994, Nisbet et al. 2007) and recent work suggests that most, if not all, cases of such mating may be a result of Type 1 errors (Jiang et al. 2013). Our small sample sizes and the fact that the relationship was significant only for SY females may support this interpretation.

We did find evidence of positive assortative mating by tarsus length, and previous investigators have noted that assortative mating is often only observed in one or a small subset of body size measurements (Wagner 1999, Forero et al. 2001, Einoder et al. 2008). Furthermore, tarsus length, the only measure of skeletal body size we recorded, is generally considered the best measure of body size in birds (Rising and Somers 1989), suggesting that male mate choice for females may be driven primarily by preference for larger size, rather than plumage coloration. Previous work with other species has revealed that female body size may be a good predictor of breeding success (Choudhury et al. 1996), and may thus present an advantage for males pairing with larger females. However, we found no evidence of increased reproductive success for larger females in our study.

In summary, we found that brighter, more UV-blue female tail coloration was related to both female age and the ability to produce larger clutches by ASY females, suggesting that males may be able to use this information to assess the age, and perhaps quality, of potential mates. Surprisingly, however, we also found evidence of negative assortative mating on the basis of plumage color, and a weak negative relationship between female plumage coloration and parental care, suggesting the possible existence of nonadaptive genetic correlation between the sexes (Lande 1987, Amundsen 2000, Amundsen and Pärn 2006). Due to the conflicting results of the potential signalling function of female plumage coloration in our study and in the literature, more studies are clearly needed, especially studies that explore the potential signalling function of female plumage in intrasexual interactions

during both the breeding and non-breeding seasons.

ACKNOWLEDGMENTS

This study would not have been possible without the support from the members of the Kamloops Naturalist Club who allowed us to use their bluebird trails. Many thanks to S. Joly for helping us capture and band bluebirds. Special thanks to G. Dreger for his extensive knowledge of, and enthusiasm for, Mountain Bluebirds and for use of his route. Thanks also to L. Dixon and P. and J. Gray for their support and use of their bluebird route. The Natural Sciences and Engineering Research Council of Canada Discovery Grant (MWR), British Ecological Society (AM), Sigma Xi (AM), the North American Bluebird Society (AM), and the TRU Comprehensive University Endowment Fund (AM) provided financial support that was instrumental to completing our research. We also thank T. Dickinson, S. McArthur, and D. Pouw for intellectual and technical assistance on this project.

LITERATURE CITED

- AMUNDSEN, T. 2000. Why are female birds ornamented? Trends in Ecology and Evolution 15: 149–155.
- —, E. FORSGREN, AND L. T. T. HANSEN. 1997. On the function of female ornaments: male Bluethroats prefer colourful females. Proceedings of the Royal Society B 264: 1579–1586.
 - —, AND H. PÄRN. 2006. Female coloration: review of functional and non-functional hypotheses. In: Bird coloration: function and evolution (G. E. Hill and K. J. McGraw, eds.), pp. 280–348. Harvard University Press, Cambridge, MA.
- BADYAEV, A. V., AND G. E. HILL. 2002. Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the House Finch. Behavioral Ecology 13: 591– 597.
- BALENGER, S., L. S. JOHNSON, J. L. BRUBAKER, AND E. OSTLIND. 2007. Parental effort in relation to structural plumage coloration in the Mountain Bluebird (*Sialia currucoides*). Ethology 113: 838–846.
 - , —, AND B. MASTERS. 2009a. Sexual selection in a socially monogamous bird: male color predicts paternity success in the Mountain Bluebird, *Sialia currucoides*. Behavioral Ecology and Sociobiology 63: 403–411.
- —, —, H. MAYS, Jr., AND B. MASTERS. 2009b. Extra-pair paternity in the socially monogamous Mountain Bluebird *Sialia currucoides* and its effect on the potential for sexual selection. Journal of Avian Biology 40: 173–180.
- BITTON, P.-P., AND R. D. DAWSON. 2008. Age-related differences in plumage characteristics of male Tree Swallows *Tachycineta bicolor*: hue and brightness signal different aspects of individual quality. Journal of Avian Biology 39: 446–452.
- BLEIWEISS, R. 1997. Covariation of sexual dichromatism and plumage colours in lekking and non-lekking birds: a comparative analysis. Evolutionary Ecology 11: 217–235.

