MATE SWITCHING IN MULTIBROODED HOUSE WRENS

NANCY E. DRILLING AND CHARLES F. THOMPSON

Ecology Group, Department of Biological Sciences, Illinois State University,
Normal, Illinois 61761-6901 USA

ABSTRACT.—We studied within-season mate switching in two populations of House Wrens (*Troglodytes aedon*) in central Illinois over nine breeding seasons. On the East Bay site, 35.2% of the monogamous pairs switched mates. On this less-preferred habitat, there were fewer potential mates. In contrast, on the Mackinaw site, 58.8% of the monogamous pairs switched mates, and there were potential mates available throughout the breeding season. There was no consistent immediate reproductive cost or benefit to mate switching. We suggest that mate switching in these House Wren populations is a consequence of varying mate availability and differing gender-related costs of facultative polygyny and territoriality. Because females incubate the eggs and brood the chicks, males have the first opportunity to desert their mate and offspring, which often results in polygynous matings. After the chicks leave the nest, males that feed fledglings may lose their territory and the opportunity to breed again. Females do not incur such a cost, and they easily move to another territory and another mate. Frequencies and relative costs and benefits of mate switching also varied considerably among three other House Wren populations. This reveals considerable flexibility in response to different demographic and environmental situations. Knowledge of the basis for this variability is important to understand mate choice in birds. *Received 14 February 1990, accepted 14 July 1990.*

THE DEGREE to which mated birds maintain the pair bond between breeding attempts within a single breeding season varies among species and among populations within a species. Multibrooded passerines often display almost complete mate fidelity, with the male caring for the offspring while his mate begins the next nest (see reviews in Nice 1930, Burns 1983). In these species, the advantages of mate fidelity (e.g. familiarity of mate and territory) outweigh the advantages of mate switching (finding a better mate or territory). Some species that regularly switch mates within seasons include European Starlings (*Sturnus vulgaris*; Feare and Burnham 1978), Prairie Warblers (*Dendroica discolor*; Nolan 1978), Indigo Buntings (*Passerina cyanea*; Carey and Nolan 1979), Winter Wrens (*Troglodytes troglodytes*; Garson 1980), Barn Swallows (*Hirundo rustica*; Shields 1984), Song Sparrows (*Melodia melospiza*; Weatherhead and Boak 1986), Fan-tailed Cisticola (*Cisticola juncidis*; Ueda 1986), and Pinon Jays (*Gymnorhinus cyanocephalus*; Marzluff and Balda 1988).

The decision of a pair to separate will depend upon the relative costs and benefits of switching to a new partner, and upon mate availability (Maynard Smith 1977). If no potential mates are available, a bird must choose between breeding with its previous mate or not breeding. If new potential mates are available, birds that suffer from low reproductive success at their first nest may have higher subsequent reproductive success if they switch mates. Thus, if there is a direct relationship between immediate reproductive success and mate switching, birds with failed nests should be more likely to switch mates than those with successful nests, and birds that switch mates after nest failure should be more successful subsequently than those not switching.

Birds switch mates for various reasons. They may be attempting to increase their reproductive success by finding a more experienced, older mate. They may be attempting to minimize the time between nesting attempts, or to obtain a higher-quality territory (Shields 1984). Switching to an older, more experienced mate may result in higher reproductive success because, in some species, more experienced or older birds have higher reproductive success than less experienced, younger individuals (Rowley 1983). If so, the frequency of mate switching should be lowest in old/experienced pairs, intermediate in mixed old/experienced–young/inexperienced pairs, and highest in young/inexperienced pairs. Switching could also increase reproductive success by minimizing the time between nesting attempts, if breeding seasons are short or reproductive success decreases as the breeding season progresses (Burns 1983).

In this case, if one parent can raise at least some of the brood alone, the other parent should abandon the first brood and switch to another mate.

We tested these predictions with the multi-brooded House Wren (*Troglodytes aedon*), a short-lived, migratory passerine that nests in central Illinois. Although mate switching (equivalent to Rowley's [1983] "resorting"; i.e. a bird mates with a different bird while its previous mate is still present on the study area) occurs regularly between the first and second brood within a season, we did not detect any immediate cost or benefit to switching mates. Our results differ in important ways from those obtained in three other House Wren populations (Kendeigh 1941, Burns 1983, Freed 1987). We hypothesize that mate switching in this central Illinois population is a consequence of variation in mate availability and differing gender-related costs of facultative polygyny and territoriality.

METHODS

Study areas and materials.—This study was conducted from 1980–1988 on two areas in McLean County, Illinois (Money Creek Township, Sect. 4-5, T 25N, R 3E). The study areas were floodplain and upland deciduous forest surrounded by agricultural fields unsuitable for breeding House Wrens. Within the 108-ha Mackinaw study area (Drilling and Thompson 1988: fig. 1a), 585 nest boxes were placed in a grid pattern. Lines in the grid were 60 m apart, and boxes within a line were 30 m apart. The 20-ha East Bay study area (Drilling and Thompson 1988: fig. 1b), with 325 nest boxes, was 1.6 km southwest of the Mackinaw tract. Distances between lines and nest boxes at East Bay varied from 15 to 60 m. Each identical, stained-pine nest box was mounted on electrical conduit covered with grease to decrease predation (box dimensions: floor, 8.4×9.0 cm; diameter of entrance, 3.2 cm; distance from bottom of entrance to floor, 13.0 cm; distance from entrance to ground, approx. 1.5 m).

