Plumage color and food availability affect male reproductive success in a socially monogamous bird

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Male reproductive success in socially monogamous birds is influenced to varying degrees by within-pair fertilization (WPF) and extrapair fertilization (EPF). In many species, males of higher phenotypic quality (e.g., plumage color) are more likely to obtain EPFs; however, predictors of WPF success have been less consistently identified. Moreover, few studies have examined the influence of ecological variables on patterns of paternity, even though environmental conditions are known to affect mating behavior of male and female birds. In this study, we examined phenotypic and ecological factors influencing patterns of paternity in broods of mountain bluebirds, *Sialia currucoides*. We show that brighter, bluer males were more likely to obtain EPFs in first broods but that plumage color did not predict the ability of males to maintain paternity in their own nest. We then examined the effect of food availability in first broods on the probability of males losing paternity in second broods within the same season. Females that were provided with supplemental food throughout first breeding attempts were less likely to produce extrapair offspring in second broods, and we suggest that supplemented females may have been less likely to seek extrapair mating opportunities because they perceived their social mates to be of higher quality under conditions of enhanced food availability. Our results demonstrate that ecological variables such as food availability can influence patterns of paternity and suggest that consideration of environmental context will be important for future research investigating mate choice and sexual selection in socially monogamous species. Key words: extrapair paternity, food availability, mountain bluebird, plumage color. [Behav Ecol 22:66–72 (2011)]
In addition, habitat characteristics that determine breeding density and synchrony can also affect rates of EPP in some species (Steen, et al. 2010). Food availability has considerable potential to affect both male and female breeding behavior, although the effects of food on patterns of paternity appear to vary depending on the species studied. For example, superb starlings, *Lamprotornis superbus*, occupying high-quality territories with abundant food were less likely to have mixed-paternity broods and had fewer extrapair offspring (EPO) in their broods compared with birds on low-quality territories (Rubenstein 2007), and female house sparrows, *Passer domesticus*, provided with food prior to breeding similarly had fewer EPO than nonsupplemented females (Václav et al. 2003). In both cases, the authors suggest that low food availability might have increased the distance females moved from the nest while foraging, and this would in turn have allowed them to encounter more potential extrapair mates as well as to escape guarding by their social mate. In contrast, female serins, *Serinus serinus*, provided with supplemental food were better able to circumvent mate guarding efforts of their social mates (consistent with the “constrained female hypothesis”; Gowaty 1996), and these supplemented females consequently had higher rates of EPP in their broods compared with control females or those with reduced food availability (Hoi-Leitner et al. 1999).

The above studies highlight the influence that food availability may have on female behavior and hence on patterns of EPP. Food availability, however, also has the potential to affect male behaviors, such as incubation feeding and investment in provisioning young. Among multiple-brooded species, increased paternal investment in first broods is associated with lower rates of EPP in second broods, suggesting that females allocate paternity to social mates according to the quality of their previous parental care efforts (Freyman-Gallant 1996; Rowe and Weatherhead 2007). Hence, food availability may also affect the probability of a male bird losing paternity in his own nest to the extent that it influences his parental investment in prior breeding attempts. This linkage between food availability in first broods and patterns of paternity in subsequent broods, however, has not previously been investigated.

In this study, we first assess the influence of male phenotypic traits on patterns of WPF and EPF success among first broods of mountain bluebirds, *Sialia currucoides*, a sexually dichromatic socially monogamous passerine. We then use a supplementation experiment to examine the effect of an ecological variable, food availability, on male WPF success. Mountain bluebirds are facultatively double brooded, and we took advantage of this characteristic by supplementing breeding pairs beginning in late incubation and continuing throughout first broods and subsequently testing the importance of food availability on the probability of females seeking extrapair mating opportunities in second breeding attempts. This experimental design allowed us to test 2 alternative predictions: First, if female bluebirds are energetically constrained from seeking EPF, food supplementation throughout first broods should increase the probability of EPF in second broods. Alternatively, if provision of supplemental food throughout first breeding attempts enhances female perception of the genetic quality of their social mate, in particular through increased male investment in mate and nestling feeding, supplemented pairs will be less likely to have EPF in second broods.

