NATAL AND BREEDING DISPERSAL IN HOUSE WRENS (*TROGLODYTES AEDON*)

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ABSTRACT.—We studied the natal and breeding dispersal of yearling and adult House Wrens (*Troglodytes aedon*) for 7 yr in central Illinois. The forested study areas contained 910 identical nest boxes placed in a grid pattern. On average 38.1% (n = 643) of the adult males and 23.3% (n = 1,468) of the adult females present in one year returned the next; 2.8% (n = 6,299) of the nestlings that survived to leave the nest returned each year. Adult male (median distance = 67 m) and adult female (median = 134 m) breeding dispersal was less than yearling male (median = 607.5 m) and yearling female (median = 674 m) natal dispersal. Females that returned had produced more offspring the previous season than had nonreturning females, and females that successfully produced at least one chick in their last nesting attempt of the previous season moved shorter distances than did unsuccessful females. There were, however, no consistent differences between returning and nonreturning females in two other measures of reproductive success. Females that were unsuccessful in their last breeding attempt of the previous year were more likely to be successful in their next attempt if they moved two or more territories than if they did not move. Reproductive success did not affect the likelihood that a male would return nor the distance that he moved. The success of subsequent nesting attempts by males was also not related to the distance moved.

Inbreeding avoidance may explain differences between breeding and natal dispersal, but it does not explain the lack of difference in dispersal of yearling females and males. Differences between adult and yearling dispersal are best explained by advantages accruing to adults that remain near former breeding sites and by the necessity for yearlings to move farther because of their late return from the wintering grounds. The advantages for adults to reoccupy previous breeding sites are counterbalanced, especially in females, by advantages associated with moving after breeding failure. *Received 15 June 1987, accepted 4 March 1988.*

IN many migratory passerines there are gender- and age-related differences in the proportion of birds that return to a breeding area and, for those returning, in the distance they settle from their former breeding or natal nest site (see reviews by Greenwood 1980, 1984). The general pattern is for adult males to return in higher proportions and settle closer to their previous nest site than adult females and for adults to settle closer to their previous nest site than yearlings to their natal site. Furthermore, individuals that produce offspring are more likely than unsuccessful birds to return to the area of their last breeding attempt.

One explanation for gender-related differences in dispersal is that territorial males gain more from being site faithful than females (Greenwood 1980). Differences in adult breeding dispersal associated with breeding success are usually explained as adaptations for improving breeding performance (e.g. Harvey et al. 1979, Beletsky and Orians 1987; cf. Nolan 1978: 461). Age-related differences in dispersal may be attributable to costs or benefits associated with inbreeding (e.g. Greenwood et al. 1978, Shields 1982). Murray (1967), Moore and Ali (1984), Liberg and von Schantz (1985), and Waser (1985) suggested that intrasexual competition for nest sites or mates is responsible for some age-related differences in dispersal.

We investigated the influence of age, gender, and reproductive success on breeding and natal dispersal in House Wrens (*Troglodytes aedon*) and examined some of the proposed explanations for differences in avian dispersal patterns.

METHODS AND MATERIALS

Study areas.—The two study areas, in McLean Co., Illinois (Money Creek Township, T 25N, R 3E), were floodplain and upland forests dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), hackberry (*Celtis occidentalis*), and ash (*Fraxinus* spp.) (Drilling and Thompson 1984). The forests were surrounded by arable fields. The 108-ha main study area was bisected by the Mackinaw River and contained 585 nest boxes distributed in north-south rows approximately 60 m apart (Fig. 1a). Nest boxes within a row were approximately 30 m apart (5.4 boxes/ha). In 1980 there were 327 nest boxes, all north of the river. The study area was expanded south of the river in 1981 by 148 nest boxes and in 1982 when another 110 nest boxes were placed in the remaining forest. The 20-ha East Bay study area (Fig. 1b), established in spring 1982, was 1.6 km west of the main study area. The 325 nest boxes there were also arranged in north-south rows, but distances between rows and nest boxes varied, with 183 nest boxes 15 × 15 m apart (43 boxes/ha), 40 nest boxes 15 × 30 m apart (23 boxes/ha), 67 nest boxes 30 × 30 m apart (10.9 boxes/ha), and 35 nest boxes 30 × 60 m apart (5.4 boxes/ha).

Each nest box, made of stained pine, had identical dimensions (floor, 8.4 × 9.0 cm; diameter of entrance hole, 3.2 cm; distance from bottom of entrance to floor, 13.0 cm; distance from entrance to ground, approximately 1.5 m). The entrance hole had a permanently mounted trapdoor. Each nest box was mounted on electrical line conduit, which was greased to reduce predation.

Definitions and procedures.—Wrens were categorized as "adults" if they were banded as breeding birds, if their age was unknown (AHY in U.S. Fish and Wildlife terminology), or if they were banded as nestlings on the study area and were 2 or more years old (TY and ATY). "Returning nestlings" and "yearlings" (SY) were banded as nestlings on the study area and returned in a subsequent year to breed.

Analyses of breeding and natal dispersal were based on data from 1,219 adult females, 547 adult males, and 6,299 nestlings that survived to leave the nest. Breeding female wrens were identified at 88–95% of the nests in 1980–1987. Females were caught in nest boxes while they incubated their eggs or brooded and fed their nestlings. Breeding males were caught either in nest boxes or in nearby mist nets or visually identified at 10–40% of the nests in 1980–1982 and at 55–85% of the nests in 1983 and 1985–1987. Because males were identified at only 2% of the 1984 nests, data for adult males and yearlings in 1984 were not included in any analyses. Adults and nestlings were banded with a numbered U.S. Fish and Wildlife Service aluminum band and three plastic color bands (2 bands/leg) in 1980, 1981, and the first half of 1982. In the second half of 1982 and in 1983–1987, each adult female and nestling was banded with a numbered aluminum band only. In 1985–1987 males were given 3 color bands and an aluminum band.

