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Males achieve greater reproductive success through multiple broods than through extrapair mating in house wrens

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In polygynous species, it is unclear whether extrapair matings provide a better reproductive payoff to males than additional social mates. Male house wrens, *Troglodytes aedon*, show three types of social mating behaviour: single-brooded monogamy, sequential monogamy (two broods) and polygyny. Thus, male reproductive success can vary depending on the number of mates, the number of broods and the number of extrapair fertilizations. We used microsatellite markers to determine the realized reproductive success (total number of young sired from both within-pair and extrapair fertilizations) of males in these three categories. We found that polygynous males were more likely to be cuckolded than monogamous males; however, half of the polygynous males had a third brood, which resulted in similar reproductive success for sequentially monogamous and polygynous males. Despite the paternity gained from extrapair fertilizations by single-brooded males, males were more successful when they produced multiple broods during a season, either sequentially (monogamy) or simultaneously (polygyny). In our population, multibrooded males were more likely to have prior breeding experience and arrived earlier in the season, which provided a better opportunity to obtain more than one brood and, thus, produce more young.

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Within species, both monogamous and polygynous matings occur in a wide variety of taxa including birds (Emlen & Oring 1977; Ligon 1999), mammals (Cavallini 1996; Fitzgibbon 1997; Digby 1999; Fietz 1999), insects (Trumbo & Eggert 1994; Reid 1999) and fish (Martin & Taborsky 1997; Tomoyuki & Nakazono 1998). Mating system theory has focused on the ability of males to become polygynous, particularly in species in which males are usually monogamous. Whether males mate monogamously or polygynously is thought to be the result of female choice based on the quality of a male and his territory (the polygyny threshold model; Verner 1964; Verner & Wilson 1966; Orians 1969), or the uneven spatial or temporal distribution of resources and mates (the environmental potential for polygamy model; Emlen & Oring 1977). Both of these models assume that polygynous males achieve higher reproductive success than monogamous males because polygynous males have more than one brood per breeding season (reviewed in Davies 1991). This assumption is based on the idea that male reproductive success is limited by the number of mates a male can obtain, and, thus, polygynous males are expected to be more successful (Trivers 1972).

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In birds, empirical studies testing these models have traditionally estimated reproductive success as the number of young fledged or the number of young recruited into the population the following year (Davies 1989; Ligon 1999; i.e. apparent reproductive success, Gibbs et al. 1990). However, it is possible that some or all of the young in a male's brood may not be his genetic progeny. Indeed, recent parentage analyses have provided evidence of extrapair paternity in many animals and it appears to be particularly widespread among avian species (reviewed in Birkhead & Møller 1998). Thus, a male may gain or lose apparent reproductive success through extrapair paternity depending on whether he is the successful extrapair sire or the male who is cuckolded. As a consequence of extrapair matings, accurate measures of male reproductive success (i.e. realized reproductive success, Gibbs et al. 1990) must include both the within-pair young a male has sired with his social mate(s) and the extrapair young he has sired in other broods.

Based on theoretical arguments, it is not clear how extrapair fertilizations should affect the reproductive success of polygynous and monogamous males. Overall, males are expected to minimize the likelihood of cuckoldry by mate guarding (Trivers 1972; Beecher & Beecher 1979; Birkhead 1979; Arak 1984) or frequent within-pair copulation (McKinney et al. 1984; Birkhead et al. 1987). However, polygynous males may not be able to guard simultaneous mates as effectively as monogamous

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males can guard a single mate, and, as a result, polygynous males may be more likely to lose paternity in their broods (mate guarding hypothesis; Arak 1984). In addition, time and energy devoted to attracting multiple mates by polygynous males may decrease their opportunity for extrapair copulations, which may reduce their chances of siring extrapair young in the broods of other males (Arak 1984; Westneat et al. 1990; Hasselquist & Bensch 1991; Smith & von Schantz 1993; Westneat 1993). If polygynous males are more likely to be cuckolded and monogamous males are more likely to be the successful extrapair sires, then monogamous males may have greater reproductive success.

