

Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds

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The number of mates, their fecundity, and the number of extra-pair fertilizations can all affect male reproductive success in biparental species. Extra-pair mating in birds has been of particular interest, because it could generate strong levels of sexual selection even when a species is socially monogamous. We examined how extra-pair fertilizations affect the opportunity for selection in the sexually dimorphic common yellowthroat (*Geothlypis trichas*) and the sexually monomorphic house wren (*Troglodytes aedon*). We were able to identify sires for at least 95% of all nestlings, and, thus, we were able to make a nearly complete accounting of male reproductive success. Although extra-pair fertilizations were common in yellowthroats (26% of young) it contributed little (21%) to the total variance in male reproductive success. Most of the variance in reproductive success (58%) was attributable to the male's within-pair success, which was influenced primarily by the number of young produced by each mate and the proportion of within-pair young sired. Despite a moderate level of extra-pair fertilizations (10% of young) in house wrens, almost all of the variance in male reproductive success (97%) was attributable to within-pair success, particularly the number of social mates. Although extra-pair fertilizations generally increase the variance in male reproductive success, within-pair reproductive success may be the major source of variation in male reproductive success. Thus, sexual dimorphism in monogamous birds may be influenced more by the number of mates and their fecundity than by extra-pair matings. *Key words:* extra-pair paternity, sexual selection, common yellowthroat, house wren. [*Behav Ecol*]

In many species, males are much larger or more ornamented than females. The evolution of these sexual differences is generally ascribed to sexual selection, which occurs as a consequence of variation in reproductive success (Andersson, 1994). For example, larger males may gain more matings than smaller males, because they are preferred by females or have an advantage in competition with other males. Traditionally, male reproductive success has been measured as the number of social mates a male acquires during the breeding season. Thus, when most of the males in a population have one mate we expect sexual selection will be weak. In contrast, when a minority of males pair with most of the available mates in a population and other males remain unmated, then we expect sexual selection will be stronger. Consistent with these predictions, monogamy is correlated with sexual monomorphism and polygamy is correlated with sexual dimorphism (Clutton-Brock, 1989; Dunn et al., 2001; Thornhill and Alcock, 1983). However, there are many exceptions to this pattern, such as monogamous species that are sexually dimorphic (Burns, 1998; Møller and Birkhead, 1994).

Three main hypotheses have been proposed to explain the evolution of sexual dimorphism in monogamous species. First, variation in male reproductive success may arise as a consequence of variation in the quality of mates obtained by males. For example, Darwin (1871: 271) suggested that males with ornamental traits gain an advantage in mating because they are preferred by the most fecund females, which are the first to breed in the spring. Females that arrive later in the

spring are less fecund and must pair with the "less vigorous and less attractive males" (see also Kirkpatrick et al., 1990). Second, not all males pair strictly with one female in monogamous species, and low levels of polygyny or males that remain unmated in the population will also increase the variance in male reproductive success (Darwin, 1871; O'Donald, 1980). Third, although males may be socially monogamous, they may gain fertilizations with extra-pair mates, which may produce a genetically polygynous mating system that increases the variance in male reproductive success (Westneat et al., 1990). This latter hypothesis is supported by comparative analyses of birds that show extra-pair mating is associated with stronger sexual dimorphism (Dunn et al., 2001; Owens and Hartley, 1998).

Although extra-pair fertilizations are widespread among avian species (Griffith et al., 2002), their effect on the opportunity for selection (the standardized variance in fitness; Arnold and Wade, 1984) has been examined in relatively few species. This is due to the inability to assign sires to all or most of the extra-pair young, which is necessary for a complete accounting of male reproductive success. In general, studies of socially monogamous species have shown that extra-pair fertilizations increased the opportunity for sexual selection in both sexually dimorphic (Johnsen et al., 2002; Richardson and Burke, 2001; Stutchbury et al., 1997; Webster et al., 2001) and monomorphic species (Kempnaers et al., 2001; Otter et al., 1998; Whittingham and Liffeld, 1995). Even fewer polygynous species have been studied. To date, two studies of red-winged blackbirds have shown that variation in extra-pair fertilizations contributed less than 13% to the total variance in male reproductive success (Weatherhead and Boag, 1997; Webster et al., 1995). To our knowledge no monomorphic polygynous species have been studied.