Nest boxes were checked twice weekly during the May–August breeding season. The day the first egg was laid (i.e. egg-1 day), clutch size, brood size, day the first chick hatched, fate of the nest, and number of chicks surviving to leave the nest were recorded for all nests.

Data analysis.—Statistical analyses were performed with Statistical Analysis System (SAS) programs (SAS Inst. 1985). Proportions were compared using a log-linear model (LM) contained in the CATMOD procedure in SAS. We used a multivariate rank test with year as a blocking factor (MRANK procedure; SAS Inst. 1986) for most analyses of distances moved. For distance analyses for which sample sizes were inadequate in some years, we used the Mann-Whitney *U*-test (M-W test) or the Kruskal-Wallis Chi-square approximation (K-W test). The distance between nest boxes was calculated as the straight-line distance. For frequency distributions of distances moved (Fig. 2), a territory was assumed to be 75 m in diameter (Kendeigh 1941).

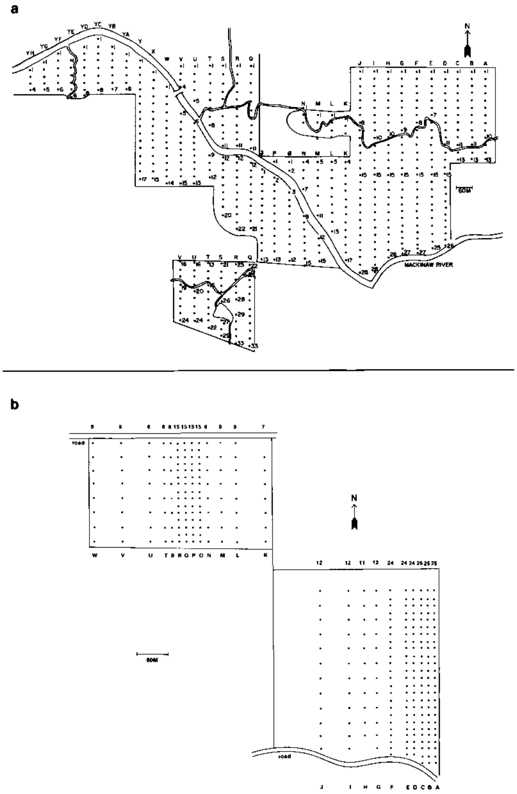

Fig. 1. Diagram of (a) main study area and (b) East Bay study area. Each dot represents 1 nest box.

To examine movements with respect to nest-box availability, we used a procedure modeled after that of Rheinwald (1975). This generated a distance distribution of empty nest boxes available at the time of return for each nest box from which a wren moved. We calculated the distances between the nest box from which a wren moved and all unoccupied boxes to which it could have moved. Each unoccupied nest box was classified as being in the former territory, in an adjacent territory, in a territory 2 territories away, and so forth, based on an average territory diameter of 75 m. We considered a nest box to be unoccupied when no nest was started in the box within 7 days

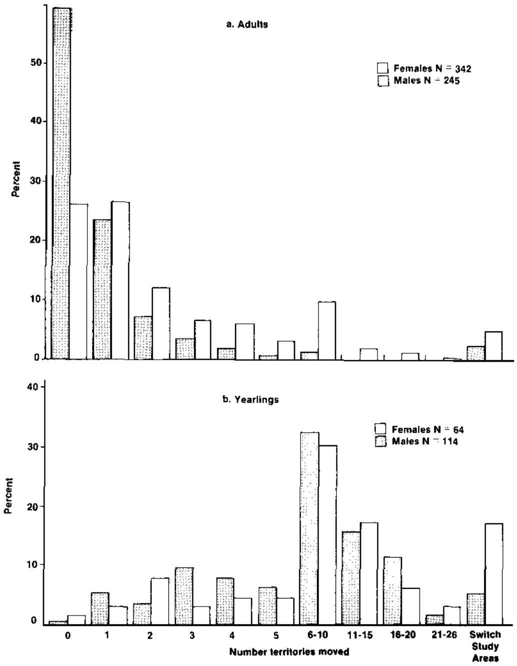

Fig. 2. Frequency distributions of movements between years by (a) adults and (b) yearlings. Males are represented by shaded bars, females by open bars.

before the date that the wren under consideration began a new nest. Seven days were used because wrens took 3-7 days to build a new nest and to begin laying eggs (pers. obs.). Each nest box from which a wren moved had a unique distance distribution dependent on its location on the study area (van Noordwijk 1984). Therefore, we did not pool distributions; instead, we standardized each individual distribution by converting the raw data for each territory distance class to a proportion of the total. For example, the first male to return in a season may have bred previously in a centrally located nest box on the main study area. In this case he had 34 nest boxes available within a distance of 2 territories away. Thus, 34 was converted to 0.058 (34 of 585 available nest boxes). The proportions for all of the territory distance classes in this converted distribution summed to 1.0. The distance the wren actually moved was plotted on the converted individual frequency distribution. The proportion of the total distribution represented by the territory distance class within which the observed distance fell and all less than that were summed. This sum was the proportion of unoccupied nest boxes that were nearer to the original nest box than was the nest box selected (Fig. 3).