Alternatively, we might predict that polygynous males will be cuckolded rarely and will be more likely to gain extrapair paternity than monogamous males. This might be the case if polygynous males are of higher quality than monogamous males, and if the social mates of polygynous males do not engage in extrapair matings as often as the social mates of monogamous males (male quality hypothesis; Birkhead & Møller 1992). In such cases, we would expect the difference in realized reproductive success between polygynous and monogamous males to be more extreme than the apparent reproductive success (the total number of fledglings).

Some studies comparing male reproductive success in monogamous and polygynous males have accounted for paternity lost through extrapair matings. In most cases, polygynous males are cuckolded more often than monogamous males (Dunn & Robertson 1993; Freeland et al. 1995; Soukup & Thompson 1998; Lubjuhn et al. 2000); however, a few studies have found similar levels of cuckoldry for monogamous and polygynous males (Dhondt 1986; Smith & von Schantz 1993), or that monogamous males are cuckolded more often than polygynous males (Freeman-Gallant 1997). However, even when levels of cuckoldry are higher for polygynous males, they still produce more genetically related young because they have more broods (Dhondt 1986; Smith & von Schantz 1993; Freeland et al. 1995; Soukup & Thompson 1998; Lubjuhn et al. 2000; but see Dunn & Robertson 1993).

Few studies have included paternity gained through extrapair matings in the assessment of male realized reproductive success and none have included comparisons with sequentially monogamous breeding males. We used genetic techniques to assign paternity and to compare the realized reproductive success of male house wrens in three breeding categories: polygynous (two or three broods), sequentially monogamous (two broods) and single-brooded monogamous. Our goal was to determine whether polygynous males have reduced within-pair and extrapair success as predicted by the mate guarding hypothesis, or enhanced within-pair and extrapair success as predicted by the male quality hypothesis.

METHODS

The house wren is a small (approximately 10 g) sexually monomorphic, migratory passerine that is distributed across most of North America. They nest in secondary cavities and readily use nestboxes in forests and forest edges (Kendeigh 1941, 1952). A male sings to defend a territory and begins building a nest with twigs, which a female later completes by lining the nest cup with grass. The female incubates four to eight eggs for approximately 13 days, and both parents feed nestlings (Kendeigh 1941).

Field work was conducted at the University of Wisconsin, Milwaukee Field Station, Saukville, Wisconsin during May–August, 1998–2000. In 1997, 180 nestboxes were placed 25 m apart along forest edge habitat (see Drilling & Thompson 1984 for nestbox design). Each nestbox was placed on a fence post covered with a greased PVC pipe (10-cm diameter) which effectively prevented predation. However, three or four clutches failed each year because the eggs were destroyed by other house wrens.

Adult males were captured in mist nets as soon as they began defending a nestbox, whereas adult females were captured inside the nestbox during incubation. Nests were checked every 1–4 days to determine the stage of breeding and reproductive success. During the 2000 breeding season, we surveyed all nestboxes from 0730 to 1500 hours daily throughout the breeding season to document the arrival dates of males. Nestlings were banded and measured 7 days after the first egg hatched. Fledging success was the number of young in the nest on day 16 (just prior to fledging) minus any nestlings found dead in the nest on day 20. All birds were banded with a U.S. Fish and Wildlife Service aluminium band and adults were marked with unique combinations of coloured leg bands for individual identification. Measurements of each bird included body mass (electronic balance to the nearest 0.1 g), tarsus length (digital callipers to the nearest 0.1 mm), wing chord and tail length (to the nearest 1.0 mm). Adult body condition was estimated as the residuals of body mass regressed against tarsus length. Birds that had bred previously in our population were considered experienced breeders, whereas newly banded birds were considered inexperienced.