**METHODS**

**Study area, species, and field procedures**

This study was conducted from 2006 to 2008 on a population of mountain bluebirds breeding in central British Columbia, Canada (lat 51°N, long 122°W). Mountain bluebirds are medium-sized (~30 g), sexually dichromatic, secondary cavity-nesting passerines that breed in western North America, and that readily use artificial nest-boxes (Power and Lombardo 1996). Females exclusively incubate eggs, although they are provisioned by their social mate during incubation, and both sexes contribute to provisioning offspring (Power and Lombardo 1996). Our study area consisted of open arid grassland with patches of large mature Douglas-fir, *Pseudotsuga menziesii*. In 2006, the site contained 72 pairs of nest-boxes mounted on fence posts; this was increased to 87 pairs beginning in 2007. Paired boxes were spaced approximately 5 m apart, and adjacent pairs were separated by approximately 200 m. Starting in late April, nests were checked every other day to determine clutch initiation date (CID) and clutch size. Completed clutches were checked daily beginning 12 days after clutch completion to determine hatching date (designated nesting day 0). When nestlings were 13 days old, we banded them with a numbered aluminum band and collected blood samples (ca. 50 μl) by puncturing the brachial vein. To assess patterns of male fertilization success, we established paternity of offspring from all fertilized eggs; we therefore also collected tissue samples from any nestlings that died prior to day 13 (n = 47), as well as from any embryos collected from unhatched eggs (n = 22). Adults were captured in nest-boxes while they were feeding nestlings during first and second broods and were banded with a unique combination of 3 colored plastic leg bands and 1 numbered aluminum band. We measured adult mass (nearest 0.25 g, using a spring balance) and used head-bill length (greatest distance from the back of the head to the tip of the bill, nearest 0.01 mm, using digital calipers) as an index of structural size. We also collected 8–10 rump feathers and approximately 50 μl of blood from all adults at the time of capture.

**Experimental design**

Within a population, up to half of all female mountain bluebirds produce a second brood after successfully fledging young from first breeding attempts (Power and Lombardo 1996). By manipulating conditions during first broods in the 2007 and 2008 breeding seasons, we were therefore able to investigate the influence of food availability on subsequent patterns of paternity in second broods. Nests were paired according to estimated hatching date, and 1 nest in each pair was randomly assigned to a feeding treatment. Supplemented birds were provided with 12 g of mealworms and waxworms daily (ca. 8 g of mealworms and 4 g of waxworms), representing approximately 50% of the energy requirements of an adult bluebird during incubation and brood rearing (Mock 1991; Merkle and Barclay 1996). Food was provided in a small dish installed on a fence post within 1 m of each nest-box, from approximately 4 days prior to the expected hatching date until nestlings were 17 days old. Control boxes had dishes installed in the same manner and were visited daily but were not provided with additional food. Mountain bluebirds defend breeding territories of up to 5 ha (Power and Lombardo 1996), and birds in neighboring territories would therefore not have had access to supplemental food. When supplements were first provided each day during incubation, the female would commonly feed first; once the female returned to the nest-box to continue incubating, the resident male would then typically continue delivering food to her. During the nestling period, both adults delivered at least some of the supplemental food to nestlings in addition to consuming it themselves (O’Brien EL, Dawson RD, personal observations). The feeding treatment is therefore likely to have directly enhanced female perception of the quality of their social mate by increasing both
his incubation feeding and his investment in feeding young. No other species were observed to feed on supplements, which were generally consumed or fed to nestlings by the resident adults within several hours each day, and we are therefore confident that supplemented birds had exclusive access to all the food provided. Once first broods had fledged, we monitored all nest sites to document initiation of second broods. We captured adults or confirmed identities by resighting colored leg band combinations during these second breeding attempts and collected blood or tissue samples from all second brood nestlings for subsequent paternity analysis.