However, extra-pair paternity does not necessarily increase the total variance in male reproductive success. Extra-pair

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fertilizations will affect the variance in realized reproductive success only if some males excel at gaining both extra-pair fertilizations and protecting their within-pair paternity while others are less adept at both (Webster et al., 1995). If there is a trade-off between gaining extra-pair fertilizations and protecting within-pair paternity (e.g., mate guarding), then males may gain extra-pair fertilizations at the same rate that they lose within-pair fertilizations. In this case, there will be little or no influence of extra-pair fertilizations on the opportunity for sexual selection (Webster et al., 1995). Few studies have examined the relative effect of extra-pair fertilization success on the opportunity for sexual selection and the variance in total male reproductive success (Webster et al., 1995, 2001).

We examined the components of variation in male reproductive success in two species of birds that exhibit extra-pair fertilizations but differ in their social mating system and level of sexual dimorphism. The common yellowthroat (*Geothlypis trichas*) is sexually dimorphic and socially monogamous, whereas the house wren (*Troglodytes aedon*) is sexually monomorphic and polygynous. Based on the difference in sexual dimorphism, we expected the variation in total male reproductive success to be greater in common yellowthroats than house wrens. Both species have moderate levels of extra-pair fertilizations (Soukup and Thompson, 1998; Thusius et al., 2001), and we could determine the sires of most extra-pair young. As a consequence, we could compare the realized reproductive success (number of within-pair and extra-pair young sired) of each male to his apparent reproductive success (number of young in the male's nests). Following the model of Webster et al. (1995), we also examined the relative influence of the number of mates (social and extra-pair), the number of young per mate (mate quality), and the proportion of young sired per mate on the variance in total male reproductive success.

METHODS

Study area and species

Fieldwork was conducted at the University of Wisconsin-Milwaukee Field Station in Saukville, WI (43° 23' N, 88° 01' W) from May–August in 1999 for common yellowthroats and 1998–2000 for house wrens. Both species are small (approximately 10 g) migratory passerines that are distributed across much of North America (Guzy and Ritchison, 1999; Johnson, 1998). Details of the field and laboratory methods are described for common yellowthroats in Thusius et al. (2001) and Peterson et al. (2001) and for house wrens in Poirier et al. (2004). Here we provide a brief summary for each species.

Common yellowthroats are socially monogamous warblers that exhibit strong sexual dimorphism. In this species, males possess a conspicuous black facial mask and bright yellow throat, breast, and belly ("bib"). These plumage characters are absent (mask) or more subdued (bib) in females. We studied common yellowthroats in 5.4 ha of mostly contiguous swamp and open sedge marsh. Upland forest or fields isolated most of the study area from other occupied habitat. For this study we examined 23 of 29 territories; six peripheral males were captured and genotyped to determine if they were extra-pair sires of young in our main study population. Females build their nests on or within a half-meter of the ground, predominantly in wet areas, and produce a clutch of two to five eggs (Guzy and Ritchison, 1999). Territories were monitored at least every other day and nests were located by observing females building nests or by watching both parents feeding nestlings. All mated males were socially monogamous and almost a third of pairs were double-brooded.

Unlike many socially polygynous species, house wrens are sexually monomorphic; both sexes are a fairly uniform brownish gray (Johnson, 1998). House wrens are secondary cavity nesters and readily use nest boxes in forests and at forest edges (Kendeigh, 1941). We had approximately 180 nest boxes available for wrens, with 41 to 53 nests each year. Each nest box was placed on a fence post covered with a greased PVC pipe (10 cm diam), which prevented predation. Males begin building the nest with twigs, which the female later completes by lining the nest cup with grass. Females produce a clutch of four to eight eggs and are often double-brooded (Kendeigh, 1941).

In both species, nests were checked every one to four days to determine the stage of breeding and mating success. Nestlings were banded and measured five and seven days after the first egg hatched for common yellowthroats and house wrens, respectively. Reproductive success was determined from the number of young genotyped (at 5 or 7 days old). All birds were banded with a U.S. Fish and Wildlife Service aluminum band, and all adults were marked with unique combinations of colored leg bands for individual identification. A small blood sample (approximately 30 μ l) was taken from each bird and stored in lysis buffer for paternity analyses.