Male Breeding Categories

A male was considered to be polygynous if he was the social mate of at least two different females for which there was an overlap in the incubation or nestling period of the primary female and the egg-laying period of the secondary female. For polygynous males, the average $\pm$ SE overlap between fledging at the first nest and the first egg at the second nest was 19 $\pm$ 3.1 days (range 3–32 days). Sequentially monogamous males had two broods during a breeding season that did not overlap temporally. For sequentially monogamous males, there was an average $\pm$ SE gap of 15 $\pm$ 1.5 days (range 7–33 days) between fledging at the first nest and the first egg at the second nest. Although all sequentially monogamous males had two broods, 56% (10/18) of them switched mates between broods, so that females mated to sequentially monogamous males could have been single or double brooded.

Behavioural Observations

We recorded male song rate during three observation periods at each nest during the female's fertile period, from 3 days before to 3 days after the first egg was laid. During

each 20-min observation period, we recorded the number of songs given by the male. We recorded male feeding rate to nestlings during 20-min observation sessions when nestlings were 4, 6, 8 and 10 days posthatching (1998–2000). In 2000, we also recorded feeding rates when nestlings were 2 days posthatching to monitor feeding rate while the female was brooding the young. We recorded male song rate from 0715 to 1611 hours (mean = 1025 hours) and observed feeding rate from 0645 to 1630 hours (mean = 1050 hours). Male song rate increased with time of day ($r^2 = 0.49$, $F_{143,220} = 1.5$, $P = 0.004$). To adjust for time of day, we used the residuals of the linear regression of male song rate and time of day for song rate analysis. Male feeding rate to nestlings did not change with time of day ($r^2 < 0.01$, $F_{1,507} = 0.48$, NS). Means of multiple observations for each male were used for analyses.

Paternity Analyses

We examined parentage for 584 nestlings from 103 broods. These included 344 nestlings from 64 nests of 29 multibrooded males and 240 nestlings from 39 broods of single-brooded males. No males were included in the data set more than once. For paternity analysis, we obtained approximately 50 µl of blood from the brachial vein of each bird and stored each sample in 800 µl of Queen's lysis buffer (Seutin et al. 1991). DNA was extracted from blood samples using a 5 M salt extraction solution (Miller et al. 1988). Parentage was determined using four microsatellite loci originally developed in other bird species (Pca3, LTR6, Mcyu4, and FhU2; Table 1). Microsatellite DNA was amplified by polymerase chain reaction (PCR) as follows. Pca3 and LTR6 reactions contained 25 ng of genomic DNA, 0.5 pmol fluorescently labelled forward primer, 0.5 pmol reverse primer, 1.5 mM $MgCl_2$, 50 mM KCl, 10 mM Tris–HCl (pH 8.3), 0.8 mM dNTPs and 0.5 U *Taq* polymerase. Mcyu4 and FhU2 reactions contained 25 ng of genomic DNA, 0.25 pmol fluorescently labelled forward primer, 0.25 pmol reverse primer, 3.0 mM $MgCl_2$, 50 mM KCl, 10 mM Tris–HCl (pH 8.3), 0.8 mM dNTPs and 0.5 U *Taq* polymerase. LTR6 amplifications were performed under the following thermal conditions (conditions for Mcyu4 and Pca3 are given in parentheses): an initial cycle at 94°C for 3 min, 44°C (50°C) for 60 s, 72°C for 60 s, followed by 34 cycles at 94°C for 30 s, 44°C (50°C) for 30 s, 72°C for 40 s, and a final cycle at 72°C for 5 min. Amplification of FhU2 was performed using a touchdown programme that consisted of an initial cycle at 94°C for 2 min, 55°C for 30 s, 72°C for 30 s, followed by 19 cycles at 94°C for 30 s, 55°C (decreased by 0.5°C per cycle) for 60 s, and 72°C for 40 s, then 10 cycles at 94°C for 30 s, 45°C for 30 s, 72°C for 40 s, and a final step at 72°C for 5 min. Finally, 5 µl of the PCR product was run on a 2% agarose gel to verify amplification.