Plumage color analysis

Feathers were stored in opaque envelopes at room temperature prior to analysis. We used an Ocean Optics USB2000 spectrometer (Dunedin, FL) with a deuterium tungsten halogen light source (Avantes, Broomfield, CO) to measure spectral characteristics of feathers across the range of wavelengths perceived by songbirds (300–700 nm; Hart 2001). Reflectance at each wavelength was determined as the proportion of light reflected relative to a WS-1 white standard (Ocean Optics, Dunedin, FL). Feathers were mounted on a nonreflective black background and overlapped to mimic the natural orientation of body contour feathers on birds (Sieferman and Hill 2003). We used a bifurcated probe fixed in a cylindrical sheath that excluded ambient light and maintained the probe perpendicular to the feather surface. We took 3 measurements at random locations on each feather sample and used the average of these values to generate individual spectral curves. The average spectral curve for rump feathers of males in our study population is shown in Figure 1.

Following the methods of Balenger et al. (2009a), we summarized the spectral curve for each individual using the measures of hue, brightness, and ultraviolet (UV)-blue chroma, which we extracted from the original spectral data using CLR v. 1.05 (Montgomerie 2008). Hue represented the wavelength of maximal light reflectance; brightness was a measure of the total amount of light reflected relative to the white standard, and UV-blue chroma represented the combined proportion of light reflected within the UV and blue wavelength range (300–512 nm) relative to the entire 300–700 nm spectrum analyzed. We then used principal components analysis to reduce these 3 correlated measures into a single color score (Montgomerie 2006). The first principal component (PC1) explained 61.6% of the variation in feather color, with the following factor loadings: hue $= -0.894$, UV-blue chroma $= 0.930$, and brightness $= 0.425$. Thus, birds with higher PC1 scores had hues shifted further into UV wavelengths, had a greater proportion of their spectral reflectance falling within the blue-UV wavelength range, and tended to be overall brighter.

Paternity assignment

We stored blood samples in 1 ml of Queen’s lysis buffer (Seutin et al. 1991) at 4 °C and extracted DNA using Qiagen DNAeasy extraction kits. To allow us to assign paternity, we genotyped adults and nestlings at 5 microsatellite loci designed for use in mountain or eastern bluebirds, including Mobl087, Mobl049, Eabl129, Eabl007 (Balenger et al. 2009a), and Mobl053 (Mays HL, personal communication; Table 1). Polymerase chain reaction (PCR) amplification was carried out in 10 μl volumes containing approximately 50 ng genomic DNA, 100 μM deoxyribonucleotide triphosphates 2.0–2.5 mM MgCl₂, 1× PCR buffer (Invitrogen), 0.2 μM forward (labeled) and reverse primers, and 0.35 U of Taq DNA polymerase (Invitrogen). We performed PCRs using an MJ Research Peltier thermal cycler under the following conditions: 1 cycle at 95 °C for 3 min, followed by 34 cycles at 94 °C for 30 s, annealing temperature for 45 s (59 °C for Mobl087 and Eabl129, 57 °C for Mobl049 and Mobl053, and 55 °C for Eabl007), and 72 °C for 45 s. This was followed by a final extension step at 72 °C for 5 min. PCR products were analyzed on a Beckman-Coulter CEQ 8000 automated sequencer.