Paternity analyses

We used microsatellite analyses to assign parentage to young and determine the realized reproductive success of males. For house wrens, parentage was determined using four microsatellite loci originally developed in other bird species: Pca3 (Dawson et al., 2000), LTR6 (McDonald and Potts, 1994), Mcyu4 (Double et al., 1997), and FhU2 (Primmer et al., 1996). Details of PCR conditions and thermal cycling profiles are given in Poirier et al. (2004). PCR products were run on a 6% polyacrylamide gel for 5 h on an ABI 373 automated sequencer. Each lane of the gel contained a fluorescently labeled size standard (Genescan 500). Genescan Analysis and Genotyper software (Applied Biosystems, Foster City, CA) were used to determine allele sizes for each individual. The number of alleles per locus ranged from 12 to 20, and the mean allele frequency ranged from 0.05 to 0.08. The observed frequency of heterozygotes (h_o ; 0.82–0.90) did not differ significantly from the expected frequency of heterozygotes (h_e ; 0.82–0.93) at any locus (see Poirier et al. 2004, for details), and there was no evidence of null alleles. The probability of paternal exclusion at each locus (P_{ei} ; Jamieson, 1994) ranged from 0.63 to 0.86 and the combined probability of paternal exclusion for all loci was 0.997.

To determine parentage and assign extra-pair sires in common yellowthroats, we used four microsatellite loci originally developed for other species of warblers: Dca24 and Dca28 (Webster et al., 2001) and Dpu01 and Dpu16 (Dawson et al., 1997). Details of the PCR conditions and thermal cycling profiles are given in Peterson et al. (2001). Radioactively labeled PCR products were run for 4500 V-h at 50°C on a 6% polyacrylamide gel, which was dried, exposed to autoradiograph film, and developed for visualization. Microsatellite allele sizes were determined by reference to a M13 mp18 DNA sequence run on each polyacrylamide gel. The number of alleles per locus ranged from 15 to 33 and the frequency of each allele ranged from 0.03 to 0.07. The observed frequency of heterozygotes (h_o ; 0.85–0.95) did not differ significantly from the expected frequency of heterozygotes (h_e ; 0.85–0.93) at any locus (see Thusius et al., 2001 for details), and there was no evidence of null alleles. The average probability of paternal exclusion (Jamieson, 1994) for each locus ranged from 0.71 to 0.90 and the combined probability of paternal exclusion at all four loci was 0.999.

In both species, all young shared an allele with their putative mother at all loci, except for one house wren nestling that mismatched both the male and female tending the nest and was not included in our analyses. Young that possessed an allele that did not match the putative father at two or more loci were considered extra-pair young. In house wrens, there were no cases in which the young mismatched the paternal allele at only one locus. In common yellowthroats, if a mismatch occurred at only one locus, multi-locus DNA fingerprinting was used to confirm paternity (Peterson et al., 2001). For both species, the paternal alleles of the extra-pair young were compared to the alleles of all males in the population at all four loci. The probability that a randomly chosen male in the population would possess the paternal alleles of a given extra-pair young at all four loci was 0.00055 ± 0.000098 SD (range: 0.0017 to 2.12×10^{-5}) for house wrens and 0.00298 ± 0.00347 SD (range: 0.0117 to 2.0×10^{-4}) for common yellowthroats (Jeffreys et al., 1992). Males were assigned as extra-pair sires if they matched the alleles of extra-pair young at all four loci. There were no cases in which more than one male matched at all loci.

Variance in mating success

All means are presented with their standard error and all tests were two-tailed. To avoid pseudoreplication, each adult house wren was included in the data set for only one year. Differences in sample sizes between analyses were the result of incomplete data for some individuals.

All calculations of reproductive success were based on the number of young genotyped (at 5 and 7 days old for common yellowthroats and house wrens, respectively). Realized reproductive success (also referred to as actual reproductive success) was estimated as the total number of young sired (i.e., both within-pair and extra-pair young) in our sample of genotyped nestlings. Apparent reproductive success was estimated by the traditional method of counting the number of young in each of the male's nests (also at 5 or 7 days old). We use 'opportunity for sexual selection' in reference to variance in male mating (Wade and Arnold, 1980) or fertilization (Webster et al., 1995) success. However, some components of male reproductive success, such as the number of young per mate (N_w and N_e below), are the outcome of both natural and sexual selection, and in these cases we use the more general term, 'opportunity for selection.'