Pooling of data.—Data from both study areas were pooled for subsequent analyses because there were no significant differences between study areas in the proportion of returning females ($\chi^2 = 0.65$, df = 1, $P = 0.42$), proportion of returning males ($\chi^2 = 0.53$, df = 1, $P = 0.47$), or distances moved by females or males (M-W test; $\chi^2 = 1.47$, df = 1, $P = 0.23$; $\chi^2 = 0.29$, df = 1, $P = 0.59$, respectively).

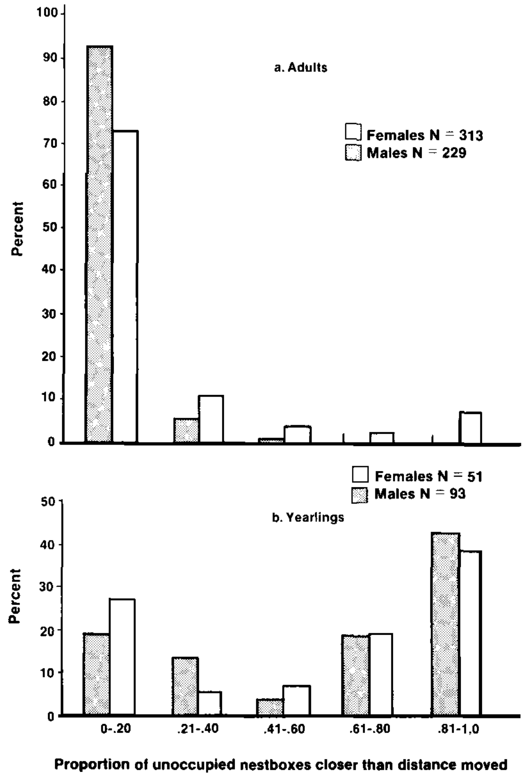

Fig. 3. Frequency distribution of the proportion of available nest boxes that (a) adults and (b) yearlings bypassed before they settled. Males are represented by shaded bars, females by open bars.

Brood and clutch sizes of many nests were altered during the course of the study (e.g. Finke et al. 1987, Baltz and Thompson 1988). These experiments could influence House Wren dispersal, so we tested for effects of brood manipulation on returns, reproductive success, and distances moved. The four brood-size treatments were enlarged broods, decreased broods, control broods, and natural (i.e. unmanipulated) broods. These treatments differ somewhat from those of Finke et al. (1987) in that decreased broods included only those that were experimentally decreased. All broods reduced in size by failure of eggs to hatch or hatchling death were classified as natural broods in this study. There were no significant differences among treatments in the proportions of adult females and males that returned ($\chi^2 = 6.21$, df = 3, $P = 0.10$; $\chi^2 = 1.05$, df = 3, $P = 0.79$, respectively), proportion of chicks that returned as yearlings ($\chi^2 = 4.92$, df = 3, $P > 0.10$), distances moved by adult females and males (K-W test, $\chi^2 = 0.37$, df = 3, $P = 0.95$; $\chi^2 = 4.45$, df = 3, $P = 0.22$, respectively), distances moved by yearlings (K-W test, $\chi^2 = 0.81$, df = 3, $P = 0.85$), proportions of successful (see Results) females and males that returned ($\chi^2 = 6.89$, df = 3, $P = 0.08$; $\chi^2 = 0.48$, df = 3, $P = 0.92$, respectively), proportions of unsuccessful females and males that returned ($\chi^2 = 3.43$, df = 3, $P = 0.33$; $\chi^2 = 3.05$, df = 3, $P = 0.38$, respectively), or total number of chicks produced in the previous season by males ($F = 2.18$, df = 3, 139, $P = 0.09$). There were significant differences among treatments in the number of chicks produced in the last breeding attempt of the previous year by females and males ($F = 21.24$, df = 3, 718, $P = 0.0001$; $F = 5.93$, df = 3, 135, $P = 0.0008$, respectively) and in the total number of chicks produced in the previous breeding season by females ($F = 16.04$, df = 3, 745, $P = 0.0001$). Therefore, only natural nests were included in analyses dealing with these two measures of reproductive success. Nests in which clutch size was altered were excluded from all analyses.

RESULTS

Return of adults.—The proportion of adult females that returned (23.3%) was significantly lower than the proportion of adult males identified each year (38.1%) (LM, $\chi^2 = 18.08$, df = 1, $P = 0.0001$) (Table 1). There was a significant difference in returns among years (LM, $\chi^2 = 17.56$, df = 6, $P = 0.007$), but there was no interaction effect between gender and year on returns (LM, $\chi^2 = 7.17$, df = 5, $P = 0.21$). The proportion of males that returned was a minimum estimate because males were not identified at all nests. A wren was included in this analysis each of the years it returned. Returns were similar when only the first return of each adult was considered (females: 19.5%, males: 34.1%) (Table 1).

A total of 251 of 1,219 different females (20.6%) and 200 of 547 different males (36.6%) returned to the study areas (i.e. bred on the study area for at least 2 seasons). Because so few males were identified in some years, we considered only females in the following analysis. Sixty-one of the 251 females (24.3%) returned twice, 19 of 61 (31.1%) returned 3 times, 7 of 19 (36.8%) returned 4 times, 3 of 7 returned 5 times, and 1 of 3 returned 6 times. Ten females and 7 males were not recaptured in the year between their first and second capture. Because these 17 wrens may have bred undetected on the study areas during the intervening year, they were excluded from further analyses.