Nest boxes were checked twice weekly. Boxes with nests were checked daily as hatching and nest-leaving approached. We recorded the date the first egg was laid (egg-1 date), clutch size, date the first chick hatched, brood size, date that either the nest failed or the chicks left the nest (termination date), and fate of nest. Because the start of breeding varied, the date that the first egg of the season was laid was subtracted from the egg-1 date of each nest to produce a standardized egg-1 date.

House Wrens are double-brooded (Fig. 1A) and both facultatively polygynous and serially monogamous in central Illinois. A nesting cycle lasts approx. 4 weeks, and fledglings are dependent on their parents for
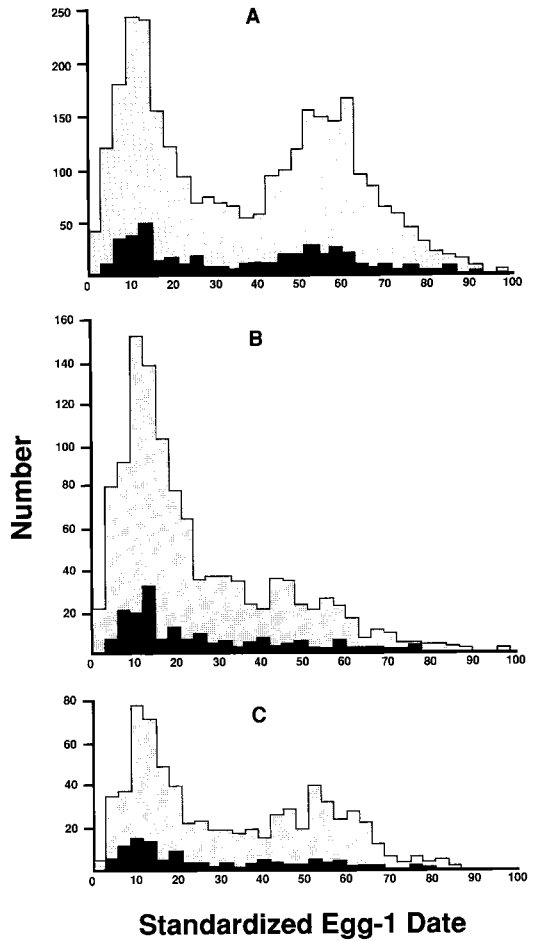

Standardized Egg-1 Date

Fig. 1. Frequency of nesting starts by standardized egg-1 date during the 1982–1988 breeding seasons. East Bay is represented by the dark shading and Mackinaw by the lighter area. (A) All nests, $n = 3,787$. (B) First known nest of previously unbanded females, $n = 1,649$. (C) First known nest of previously unbanded males, $n = 982$.

food for an additional 2 weeks. Only females incubate the eggs and brood the nestlings until the chicks are 6–7 days old. If a female abandons her brood after it is 6–7 days old, the male can raise the nestlings. Alternatively, if the male abandons at any point during the nesting cycle, the female can raise at least some of the chicks (Bart and Tornes 1989; pers. obs.).

All adults were captured at their nest and banded with a numbered aluminum USFWS band. In most years, males were banded with three plastic color bands (up to 2 bands per leg) to form a unique color combination (see Drilling and Thompson 1988 for additional details). All nestlings were weighed when banded (usually when they were 12 or 13 days old) except in 1984 and 1985. Because heavier 12-day-old

nestlings were more likely than lighter ones to be recaptured as juveniles in nets near the study areas and were more likely to be recruited to subsequent breeding populations (Thompson unpubl. data), we used the mean mass of the nestlings in a brood at banding as a measure of nestling quality.

Data set and statistics.—The percentage of nests at which both the male and female were identified varied greatly among years (minimum 7.4% in 1980, maximum 81.0% in 1988). Our data set includes only males that had more than one nest in a season and only those cases in which the female was known for both the first and second nest. This subset of the population had a higher proportion of successful nests than did the entire population because unsuccessful nests often did not survive long enough for us to identify both parents. A male was included in the data set more than once within a year if he had three or more nests within a season and his mate was identified at all of these nests (e.g. a male with three nests was listed once for his first and second nests and listed again when we compared the second and third nests). To avoid the problem of repeated measures, we used the first record for each pair in all statistical analyses involving pairs, the first female record for female-only analyses, and the first male record for male-only analyses.

We did not know the age of House Wrens on our study areas except for the 2.8% of the fledglings that subsequently returned as breeders. Therefore, in the breeding experience analyses, *experienced* (E) refers to birds that were unbanded when first caught breeding but that subsequently bred one or more seasons on the study area, as well as birds produced on our study areas that we knew were two or more years old. *Inexperienced* (I) refers to birds of unknown age in their first breeding season on the study areas and birds that we knew were yearlings because we had banded them as nestlings.