We calculated an index of the opportunity for sexual selection (I_s ; the variance in fertilization success divided by the square of mean success; Wade and Arnold, 1980) to compare realized and apparent reproductive success. To examine the opportunity for selection, we included components of the variance in male reproductive success arising from both sexual and natural selection (Arnold and Wade, 1984). We used Equation 16 in Webster et al. (1995), which partitions the total variation in male reproductive success into variation due to the number of social (M_w) and extra-pair (M_e) mate, the number of young per social (N_w) and extra-pair (N_e) mate, the proportion of young sired per social (P_w) and extra-pair (P_e) mates, and their covariances and remainders (D_T).

There was no nest predation in our sample of house wrens; however, in species, such as common yellowthroats, with frequent nest predation (41% of broods) and multiple broods it may be difficult to obtain accurate estimates of reproductive success (Ketterson et al., 1997). In our sample of common yellowthroats, we were able to obtain blood samples of nestlings for paternity analysis from the territories of 19 of 21 mated males (an additional two males remained unmated). Two mated males were excluded from all calculations because

their nests failed before sampling and, thus, their within-pair success was unknown (one of them sired two extra-pair young in neighboring nests and these numbers were also excluded from calculations of extra-pair success). Our results were qualitatively similar when we included these two males and assumed that they sired all young in their own nest (percentages of standardized variances changed by <2.4%). Thus, all males sampled here had at least one nest on their territory genotyped (except for the two unmated males), so we could examine both within-pair and extra-pair reproductive success.

RESULTS

We examined the reproductive success of 21 male common yellowthroats that established territories in our main study area in 1999. Of these, 12 males were single-brooded, seven males were double-brooded, and two males remained unmated throughout the breeding season. We obtained paternity data from 26 broods and 93 nestlings. Extra-pair young were present in 17 (65%) broods and accounted for 24 (26%) of all young. Extra-pair sires were identified for 20 (83%) of the extra-pair young. Males that sired extra-pair young had significantly greater realized reproductive success (5.1 ± 0.88 young) than males that did not gain extra-pair fertilizations (2.53 ± 0.64 young; Mann-Whitney U test: $Z = 2.05$, $p = .04$). As a result, the variance in realized reproductive success ($I_{sr} = 0.48$) was 1.7 times greater than the variance in apparent reproductive success ($I_{sa} = 0.28$; Table 1). Most of the total variance was attributable to within-pair success (58%; Table 1), and the remainder of the variance was divided between extra-pair success (21%) and the covariance between within-pair and extra-pair success (22%; Table 1). Nine of the 21 males were successful as extra-pair sires and sired an average of 1.9 ± 0.45 extra-pair young (range 1 to 5). Most extra-pair males (7/9) sired only one or two extra-pair young. Neither of the two unmated males sired extra-pair young.

For house wrens we determined parentage for 584 nestlings from 103 broods. Our sample included 68 males and 70 females. There was no predation and there were no unmated males in our population. Overall, 29 (28%) broods contained at least one extra-pair young and 59 (10%) nestlings were sired by extra-pair males (Poirier et al., in press). Extra-pair sires were identified for 52 (88%) extra-pair young. Males had one to three broods per season; they were single-brooded, sequentially monogamous or polygynous. Females had either one or two broods per season. Individuals that were sequentially monogamous often switched mates between broods (Poirier et al., 2003).

Realized reproductive success of male house wrens averaged $7.4 (\pm 0.4)$ young but varied substantially among males (range 0–19). Males with more than one brood (either polygynous or sequentially monogamous) sired more young (11.6 ± 0.5) than single-brooded males (5.6 ± 0.3 ; Mann-Whitney U test: $Z = 6.8$, $p < .0001$; Poirier et al., in press). Nearly a third of the males (23/68) sired extra-pair young and improved their reproductive success by an average of 1.8 ± 0.1 offspring (range 1 to 6). Most extra-pair males (18/23) sired only one or two extra-pair young.