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 labelled size standard (Genescan 500). Genescan Analysis and Genotyper software (PE Biosystems) were used to determine allele sizes for each individual.

For each locus, the frequency of each allele (p_i) was calculated from 104 unrelated adults. The expected frequency of heterozygotes (h_e) was calculated for each locus using the equation: $h_e = 1 - \sum(p_i)^2$, where p_i is the allele frequency at locus i. The parentage exclusion probability for each locus was calculated as (Jamieson 1994):

$$P_{ei} = 1 - 2\sum p_i^2 + \sum p_i^3 + 2\sum p_i^4 - 3\sum p_i^5 - 2\left(\sum p_i^2\right)^2 + 3\sum p_i^2 \sum p_i^3.$$

The total probability of exclusion (P_{et}) was calculated for all four loci: $P_{et} = 1 - \pi(1 - P_{ei})$. P_{et} is the probability that a randomly chosen male will not possess the paternal allele found in a given offspring for one or more of the four loci examined, given that the mother is known.

The four microsatellite markers used to determine parentage were highly polymorphic (Table 1). The number of alleles per locus ranged from 12 to 20, and the mean allele frequency ranged from 0.05 to 0.08. Expected heterozygosity (h_e; 0.82–0.93) was similar to the observed heterozygosity (h_o; 0.82–0.90). The probability of paternal exclusion at each locus (P_{ei}) ranged from 0.63 to 0.86 and the combined probability of paternal exclusion for all loci was 0.997. All nestlings except one shared an allele with the social female at each locus. Young that mismatched the paternal allele at two or more loci were considered to be extrapair young. There were no cases in which the young mismatched the paternal allele at only one locus.

Extrapair sires were identified for 88% of extrapair young. At all four loci, the paternal alleles of the extrapair young were compared to the alleles of all males in the population. The probability that a randomly chosen male in the population would possess the paternal alleles of

Table 1. Allele frequencies, exclusion probabilities (P_{ei}), and heterozygosity indexes (h_e = expected, h_o = observed) of four microsatellite loci used to assess paternity in house wrens

Locus	Number of alleles (N=104 adults)	Mean allele frequency	P_{ei}	h_e	h_o	Reference
Pca3	12	0.08	0.63	0.82	0.82	Dawson et al. 2000
LTR6	19	0.06	0.81	0.90	0.83	McDonald & Potts 1994
Mcyu4	20	0.05	0.86	0.93	0.90	Double et al. 1997
FhU2	17	0.06	0.68	0.87	0.85	Primmer et al. 1996

The total probability of paternal exclusion (P_{et}) for all loci was 0.997.

a given extrapair young at all four loci by chance was calculated as (Jeffreys et al. 1992):

$$(2p_{i1} - p_{i1}^2)\times(2p_{i2} - p_{i2}^2)\times(2p_{i3} - p_{i3}^2)\times(2p_{i4} - p_{i4}^2),$$

where p_i was the paternal allele frequency at locus i. The mean probability that an extrapair young would share the paternal allele at all four loci with a randomly chosen male in the population was 0.00055 ± 0.000098 (range $0.0017-2.12\times10^{-5}$; $N = 29$ extrapair young).

JMP (version 4.0) was used for all statistical analyses, except the analysis of 2×3 contingency tables, which were analysed using the Fisher-Freeman-Halton test in StatXact 4 (Cytel Software 1989), which is an extension of Fisher's exact test. All means are presented with their standard errors and all tests were two tailed unless noted otherwise. We tested dependent variables for normality using the Shapiro–Wilk test and nonparametric tests were used in all cases in which data were not distributed normally.

RESULTS

The number and timing of broods varied substantially for male house wrens. Over all 3 years, 57% (39/68) of males were single brooded and 43% (29/68) of males were multibrooded. Of the multibrooded males, 62% (18/29) were sequentially monogamous and 38% (11/29) were polygynous. Fifty-five per cent (6/11) of polygynous males had a third brood. The proportion of males in each breeding category tended to differ between years (Fisher's exact test: $\chi_4^2 = 9.3$, $P = 0.053$) because fewer males were single brooded in 1998 ($N = 4$) than in 1999 ($N = 16$) and 2000 ($N = 19$).