- BUDDEN, A., AND J. L. DICKINSON. 2009. Signals of quality and age: the information content of multiple plumage ornaments in Western Bluebirds, *Sialia mexicana*. Journal of Avian Biology 40: 18–27.
- BURLEY, N. 1988. The differential-allocation hypothesis: an experimental test. American Naturalist 132: 611– 628.
- CHOUDHURY, S., J. M. BLACK, AND M. OWEN. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. Ibis 138: 700–709.
- CLUTTON-BROCK, T. 2009. Sexual selection in females. Animal Behaviour 77: 3–11.
- COADY, C. D., AND R. D. DAWSON. 2013. Subadult plumage of female Tree Swallows reduces conspecific aggression during the breeding season. Wilson Journal of Ornithology 125: 348–357.
- DEL VAL, E., J. QUESADA, AND J. C. SENAR. 2010. Agerelated differences in a carotenoid-based coloration trait are due to within-individual changes in Great Tits *Parus major*. Ardea 98: 179–184.
- DELESTRADE, A. 2001. Sexual size dimorphism and positive assortative mating in Alpine Choughs (*Pyrrhocorax graculus*). Auk 118: 553–556.
- DOUTRELANT, C., A. GREGOIRE, N. GRNAC, D. GOMEZ, M. M. LAMBRECHT, AND P. PERRETT. 2008. Female coloration indicates female reproductive capacity in Blue Tits. Journal of Evolutionary Biology 21: 226– 233.
- —, —, A. MIDAMEGBE, M. LAMBRECHTS, AND P. PERRET. 2012. Female plumage coloration is sensitive to the cost of reproduction: an experiment in Blue Tits. Journal of Animal Ecology 81: 87–96.
- DROBNIAK, S. M., D. WIEJACZKA, A. ARCT, A. DUBIEC, L. GUSTAFSSON, AND M. CICHON. 2013. Low crosssex genetic correlation in carotenoid-based plumage traits in the Blue Tit nestlings (*Cyanistes caeruleus*). PLoS ONE 8: e69786.
- EINODER, L. D., B. PAGE, AND S. D. GOLDSWORTHY. 2008. Sexual size dimorphism and assortative mating in the Short-tailed Shearwater *Puffinus tenuirostris*. Marine Ornithology 36: 167–173.
- EDWARD, D., AND T. CHAPMAN. 2011. The evolution and significance of male mate choice. Trends in Ecology and Evolution 26: 647–654.
- FLOOD, N. J. 2002. Scott's Oriole (*Icterus parisorum*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- FORERO, M. G., J. L. TELLA, J. A. DONAZAR, G. BLANCO, M. BERTELLOTTI, AND O. CEBALLOS. 2001. Phenotypic assortative mating and within-pair sexual dimorphism and its influence on breeding success and offspring quality in Magellanic Penguins. Canadian Journal of Zoology 79: 1414–1422.
- FORSLUND, P., AND T. PÄRT. 1995. Age and reproduction in birds: hypotheses and tests. Trends in Ecology and Evolution 10: 374–378.
- FOWLER, G. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pairbond duration and reproductive experience. American Zoologist 35: 318–328.
- GIBSON, K. W., AND A. MOEHRENSCHLAGE. 2008. A sex difference in the behavioural response of nesting Mountain Bluebirds (*Sialia currucoides*) to a mounted predator. Journal of Ethology 26: 185–189.

GRIGGIO, M., F. VALERA, A. CASAS, AND A. PILASTRO. 2005. Males prefer ornamented females: a field experiment of male choice in the Rock Sparrow. Animal Behaviour 69: 1243–1250.

—, A. DEVIGILI, H. HOI, AND A. PILASTRO. 2009. Female ornamentation and directional male mate preference in the Rock Sparrow. Behavioral Ecology 20: 1072–1078.