In contrast to common yellowthroats, extra-pair paternity had very little effect on the variance in reproductive success for male house wrens. The standardized variance in realized reproductive success ($I_{sr} = 0.22$) was only 1.2 times greater than the standardized variance in apparent reproductive success ($I_{sa} = 0.18$; Table 1). Almost all of the total variance was attributable to within-pair success (97.3%), while a small portion was due to extra-pair success (10.4%; Table 1). However, the covariance between within-pair and extra-pair

Table 1
Extra-pair mating and the variance in male reproductive success

species	% EP broods	% EP young	% EPY assigned	I_s apparent	I_s realized	V_r/V_a	% Total variance					Reference
							WP	EP	Cov	MS	SD	
Common yellowthroat (<i>Geothlypis trichas</i>)	65	26	83	0.28	0.48	1.7	57.7	20.8	21.5	M	Y	this study
House wren (<i>Troglodytes aedon</i>)	28	10	88	0.18	0.22	1.2	97.3	10.4	-7.7	P	N	this study
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	41	25	60	0.34	0.49	1.4	69.3	9.7	20.1	P	Y	Westneat, 1993; Webster et al., 1995
Black-throated blue warbler (<i>Dendroica caerulescens</i>)	31	21	70	0.49	0.71	1.4	76.6	13.9	9.3	M	Y	Webster et al., 2001 ^a
Tree swallow ^b (<i>Tachycineta bicolor</i>)	76	52	65	0.09	0.99	11.0	36.0	38.1	25.8	M	N	Kempnaers et al., 2001
House martin ^c (<i>Delichon urbica</i>)	35	19	100	0.06	0.31	5.2	41.5	56.6	1.9	M	N	Whittingham and Liffield, 1995

^a Means of 1997 and 1998 data presented in Tables 3 and 4 of Webster et al. (2001).

^b Variance partitioned using data in Figure 1 of Kempnaers et al. (2001).

^c Variance partitioned using data in Figure 2 of Whittingham and Liffield (1995).

The extent of extra-pair mating for each species is shown as the proportion of broods with extra-pair young (% EP broods), the proportion of extra-pair young (% EP young in the population), and the proportion of extra-pair young for which extra-pair sires were assigned (% EP assigned). Male reproductive success is presented as the standardized variance (I_s) in apparent and realized reproductive success (within-pair plus extra-pair young sired) and the ratio between them (V_r/V_a). The percentage of total variance in male reproductive success is shown divided into its components: variance due to within-pair success (WP), extra-pair success (EP), and the covariance between within-pair and extra-pair success (Cov). Mating system (MS) is shown as polygynous (P) or monogamous (M) and sexual dimorphism (SD) is shown as yes (Y) or no (N).

success was negative (-7.7%), suggesting a possible trade-off between the two components.

The total variance can be partitioned further into the variance due to the number of mates (M), the average number of young per mate (N), and the proportion of young sired (P) for both within-pair and extra-pair mates (Webster et al., 1995: Equation 16). In the polygynous house wren most of the total variance in male reproductive success resulted from variance in the number of social mates (71%) and a smaller component (23%) from variation in within-pair paternity (P_w ; Table 2). This pattern was similar to red-winged blackbirds (Table 2). In common yellowthroats, polygyny is rare and males in this study had either zero (two unmated males) or one social mate; thus, variation in the number of social mates contributed just 10.6% to the total variation in reproductive success (Table 2). The main components of variation in reproductive success were the average number of within-pair young per mate (20.6%, N_w), the proportion of within-pair young sired (22.6%, P_w), and the number of extra-pair (22.7%, M_e) mates (Table 2). There was a tendency for male common yellowthroats to have more extra-pair mates (0.7 ± 0.2 , range 0–4) than male house wrens (0.4 ± 0.1 , range 0–2; t test: $t = 1.82$, $p = .07$), but there was no difference in the average number of extra-pair young sired by male common yellowthroats (0.8 ± 0.3) and house wrens (0.7 ± 0.1 ; t test: $t = 0.3$, $p = .7$; including males that sired no extra-pair young).

Overall, male house wrens sired more within-pair young (7.5 ± 0.5) than male common yellowthroats (3.3 ± 0.5 ; t -test for unequal variances: $t = 6.4$, $p < .0001$) because of their greater number of broods and mates, and they had greater variance in the number of within-pair young (Bartlett test for unequal variances: $F = 7.8$, $df = 1$, $p = .005$).