An *interbrood interval* was defined as the number of days between the termination date of a wren's nest and the egg-1 date of its next nest. We used the interbrood interval to estimate the extent of parental care given to fledglings following nest-leaving. Assuming that parents fed fledglings for 13 days after nest-leaving (Kendeigh 1941), we applied the following criteria to determine if a parent deserted its brood after nest-leaving but before the fledglings achieved independence. If the pair switched mates, the bird with an interbrood interval of ≤ 14 days either deserted or, in the case of the male, at least greatly reduced his contribution to the brood. If both the female's and the male's interbrood interval was >14 days, neither parent deserted the brood. These categories eliminated most pairs whose fledglings died before independence, as well as those pairs whose desertion pattern could not be inferred from the interbrood interval.

Statistical analyses were performed with SAS sta-tistical programs (SAS Institute 1985). To compare frequencies with the SAS program CATMOD, we used either a log-linear model for saturated designs or a maximum likelihood model when there were empty cells. We used analysis of variance (with Type III sums of squares), analysis of covariance (ANCOVA), or logistic regression in analyses using the variables "number of chicks to leave the nest" and "standardized egg-1 date."

In many nests, clutch size or brood size was manipulated (e.g. increased or decreased) for other studies (Finke et al. 1987, Baltz and Thompson 1988). Mate switching after the first nest was not significantly different among the three treatments (after manipulation of clutch size, 50.0%; after manipulation of brood size, 57.7%; no manipulation, 54.0%; $\chi^2 = 0.7$, df = 2, $P = 0.70$). Therefore, treatments were combined in all analyses.

The frequency of mate switching was significantly different between the two study areas. Therefore, we performed logistic regression and Chi-square analyses separately for each study area. We included the effects of study area and of interaction between treatment and study area in all other analyses. We do not report the interaction effects because none was statistically significant at the 5% level.

RESULTS

Polygyny and mate switching.—A male was considered polygynous if the egg-1 date of his second nest preceded the termination date of his first nest. There were 156 (24.2%) cases of bigamy and one case of trigamy in 645 cases in which the female was identified at each of the male's nests. These 156 bigamous cases included 18 males listed twice because they had two bigamous matings in one season and one male listed three times because he had three bigamous matings in one season (see Table 1). Twenty-four of 53 males (45.3%) with three nests in one season had a different mate for each nest and 2 of 6 males with four nests in a season had four different mates. The trigamous male, with a total of five nests in the season, mated with four different females. Polygynous matings and pairs in which the first female did not breed on the study area again in that season were excluded from all subsequent analyses.

Mate switching and mate availability.—For all monogamous matings, 210 individuals of 379 pairs (55.4%) switched mates for the following nest, while 169 pairs (44.6%) stayed together. Frequency of mate switching differed significantly between the two study areas ($\chi^2 = 10.4$, df = 1, $P = 0.001$) but did not differ significantly

TABLE 1.   Mate fidelity in polygynous males that had three or more nests in one breeding season. Frequency of occurrence is in parentheses. "Female nest x = female nest y" indicates that females at nests x and y were the same.

I. Three nests in one season (53)
   A. One bigamous and one monogamous mating (38)
      1. Nest 1 monogamous, nests 2 & 3 bigamous (20)
         a. Female nest 1 = female nest 2 (7)
         b. Female nest 1 = female nest 3 (2)
         c. Three different females (11)
      2. Nests 1 & 2 bigamous, nest 3 monogamous (18)
         a. Female nest 2 = female nest 3 (6)
         b. Female nest 1 = female nest 3 (5)
         c. Three different females (7)
   B. Nests 1 & 2 bigamous, nests 2 & 3 bigamous (15)
      1. Female nest 1 = female nest 3 (9)
      2. Three different females (6)
II. Four nests in one season(6)
   A. Nests 1 & 2 bigamous, nests 2 & 3 bigamous, nest 4 monogamous (1)
      — Female nest 1 = female nest 3 = female nest 4
   B. Nests 1 & 2 bigamous, nests 3 & 4 bigamous, nest 2 monogamous (2)
      1. Female nest 2 = female nest 4 (1)
      2. Four different females (1)
   C. Nest 1 monogamous, nests 2 & 3 bigamous, nest 4 monogamous (1)
      — Female nest 2 = female nest 4
   D. Nest 1 monogamous, nests 2 & 3 bigamous, nests 3 & 4 bigamous (1)
      — Female 1 = female 2
   E. Nests 1 & 2 bigamous, nests 2 & 3 bigamous, nests 3 & 4 bigamous (1)
      — Four different females
III. Five nests in one season (1)
    — Nest 1 monogamous, nests 2 & 3 & 4 trigamous, nest 5 monogamous
    — Female 1 = female 3

TABLE 2.   Percentage of mate switching (sample sizes in parentheses).