We used CERVUS 3.0 (Kalinowski et al. 2007) to determine allele frequencies and exclusion probabilities for all microsatellite loci and to identify extrapair sires where possible. We genotyped 139 adult females, 118 adult males, and 1170 nestlings (first and second broods over 3 years) at 5 loci, with the exception of 1 adult male and 5 nestlings that we were unable to genotype at 1 locus. Nestlings were classified as within-pair offspring if they matched the resident male at all loci, and EPO if they mismatched the attending male at a minimum of 1 locus. Only 32 of 371 young mismatched at a single locus, and these nestlings commonly shared the mismatching allele with at least 1 sibling that mismatched the attending male at 1 or more additional loci. We are therefore confident with our paternity assignments using this criterion. No nestlings mismatched the maternal genotype, so all were assumed to be genetically related to the resident female. Observations of banded birds in our study population indicate that males are very rarely able to usurp occupied territories during the egg laying period (O’Brien EL, Dawson RD, unpublished)

Table 1

<table>
<thead>
<tr>
<th>Locus</th>
<th>n</th>
<th>No. of alleles</th>
<th>$P_e$</th>
<th>$h_e$</th>
<th>$h_o$</th>
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<tr>
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<td>7</td>
<td>0.46</td>
<td>0.76</td>
<td>0.69</td>
<td>-0.005</td>
</tr>
<tr>
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<td>20</td>
<td>0.61</td>
<td>0.76</td>
<td>0.77</td>
<td>0.003</td>
</tr>
<tr>
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<td>0.79</td>
<td>0.90</td>
<td>0.89</td>
<td>-0.006</td>
</tr>
</tbody>
</table>

$P_e$ is the probability of exclusion with 1 parent (female) known, $h_e$ is the observed heterozygosity, and $h_o$ is the expected heterozygosity. Also shown is the frequency of null alleles (null). The combined probability of paternal exclusion was 0.996.
data), and we are therefore confident that paternal mismatches reflected extrapair mating by the resident female rather than social mate replacement. We had complete paternity information for 51 breeding pairs in 2006, 59 in 2007, and 67 in 2008 (177 total). For each male that fledged young from at least 1 brood \((n = 160)\), we calculated total annual reproductive success as the sum of all surviving nestlings that were identified as his biological offspring within a study year.

**Statistical analyses**

We used analysis of covariance (ANCOVA) to examine the influence of within-pair paternity (WPP; whether or not a male lost paternity in his own nest) and EPP (whether a male gained EPP in at least one other nest in the study population) on total annual reproductive success of individual males \((\text{i.e., total number of young fledged})\). We included all males in each of 3 years that successfully fledged young from at least 1 brood, and for which we had paternity data, and entered male identity as a random factor to account for repeated measures of the same male among years. We also included as a fixed factor whether or not a male’s social mate produced a second brood because this has the potential to nearly double the total number of young produced within a season \((O’Brien EL, Dawson RD, unpublished data)\). The initial model contained all first-order interactions among WPP success, EPP success, and second brooding, and nonsignificant terms were sequentially removed by backward elimination.

Binomial logistic regression allowed us to test the effect of plumage color \((\text{above})\) and body condition of males during first broods on the probability of (a) losing paternity in their own nest and (b) gaining paternity in at least one other nest. Male body condition in each study year was estimated as the residuals from a linear regression of body mass on head-bill length; this measure was not correlated with plumage-color score \((r = 0.11, n = 125, P = 0.29)\). We only included first nesting attempts over 3 years \((\text{i.e., excluding renesting attempts after a failed first attempt as well as second nests initiated after fledging young from first broods})\) and restricted this analysis to a single observation for each male; thus, for those males that we captured over successive breeding seasons, we only used data for their phenotypic measurements and paternity gains in the first year they were captured \((n = 118)\). Year was included as a categorical covariate in initial models to account for possible annual variation in patterns of paternity. CID is correlated with female age and/or quality in many songbirds, including our population of bluebirds \((O’Brien EL, Dawson RD, unpublished data)\), and older females or those in better condition may be more likely to seek EPFs \((Bouwman and Komdeur 2005)\); males paired with high quality or older females that initiate breeding earlier in the season may therefore be more likely to lose paternity in their own nest. Alternatively, females that initiate breeding earlier in the season may be paired with higher quality social mates and may therefore be predicted to be less likely to seek EPF. Early-breeding males may also be freed from the constraints of mate guarding earlier in the season and so have more opportunities to obtain EPF in clutches initiated later in the season, once their social mate has begun incubation \((van Dongen and Mulder 2009)\). We therefore also included CID of a male’s social mate as a covariate in initial models.