We also examined the factors influencing the variation in reproductive success of females for both species. Overall, female house wrens produced larger clutches (6.4 ± 0.1) than female yellowthroats (4.4 ± 0.1 ; Mann-Whitney U test: $Z = -6.5$, $p < .0001$), and the variance in house wren clutch size (0.60) was greater than that of common yellowthroats (0.26; Bartlett test for unequal variances: $F = 3.8$, $df = 1$, $p = .05$). In common yellowthroats, the standardized variance in number

of related young (at 5 days of age) was 3.2 times greater ($I_{sm} = 0.48$) for males than for females ($I_{sf} = 0.15$). In house wrens, the standardized variance in the number of related young (at 7 days of age) was 1.4 times greater ($I_{sm} = 0.22$) for males than females ($I_{sf} = 0.16$). Overall, the opportunity for sexual selection was greatest for male common yellowthroats and relatively low for male house wrens and females of both species.

Lastly, we compiled data from other species to examine the effect of extra-pair fertilizations on estimates of the opportunity for selection. Extra-pair fertilizations increased the opportunity for sexual selection more in monogamous species (mean $V_r/V_a = 3.6 \pm 0.9$, $n = 11$) than in polygynous species (mean $V_r/V_a = 1.3 \pm 0.1$, $n = 4$; Mann-Whitney U test, $Z = 2.35$, $p = .02$; Tables 1 and 3). Also, extra-pair fertilizations

Table 2
Percentage of standardized variance in total reproductive success partitioned into variance due to the number of mates (M), the average number of young produced by each mate (N), and the proportion of the mates' young sired by the male (P) for both within-pair and extra-pair reproduction, and the portion attributable to covariances and D

Components	Common yellowthroat	House wren	Red-winged blackbird
Within-pair terms			
N mates (M_w)	10.6	71.3	41.7
N young/mate (N_w)	20.6	9.0	12.7
Proportion sired (P_w)	22.6	22.9	35.2
Extra-pair terms			
N mates (M_e)	22.7	8.3	10.2
N young/ mate (N_e)	0.5	0.1	0.2
Proportion sired (P_e)	2.1	1.4	1.1
Covariances + D	20.9	-13.0	-1.1

D is the remainder term that reflects multivariate skewness (Webster et al., 1995: Equation 16). Red-winged blackbird data are from Webster et al. (1995). Note that the within-pair and extra-pair terms do not sum to the same values as in Table 1 because of covariances and D.

Table 3

Extra-pair mating and the variance in male reproductive success (species in which variance was not partitioned)

Species	% EP broods	% EP young	% EPY assigned	I _s apparent	I _s realized	Vr/Va	MS	SD	Reference
Bullock's oriole (<i>Icterus galbula bullockii</i>)	46	32	45	0.07	0.17	2.4	M	Y	Richardson and Burke, 2001
Bluethroat (<i>Luscinia s. svecica</i>)	54	29	56	0.08	0.37	4.6	M	Y	Johnsen et al., 2002
Hooded warbler (<i>Wilsonia citrina</i>)	35	27	55	0.18	0.46	2.6	M	Y	Stutchbury et al., 1997
Collared flycatcher (<i>Ficedula albicollis</i>)	33	16	93	0.03	0.14	4.7	M	Y	Sheldon and Ellegren, 1999
Black-capped chickadee (<i>Poecile atricapillus</i>)	29	9	88	0.04	0.10	2.5	M	N	Otter et al., 1998; Otter K, personal communication
Dark-eyed junco (<i>Junco hyemalis</i>)	45	28	100	0.55	0.72	1.3	M	N	Ketterson et al., 1997; Ketterson ED, personal communication
Blue tit (<i>Parus caeruleus</i>)	31	11	73	0.16	0.27	1.7	M	N	Kempnaers et al., 1992
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	5	3	100	1.00	1.02	1.0	P	N ^a	Hasselquist et al., 1995
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	45	28	93	0.25	0.39	1.6	P	Y	Gibbs et al., 1990

^a Small sexual difference in body mass (8%) but not dimorphic in plumage.

