Articles

Extra-pair paternity in the socially monogamous mountain bluebird *Sialia currucoides* and its effect on the potential for sexual selection

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Sexual selection theory posits that ornamental traits can evolve if they provide individuals with an advantage in securing multiple mates. That male ornamentation occurs in many bird species in which males pair with a single female is therefore puzzling. It has been proposed that extra-pair mating can substantially increase the variance in reproductive success among males in monogamous species, thus increasing the potential for sexual selection. We documented the frequency of extra-pair paternity and examined its effect on variation in male reproductive success in the mountain bluebird *Sialia currucoides*, a socially monogamous songbird in which males possess brilliant plumage ornamentation. Extra-pair paternity was common in our Wyoming study population, with 72% of broods containing at least one extra-pair offspring. The standardized variance in actual male reproductive success (i.e., the total number of within-pair and extra-pair offspring sired) was more than seven times higher than the variation in apparent success (i.e., success assuming that no extra-pair mating occurred). Success at siring within-pair and extra-pair offspring both contributed to the variation in overall male reproductive success. Within-pair success, however, did not predict a male's level of extra-pair success, suggesting that males do not sacrifice within-pair paternity to gain extra-pair paternity. Calculation of the sexual selection (Bateman) gradient showed that males sire approximately two additional offspring for each extra-pair mate that we identified. Thus, in this sexually dichromatic species, extra-pair mating increases the variance in male reproductive success and provides the potential for sexual selection to act.

The presence of male ornamentation in species in which most or all males form long-term pairbonds with a single female presents something of a conundrum given that ornamentation is often thought have evolved because it gives males an advantage in securing multiple mates (Darwin 1871). It has been suggested that extra-pair (EP) mating can substantially increase the variance in reproductive success among males, thus increasing the opportunity for sexual selection (Webster et al. 1995, Møller and Ninni 1998). The potential for sexual selection to operate on individuals of a given sex is proportional to the variance in reproductive success for that sex, to the extent that this variance reflects differences in the number (and/or quality) of mates (Webster et al. 1995, and references therein). However, a high rate of extra-pair mating alone will not necessarily increase the variance in male reproductive success. For example, if males that seek EP fertilizations do so at the expense of within-pair (WP) paternity (e.g., as a result of spending less time guarding their WP mate), then EP mating may ultimately have little effect on the overall variation in male reproductive success (Webster et al. 1995, Freeman-Gallant et al. 2005, Whittingham and Dunn 2005). In fact, several studies of socially monogamous species found that taking into account the effects EP paternity did not substantially increase estimates of the variation in male reproductive success (reviewed in Freeman-Gallant et al. 2005, Whittingham and Dunn 2005; see also Kraaijeveld et al. 2004, O'Connor et al. 2006, Webster et al. 2007). Other studies, however, have shown that EP mating does increase such variation (e.g., Byers et al. 2004, Albrecht et al. 2007, Dolan et al. 2007).

The mountain bluebird *Sialia currucoides* is a socially monogamous songbird with striking male plumage ornamentation. We documented the frequency of extra-pair paternity in this species and quantitatively assessed the degree to which extra-pair paternity affected variance in male reproductive success and thus the potential for sexual selection to operate.

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 have UV-blue plumage that is particularly brilliant on the back, rump, head, and throat. In contrast, females have some dull blue coloring on their rump, tail, and wings but are primarily buffy-brown and gray. This species is a short-distance migrant that returns to its breeding grounds starting in late winter. Pairs nest naturally in pre-formed cavities such as old woodpecker holes and readily use human-made nest boxes. Males are territorial, vigorously defending the area surrounding their nest site. Only females incubate the eggs and brood the hatchlings. Both sexes feed offspring during the 19–21 d nestling period and the 2–6 week fledging period. Social polygyny is extremely rare in this species and no male in our study had two social mates.

Study site and field methods

We conducted this study in 2004 and 2005 in the Bighorn Mountains of north-central Wyoming, USA. All observed pairs utilized nest boxes erected in pastures or meadows. We observed birds at two sites, a low-elevation site (1,258–1,620 m a.s.l.) in the foothills (44º 38′N, 107º 01′W), and a high-elevation site (2,443–2,582 m a.s.l.) on a mountain plateau (44º 46′N, 107º 32′W; see Johnson et al. 2006 for a more detailed description of the two sites).