- HAWKINS, G. L., G. E. HILL, AND A. MERCADANTE. 2012. Delayed plumage maturation and delayed reproductive investment in birds. Biological Reviews 87: 257–274.
- HENDERSON, L. J., B. J. HEIDINGER, N. P. EVANS, AND K. E. ARNOLD. 2013. Ultraviolet crown coloration in female Blue Tits predicts reproductive success and baseline corticosterone. Behavioral Ecology 24: 1299–1305.
- HILL, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the House Finch. Evolution 47: 1515–1525.
- 2006. Female mate choice for ornamental coloration. In: Bird coloration: function and evolution (G. E. Hill and K. J. McGraw, eds.), pp. 137–200. Harvard University Press, Cambridge, MA.
- HOELZER, G. A. 1989. The good parent process of sexual selection. Animal Behaviour 38: 1067–1078.
- HOUTMAN, A. M., AND J. B. FALLS. 1994. Negative assortative mating in the White-throated Sparrow, *Zonotrichia albicollis*: the role of mate choice and intra-sexual competition. Animal Behaviour 48: 377–383.
- JAWOR, J. M., N. GRAY, S. M. BEALL, AND R. BREITWISCH. 2004. Multiple ornaments correlate with aspects of condition and behaviour in female Northern Cardinals, *Cardinalis cardinalis*. Animal Behaviour 67: 875–882.
- JIANG, Y., D. I. BOLNICK, AND M. KIRKPATRICK. 2013. Assortative mating in animals. American Naturalist 181: e125–e138.
- JOHNSEN, A., K. DELHEY, E. SCHLICHT, A. PETERS, AND B. KEMPENAERS. 2005. Male sexual attractiveness and parental effort in Blue Tits: a test of the differential allocation hypothesis. Animal Behaviour 70: 877– 888.
- JOHNSON, K. 1988. Sexual selection in Pinyon Jays. II. Male choice and female:female competition. Animal Behaviour 36: 1048–1053.
- JONES, I. L., AND F. M. HUNTER. 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a Crested Auklet ornament. Animal Behaviour 57: 521–528.
- KEYSER, A. J., AND G. E. HILL. 1999. Conditiondependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. Proceedings of the Royal Society B 266: 771–777.
- _____, AND _____. 2000. Structurally based plumage coloration is an honest signal of quality in male Blue Grosbeaks. Behavioral Ecology 11: 202—209.
- KRAAIJEVELD, K., F. J. L. KRAAIJEVELD-SMIT, AND J. KOMDEUR. 2007. The evolution of mutual ornamentation. Animal Behaviour 74: 657–677.
- LANDE, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. In: Sexual selection: testing the alterna-

tives (J. W. Bradbury and M. B. Andersson, eds.), pp. 83–94. John Wiley, Berlin, Germany.

- LEBAS, N. 2006. Female finery is not for males. Trends in Ecology and Evolution 21: 170–173.
- LINVILLE, S. U., R. BREITWISCH, AND A. J. SCHILLING. 1998. Plumage brightness as an indicator of parental care in Northern Cardinals. Animal Behaviour 55: 119–127.
- MACDOUGALL, A. K., AND R. MONTGOMERIE. 2003. Assortative mating by carotenoid-based plumage colour: a quality indicator in American Goldfinches, *Carduelis tristis*. Naturwissenschaften 90: 464– 467.
- MARTIN, T. E. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist 35: 340–348.
- MCGRAW, K. J., E. A. MACKILLOP, J. DALE, AND M. E. HAUBER. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. Journal of Experimental Biology 205: 3747–3755.
- MIDAMEGBE, A., A. GREGOIRE, P. PERRET, AND C. DOUTRELANT. 2011. Female-female aggressiveness is influenced by female coloration in Blue Tits. Animal Behaviour 82: 245–253.
- MØLLER, A. P., AND R. THORNHILL. 1998. Male parental care, differential parental investment by females and sexual selection. Animal Behaviour 55: 1507–1515.
- MONTGOMERIE, R. [online]. 2008. RCLR, version 0.9.28. Queen's University, Kingston, Canada. http://post. queensu.ca/~mont/color/analyze.html (Accessed 12 April 2013).
- MORALES, J., J. MORENO, S. MERINO, J. J. SANZ, G. TOMÁS, E. ARREIRO, E. LOBATO, AND J. MARTÍNEZ-DE LA PUENTE. 2007. Female ornaments in the Pied Flycatcher *Ficedula hypoleuca*: associations with age, health and reproductive success. Ibis 149: 245– 254.
- MURPHY, T. G., D. HERNANDEZ-MUCINO, M. OSORIO-BERISTAIN, R. MONTGOMERIE, AND K. E. OMLAND. 2009. Carotenoid-based status signaling by females in the tropical Streak-backed Oriole. Behavioral Ecology 20: 1000–1006.
- NISBET, I. C. T., E. S. BRIDGE, P. SZCZYS, AND B. J. HEIDINGER. 2007. Sexual dimorphism, femalefemale pairs, and test for assortative mating in Common Terns. Waterbirds 30: 169–179.
- OSMOND, M. M., M. W. REUDINK, R. R. GERMAIN, P. P. MARRA, J. J. NOCERA, P. T. BOAG, AND L. M. RATCLIFFE. 2013. Relationships between carotenoidbased female plumage and age, reproduction and mate colour in the American Redstart (*Setophaga ruticilla*). Canadian Journal of Zoology 91: 589– 595.
- PETERS, A., R. H. KURVERS, M. L. ROBERTS, AND K. DELHEY. 2011. No evidence for general conditiondependence of structural plumage colour in Blue Tits: an experiment. Journal of Evolutionary Biology 24: 976–987.
- POWER, H. W., AND M. P. LOMBARDO. 1996. Mountain Bluebird (*Sialia currucoides*). In: The birds of North America, No. 222 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and