The extent of extra-pair mating for each species is shown as the proportion of broods with extra-pair young (% EP broods), the proportion of extra-pair young (% EP young in the population), and the proportion of extra-pair young for which extra-pair sires were assigned (% EP assigned). Male reproductive success is presented as the standardized variance (I_s) in apparent and realized reproductive success (within-pair plus extra-pair young sired) and the ratio between them (Vr/Va). Mating system (MS) is shown as polygynous (P) or monogamous (M) and sexual dimorphism (SD) is shown as yes (Y) or no (N).

appeared to contribute more to variation in total reproductive success in monogamous (range 13.9–56.6%; $32.4 \pm 9.6\%$, $n = 4$) than polygynous (range 9.7–10.4%; $10.1 \pm 0.4\%$, $n = 2$; Table 1) species. If we considered only socially monogamous species, extra-pair fertilizations did not contribute more to variation in total reproductive success (Vr/Va) in sexually dimorphic species (2.9 ± 0.6 ; $n = 6$) than in sexually monomorphic species (4.3 ± 1.8 ; $n = 5$; Mann-Whitney U test, $Z = 0.18$, $p = .85$; Tables 1 and 3).

DISCUSSION

The discovery of widespread extra-pair mating in birds has led to two general expectations about the influence of extra-pair paternity on male reproductive success. First, extra-pair fertilizations will increase the variance in male reproductive success and, as a consequence, the opportunity for selection (Webster et al., 1995). Second, the increase in the variance in male fertilization success is likely to be extreme because a few high quality males will be winners at both within-pair and extra-pair fertilizations, while most males will be losers (Birkhead and Møller, 1992; Møller, 1992). We have shown in house wrens that, despite a moderate level of extra-pair paternity, the total variance in male reproductive success was relatively unaffected by extra-pair fertilizations. Variance in male reproductive success was produced mostly by variance in within-pair success, which was influenced primarily by the number of social mates and the proportion of within-pair young sired (Table 2). In contrast, extra-pair fertilizations increased the variance in reproductive success for male common yellowthroats; however, more than half of the variance in reproductive success was the result of within-pair success (Table 2). In addition, almost half of the males in the population were successful at both within-pair and extra-pair fertilizations (Thusius et al., 2001). As a consequence, success was not biased toward only a small subset of males in the population, and there was a weak positive covariance between within-pair and extra-pair success (Table 1). Thus, the two general expectations mentioned above were only partially supported by our study.

When we looked across species, we also found that the two general expectations were not fulfilled. In the common yellowthroat, black-throated blue warbler, and red-winged blackbird, extra-pair fertilizations were fairly common, but the total variance in reproductive success increased only moderately as a consequence (≤ 1.7 times), and most of the variance was attributed to within-pair reproductive success (Table 1). In contrast, tree swallows and house martins showed the largest increase in the opportunity for selection (11.0 and 5.2 times, respectively), yet the total variance in male reproductive success was distributed equally between within-pair and extra-pair success (Table 1). Only three species (common yellowthroats, red-winged blackbirds, and tree swallows) had a substantial positive covariance ($>20\%$), suggesting that some males were successful as both within-pair and extra-pair sires.

It is important to caution that these interspecific comparisons of variances need to be made using similar estimates of mating or fertilization success. Ideally, estimates of mating and fertilization success should be made from fertilized ova (Trail, 1985), but estimates are typically made some time after hatching, when a blood sample can be obtained for genotyping. In this case, any mortality of young (e.g., nest predation, hatching failure) prior to the time of sampling will often increase the variance in reproductive success (Trail, 1985). In the studies to date (Table 1), nest predation prior to sampling young may have contributed to total variation in reproductive success in common yellowthroats, red-winged blackbirds, and black-throated blue warblers; the other species had little or no nest predation and, thus, researchers sampled almost all of the eggs. Nevertheless, relative comparisons of the components of fertilization success (e.g., within-pair versus extra-pair) are unlikely to be biased, unless predation or hatching failure affects one component more than another. These potential biases need to be considered in future studies.