There were 84 cases in which both members

TABLE 1. Return of House Wrens to the study areas. "All captures" includes wrens each time they returned. "First captures" includes only the first return of wrens banded as breeding birds. For "Chicks" female and male returns were calculated by assuming an equal sex ratio at nest departure. Numbers are percentages, with sample sizes in parentheses.

	Year from							
	1980	1981	1982	1983	1984	1985	1986	Total
All captures								
Adult females	16.1 (31)	19.3 (150)	19.3 (223)	21.6 (254)	28.0 (236)	22.8 (232)	26.6 (342)	23.3 (1,468)
Adult males	36.4 (11)	25.0 (28)	27.7 (119)	— —	23.5 (34)	42.6 (183)	42.9 (268)	38.1 (643)
First captures								
Adult females	16.1 (31)	17.4 (144)	19.4 (191)	17.2 (198)	20.6 (180)	20.7 (155)	21.5 (260)	19.5 (1,159)
Adult males	36.4 (11)	26.9 (26)	26.2 (103)	— —	20.0 (30)	40.9 (154)	36.5 (148)	34.1 (472)
Chicks								
Females	2.6	0.6	2.0	—	1.8	3.7	0.9	2.0
Males	4.0	1.9	2.1	—	11.0	5.2	2.5	3.6
Total	3.3 (151)	1.3 (930)	2.1 (1,306)	— —	6.4 (328)	4.4 (1,853)	1.8 (1,731)	2.8 (6,299)

TABLE 2. Median distances (m) moved between years from the last breeding attempt (adults) or the natal nest (yearlings).

Year from	Adult females			Adult males			Yearling females			Yearling males		
	n	Median	Range	*n*	Median	Range	*n*	Median	Range	*n*	Median	Range
1980	4	187.0	90-931	2	90.0	30-150	2	634.5	543-726	3	603.0	570-666
1981	29	242.0	0-882	6	76.0	30-339	2	947.5	808-1,087	8	520.0	301-725
1982	34	213.0	0-1,634	29	85.0	0-684	13	750.0	218-1,728	13	450.0	120-1,572
1983	46	87.5	0-1,538		—			—			—	
1984	61	135.0	0-1,262	7	154.0	15-242	3	360.0	323-663	13	655.0	210-1,437
1985	49	124.0	0-1,129	71	60.0	0-384	25	603.0	150-1,440	40	740.0	120-1,707
1986	71	134.0	0-1,445	99	67.0	0-513	5	685.0	124-1,641	17	513.0	192-1,323
Total	294	134.0	0-1,634	214	67.0	0-684	50	674.0	124-1,728	94	607.5	120-1,707

of a pair returned the following year. Only 3 pairs remated.

Distances moved by adults.—Adult females moved significantly farther than adult males between their last breeding site of the previous year and their first breeding site after they returned (MRANK, $\chi^2 = 55.95$, df = 1, $P = 0.0001$) (Table 2, Fig. 2a). Most returning adult males (>90%) and females (>70%) bypassed fewer than 20% of the nest boxes available when they returned (Fig. 3a). Males bypassed significantly fewer unoccupied nest boxes than did females ($\chi^2 = 42.89$, df = 4, $P = 0.0001$). Wrens that switched study areas were excluded from these analyses.

Female reproductive success and return.—To measure breeding success we used (1) the outcome of the last breeding attempt of the previous season (i.e. successful, producing at least 1 chick that survived to leave the nest, or failed) (Table 3), (2) the number of chicks produced from the last breeding attempt of the preceding season (Table 4), (3) the total number of chicks produced during the previous breeding season (Table 4), and (4) whether or not an adult raised chicks that returned to breed on one of the study areas. Only birds from natural nests were included in the analyses for measures 2 and 3 (see Methods).

The outcome of the previous breeding attempt did not affect the likelihood that a female would return (LM, $\chi^2 = 1.40$, df = 1, $P = 0.24$) (Table 3), and there was no significant difference among years in returns (LM, $\chi^2 = 8.12$, df = 6, $P = 0.23$). There was no significant interaction effect between the variables previous outcome (successful/failed) and year on returns (LM, $\chi^2 = 4.11$, df = 6, $P = 0.66$).

There was an interaction between the class variables return (yes/no) and year when the number of chicks produced in the last nest of the previous year was analyzed ($F = 3.00$, df = 6,940, $P = 0.006$). Therefore, the simple effects of return within each year were analyzed (Table 4). Females that returned from the 1983 breeding season produced significantly more chicks at their last attempt than did nonreturning females ($t = 3.01$, df = 57, $P = 0.004$). Females that returned from 1985 produced significantly fewer chicks than did nonreturning females ($t = 2.23$, df = 207, $P = 0.03$). In all other year-by-year analyses, the probability exceeded 0.05.

Females that returned had produced significantly more chicks in the previous breeding

TABLE 3. Percentage returns and median distances moved (m) between years from previous nest of successful (produced at least 1 chick that survived to leave the nest) and unsuccessful adults.