In both years we monitored only first broods. We checked boxes every 1–5 d to record clutch size and 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 µl) 4–7 d after hatching occurred. Adults were trapped as they entered boxes to feed nestlings 5–10 d post-hatching. Upon capture, we collected a blood sample and marked adults with individually colored leg bands and a numbered aluminum band.

We excluded from our study a handful of nests with less than three nestlings because our aim was to estimate frequencies of EP paternity and because time constraints prevented us from working with every available nest. At such nests we typically only trapped, bled, and marked males. We discuss below the ramifications of including only first broods of a certain size in this study.

Genotyping

Microsatellite loci were identified from microsatellite enriched genomic libraries from mountain and eastern bluebirds following methods outlined in Poláková et al. (2007). We analyzed adult and nestling genotypes at between three and five highly polymorphic microsatellite loci using M13-tailed primers (Boutin-Ganache et al. 2001) designed for use in mountain bluebirds (*Mobl087* and *Mobl049*) and in eastern bluebirds (*Sialia37*, Faircloth et al. 2007; *Eabl129* and *Eabl007*; Table 1).

We PCR amplified *Sialia37*, *Mobl087*, *Eabl129* and *Eabl007* using the touchdown protocol in Johnson et al. (2002). We PCR amplified *Mobl049* according to the following protocol: 95° C for 30 s; 35 cycles at 94° C for 30 s, 57° C for 45 s, 72° C for 45 s; and one cycle at 72° C for 5 min. We estimated PCR fragment sizes using a Beckman Coulter CEQ 8000 capillary sequencer and CEQ software version 8.0.

We estimated that we sampled ≥75% of males within the boundaries of our study areas each year. The average probability of exclusion ranged from 0.972 to 0.984 at three loci, was 0.994 at four loci, and 0.998 for 5 loci (Table 1). Allelic frequencies and exclusion probabilities were determined with Cervus 3.0 (Kalinowski et al. 2007). We also performed a simulation of parentage analysis in Cervus 3.0 using 10,000 iterations of paternity assignment given a known mother and 75% of local males being sampled. We assumed a 1% mutation rate and 1% genotyping error. Under a strict confidence of 95%, more than 98% of paternity assignments were estimated to identify the true sire, and 1% were expected to be incorrectly assigned to a male due to incomplete sampling.

We genotyped a total of 99 adult males, 86 adult females, and 465 nestlings. Of these 650 individuals, 81% were genotyped at four loci. We were unable to PCR amplify and/or confidently determine the length of one microsatellite locus for 12% of individuals. In some cases (7%), individuals were genotyped at a fifth locus to clarify paternity. In cases where identical pairs returned to breed at the same location as the previous year (n = 3), we randomly selected the data from one year for inclusion in analyses. When individuals returned to breed with a different mate at a new location (seven males and four females), or returned

Table 1. Summary of allelic distributions for microsatellite loci used in determining parentage in the study population of mountain bluebirds. Shown for each locus is the number of alleles (N_A) detected, observed (H_O) and expected (H_E) heterozygosities, probability of excluding the father (Ex), and frequency of null alleles (Null). The M13 prefix in the primer sequence denotes a 5′-M13 tail (CACGACGTTGTAAAACGAC) attached to the forward primer sequence. All χ^2 tests for deviation from a Hardy-Weinberg equilibrium were non-significant (all P > 0.15).

Repeat Locus	motif in clone	GenBank Primer sequence (5′–3′)	Accession no.	N_A	n	H_O	H_E	Ex	Null	Citation
Eabl007	$(CA)_{11}$	F: M13-CCTGCACAAAGTCACCTCCT R: TGACACTAGGTGGGGATTGA	EU660861	22	179	0.79	0.77	0.61	−0.03	This paper
Eabl129	$(CA)_{12}$	F: M13-CCAGACAGTGTCCTCCCACT R: GAATTCAGCCCCATCAACAG	EU660862	18	180	0.92	0.89	0.79	−0.02	This paper
Mobl087	$(CA)_{13}$	F: M13-TGCCACATTAACAGGAATGG R: CCTTAAAATGCTGCAGAAGAGG	EU660863	20	181	0.86	0.87	0.73	0.01	This paper
Mobl049	$(TG)_7$ $TA(TG)_3$	F: M13-TCAAATGCACAGGAGAGGTT R: GGATGCTATTCACTGCTCACTC	EU660864	20	179	0.88	0.87	0.73	−0.01	This paper
Sialia37	$(AGAT)_6$	F: M13-AGTTCATTAGCAAAACAAG R: GTTTGATGGTTATCTCAGTCACAG	DQ279189	9	29	0.90	0.82	0.62	−0.06	Faircloth et al. (2006)

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 (one pair), we treated each year's breeding attempt as independent, and included both in analyses.