Year	Mackinaw	East Bay
1980	0.0 (1)	—
1981	100.0 (6)	—
1982	64.0 (25)	—
1983	67.7 (34)	25.0 (16)
1984	—	40.0 (10)
1985	67.5 (40)	33.3 (9)
1986	50.6 (77)	—
1987	51.5 (66)	44.4 (9)
1988	60.5 (76)	40.0 (10)
Total	58.8 (325)	35.2 (54)

man-caused failures (14.8%); and abandonment or disappearance of eggs or chicks (69.1%). The number of chicks produced in each nest in which at least one egg was laid also decreased significantly throughout the season (cubic polynomial regression, $R^2 = 0.79$, $P = 0.0001$) (Fig. 2B).

Wrens from successful and unsuccessful pairs were equally likely to switch mates (successful wrens, 55.6%; unsuccessful, 54.1%) (log-linear model: $\chi^2 = 2.1$, df $= 1$, $P = 0.15$). The probability of mate switching did not depend on the number of chicks produced in the first nest at either East Bay or Mackinaw (logistic regression: $\chi^2 = 3.0$, df $= 1$, $P = 0.08$; $\chi^2 = 0.9$, df $= 1$, $P = 0.35$, respectively). Mate-faithful wrens and individuals that switched mates both produced, on average, 4.3 fledglings in their first nest.

Mate switching did not affect the success of the next breeding attempt either for previously successful females or for previously unsuccessful females (Table 3). Mate switching did not affect the number or quality of fledglings produced by previously successful or previously unsuccessful females in their next nest (Table 3). Among females not switching mates, previously unsuccessful females had lower nest success and produced fewer fledglings than did previously successful females. The same results were obtained for previously successful and previously unsuccessful males (Table 3).

Experience and mate switching.—The proportion of wrens that switched mates was not significantly different among the four types of pairs made up of experienced (E) and inexperienced (I) birds (E-E pairs, 59.6%; I-I pairs, 53.4%; E female–I male pairs, 54.0%; I female–E male pairs, 56.6%) (log-linear model: $\chi^2 = 2.4$, df $= 3$, $P = 0.49$). Neither the experience level of the subsequent mate nor mate switching affected

among years (maximum likelihood model: $\chi^2 = 1.7$, df $= 7$, $P = 0.98$; 1980 not included) (Table 2).

Unbanded adults (i.e. without known previous breeding experience on the study areas) were available and recruited to the population throughout the breeding season (Fig. 1B, C).

Reproductive success and mate switching.—The proportion of all nests that were successful (i.e. produced at least one fledgling) decreased significantly throughout the season (cubic polynomial regression: $R^2 = 0.52$, $P = 0.0001$) (Fig. 2A). Nests failed completely because of predation by raccoons (*Procyon lotor*), small mammals, snakes, and birds (12.6%); drowning (3.4%); hu-
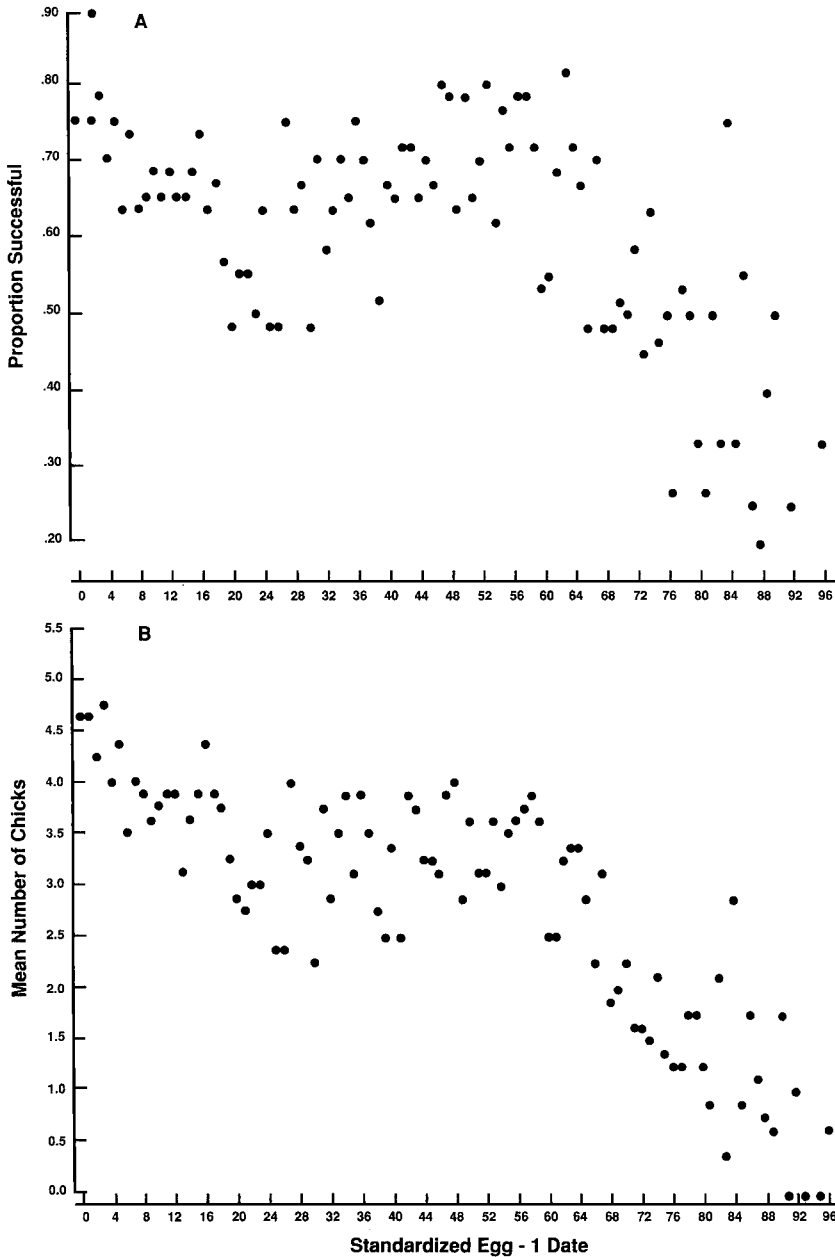
Fig. 2.   Seasonal decline in reproductive success of 1980–1988 nests in relation to their standardized egg-1 date. (A) Proportion of successful nests. (B) Mean number of chicks produced per active nest.