Paternity

Overall, 28% (29/103) of broods contained at least one extrapair young and 10% (59/584) of nestlings were sired by extrapair males. The proportion of nests with at least one extrapair young tended to be greater in 1998 than in 1999 or 2000 ($\chi_2^2 = 5.2$, $P = 0.07$). In broods of cuckolded males, the mean number of extrapair young per brood was 2.1 ± 0.2 (range 1–6). One nestling was not related to either the male or female tending the nest and was not included in our analyses.

The occurrence of extrapair young differed between the three categories of breeding males ($\chi_2^2 = 9.1$, $P = 0.01$; Fig. 1). Seven of 11 (67%) polygynous males, 2 of 18 (11%) sequentially monogamous males and 14 of 39 (36%) single-brooded males had at least one nest containing extrapair young. This difference was related to mating system rather than number of broods. Polygynous males were more likely to be cuckolded (7/11 males) than monogamous males (16/57 sequentially monogamous and single-brooded males; Fisher's exact test: $P = 0.035$). In contrast, males with multiple broods (9/29) were not more likely to have extrapair young than were single-brooded males (14/39; Fisher's exact test: $P = 0.80$).

The occurrence of extrapair young in first and second broods differed for polygynous and sequentially monogamous males. Considering both first and second broods, polygynous males were more likely to be cuckolded than were sequentially monogamous males (Fisher's exact test: $P = 0.001$; Fig. 1). For polygynous males, we did not detect any difference between primary (3/11) and secondary broods (7/11) in the level of extrapair paternity (Fisher's exact test: $P = 0.2$; Fig. 1). Of the six polygynous males that had a third brood within a breeding season, two (33%) of those broods contained extrapair young (Fig. 1). For sequentially monogamous males, there were no extrapair young in first broods, and in second broods, only two of 18 (11%) males were cuckolded (Fisher's exact test: $P = 1.0$; Fig. 1).

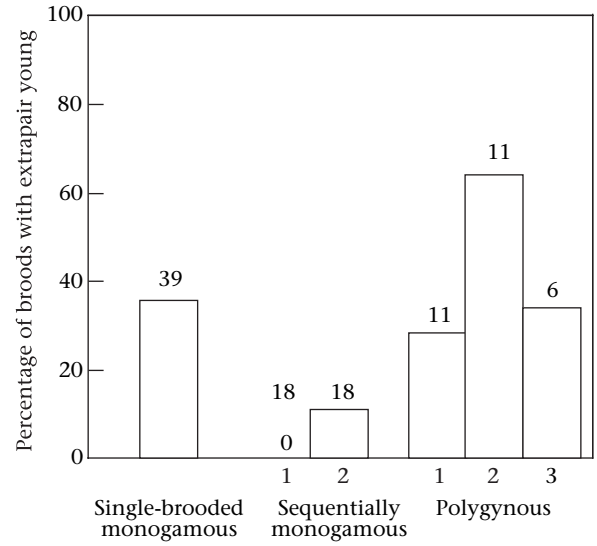

Figure 1. Percentage of first, second or third broods with extrapair young of single-brooded, sequentially monogamous and polygynous male house wrens. Number of males in each group is presented above the bars; brood numbers are presented below the bars.