	Percentage returns				Median distances moved					
	Successful		Unsuccessful		Successful			Unsuccessful		
Year from	*n*	%	*n*	%	*n*	Median	Range	*n*	Median	Range
Females										
1980	22	13.6	9	22.2	2	187.0	134–240	2	510.5	90–931
1981	111	21.6	39	12.8	24	244.5	0–600	5	242.0	90–882
1982	149	19.5	71	18.3	24	163.5	0–1,634	10	366.0	162–955
1983	190	22.1	58	12.1	40	87.5	0–1,538	6	117.5	0–1,368
1984	170	30.6	54	18.5	50	134.0	0–1,262	10	202.5	30–1,020
1985	177	21.5	51	21.6	37	90.0	0–633	11	170.0	85–1,129
1986	190	27.9	95	24.2	50	116.0	0–1,445	21	242.0	0–997
Total	1,009	23.9	377	18.8	227	134.0	0–1,634	65	215.0	0–1,368
Males										
1980	7	14.3	3	66.7		—		2	90.0	30–150
1981	25	16.0	2	100.0	4	109.5	67–339	2	48.5	30–67
1982	97	30.9	21	9.5	27	85.0	0–684	2	60.0	60
1984	20	30.0	14	14.3	5	62.0	15–242	2	178.0	154–202
1985	160	40.6	18	50.0	62	60.0	0–384	9	60.0	0–384
1986	179	45.3	40	47.5	81	60.0	0–513	18	102.0	30–192
Total	488	38.3	98	36.7	179	62.0	0–684	35	85.0	0–384

season (measure 3) ($\bar{x} = 6.7$) than had nonreturning females ($\bar{x} = 5.7$) ($F = 5.23$, df = 1, 1,141, $P = 0.022$) (Table 4). There was a significant difference among years ($F = 9.78$, df = 6, 1,141, $P = 0.0001$). Significantly more chicks were produced in 1985 than in all other years, and chick production in 1984 was significantly different from that in 1982 and 1986. There was no interaction effect between return and year on total chick production ($F = 0.65$, df = 6, 1,141, $P = 0.69$).

The likelihood that a female would return was independent of her having offspring that returned in any subsequent year. Thirty-five of 277 (12.6%) returning successful females and 102 of 884 (11.5%) nonreturning successful females had at least one of their offspring return to breed on the study areas ($\chi^2 = 0.24$, df = 1, $P = 0.62$).

Male reproductive success and return.—There was no significant difference in the proportions of males that returned and whether or not they previously had bred successfully (LM, $\chi^2 = 1.79$, df = 1, $P = 0.18$). There was no interaction effect between the variables previous success and year on the proportions of males that returned (LM, $\chi^2 = 10.82$, df = 5, $P = 0.055$). There was a significant difference in the returns of males among years (LM, $\chi^2 = 15.54$, df = 5, $P = 0.008$) (Table 3).

Returning and nonreturning males did not differ significantly in the number of chicks produced in their last nest of the previous year ($F = 0.48$, df = 1, 465, $P = 0.49$) (Table 4). There was no interaction effect between the variables return and year on the number of chicks produced ($F = 1.26$, df = 4, 465, $P = 0.29$). There was a difference among years ($F = 4.43$, df = 5, 465, $P = 0.0006$), with significantly more chicks produced per nest in 1985 than in 1984 and 1986.

There was no difference between returning and nonreturning males in the total number of chicks produced in the previous season ($F = 0.96$, df = 1, 495, $P = 0.33$) and no interaction effect between the variables return and year on total number of chicks produced ($F = 1.10$, df = 5, 495, $P = 0.36$) (Table 4). There was a significant difference among years in the total number of chicks produced ($F = 4.60$, df = 5, 495, $P = 0.0004$), with 1985 differing significantly from 1982, 1984, and 1986. These differences were caused, in part, by differences in the proportions of nests at which males were identified in those years (see Methods).

Male return was independent of the likelihood that any of his offspring returned to breed in any subsequent year. Twenty-five of 196 (12.8%) returning successful males and 43 of 318 (13.5%) nonreturning successful males had off-

TABLE 4. Number of chicks ($\bar{x}$ ± SE) produced by adults from natural nests, in relation to return. Sample sizes are in parentheses.

	No. chicks produced in last nest		No. chicks produced in season	
Year from	Returned	Did not return	Returned	Did not return
Females				
1980	2.5 ± 2.5 (2)	4.2 ± 0.9 (9)	6.0 ± 1.0 (2)	3.5 ± 0.9 (11)
1981	3.9 ±.0.7 (12)	3.8 ± 0.3 (68)	5.7 ± 0.9 (14)	5.6 ± 0.4 (83)
1982	4.6 ± 0.7 (12)	3.6 ± 0.3 (68)	5.7 ± 0.7 (26)	4.6 ± 0.4 (106)
1983	4.7 ± 0.3 (29)	3.5 ± 0.2 (124)	7.7 ± 0.7 (33)	5.6 ± 0.3 (143)
1984	4.7 ± 0.3 (56)	4.1 ± 0.2 (141)	7.1 ± 0.5 (63)	6.1 ± 0.3 (160)
1985	3.9 ± 0.3 (47)	4.7 ± 0.2 (162)	8.1 ± 0.6 (50)	7.6 ± 0.3 (179)
1986	3.5 ± 0.3 (62)	3.8 ± 0.2 (162)	5.4 ± 0.4 (76)	4.7 ± 0.2 (209)
Males				
1980	—	2.3 ± 1.4 (3)	0.0 (1)	4.7 ± 1.4 (3)
1981	4.3 ± 1.5 (4)	4.6 ± 0.4 (11)	3.4 ± 1.5 (5)	6.5 ± 0.6 (11)
1982	4.9 ± 0.5 (14)	3.9 ± 0.4 (37)	6.2 ± 0.7 (15)	5.0 ± 0.6 (40)
1984	3.9 ± 0.9 (8)	2.9 ± 0.6 (25)	5.8 ± 1.6 (8)	4.9 ± 0.9 (26)
1985	4.7 ± 0.3 (74)	5.2 ± 0.2 (102)	7.3 ± 0.5 (74)	7.2 ± 0.3 (105)
1986	4.1 ± 0.2 (91)	4.1 ± 0.2 (107)	6.2 ± 0.4 (100)	5.6 ± 0.3 (119)

spring return to breed ($\chi^2 = 0.06$, df = 1, $P = 0.80$).