subsequent reproductive success of females or males (Table 4).

Desertion and subsequent reproductive success.— In these analyses, desertion pertains only to deserting the mate after the chicks left the nest but before they were independent (see Methods). Therefore, we used only those wrens that

switched mates after having a successful first nest. Because reproductive success declined during the season (Fig. 2), analyses involving percentage of successful nests included only nests begun before the standardized egg-1 date of 68 (ca. 25 July), and ANOVA used standardized egg-1 date as a covariate.

TABLE 3. Mate switching and subsequent reproductive success. The measures of subsequent reproductive success are percentage of successful nests, number of chicks produced ($\bar{x} \pm$ SE), and nestling mass ($\bar{x} \pm$ SE). Sample sizes are in parentheses.

	Nests successful (%)	No. of chicks	Nestling mass (g)
Females			
Previously successful			
Switched	78	3.7 ± 0.2 (149)	9.8 ± 0.1 (79)
Did not switch	84	3.9 ± 0.2 (118)	9.8 ± 0.1 (71)
Previously unsuccessful			
Switched	71	3.3 ± 0.4 (42)	9.8 ± 0.2 (25)
Did not switch	60	2.8 ± 0.5 (36)	10.0 ± 0.1 (19)
P^a	0.31	0.30	0.51
P^b	0.60	0.79	0.38
P^c	0.28	0.08	0.52
P^d	0.001	0.001	0.94
Males			
Previously successful			
Switched	85	3.8 ± 0.2 (147)	9.9 ± 0.1 (73)
Did not switch	82	3.9 ± 0.2 (110)	9.8 ± 0.1 (62)
Previously unsuccessful			
Switched	82	3.4 ± 0.4 (36)	9.8 ± 0.1 (25)
Did not switch	59	2.9 ± 0.5 (31)	10.0 ± 0.1 (19)
P^a	0.69	0.79	0.33
P^b	0.37	0.62	0.79
P^c	0.34	0.23	0.51
P^d	0.002	0.002	0.77

[a] P value for comparison of previously successful wrens that did and did not switch.
[b] P value for comparison of previously unsuccessful wrens that did and did not switch.
[c] P value for comparison of previously successful and previously unsuccessful wrens that switched.
[d] P value for comparison of previously successful and previously unsuccessful wrens that did not switch.

Male reproductive success at subsequent nests was not dependent on whether or not he had been abandoned by his mate, if he abandoned his mate, or if neither parent deserted during the postfledging period (Table 5). Similar results were obtained for females, although females tended to have lower subsequent reproductive success if both parents cared for the fledglings (Table 5).

To investigate further if there was an advantage to deserting a mate, we combined two categories ("did not desert" and "deserted by mate") from Table 5 to compare wrens that stayed to feed their fledglings with those that deserted. We found no significant difference in future reproductive success between females that stayed with their fledglings and females that deserted their mate and brood (% success: $\chi^2 = 1.0$, df = 1, $P = 0.32$; number of nestlings: ANCOVA $F = 0.03$, df = 1, 69, $P = 0.86$). Similarly, the future reproductive success of males that stayed with their fledglings was not significantly different from that of males that de-

serted their females and broods (% success: $\chi^2 = 1.3$, df = 1, $P = 0.25$; number of nestlings: ANCOVA $F = 0.03$, df = 1, 61, $P = 0.85$).

Mate and site switching.—Wrens that did not switch mates moved a median of 30 m (i.e. one nest box away on the Mackinaw tract) (range: 0–153 m at East Bay and 0–120 m at Mackinaw). Females that switched mates moved a median of 61 m (range: 0–262 m) at East Bay and 122 m (range: 0–1,063 m) at Mackinaw. Males that switched mates moved a median of 18 m (range: 0–90 m) at East Bay and 30 m (range: 0–1,080 m) at Mackinaw. Females that switched mates moved significantly farther than did mate-faithful females ($\chi^2 = 140.7$, df = 1, $P = 0.0001$), and males that switched moved significantly farther than did males that did not switch ($\chi^2 = 11.4$, df = 1, $P = 0.0007$) (multivariate rank test [SAS Inst. 1986], using study area as a blocking variable).