Paternity assignment

In total, we determined offspring paternity in 92 families with 3–7 nestlings (mean: 5.1), including 29 and 63 families in 2004 and 2005, respectively. We considered nestlings to be WP offspring if they matched both female and male attending the nest at 100% of loci genotyped and their probability of being randomly assigned to the WP male (probability of inclusion; p.o.i.) was < 0.05. We classified offspring that mismatched the WP male at two or more loci as EP. A total of seven nestlings in two nests did not match the within-pair female at all loci genotyped and were excluded from further analysis. All other nestlings matched the attending female at 100% of loci genotyped and were considered to be her genetic offspring.

Nestlings that mismatched the WP male at only one locus may truly be EP offspring, or the mismatch may be the result of null alleles, genotyping error, or mutation. The Hardy-Weinberg test for null alleles was not significant for any of the loci used (Table 1), and therefore null alleles are not likely to affect paternity assignment in this study. We therefore re-genotyped all male-female-nestling trios where the male and nestling mismatched at one locus to reduce the likelihood of genotyping error. If re-genotyping did not produce the expected allelic match, we genotyped the male-female-nestling trio at an additional locus (*Sialia37*, Faircloth et al. 2006). Following Masters et al. (2003) we then recalculated the p.o.i. after removing the mismatched locus from consideration and assigned paternity to the WP male if his p.o.i. was < 0.05.

When possible, we assigned the EP sires by identifying which males (if any) matched the nestling at all loci typed. All males captured within the same year and elevation were considered as possible EP sires. We considered an EP male to be the true sire if: 1) the WP male was excluded as a possible sire, 2) the EP male matched the nestling at 100% of loci genotyped, and 3) the EP male's probability of falsely being assigned as sire was less than 0.05. Only one nestling matched more than one EP male at all loci genotyped. In this instance, one matched male had a nest nearly six km away, while the other male was at the nearest neighboring nest, 225 m away. We assigned paternity to the latter male.

Male reproductive success and the potential for sexual selection

We defined the reproductive success of an individual as the number of offspring that reached the age at which we collected blood samples (d 4–7). We calculated the standardized variance (i.e., variance divided by mean^2; Arnold and Wade 1984) in *apparent* reproductive success, defined as the number of offspring in a male's own nest (regardless of paternity) and compared it to that of *actual* reproductive success, the total number of offspring that a male sired in all nests. We partitioned the total variation in actual reproductive success into WP and EP components (as in Webster et al. 1995). Finally, we calculated the so-called sexual selection or Bateman gradient for males by regressing male actual reproductive success on mating success, with the latter defined as the number of females with whom the male produced offspring (Arnold and Duvall 1994). The slope of this regression gives the expected number of offspring produced for each additional successful mating, and provides an effective measure of the intensity of selection for mating with multiple females (Arnold 1994, Jones et al. 2002, Webster et al. 2007).

Failure to identify the sires of a large portion of EP offspring can inflate the standardized variance in male reproductive success (Dunn et al. 2001, Freeman-Gallant et al. 2005, Whittingham and Dunn 2005). Overall, we identified the true sires of 47% of EP offspring. Prior to conducting detailed analyses of male reproductive success, we chose to remove several clusters of nests in which, collectively, we identified relatively few EP sires. 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. Specifically, we excluded all nests (n = 18) in two small, isolated clusters of nest boxes as well as nests (n = 15) that were in boxes located on either end of clusters of boxes arranged in linear fashion. Ultimately, we retained for analyses 59 nests in which we identified sires for 70% of the EP offspring. Interspersed among these 59 nests were five additional nests that were excluded from study because they contained only two nestlings at bleeding age. Females at two such nests laid only two eggs, only two eggs hatched at two other nests, and only two survived to bleeding age at the fifth nest. 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).