Adult reproductive success and distance moved.—Females unsuccessful at their last nesting attempt of the previous season moved significantly farther than did successful females (MRANK, $\chi^2 = 10.63$, df = 1, $P = 0.001$) (Table 3). In contrast, there was no significant difference in the distances moved by successful and unsuccessful males (MRANK, $\chi^2 = 0.75$, df = 1, $P = 0.38$).

Distance moved and subsequent reproductive success.—Adults were categorized as birds that nested on the same or an adjacent territory and birds that moved 2 or more territories from the site of their last nest of the previous year (Table 5).

The distance moved by previously successful females was not related to the outcome (i.e. success or failure) of the next breeding attempt ($\chi^2 = 0.09$, df = 1, $P = 0.77$) (Table 5). Previously unsuccessful females, however, tended to be more successful if they moved 2 or more territories than if they stayed within 1 territory of their previous breeding site ($\chi^2 = 3.15$, df = 1, $P = 0.076$).

There was no significant difference in the number of chicks produced in the subsequent breeding attempt by females that moved only 1 territory compared with those that moved 2 or more territories ($F = 1.10$, df = 1, 209, $P = 0.30$) (Table 5). The outcome of the previous nesting attempt did not significantly affect the number of chicks produced in the subsequent attempt ($F = 0.34$, df = 1, 209, $P = 0.56$). There was no interaction effect between the variables distance category and previous outcome on the number of chicks produced in the subsequent attempt ($F = 0.73$, df = 1, 209, $P = 0.39$).

The reproductive success of males that moved 2 or more territories and those that stayed within 1 territory did not differ significantly, regardless of the outcome of their previous breeding attempt (previously successful: $\chi^2 = 0.01$, df = 1, $P = 0.92$; previously unsuccessful: $\chi^2 = 0.72$, df = 1, $P = 0.39$) (Table 5).

Distance moved and the outcome of the previous nest did not significantly affect the number of chicks produced in the subsequent breeding attempt by males (outcome: $F = 0.27$, df = 1, 156, $P = 0.60$; territory: $F = 1.61$, df = 1, 156, $P = 0.21$; interaction: $F = 0.14$, df = 1, 156, $P = 0.71$) (Table 5).

Return of chicks.—More male than female chicks returned to the study areas in 5 of 6 yr (Table 1). A significantly higher proportion of chicks (148 of 3,825, 3.9%) from early-season nests (those begun before the median egg-1 date of the year) returned than from late-season nests (those begun on or after the median egg-1 date) (28 of 2,474, 1.1%) ($\chi^2 = 41.45$, df = 1, $P = 0.0001$). The proportions of chicks that left early- or late-season nests and returned to breed were significantly lower than the proportions of adult females and males that returned, assuming a 1:1 sex ratio at nest departure (females: adult vs.

early-season chicks, $\chi^2 = 343.94$, df = 1, $P = 0.0001$; adult vs. late-season chicks, $\chi^2 = 294.21$, df = 1, $P = 0.0001$) (males: adult vs. early-season chicks, $\chi^2 = 453.06$, df = 1, $P = 0.0001$; adult vs. late-season chicks, $\chi^2 = 475.84$, df = 1, $P = 0.0001$).

Distances moved by yearlings.—The median distances moved by female and male yearlings from their natal nest boxes to their first breeding nest boxes were not significantly different (MRANK, $\chi^2 = 2.97$, df = 1, $P = 0.09$) (Fig. 2b, Table 2). The median distance moved by early-season yearlings (661 m) was greater than that by late-season yearlings (493.5 m) (M-W test, $\chi^2 = 6.58$, df = 1, $P = 0.01$). Yearlings settled farther from their natal nest boxes (median = 644 m) than returning adults did from their last breeding site of the previous year (median = 98 m), when controlling for year, season, and sex (MRANK, $\chi^2 = 134.08$, df = 1, $P = 0.0001$). Male and female yearlings did not differ in the proportion of unoccupied nest boxes that they bypassed ($\chi^2 = 4.40$, df = 4, $P = 0.35$) (Fig. 3b). Yearlings bypassed significantly more unoccupied nest boxes than did adults (males: $\chi^2 = 208.51$, df = 4, $P = 0.0001$; females: $\chi^2 = 70.39$, df = 4, $P = 0.0001$).

Date of first nesting attempt.—Age and gender of wrens may affect their time of return to the breeding ground, which may in turn influence their dispersal patterns. To evaluate this we compared the egg-1 dates in the first nest of the early season by adult females and males (i.e. at least 2 yr old), yearling females and males, and females and males of unknown age (i.e. 1 or more years old). To adjust for annual variation in the start of the breeding season, the egg-1 date of each clutch was expressed as the number of days that had elapsed from the laying of the first egg in that year. There was a significant difference in the median date that wrens in the six age and gender categories began their first nesting attempt of the early season (K-W test, $\chi^2 = 72.72$, df = 5, $P = 0.0001$). In follow-up tests (Dunn's method, Zar 1984), adult females (median = 11 days) and adult males (median = 11 days) did not differ significantly from each other. Both adult females and males began their clutches significantly earlier than did wrens in the other four categories. There were no significant differences among yearling males (median = 15 days), unknown-age females (median = 14 days), and unknown-age males (median = 14 days). Yearling females (median = 18.5 days)

TABLE 5. Percentage successful nesting attempts (at least 1 chick survived to leave the nest) and mean number (±SE) of chicks produced at the subsequent nesting attempt, as a function of past reproductive success and the number of territories moved. Sample sizes are in parentheses.