Assuming that a territory is 75 m in diameter (Kendeigh 1941), all but one of the pairs that remained together stayed within their old ter-

TABLE 4. Relationships among experience, mate switching, and subsequent reproductive success. Initial pairs include only pairs that were successful at their first attempt. Experienced birds (E), inexperienced (I), females (F), and males (M) are denoted. Samples sizes are in parentheses. A = frequency of initial pairings occurring in each of the three subsequent mate's experience levels; B = percentage of subsequent nests that were successful (P values are results of log-linear model tests); and C = mean (±SE) number of chicks produced in the subsequent nest (P values are results of ANOVAs).

| | Subsequent mate | | | |
Initial pair	Same	Switch-E	Switch-I	P
		Female		
EF-EM				
A. Freq. (54)	0.43	0.31	0.26	
B. % successful	90.5 (21)	87.5 (16)	100 (13)	0.99
C. No. of chicks	4.3 ± 0.4 (23)	3.9 ± 0.6 (17)	4.9 ± 0.5 (14)	0.60
EF-IM				
A. Freq. (67)	0.52	0.11	0.37	
B. % successful	87.9 (33)	85.7 (7)	90.5 (21)	0.99
C. No. of chicks	3.8 ± 0.4 (35)	4.4 ± 0.9 (7)	4.3 ± 0.4 (25)	0.87
IF-EM				
A. Freq. (102)	0.48	0.22	0.30	
B. % successful	84.4 (45)	100 (15)	93.1 (29)	0.99
C. No. of chicks	3.7 ± 0.3 (48)	3.7 ± 0.4 (22)	4.8 ± 0.4 (30)	0.65
IF-IM				
A. Freq. (109)	0.54	0.19	0.27	
B. % successful	72.5 (51)	79.0 (19)	90.9 (22)	0.38
C. No. of chicks	3.6 ± 0.3 (57)	3.6 ± 0.6 (21)	3.3 ± 0.4 (28)	0.91
		Male		
EM-EF				
A. Freq. (57)	0.40	0.23	0.37	
B. % successful	90.5 (21)	61.5 (13)	78.6 (14)	0.97
C. No. of chicks	4.3 ± 0.4 (23)	3.1 ± 0.7	3.4 ± 0.6 (20)	0.32
EM-IF				
A. Freq. (113)	0.43	0.22	0.35	
B. % successful	84.4 (45)	82.3 (17)	86.5 (37)	0.91
C. No. of chicks	3.7 ± 0.3 (48)	3.7 ± 0.5 (25)	4.0 ± 0.4 (38)	0.90
IM-EF				
A. Freq. (76)	0.46	0.14	0.40	
B. % successful	87.9 (33)	90.9 (11)	95.2 (21)	0.99
C. No. of chicks	3.8 ± 0.4 (35)	4.5 ± 0.5 (11)	4.3 ± 0.4 (27)	0.33
IM-IF				
A. Freq. (130)	0.47	0.12	0.41	
B. % successful	69.8 (53)	100 (11)	92.7 (41)	0.34
C. No. of chicks	3.5 ± 0.3 (59)	3.9 ± 0.5 (15)	3.6 ± 0.3 (54)	0.98

ritory for the next breeding attempt. Males that switched mates stayed within their old territory (75.4% did not move), while females that switched tended to move to a new territory (36.3% did not move).

DISCUSSION

House Wrens were as likely to switch mates after a successful nest as after an unsuccessful nest, and wrens that switched after failure did not do better reproductively than those that did not switch. The failure of unsuccessful wrens to improve their success by switching is expected if birds that failed were of intrinsically poorer quality than were successful birds. Our results support this prediction because previously unsuccessful females did worse at their next breeding attempt than did previously successful females (see Table 3). The likelihood of mate switching was not related to the age/experience levels of pair members. Much of the

evidence for a positive relationship between age and reproductive success has been obtained in large, long-lived passerines and in nonpasserines (see Rowley 1983). The lack of such a relationship in the House Wren may be a consequence of the species' short life span. However, our classification based on experience undoubtedly included some older birds (which had bred previously beyond the bounds of the study area) with yearling, inexperienced birds. This reduced any difference between the two categories of experience. Finally, we found no evidence that wrens enjoy an immediate reproductive advantage by deserting their mate and thereby beginning another brood more quickly. These results with respect to frequency and costs and benefits of mate switching differ from those reported in other House Wren populations.

The frequency of mate switching, mate availability, and reproductive costs of switching differed among five populations of House Wrens in Ohio (41°N; Kendeigh 1941), Minnesota (45°N; Burns 1983), Panama (11°N; Freed 1987), and Illinois (40°N; this study). The incidence of mate switching in Illinois House Wrens on the Mackinaw study site was similar to the frequency in populations in Ohio and Minnesota. Mate switching in these areas was much higher than on the East Bay study area in Illinois and in a nonmigratory House Wren population in Panama.