For second broods, we used binomial logistic regression to examine the effect of food supplementation during first breeding attempts on the probability of males losing paternity in these subsequent broods. For this analysis, models included the food supplementation treatment, year, and paternity loss in first broods as categorical covariates. In both study years, first broods were also subjected to a hatching date manipulation as part of another study; we therefore also included this timing treatment as a categorical covariate in the model. We assessed the significance of individual variables and interaction terms in all logistic regression models using Wald \(X^2\) values.

**RESULTS**

Patterns of paternity and male reproductive success

Among first breeding attempts, 65% \((115/177)\) of broods contained at least 1 nesting that was not related to the resident male, whereas at the population level, 288 of 900 first brood young \((32\%)\) were sired by extrapair males. However, despite having captured nearly all males breeding in nest-boxes on the study site, we were only able to identify the genetic father of 56% \((161/288)\) of EPO in first broods. The study area contains abundant natural tree cavities, and this suggests that many extrapair sires may be birds occupying these natural nest sites. Among second broods, 50% \((33/66)\) of nests contained at least 1 EPO, and 31% \((83/270)\) of all second brood nestlings were the result of EPFs. Males that obtained EPFs were not more likely to lose paternity in their own nests, suggesting that males did not experience a trade-off between obtaining EPF and maintaining paternity in their own nest \((X^2 = 0.21, df = 1, P = 0.65)\). Total annual reproductive success among males that fledged young from at least 1 brood ranged from 0 to 21 young, including all surviving offspring sired \((mean: 5.2 \pm 0.3, n = 160)\), and was greater for males that obtained EPFs compared with males that did not gain EPP \((EPP: F_{1,40} = 29.49, P < 0.001; Figure 2)\). Males that maintained paternity in their own nest \((WPP)\) also produced more offspring than males raising at least 1 unrelated nesting but only when their social mate initiated a second brood within the same breeding season \((WPP \times \text{second brood}: F_{1,40} = 4.72, P = 0.04; Figure 3)\).

**Predictors of fertilization success among first broods**

We obtained morphological and genetic data for 118 males in the first year they were captured breeding in nest-boxes on the study site. There was no evidence for annual variation in the effects of

**Figure 2**

Number of offspring sired by male mountain bluebirds in relation to their EPF success. Males that did not gain EPP (no EPP gain) produced fewer offspring within a breeding season than males that gained EPP in at least 1 nest (EPP gain). Shown are least-square means ± SEs, calculated after accounting for effects of WPF success and double brooding. Sample sizes in each group are indicated above SE bars.
CID, plumage color, or body condition on the probability of male bluebirds gaining EPFs (all interactions with year: $P > 0.11$). Body condition of males also did not predict their ability to obtain EPFs ($\chi^2 = 0.19$, $P = 0.67$) nor was there variation among years in the overall probability of males producing EPO (year: $\chi^2 = 2.0$, $P = 0.37$). However, both plumage color score and CID at their own nest predicted whether male bluebirds obtained EPFs (plumage: $\chi^2 = 4.7$, $P = 0.03$; CID: $\chi^2 = 4.4$, $P = 0.04$). Specifically, males with higher plumage color scores, and whose social mates initiated clutches earlier in the season, had a greater probability of obtaining EPFs (plumage: $B = 0.53 \pm 0.24$ standard error [SE]; CID: $B = -0.05 \pm 0.03$ SE). In contrast, we did not identify any variables that predicted whether a male lost paternity in his own nest during first broods (all $P > 0.15$).