	Successful previous year				Unsuccessful previous year			
	0-1 territory		2+ territories		0-1 territory		2+ territories	
Females	83.6%	5.1 ± 0.2 (105)	85.1%	5.9 ± 0.2 (63)	57.1%	5.2 ± 0.8 (14)	78.6%	5.3 ± 0.4 (31)
Males	77.8%	5.1 ± 0.2 (118)	76.9%	6.0 ± 0.3 (16)	85.2%	5.0 ± 0.4 (20)	71.4%	5.5 ± 1.3 (6)

began their clutches significantly later than did unknown and adult female and male wrens.

DISCUSSION

Breeding dispersal.—Female House Wrens, like many other migratory passerines (Greenwood 1980), were less likely to return to their previous breeding area than were males. An average of 23.3% of the females and at least 38.1% of the males returned to the study tract each year. Similar results were obtained by Baldwin and Bowen (1928), who reported that 13.7% (11 of 88) of the female and 16.9% (11 of 65) of the male House Wrens returned to an Ohio study area in 1927. Kendeigh (1971) described a population crash of House Wrens in Ohio in 1926 and a recovery in 1927, which may be responsible for the lower returns in 1927 compared with those we obtained in Illinois. Caution must be exercised, however, when comparing returns from different studies because results are dependent on the size and arrangement of the study areas (Barrowclough 1978).

There were five possible fates for wrens not found on the study area subsequent to the year they were banded: (1) they died, (2) they settled elsewhere, (3) they returned to the study area but did not breed, (4) they returned but bred undetected in our nest boxes, or (5) they returned but nested in natural cavities. Some males returned to the study area but were not identified as breeders (fates 3 and 4). We netted one previously banded male that was never identified as a breeder that year, and a few males established territories but failed to attract mates. Few males were likely to have been overlooked because they nested in natural cavities. An intensive census of two tracts on the study area in 1987 revealed 6 nests in natural cavities (approximately 5% of the nests on those tracts), and the males were identified at 5 of these (Harshman and Thompson MS). Three of the 5 males were also associated with a nest in a box at some other time of the season. The possibility that a substantial proportion of the missing males settled elsewhere is also unlikely, because only 2.5% of the males switched study areas to breed (Fig. 2). The study tracts encompassed much of the available breeding habitat in the area, and males that returned to the study area moved very short distances between breeding attempts. A majority of the missing males was probably dead. In 1986 and 1987 males were identified at over 75% of the nests, and 43% of the males returned from the previous years (i.e. 1985 and 1986). This may approach, but probably underestimates, annual survival. The 43% minimum estimate of survival for male House Wrens is lower than that estimated for other small, migratory passerines at this latitude. For example, Nolan (1978: 469) estimated annual survival at 65% for adult Prairie Warblers (*Dendroica discolor*). Thus, many, but not all, of the missing males were dead, and a few were probably nonbreeders or bred undetected on the study area.

In contrast to males, only 23% of adult females returned to the study areas. It is unlikely that annual mortality approached 80%, especially as the return rate increased to more than 30% each year after a female had returned twice to the study areas. Natural cavities were used for about 5% of all the nests on the study area, so a small proportion of the unaccounted females probably nested in natural cavities. We identified the female at 3 of the 6 nests found in natural cavities in 1987, and 1 of these females also bred in a nest box (pers. obs.). We have no information on nonbreeding females, if any occur. Most of the missing females that had not died probably settled off the study areas, given their willingness to settle far from their former nest sites (Fig. 2).

Greenwood (1980, 1984) proposed that males are more site faithful than females because most birds have a resource-based mating system. Males typically defend a fixed resource, such as a territory or a nest site (von Haartman 1957), which is used to attract a mate. Presumably it is more advantageous and easier for a male to reestablish his territory of the previous year than to obtain a new territory, so males are site faithful. In contrast, females do not defend a fixed resource and have the flexibility to move and find the best mate or nest site, or both. Therefore, they are less site faithful.

Our results are consistent with Greenwood's hypothesis, but they are also consistent with other hypotheses. For example, gender-related differences in the availability of new nest sites may be responsible for differences in dispersal distances if adults return to near the site of their last breeding attempt. Males may move until they find suitable nest sites, often near their previous breeding sites. Females also may move until they find suitable nest sites, but if there are no suitable males at the sites, females must move farther to find both suitable nest sites and suitable mates. In this case, females should, on average, disperse farther than males, as predicted by Greenwood's hypothesis.

Breeding dispersal may be influenced either indirectly or directly by previous reproductive success. Nolan (1978: 461) suggested that females return to the area where they spent the postbreeding period, an indirect influence. Unsuccessful females leave the area of the nest site after a nest failure, whereas successful birds stay because they are feeding fledglings. Thus, differences in the proportion that return could be the result of differences in where the birds spent the postbreeding period, which in turn is affected by reproductive success. Reproductive success may also influence breeding dispersal directly. Successful birds should be more likely than unsuccessful birds to return if previous success is a good predictor of future success.