Except where noted, means are given with 95% confidence intervals. All statistical analyses were performed using SAS v. 9.1 (SAS Institute).

Results

Rates of extra-pair paternity and identity of extra-pair fathers

Multivariate logistic regression revealed no significant effect of year ($\chi^2_1 = 0.09$, P = 0.77) or elevation ($\chi^2_1 = 1.05$, P = 0.31), on rate of EP paternity among broods, nor any significant interaction between year and elevation ($\chi^2_1 = 0.009$, P = 0.93; Table S1). Across elevations and years, 66 of 92 broods (72%) observed contained ≥ 1 EP offspring. In total, 169 of the 465 nestlings (36%) sampled were sired by EP males. When females produced multiple EP offspring it was common for two or more different EP males to sire offspring. We identified most or all of the sires of EP offspring in 32 of the 66 broods that contain ≥ 1 EP offspring. More than one male sired EP offspring in 20 (65%) of these broods (46 males in all; average of 1.4 EP sires per brood).

Table 2. Mean reproductive success (with 95% confidence intervals) of male mountain bluebirds that did and did not sire all offspring within their own nests. Values for brood size and number of within-pair (WP) offspring sired were calculated using the complete data set and included 26 and 66 males that were and were not cuckolded, respectively. Values for number of extra-pair (EP) offspring sired and total offspring sired were based on a reduced data set (see Methods) and included 42 and 17 males that were and were not cuckolded, respectively.

	Cuckolded	Not cuckolded	Statistic	P
Brood size	5.0 (4.8–5.3)	5.1 (4.7–5.5)	$t_{90} = -0.39$	0.70
WP offspring	2.5 (2.1–2.9)	5.1 (4.7–5.5)	$t_{72} = -9.60$	<0.001
EP offspring	0.7 (0.3–1.2)	0.6 (0.1–1.1)	$t_{57} = 0.41$	0.68
Total offspring	3.5 (2.8–4.1)	5.6 (4.8–6.3)	$t_{57} = -3.81$	<0.001

Whether a nest contained EP offspring was unrelated to distance to the nest of the nearest neighboring male (logistic regression: $\chi_1^2 = 0.06$, P > 0.80). This was not surprising given that sires of EP offspring did not typically occupy the nest that was nearest to or even adjacent to the focal nest. Indeed, the nearest neighboring male was excluded as the sire of any and all EP offspring in 77% of nests with EP offspring (including 82% of all EP offspring). Only 15% of EP sires occupied the nearest neighboring nest box, while only 24% nested in an adjacent (but not nearest) box. Nests of the 46 identified EP sires were, on average, 812 m (range: 99–3624 m) from the nests where they sired EP offspring.

Extra-pair paternity, male reproductive success, and the potential for sexual selection

Forty-one of 59 (69%) broods in the reduced data set that we used to calculate male reproductive success (see Methods) contained one or more EP offspring. Of the 295 offspring in these broods, 94 (32%) were sired by an EP male. We identified the male siring 70% of these 94 EP offspring.

Mean brood size did not significantly differ between males siring one or more EP offspring and males with no EP offspring (5.1, 4.7–5.6 vs. 5.0, 4.6–5.3, respectively; $t_{57} = -0.57$, P = 0.57). Males that sired one or more EP offspring sired significantly more total offspring on average, than did males with no EP offspring ($\bar{x} = 6.0$, 5.0–6.9 vs. 3.2, 2.6–3.7, respectively; $t_{57} = -5.72$, P < 0.001). Males that did and did not sire EP offspring differed little in the mean number of WP offspring produced (3.8, 3.1–4.6 vs. 3.2, 2.6–3.7, respectively; $t_{57} = -1.49$, P = 0.14), indicating that males who seek EP matings do not necessarily lose paternity in their own brood.

Males that were not cuckolded sired significantly more offspring overall than did males that were cuckolded (Table 2). Males that were and were not cuckolded sired a similar number of EP offspring.