**Effect of food supplementation on patterns of paternity in second broods**

Of 30 pairs that produced second broods over the 2 years of the food supplementation experiment, we had morphological data for 18 males and 24 females in both broods. Supplemental feeding did not affect body condition of either sex during first broods (ANOVA, males: $F_{1,64} = 0.70$, $P = 0.41$; females: $F_{1,73} = 2.25$, $P = 0.14$) nor did it influence change in body mass between broods (independent samples $t$-test, males: mean difference between first and second brood, control–fed $= -0.02$ g, $df = 16$, $t = -0.03$, $P = 0.97$; females: mean difference, control–fed $= 0.33$ g, $df = 22$, $t = 0.62$, $P = 0.54$). We had complete paternity data for 26 second broods produced by pairs that were included in the feeding experiment; there were no differences between study years in the probability of males losing paternity in second broods (year: $\chi^2 = 0.96$, $P = 0.33$), and paternity loss in first broods did not predict subsequent loss of paternity in second broods ($\chi^2 = 0.44$, $P = 0.51$). Second broods produced by supplemented birds, however, were less likely to contain EPO compared with second broods of control birds (food: reference = controls; $B = -2.21 \pm 0.99$ SE; $\chi^2 = 5.0$, $P = 0.03$). There was no additional effect of the timing treatment (timing: $\chi^2 = 0.96$, $P = 0.62$).

**DISCUSSION**

We provide experimental evidence that increased food availability in first broods reduced the probability of male mountain bluebirds losing paternity in their own nest during subsequent broods in the same breeding season. We suggest that this effect may have been a consequence of enhancement of female perception of the quality of their social mate, due to the direct effects of food provisioning on male behaviors, such as mate and nestling feeding, and that this reduced the probability that females would seek extrapair mating opportunities in second broods. In our study population, plumage color predicted male EPF success in first broods over 3 years but was not associated with male reproductive success in either brood. Filled circles indicate males that lost paternity in at least 1 of their broods, whereas open circles show males that did not lose paternity in either first or second broods. Benefits of double brooding were most evident among males that did not raise any unrelated offspring. Shown are least-square means $\pm$ SEs, calculated after accounting for effects of EPF success. Sample sizes in each group are indicated above SE bars.

![Figure 3](image_url)  
**Figure 3** Number of offspring sired by male mountain bluebirds in relation to whether their social mate produced a second brood after successfully fledging young from first broods and whether they lost paternity in either brood. Filled circles indicate males that lost paternity in at least 1 of their broods, whereas open circles show males that did not lose paternity in either first or second broods. Benefits of double brooding were most evident among males that did not raise any unrelated offspring. Shown are least-square means $\pm$ SEs, calculated after accounting for effects of EPF success. Sample sizes in each group are indicated above SE bars.

Despite abundant evidence that EPP occurs in socially monogamous birds, few studies have been able to distinguish between hypotheses based on male versus female behavior in explaining patterns of EPP within or among species (Westneat and Stewart 2003; Eliassen and Kokko 2008). By supplementing pairs throughout first broods and examining subsequent patterns of paternity in second breeding attempts, we were able to exclude several alternative explanations for the effect of food availability on male WPF success. The amount of food provided each day was not sufficient to prevent females from moving around the entire territory to forage once supplemental food was consumed (see Methods) nor did supplements alter female condition in first broods or their change in mass between broods. Our food supplementation treatment was
therefore unlikely to have restricted the ability of females to encounter prospective extrapair mates on the margins of their territories by limiting their movements away from the nest site (as shown by Václav et al. 2003 in house sparrows). Moreover, supplements were discontinued once first brood nestlings reached 17 days of age; hence, when female bluebirds were again fertile and preparing to initiate second clutches, they would no longer have been receiving supplemental food, and direct effects of supplements on female extrapair mating behavior are therefore unlikely. Males provided with supplemental food may be able to guard their social mate more effectively because mate guarding is energetically costly (Komdeur 2001); however, male birds generally have little opportunity to mate guard during second breeding attempts in multiple-brooded species because they often provide considerable post-fledging care of first brood young at this time (Power and Lombardo 1996; Conrad et al. 1998). Moreover, food supplementation did not affect male body condition during first broods or the change in body mass between broods, and so we have no evidence that supplemented males had more energy reserves available to allocate to mate guarding. This lack of an effect on male condition also makes it unlikely that supplemented males were able to invest more resources in sperm production (Burness et al. 2008). The constrained female hypothesis (Gowaty 1996) predicts that females are energetically limited from escaping male paternity guards and that supplemental food should increase their ability to obtain extrapair copulations; our results, however, showed the opposite effect in that supplemented females were less likely to have EPP in second broods. It is also unlikely that supplemented females engaged in fewer extrapair copulations during formation of second clutches to avoid losing the high level of parental investment received from their social mate in first broods, because males in the majority of bird species are either unable to assess paternity loss, or do not respond by reducing their parental investment (Kempenaers and Sheldon 1996, and references therein). Male bluebirds typically responded to food provisioning by delivering supplements to the incubating female or to nestlings, and the results of this study therefore more likely reflect female mating decisions in response to enhancement of the perceived quality of their social mate or his territory by food supplementation.