Sires were identified for 88% (52/59) of extrapair young. In addition to the 29 multibrooded males and 39 single-brooded males, eight additional males were included in our analysis as possible extrapair sires. These were males that defended a nestbox but did not produce young because they did not attract a mate, the nestbox was usurped by another male, or the eggs were destroyed by other house wrens. Thus, all known males in the population were included in paternity analyses. The 29 extrapair sires that were identified included 21 single-brooded males, six multibrooded males and two males that did not nest successfully. Extrapair sires improved their reproductive success by an average of 1.8 ± 0.1 offspring (range 1–6). Neither the number of extrapair young sired ($F_{2,65} = 0.35$, $P = 0.7$), nor the likelihood of being an extrapair sire ($\chi_{65}^2 = 1.7$, $P = 0.4$) was related to male breeding category. Overall, monogamous males (both categories) were not more likely to be extrapair sires than were polygynous males (Fisher's exact test: $P = 0.3$).

Male Reproductive Success

Realized reproductive success of males was estimated as the total number of fledglings sired (i.e. both within-pair

and extrapair young) over an entire season. Overall, males sired an average of 7.4 ± 0.4 young (range 0–19); however, realized reproductive success differed between the three categories of breeding males ($F_{2,65} = 52.6$, $P = 0.01$; Fig. 2). Polygynous and sequentially monogamous males sired a similar number of fledglings (11.8 ± 1.1 and 11.3 ± 0.4, respectively), whereas single-brooded males sired fewer fledglings (5.6 ± 0.3; Tukey–Kramer tests: $P<0.05$; Fig. 2). These differences in reproductive success were not due to differences in female fecundity, because clutch size in the first brood did not differ between single-brooded and multibrooded males (Mann–Whitney U test: $Z = 1.41$, $N_1 = 29$, $N_2 = 39$, $P = 0.18$). There was also no difference between single-brooded and multibrooded males in overall fledging success (percentage of hatchlings fledged; $Z = 0.9$, $N_1 = 29$, $N_2 = 39$, $P = 0.40$). When only first and second broods were considered for multibrooded males, sequentially monogamous males ($\bar{X} \pm \mathrm{SD} = 11.3 \pm 1.7$, $N = 18$) sired a greater number of young than polygynous males (9.5 ± 2.8, $N = 11$; $Z = 2.0$, $P = 0.046$). The variance in reproductive success also tended to be lower for sequentially monogamous than polygynous males (Bartlett test: $\chi^2_1 = 3.2$, $P = 0.07$). Males with previous breeding experience in our nestbox population were more likely to be multibrooded (Fisher's exact test: $P<0.01$) and sired more fledglings than males that bred for the first time (10.1 ± 0.8 and 7.9 ± 0.5 young, respectively; Mann–Whitney U test: $Z = 2.0$, $N_1 = 8$, $N_2 = 60$, $P = 0.04$).

To examine the potential influence of other factors on realized reproductive success, we performed a series of multiple regressions with breeding category (polygynous, sequentially monogamous, single brooded), year, male breeding experience, male body condition and laying date of the first brood (a potential index of time available for multiple broods) as predictors. In the full model (without interactions), only breeding category ($F_{2,54} = 24.7$, $P<0.001$) was significant (overall model: $R^2 = 0.64$, $F_{6,54} = 16.7$, $P<0.001$). After exploring several models that included interactions (none significant), we found that breeding category ($F_{2,64} = 45.1$, $P<0.001$) and year ($F_{1,64} = 5.5$, $P = 0.02$) provided the most parsimonious predictors of realized reproductive success. Breeding experience was not a significant predictor of realized reproductive success (all P values NS) in any multiple regression that included breeding category. Similarly, male body condition and laying date were also not significant predictors of realized reproductive success (all P values NS) in any multiple regression.

The apparent reproductive success of males was estimated as the total number of young fledged from the males' own nests. In this case, polygynous males appeared to sire significantly more young than sequentially monogamous males (13.2 ± 1.0 and 10.9 ± 0.3, respectively), and single-brooded males sired fewer young than each group of multibrooded males (5.6 ± 0.3; Tukey–Kramer tests: $P<0.05$; Fig. 2).