In Minnesota (the northernmost population studied) unmated wrens acquired mates throughout the breeding season. Previous nest success was not a good predictor of mate switching. Birds that deserted their first nests and mates minimized the time between nesting attempts, a tactic possible because the remaining parent could raise the offspring alone. Wrens that deserted their first nest and mate could begin their second nest 5.6 days earlier, on average, than those that stayed with their first mate. Wrens that were deserted did not begin a second nest because the Minnesota breeding season was short. If reproductive success declined as the Minnesota season progressed (Burns [1983] did not present these data), the optimal strategy for either males or females was to desert. A female, however, is constrained from deserting too early because she alone broods the chicks until they can thermoregulate effectively (i.e. ca. 6 days of age) (Kendeigh 1952). Thus, the male that deserts should do so early in the nesting cycle. However, all pairs at first nests (Burns

TABLE 5. Percent subsequent successful nests and mean ($\pm$SE) number of chicks produced in subsequent nest in relation to mate desertion after chicks left the nest but before fledgling independence. P values for percent successful nests are results of Chi-square tests; P values for means are results of ANCOVAs using standardized egg-1 date as the covariate. Sample sizes are in parentheses.

	% successful	No. of chicks
Female		
Deserted by mate	100% (17)	4.4 ± 0.4 (22)
Deserted mate	95.5% (22)	4.5 ± 0.4 (22)
Did not desert	79.2% (24)	3.6 ± 0.6 (28)
P	0.05	0.54
Male		
Deserted by mate	68.8% (16)	3.3 ± 0.6 (22)
Deserted mate	86.4% (22)	4.2 ± 0.5 (22)
Did not desert	76.9% (26)	4.0 ± 0.6 (28)
P	0.42	0.77

1983) fed the nestlings until the nestlings were at least 10 days old, and in half of the cases the deserter was the female. Both facts contradict the predication.

In Panama, the southernmost population studied, there were no costs or benefits for mate switching in terms of immediate reproductive success or time saved (Freed 1986a, 1987). Instead, and despite the existence of a floater population, there were few available unpaired potential mates on territories because territories were maintained year-round, all territories were occupied, and mortality was low. Females were constrained from mate switching because there were few unmated males with a territory. Males were constrained from switching because there were few empty territories, and they could rarely usurp territory-holders (Freed 1986b).

In Ohio, the breeding season was long enough for deserted birds to complete successfully a second brood, and potential mates were available throughout the season (Kendeigh 1941). Mate switching was not related to the reproductive success of the first nest. In contrast, Burns' (1983) reanalysis of a small data set from Kendeigh revealed that switching individuals incurred a cost in the subsequent reproductive attempt. Previously successful wrens that switched mates produced significantly fewer offspring than did previously successful wrens that did not switch. Yet, the frequency of mate switching was high (60%). Kendeigh described 42 cases in which House Wren parents fed fledglings. In 21 cases, both parents fed the

fledglings, and 65% of these males remated with their previous mate. In the remaining 21 cases, the males did not feed fledglings (and presumably abandoned the brood to the female), and only 33% remated with their former mate. If desertion saves time, wrens that abandoned their brood and quickly began another should have higher subsequent reproductive success than those that cared for their fledglings. Bart (1990) reanalyzed Kendeigh's data and found that subsequent reproductive success was not significantly different among wrens that did and did not abandon their fledglings. He did detect a cost to males that fed fledglings. House Wrens usually fed their fledglings off their territories. Fifty-five percent of the males that fed fledglings lost their territory, and 33% of these males that fed fledglings failed to obtain another territory and never bred again on the study area in that season. For males that did not feed fledglings, only 9% lost territories, and, of these, only 15% failed to obtain another territory.

Our two study areas had significantly different frequencies of mate switching. This difference is not attributable to differential reproductive success between the two sites, as shown by the lack of any significant interactions in our reproductive success analyses. We believe that there were fewer available mates on the East Bay site because of habitat quality. Only an average of 21% of East Bay nest boxes had nests each year (3.39 nests/ha) compared with 74% at Mackinaw (3.97 nests/ha). Further, the East Bay breeding season began an average of 6 days later than at Mackinaw. This difference in House Wren site preferences, and difference in mate availability, probably accounts for the significant difference in levels of mate switching between the two areas.

On the Mackinaw study area, mates were readily available throughout the breeding season (Fig. 1B, C). The number of available mates is underestimated because available banded birds and territorial males previously unsuccessful in obtaining mates were excluded. In contrast to the Minnesota population, breeding season length was not a factor in Illinois because females could raise up to three broods in one season (pers. obs.). We found no immediate reproductive costs or benefits to switching mates. Of course, costs and benefits may be expressed as differences in survival or in lifetime reproductive success, which we did not measure. In addition, costs may have been under-

estimated because we excluded wrens that did not renest. This group probably included birds that were deserted and never obtained another mate. Another possibility is that we failed to detect a benefit or cost to mate switching because we used standardized nest boxes. If the abundance or quality of nest cavities affected mate switching, then we may have negated the effects of switching. However, there was evidence of a cost to mate switching in Kendeigh's population, which bred in nest boxes (Burns 1983).