the American Ornithologists' Union, Washington, D.C.

- PRUM, R. 2006. Anatomy, physics, and evolution of structural colors. In: Bird coloration: mechanisms and measurements (G. E. Hill and K. J. McGraw, eds.), pp. 295–353. Harvard University Press, Cambridge, MA.
- PYLE, P. 1997. Identification guide to North American birds, part 1. Slate Creek Press, Bolinas, CA.
- RISING, J. D., AND K. M. SOMERS. 1989. The measurement of overall body size in birds. Auk 106: 666–674.
- ROBERTSON, R. J., AND W. B. RENDELL. 1990. A comparison of the breeding ecology of a secondary cavity nesting bird, the Tree Swallow (*Tachycineta bicolor*), in nest boxes and natural cavities. Canadian Journal of Zoology 68: 1046–1052.
- ROHDE, P. A., A. JOHNSEN, AND J. T. LIFJELD. 1999. Female plumage coloration in the Bluethroat: no evidence for an indicator of maternal quality. Condor 101: 96–104.
- ROSVALL, K. 2011. Intrasexual competition in females: evidence for sexual selection? Behavioral Ecology 22: 1131–1140.
- SAS INSTITUTE. 2012. JMP, version 10. SAS Institute, Inc., Cary, NC.
- SIEFFERMAN, L., AND G. E. HILL. 2005. Evidence for sexual selection on structural plumage coloration in female Eastern Bluebirds (*Sialia sialis*). Evolution 59: 1819–1828.
 - —, AND ——. 2007. The effect of rearing environment on blue structural coloration of Eastern Bluebirds. Behavioral Ecology and Sociobiology 61:1839–1846.

—, —, AND F. S. DOBSON. 2005. Ornamental plumage coloration and condition are dependent on age in Eastern Bluebirds *Sialia sialis*. Journal of Avian Biology 36: 428–435.

- Biology 36: 428–435.
 SMISETH, P. T., AND T. AMUNDSEN. 2000. Does female plumage coloration signal parental quality? A male removal experiment with the Bluethroat (*Luscinia s. svecical*). Behavioral Ecology and Sociobiology 47: 205–212.
- J. ÖRNBORG, S. ANDERSSON, AND T. AMUNDSEN. 2001. Is male plumage reflectance correlated with paternal care in Bluethroats? Behavioral Ecology 12: 164–170.
- WAGNER, R. H. 1999. Sexual size dimorphism and assortative mating in Razorbills (*Alca torda*). Auk 116: 542–544.
- WEST-EBERHARD, M. J. 1979. Sexual selection, social competition, and evolution. Proceedings of the American Philosophical Society 123: 222–234.
- WHITTINGHAM, L. A., A. KIRKCONNELL, AND L. M. RATCLIFFE. 1992. Differences in song and sexual dimorphism between Cuban and North American Red-winged Blackbirds (*Agelaius phoenicius*). Auk 109: 928–933.
- , ____, AND _____. 1996. Breeding behavior, social organization and morphology of Redshouldered (*Agelaius assimilis*) and Tawny-shouldered (*A. humeralis*) blackbirds. Condor 98: 832–836.
- WINKLER, D. W., K. K. HALLINGER, D. R. ARDIA, R. J. ROBERTSON, B. J. M. STUTCHBURY, AND R. R. COHEN. 2011. Tree Swallow (*Tachycineta bicolor*). In: The birds of North America online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.