Accounting for extra-pair paternity increased our estimate of the variance in male reproductive success (Fig. 1). Indeed, the standardized variance in actual male reproductive success was 7.3 times greater than the variance in apparent reproductive success (Table 3). Both success at siring offspring in one's own nest and success at siring offspring in the nests of other males contributed to the variance in actual male reproductive success, accounting for 60 and 34% of the variance, respectively (Table 3). As suggested above, WP and EP success were not significantly related (Fig. 2). The covariance between the number of WP offspring sired and the number of EP offspring sired was positive but accounted for only 6% of the variance in actual male reproductive success.

The sexual selection gradient showed that, for males, reproductive success increased significantly with the number of mates successfully fertilized (Fig. 3). On average, males produced 2.0 (1.4–2.6) additional offspring for each mate obtained. The relationship between reproductive success remained positive and significant when we repeated the analysis without the three males that fathered no WP and no known EP offspring ($R^2 = 0.32$, $F_{1,54} = 25.8$, P < 0.001, n = 56). In this analysis, paired males that sired at least one offspring in their own nest gained an average of 1.7 (1.1–2.4) offspring for each EP mate that they acquired.

In contrast to males, the reproductive success of females was unaffected by the number of mates (y = 4.9 + 0.0x, −0.2–0.3; n = 59, $r^2 < 0.001$, $F_{1, 58} = 0.10$, P = 0.75; Fig. 3). The sexual selection gradient for males was significantly different from that for females (test for homogeneity of slopes in an ANCOVA: $F_{1,114} = 35.2$, P < 0.001).

Discussion

Our data suggest that EP mating is unusually common in our study population of mountain bluebirds. Overall, 72% of broods had mixed paternity and 36% of all offspring were sired by EP males. This is among the highest frequencies of EP paternity reported for a passerine bird (Griffith et al. 2002). It is substantially higher than frequencies reported for the congeneric eastern bluebird *Sialia sialis* (24% of broods, 8% of offspring; Meek et al. 1994), and western bluebird *Sialia mexicana* (45% of broods; 19% of offspring; Dickinson and Akre 1998). In
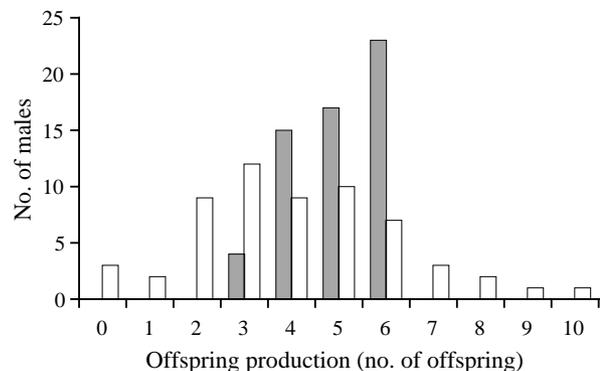

Figure 1. Distribution of apparent (gray bars; offspring in own nest), and actual reproductive success (white bars; total within- and extra-pair offspring sired) of 59 male mountain bluebirds.

Table 3. Comparison of apparent and actual male reproductive success (number of offspring sired) based on a sample of 59 breeding males. Std. var. (standardized variance) is the variance divided by the mean total reproductive success squared. Standardized variance in total offspring sired is partitioned into the amount of variance contributed by within-pair (WP) and extra-pair (EP) paternity success, along with their covariance. WP and EP success are each further partitioned into contributors to overall variance in success. Note that remainder terms and all covariances are not presented which results in a summation not equal to 100%

	Range	Mean	Std. var.	Percent
Apparent reproductive success	3–6	5.00	0.037	
Actual reproductive success	0–10	4.14	0.271	100.0
Within-pair success	0–6	3.39	0.164	60.4
Extra-pair success	0–5	0.68	0.091	33.6
$2 \times$ Covar (WP, EP)			0.016	6.0
Within-pair sources of variance				
Proportion of young sired	0–1	0.68	0.025	9.2
No. of young in nest	3–6	3.39	0.130	48.0
Extra-pair sources of variance				
No. of mates	0–2	0.41	0.026	9.5
Proportion of young sired	0.17–0.67	0.31	0.004	1.3
No. of young in nest	4–6	5.15	0.045	16.5

a Colorado population of mountain bluebirds, Monk (1999) found that 59% of 17 nests contained one or more EP offspring (32% of all offspring were extra-pair), which suggests that the frequency of EP paternity in our population may not be atypical for this species.