Contrary to several studies (e.g. von Haartman 1949, Delius 1965, Darley et al. 1971, Nolan 1978, Freer 1979, Harvey et al. 1979, Shields 1984, Gavin and Bollinger 1988), we found no association between success or failure at the last breeding attempt of the previous year (measure 1) and the likelihood that a female House Wren would return. Assuming that reproductive success and female survival the subsequent winter are independent, this lack of a difference may be attributable to the size and isolation of the study areas, where an unsuccessful female that returned would find a better site within the borders. This seems to be the case, because many unsuccessful females returned to breed on the study area, but moved farther than successful females. There were benefits for unsuccessful female House Wrens that moved. Unsuccessful females that moved were more likely to produce chicks in their subsequent attempt than were unsuccessful females that returned either to their former or adjacent territories. Females that returned had produced more chicks the previous season, however, than had females that did not return (measure 3). This could have resulted from a positive correlation between female survival and number of chicks raised in a season. More likely, low total chick production may have provided adequate information to make a decision to abandon entirely the study area. In contrast, failure of the last breeding attempt (measure 1) may warrant only a short move within the study area.

Because dispersing males must find and establish a territory in a new locale, they face costs that females escape. By moving, males risk not finding a suitable site, or of finding one from which they are expelled when the former owner returns (Nolan 1978, Lanyon and Thompson 1986). Thus, males should be less likely than females to move, regardless of their previous reproductive success. Indeed, there was no relationship between dispersal and previous reproductive success in male House Wrens.

Natal dispersal.—Low return to the natal site is almost universal among passerines (Gauthreaux 1982), and House Wrens are no exception. The return of chicks as breeders in this study (2.8%) was similar to an Ohio population (2.6%) (Kendeigh 1941).

A combination of high mortality and low philopatry is responsible for the low return to the natal area. One explanation for low fidelity to the natal site is that it prevents or reduces inbreeding (Bulmer 1973, Greenwood et al. 1978, Greenwood 1984). If so, one sex should disperse farther than the other to avoid mating with siblings, and yearlings should disperse differently from adults to avoid mating with their parents. We found that natal dispersal was significantly greater than breeding dispersal, and this may be explained by inbreeding avoidance. The median distances moved by male and female yearlings were similar, however. If inbreeding avoidance were an important consideration, gender-based differential dispersal of yearlings surely would also occur within the study area. Despite the potential for brother-sister breeding pairs, apparently none occurred in our study, nor were there instances of other close-kin matings. The likelihood of sibling matings was reduced by the lower return of female than of male yearlings. Assuming this difference was not attributable to lower survival of yearling females than of yearling males and that there was an equal sex ratio at nest departure, a larger proportion of surviving yearling females than males must have settled elsewhere. We conclude that our results are inconsistent with the hypothesis that all dispersal patterns are a result of inbreeding avoidance.

Murray (1967), Moore and Ali (1984), Liberg and von Schantz (1985), and Waser (1985) proposed an intrasexual-competition hypothesis to explain age-related differences in dispersal. Natal dispersal would exceed breeding dispersal if yearlings were subordinate to adults and were forced to move until they found a nest site not occupied by a dominant older bird. To examine this hypothesis, we excluded all occupied nest boxes from the analysis (Fig. 3). If the model is correct and yearlings begin their search for a suitable site from near their natal nest boxes, yearlings might be expected to pass over nest boxes in unsuitable habitat, but they should not consistently bypass large numbers of unoccupied nest boxes. Yet, most yearlings avoided a large proportion of the available nest boxes (median = 74.3%) before they settled. This indicates that yearlings moved much farther than the first unoccupied site, which is not consistent with the competition hypothesis. Alternatively, yearlings may pick the first acceptable, unoccupied site without regard to the location of their natal site.

One overlooked aspect of natal dispersal is that in migratory species, yearlings typically return to the breeding grounds later than adults (e.g. Kendeigh 1941, Nolan 1978, Lanyon and Thompson 1986). We found that adult House Wrens began laying eggs before yearlings, suggesting that adults returned before yearlings. Although the date of clutch initiation is not a good indication of arrival time in some species (Stutchbury and Robertson 1987), we found that the date of clutch initiation of wrens on the study area agreed with Kendeigh's (1941) direct observation that yearling House Wrens arrived later than adults on the breeding ground. As a consequence of later arrival, many yearlings must move farther than adults, which have returned to the vicinity of their previous breeding sites. Thus, differences between natal and breeding dispersal may be a consequence of age-specific differences in timing of migration, which in turn are under the control of other factors (Ketterson and Nolan 1983).

Fledglings from early-season nests were more likely to return than were those from late-season nests. Possible explanations for this are that a greater proportion of fledglings from early-season nests survived than from late-season nests or that late-season yearlings were more likely to breed off the study area than were early-season yearlings, or both. The first explanation is the most plausible. Late-season fledglings left the nest from early August to mid-September. This provided, at most, 2 months to achieve independence, molt, and accumulate reserves for migration in early October. In contrast, early-season fledglings had up to 4 months for these tasks. Thus, older juveniles may have survived better during migration and winter than younger juveniles given that all juveniles had to migrate at about the same time. Our results were contrary to the second explanation. Tetzlaff (pers. comm.) found a positive correlation between juvenile age and recapture distance from the natal nest box during the first summer. Similarly, early-season yearlings dispersed farther from their natal nest boxes to the sites of their first breeding attempts than did late-season yearlings. Based on these results, we would expect fewer, not more, yearlings from early-season nests to return. Thus, differences in survival rather than in dispersal probably accounted for the greater return of early-season than late-season yearlings.

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