In addition to the effects of plumage color on male EPP success in first broods, the CID of a male’s social mate also independently predicted his ability to obtain EPP but did not affect the probability of that male losing paternity in his own nest. Thus, older or higher quality female mountain bluebirds in our population (that initiate first broods earlier) are neither more nor less likely to produce EPO, but males paired with these high-quality females are more successful at obtaining EPP in other nests. This suggests that, while early-breeding male bluebirds may not be more effective at mate guarding in terms of loss of WPP, they are liberated from the constraints of guarding their social mates earlier in the season, and so may have more opportunities to obtain EPF once their social mate has begun incubating (Foote and Barber 2009). If these males were themselves of higher quality according to phenotypic traits that influenced their ability to secure EPF, independent of plumage color (e.g., sperm quality; Pizzari et al. 2007), one might expect that they would also be better able to maintain WPP. Because this was not the case, it is more likely that early-breeding male bluebirds were simply able to allocate more time to seeking extrapair mating opportunities. Attracting a high-quality social mate that initiates breeding early in the season may have considerable advantages for male birds in terms of offspring number or quality (e.g., Smith and Moore 2005); because EPF success significantly increased total male reproductive success in this population (Figure 2), our results suggest that an additional benefit of attracting an early-breeding social mate may be in the additional offspring a male will have the potential to sire in other nests. Anthropogenic food supplements have a wide range of consequences for birds, affecting life history traits ranging from egg quantity and quality to adult survival (Robb et al. 2008). Results of our study suggest that such artificial enhancements of food availability may have additional effects on reproductive behavior, patterns of female paternity allocation, and ultimately sexual selection and genetic variation within temperate songbird populations, and these effects may be particularly important when supplementation extends into the breeding season. Carry-over effects of supplemental feeding in subsequent breeding seasons have also been shown in some measures of avian reproductive investment (e.g., clutch size and timing of breeding; Brommer et al. 2004), and in light of our results, we suggest that future studies should address the potential for supplemental feeding to affect male reproductive investment and female mating decisions in a wider range of bird species, both within and between breeding seasons.

Our results indicate that maintenance of WPP may be as important as EPF gains in determining total reproductive success of male mountain bluebirds, and plumage color or other morphological traits may have less of an influence than behavioral and/or ecological factors on WPP success of males in this species. It is also important to note, however, that this study only examined reproductive success of individual males within a breeding season. If brightly colored males invest more energy into obtaining EPF and less into arguably more costly behaviors associated with parental care and maintenance of WPP, they may have a higher annual survival probability and so ultimately have greater lifetime reproductive success; longitudinal studies that measure relative investment in within- and extrapair mating opportunities over the lifetime of individual male birds will be necessary to address this question. However, our results demonstrate the influence that ecological variables, such as food availability, can have on annual patterns of paternity in populations of socially monogamous birds and suggest that consideration of environmental context will be a productive direction for future research investigating mate choice and sexual selection in socially monogamous species.

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