Mate switching in the Mackinaw population is a consequence of territoriality and the facultatively polygynous mating system. When one member of the pair benefits from a move but not the other, mate switching may result. Males in our population were more site-faithful than females. Greenwood (1980) argued that males are site-faithful because they defend territories and would incur a cost in time and energy if they moved, whereas females can move about because they do not use territories to attract a mate (see also Shields 1984). When female wrens choose a different site, mate switching may be an incidental consequence of the differing costs of switching nest sites in males and females. This is consistent with the behavior of female Pied Flycatchers (*Ficedula hypoleuca*), which select mates on the basis of nest-site characteristics rather than on physical attributes of the males (Alatalo et al. 1986, Slagsvold 1986; but cf. Lifjeld and Slagsvold 1988). Although we did not detect an advantage in moving to a new site, this topic warrants further study.

Male and female House Wrens also incur different costs and benefits as a result of the opportunity for polygyny. Facultative polygyny allows males to attempt more breeding each season (up to four successful attempts in central Illinois). Because females incubated the eggs and brooded the chicks, female desertion was rare and only one female began a second nest before her first brood left the nest. In contrast, males often tried to attract other females as soon as the first nest was begun (pers. obs.). Almost a quarter of the matings were polygynous and an additional unknown proportion of males were at other nest boxes trying unsuccessfully to attract another female. Male House Wrens on the Mackinaw study area were less attentive to their early nests and had lower feeding rates than did females when the chicks were older than 6

days (Morton 1984). Late in the season, these differences disappeared. Thus, many males may have deserted their brood or reduced their contribution before the chicks left the nest, especially early in the season when there were more potential mates and more time to raise another brood successfully. This agrees with Maynard Smith's (1977) prediction that mate desertion should occur when one parent is as effective as two in raising the offspring, as occurs in the House Wren after the nestlings can thermoregulate (Bart and Tornes 1989).

If desertion does not occur while the chicks are in the nest, it could occur during the 2 weeks following nest-leaving. We found no relationship between desertion during the fledgling period and subsequent reproductive success. This analysis included only wrens that bred again on the study area. Thus, just as in the Ohio population, males feeding fledglings may have lost their territory and the opportunity to breed again, a cost that females did not incur. This potential male cost is worthy of additional study in the Illinois populations. We hypothesize that females switched mates in the Mackinaw population because their first mate was occupied with attempting to attract additional mates. Females that did not switch may have been mated to males that did not attempt to attract another mate. The variability in mate-switching frequencies, as well as in potential costs and benefits, that occurs in five House Wren populations illustrates the species' ability to respond flexibly to different demographic conditions.

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100 Years Ago in The Auk

From "The habits of the Golden Plover (Charadrius dominicus) in Massachusetts"
by George H. MacKay (1891, Auk 8: 17-24):

". . . As far as my observation shows on the Island of Nantucket, the Golden Plover usually seeks land about dusk and during the first half of the night. I can recall but three occasions when they landed during daytime, and on two of those in very inconsiderable numbers. It is usual several times during the migrating period to hear them whistling as they pass low down over the town of Nantucket; but on these occasions, unless it is storming hard, they do not stop, but pass on, if the wind is fair (northeast). I have been many times disappointed on driving over the Plover ground at daylight on the following morning to find that no birds had stopped. In other words, it is a most difficult matter to 'hit the flight,' for it requires a combination of circumstances and weather which rarely happens, to enable one to obtain any number of these birds on the Atlantic coast.

In regard to the numbers of these birds formerly, and at the present time, I would say that it is extremely difficult to arrive at any correct conclusion, this arises from the fact that the migration almost always passes by, or over the Island, after dark, and our means of judging is by comparison with others of the number of flocks heard whistling as they flew overhead. It is however certain that for a number of years fewer birds have stopped on the coast than formerly, and

for a shorter period. We are, however, liable any year, when all the conditions are favorable, to have an immense landing.

To those interested in this direction I give the following result of some inquiry I made recently of two game dealers in Boston. About four years ago the shipment of Golden Plover, Eskimo Curlew, and Bartramian Sandpipers first commenced in the spring, and it has been on the increase up to date. Last spring (1890) these two firms received from Nebraska (principally), Saint Louis, and Texas (Fort Worth) twenty barrels of birds, one-third of which were Golden Plover, two-thirds Bartramian Sandpipers; eight barrels of Eskimo Curlew; twelve barrels of Eskimo Curlew and Golden Plover. As there are twenty-five dozen Curlew, and sixty dozen Plover each to a barrel, it will be realized what this means, if other large cities are similarly supplied. All were killed on their northern migration to their breeding grounds. Therefore while we may not be able now to answer the question: are they fewer than formerly, we shall be ably fitted to do so in a few years."

Vol. 8 (1) also included a color plate. The illustration, drawn by J. L. Ridgway, was of an adult and young male Icternus northropi in an article "The birds of Andros Island, Bahamas" by John L. Northrop.—Ed.