Several lines of evidence suggest that EP mating substantially increases the potential for sexual selection in our population. First, after accounting for the effects of EP mating on paternity, variance in *actual* male reproductive success was over seven times greater than the variance in *apparent* reproductive success. We caution that our inability to identify the sires of 30% of EP offspring will have inflated the difference between apparent and actual reproductive success, as well as WP and EP components, to some degree (see Freeman-Gallant et al. 2005). Estimates of actual male reproductive success in this study, therefore, represent minimum values given that we undoubtedly did not identify every EP offspring sired by males in our study population. It is noteworthy, however, the difference that we found between apparent and actual reproductive success is several fold larger than reported in other studies where researchers assigned parentage to ~70% of EP offspring (cf. Kempenaers et al. 1992, Albrecht et al. 2007).

Second, we found that variance among males in success at siring offspring in the nests of other males and siring offspring in their own nest were both important in the total
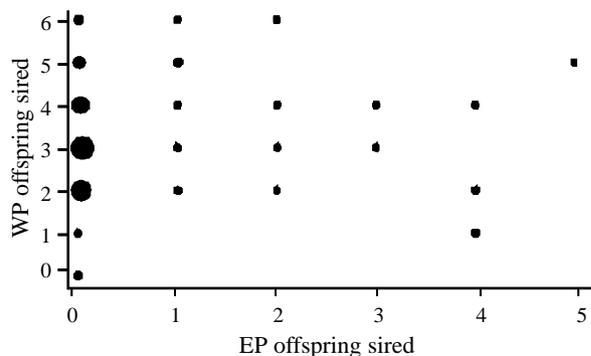
variance in male reproductive success. Certainly, some care must be taken in interpreting this type of result. If males typically tradeoff WP for EP mating success (e.g., if extensive pursuit of EP matings reduces time spent guarding WP paternity), this will negate the positive effects of EP paternity on total male reproductive success. Although we found no evidence of an inverse relationship between EP and WP paternity (e.g., the covariance between the two was small and positive), we cannot know whether individuals
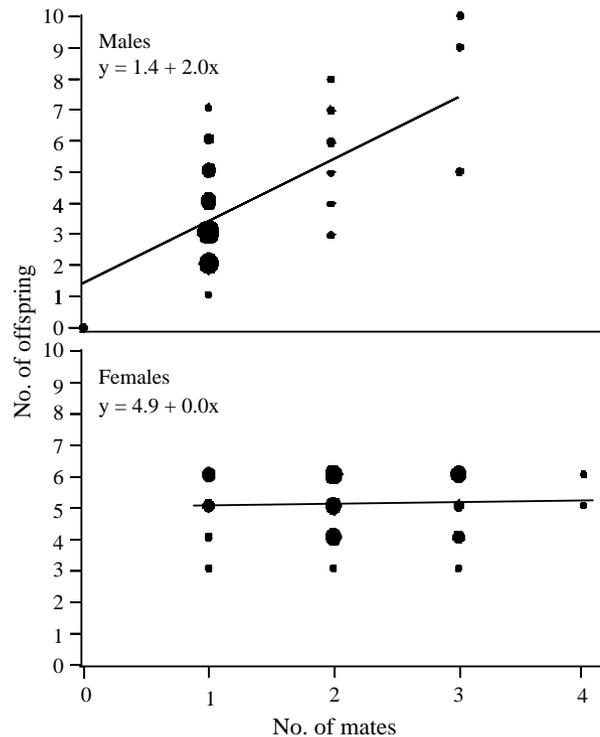

Figure 3. Sexual selection gradients showing the relationship between number of mates (i.e., number of individuals with whom offspring were produced), and total number of offspring sired. Males: n = 59, r^2 = 0.42, $F_{1,58}$ = 42.0, P = 0.003; females: n = 59, r^2 < 0.01, $F_{1,58}$ = 0.10, P = 0.75. The size of each filled circle represents the number occurrences at each intersection (range: 1–10).

Figure 2. The relationship between the number of extra-pair (EP) and within-pair (WP) offspring that a male sired (n = 59, r = 0.07, P = 0.61). The size of the circle represents the frequency of each observation (range: 1–12).

are (or are not) actually trading off WP and EP paternity without further experimental work.