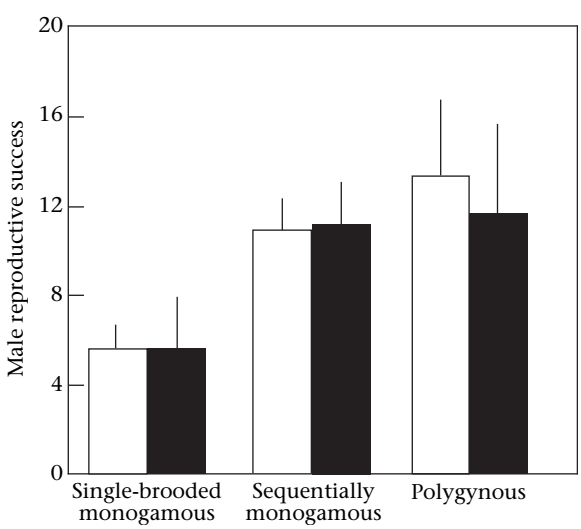

Figure 2. Mean ± SD male reproductive success of single-brooded (N=39), sequentially monogamous (N=18) and polygynous (N=11) male house wrens within a breeding season. Open bars indicate apparent reproductive success (the number of young fledged from the nests of the male's social mates) and filled bars indicate male realized reproductive success (the total number of fledglings sired through within-pair and extrapair paternity).

Multibrooded Males

Because multibrooded males were more successful than single-brooded males, we examined factors that might allow males to produce multiple broods. A multiple logistic regression with year, laying date of the first nest, male body condition and breeding experience as predictors revealed that males were more likely to have multiple broods if they had a female that started breeding early in the season (laying date for the first nest: $\chi^2_1 = 7.6$, $P = 0.006$). There was also a tendency for males to be multibrooded if they had prior breeding experience ($\chi^2_1 = 3.3$, $P = 0.07$) or bred in 1998 ($\chi^2_2 = 5.9$, $P = 0.053$). Male body condition was not related to breeding category ($\chi^2_1 = 2.4$, $P = 0.12$) in the multiple logistic regression. Finally, we compared males in different breeding categories to determine whether they differed in their behaviour. Breeding category was not associated with year ($\chi^2_2 = 1.4$, $P = 0.3$), song rate (multiple logistic regression; $\chi^2_1 = 0.06$, $P = 0.8$) or male feeding rate to nestlings ($\chi^2_1 = 1.2$, $P = 0.3$) at first nests.

Extrapair Sires and Cuckolded Males

We identified 29 extrapair sires for 52 extrapair young. Females may make direct comparisons of social mates and extrapair males; therefore, we compared morphological and behavioural characteristics of extrapair males and the males they cuckolded. There was no difference between successful extrapair sires and the males they cuckolded in body condition (paired t test: $t_{19} = 0.54$, $P = 0.3$), prior breeding experience (Fisher's exact test: $P = 1.0$), or the likelihood that the male would return to breed the following year (Fisher's exact test: $P = 0.6$).

Unlike other studies in which extrapair sires were usually neighbouring males (Thusius et al. 2001; Webster

et al. 2001), house wrens sired extrapair young primarily in the broods of non-neighbouring females. The mean distance between the nest of an extrapair sire and the nest where he sired extrapair young was 330 m (range 40–785 m). Of the 27 known extrapair males resident at a nestbox, only 26% (7/27) sired young in the nest of a neighbouring female, whereas 74% (20/27) sired young in nests further away than the nearest fertile female. The timing of extrapair paternity suggested that extrapair matings occurred when the social mates of extrapair males were not fertile. The majority of extrapair young were sired before or after the fertile period of the extrapair sire's social mate (20/27 extrapair males).