Overall, there has been little published support for the idea that a minority of males sire most of the extra-pair young (see Dunn and Cockburn, 1999 for an exception). Instead, we found that a fairly large proportion of males (34% and 45% in house wrens and common yellowthroats, respectively) sired extra-pair young. For common yellowthroats males are

successful as extra-pair sires primarily on neighboring territories (Thusius et al., 2001). If females interact and copulate only with males on neighboring territories (e.g., on a local scale), then the opportunity for selection generated by extra-pair fertilization success will be relatively low (Webster et al., 2001). In contrast, if only a small number of males gain most of the extra-pair fertilizations in the population (e.g., success on a global scale), then the opportunity for selection may be quite strong (Webster et al., 2001). For other species, there was either no evidence of a relationship between within-pair and extra-pair reproductive success (e.g., house martins) or there may have been a trade-off between these two components of reproductive success (e.g., house wrens; Table 1).

It has been suggested that extra-pair fertilizations provide an explanation for the paradox of sexual dimorphism in socially monogamous species (Møller and Birkhead, 1994; Owens and Hartley, 1998). However, these comparative studies were based solely on the percentage of within-pair young in a brood and not on the relative contribution of extra-pair fertilizations to variation in total reproductive success (V_r/V_a). Although it is clear that more studies need to be done, our analysis of V_r/V_a among species (Tables 1 and 3) revealed no clear association between extra-pair fertilizations and sexual dimorphism. One potential problem may be that sexual dimorphism has been based on differences observable only in the human visible range and does not take into account differences between the sexes detectable by birds in the ultraviolet range. For some species considered here this might not be a problem, as there is little difference between the sexes in ultraviolet plumage reflectance in tree swallows or house wrens (unpublished data). However, in blue tits the sexes are strongly dimorphic in the ultraviolet range (Andersson et al., 1998) and in black-capped chickadees (*Poecile atricapillus*) there are sexual differences in the contrast between adjacent light and dark plumage regions (Mennill et al., 2003). Thus, differences between the sexes detectable to birds but not to humans will need to be considered in future studies.

Although the number of studies is limited (Table 1 and 3), it appears that the social mating system was associated with particular components of variation in reproductive success. For example, extra-pair fertilizations were relatively more important to total variation in male reproductive success in monogamous (mean $V_r/V_a = 3.4$) than polygynous species (mean $V_r/V_a = 1.3$). In polygynous species, any reproductive advantages of having additional social mates could be eroded by a greater risk of extra-pair paternity (e.g., Dunn and Robertson, 1993); however, this does not appear to be case in house wrens and red-winged blackbirds. In both of these polygynous species, the number of social mates was the largest single contributor to the total variation in male reproductive success (Table 2). Thus, in polygynous species, acquiring additional mates appears to contribute more to the total opportunity for selection than acquiring extra-pair fertilizations, although protecting paternity in the nests of within-pair mates is also important (Table 2).

Darwin suggested that variance in the number of young produced by a mate (fecundity, N_w) could influence sexual selection in monogamous species. Combined with variation in the number of mates (zero or one in monogamous species), these within-pair components of reproductive success contributed to approximately 31% of the total variation in reproductive success in common yellowthroats (Table 2). Another 23% of the variation was the result of within-pair paternity. Thus, male common yellowthroats have four main avenues through which they can gain (or lose) reproductive success: acquiring a social mate, female fecundity, within-pair paternity, and acquiring extra-pair mates.

Although extra-pair mating occurs in 75% of bird species (Griffith et al., 2002), the average percentage of extra-pair young is just 11%, and sexual dimorphism is related more consistently to the social mating system than to testes size, which is an index of sperm competition and extra-pair mating (Dunn et al., 2001). Thus, we think the current emphasis on extra-pair fertilizations as the driving force in the evolution of sexual dimorphism in birds is misplaced. As we have shown for house wrens, the presence of extra-pair fertilizations will not necessarily increase the opportunity for sexual selection. Even when extra-pair fertilizations increase the variance in male reproductive success, the effect may not be extreme if extra-pair fertilizations occur primarily among immediate neighbors on a local scale and are not biased toward a small subset of males in the population. Furthermore, when extra-pair fertilizations are common, most of the variance in male reproductive success comes from within-pair success, which is often influenced strongly by the number of social mates and by the number of young produced by each female. Thus, although extra-pair fertilizations can influence the opportunity for selection, we must also consider the influence of other components, as Darwin (1871) suggested.

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