Third, we found a significant, positive sexual selection gradient for males indicating that the more females that a male successfully mates with beyond his WP mate, the more offspring he produces overall. Indeed, males that achieved EP paternity sired, on average, about two extra offspring for every EP mate with whom they produced offspring. The strong, positive relationship between reproductive success and number of mates is further evidence that males were not trading off WP and EP fertilization success. When examining the effect of EP mating on the potential for sexual selection, the sexual selection gradient is particularly informative because one's estimation of the gradient will not be strongly affected by an inability to either identify the sires of certain EP offspring or account for all EP offspring sired by particular males.

In many territorial passerines studied to date, males tend to sire EP offspring in nests on territories adjacent to or at least near their own nests (e.g., Stutchbury et al. 1994, 1997, Yezerinac et al. 1995, Webster et al. 2001, Johnson et al. 2002, Freeman-Gallant et al. 2005). When social or ecological factors restrict males to siring EP offspring only with nearby females, this can limit the degree to which EP mating increases variance in male reproductive success (Webster et al. 2001, Schuster and Wade 2003). In our study, sires of EP offspring were not typically males at neighboring nests. Indeed, in most cases EP sires came from nests that were more than 500 m away. Most nests in our study were surrounded by large expanses of meadows and pastureland on at least two sides. Such areas are largely undefended and may facilitate the ability of males to move long distances unimpeded and approach multiple females. All else being equal, this should increase the number of receptive females that a male encounters and, again, increase the potential for sexual selection. High rates of EP paternity have also been found in several other territorial species in which males can regularly gain access to females on non-neighboring territories (e.g., Woolfenden et al. 2005, Dolan et al. 2007).

Although our results do strongly suggest that extra-pair mating increases the variance in male reproductive success in our population, we caution that both our exclusion of certain males and nestlings from the study and our use of artificial nest boxes may have led us to overestimate the proportional contribution of EP mating to the overall variance in reproductive success to some degree. We excluded from our study a handful of nests that contained two or fewer offspring surviving to bleeding age. Thus, we eliminated some paired, settled males that had little or no WP reproductive success, which would have caused us to underestimate the variation in WP reproductive success to some degree. In addition, our analyses do not include contributions to (annual) reproductive success from second breeding attempts. Although we did not closely monitor such attempts, it was clear that only a fraction of pairs in our population made such attempts, as has been found in other populations of this species (e.g., Power 1966). We do not know whether males that have high (or low) WP and/or EP reproductive success during first breeding attempts are more or less likely to be involved in second breeding attempts. We also do not know whether and how patterns of paternity in second attempts differ from those in first attempts (Kleven et al. 2006).

Our use of nest boxes may also have influenced our results to some degree. Studies of mountain bluebirds elsewhere suggest that under natural conditions (i.e., when no nest boxes are present), suitable nest sites are in such limited supply that, in any given year, some fraction of males fail to nest at all (and hence have no WP reproductive success). For example, when artificial nest sites are erected, the number of nesting pairs in an area typically increases (e.g., Bock and Fleck 1995). At one British Columbia site, boxes that were erected after all breeding pairs in the local area had begun egg-laying were quickly occupied by new breeding pairs (Holt and Martin 1997), suggesting the existence of a considerable number of "floating" individuals or perhaps pairs (see also Power 1975). If this is the norm for this species, then actual variation in male reproductive success may be much higher than we have estimated, with success at securing a nest site contributing substantially to this variance. Furthermore, if under natural conditions mountain bluebird pairs nest at relatively low densities because nest sites are in limited supply, then settled males may normally have less opportunity to sire EP offspring than they did in our study (Gowaty and Bridges 1991; Charmantier and Perret 2004). In either case, the relative impact of EP mating on the overall variance in male reproductive success under more natural conditions would be less than what our calculations suggest. However, some of this impact may be counteracted if floating males have some success at cuckolding mated males.

In summary, our results show that EP mating occurs frequently in mountain bluebirds and suggest that it has a notable effect on variation in male reproductive success. This provides potential for sexual selection to favor traits that reduce the risk of cuckoldry and/or increase the probability of males siring offspring outside the pairbond. Whether plumage color is one such trait will be the subject of future analyses.

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