Return Nestlings

Male reproductive success is ultimately influenced by the recruitment of offspring into the breeding population. Although recruitment was low in our population, we genotyped all ($N = 12$) nestlings that returned to the population following their hatch year (nestlings that returned in 2001 were included in this analysis). Eleven of 12 (92%) nestlings that recruited into our breeding population were within-pair young that were reared in the nests of monogamous males. Six of these 11 recruits (55%) were produced in broods of sequentially monogamous males and five (45%) were produced in broods of single-brooded males. Only one of the 12 returning nestlings was an extrapair young, and it was reared in the brood of a polygynous male and sired by a single-brooded monogamous male. Polygynous males did not sire any of the 12 nestlings that recruited to this population. There was no difference in the number of young recruited for sequentially monogamous males (6/204), single-brooded males (6/237) and polygynous males (0/133; Fisher-Freeman-Halton exact test: $P = 0.13$). Furthermore, there was no difference in the recruitment of within-pair (11/525) and extrapair young (1/59; Fisher's exact test: $P = 1.0$).

DISCUSSION

The reproductive success of male house wrens differed primarily as a consequence of the number of broods produced during a season. Multibrooded males were more successful than single-brooded males regardless of extrapair paternity. Among multibrooded males, polygynous males appeared to have greater reproductive success on average, because half of them had three broods. However, polygynous males were more likely to be cuckolded, which resulted in a similar number of fledglings sired for polygynous and sequentially monogamous males. The tendency towards greater variance in reproductive success for polygynous males suggests that polygyny may be more risky than sequential monogamy for male house wrens. Despite paternity gained from extrapair matings, single-brooded males still produced fewer offspring than multibrooded males.

Several studies have investigated male reproductive success in terms of the number of young sired within a male's social brood. Most of these studies have also detected paternity costs for polygynously paired males, but in most cases, polygynous males sire more young overall because they produce more broods than monogamous males (Freeland et al. 1995; Soukup & Thompson 1998; Lubjuhn et al. 2000; but see Dunn & Robertson 1993). For example, in an Illinois population of house wrens, polygynous males were cuckolded more frequently, yet sired more within-pair young than did monogamous males (Soukup & Thompson 1998). Even when monogamous males were hypothetically assigned all of the extrapair young, they still produced fewer young than polygynous males (Soukup & Thompson 1998). Soukup & Thompson (1998) did not examine the separate effects of number of broods (single and multiple) and mating behaviour (monogamy or polygyny) on total reproductive success, because they treated single-brooded and sequentially monogamous males as one group. Our study reveals that sequentially monogamous males can achieve similar reproductive success to polygynous males by producing multiple broods.

The results of this study are consistent with Arak's (1984) prediction that polygynous males will experience higher levels of cuckoldry in their broods as a consequence of reduced mate guarding. Secondary nests of polygynous males have a higher proportion of extrapair young than primary nests (Soukup & Thompson 1997; this study) and extrapair paternity tends to increase with temporal overlap between primary and secondary broods (Soukup & Thompson 1997); however, male mate guarding behaviour has not yet been examined directly. Arak (1984) also predicted that the difference in cuckoldry would result in similar reproductive success among polygynous and monogamous males. Despite a higher cuckoldry rate, polygynous males in our population still sired substantially more young than single-brooded monogamous males.

Alternatively, the male quality hypothesis predicts that females choose to pair with higher-quality polygynous males and will not engage in extrapair matings with lower-quality monogamous males (Birkhead & Møller 1992). Results from house wrens do not support this prediction. First, polygynous males were cuckolded more frequently than monogamous males. Second, polygynous males were not more likely to be successful extrapair sires than were monogamous males. Finally, we found no differences in male condition or behaviour between polygynous and single-brooded males.

Despite the success of single-brooded male house wrens as extrapair sires, they had the lowest reproductive success in our population, suggesting that brood number was an important constraint on male reproductive success. Males that started breeding earlier were more likely to be multibrooded (see also Gil & Slater 2000), which led to their higher reproductive success. Overall, sequentially monogamous and polygynous males produced a similar number of young; however, polygynous males incurred paternity costs and only half were able to compensate with a third brood. Studies comparing reproductive success of monogamous and polygynous males have largely ignored sequential monogamy even though it is common in many species of birds (Burns 1983; Black

1996). In this population, sequential monogamy provided male house wrens with high realized reproductive success and a lower risk of cuckoldry.

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