FACTORS AFFECTING NEST AND SITE FIDELITY IN ADIRONDACK BARN SWALLOWS (*HIRUNDO RUSTICA*)

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ABSTRACT.—During 1979–1983, I documented the natal and breeding dispersal of the Barn Swallow (*Hirundo rustica*) in the Cranberry Lake, New York, region of the Adirondacks by following the lifetime movements and breeding histories of individually marked birds. During the study, 847 birds were marked, and the movements of most were followed during the season they were marked. About 40% of the adults and 2% of the nestlings and juveniles were resighted or recaptured in two or more years. All recovered nestlings had dispersed from their natal colonies (median distance = 6.37 km). Most breeding adults remained faithful to previously used colonies, as well as to clusters within colonies, nests, and mates, when the latter were alive and available. Some individuals, however, did disperse. More females than males dispersed and usually moved farther both within and between breeding seasons. Males and, especially, females that had nested unsuccessfully with a particular mate in a particular location had a higher probability of deserting and dispersing than did successful breeders, both within and between breeding seasons. Old nests were reused at high frequencies for consecutive breeding attempts across breeding seasons. After successful first nests, breeders tended to move to secondary nests within 25 m of their first nests. *Received 8 December 1983, accepted 28 March 1984.*

POPULATION structure is considered to be a major influence on evolution and social behavior. Dispersal and demography are the prime determinants of population structure. They have important influences on mating systems (for review, see Murray 1984), on local patterns of relatedness and, hence, on the degree of cooperation and competition characterizing different kinds of social interactions (e.g. Hamilton 1964; Sherman 1980, 1981; Hoogland 1981, 1983), on whether particular cases of apparent altruism are more likely to be the result of individual selection, kin selection, reciprocity, or group selection (e.g. Zahavi 1974, Brown 1978, Emlen 1978, Woolfenden and Fitzpatrick 1978, Ligon and Ligon 1978, Wilson 1980), and on any group's tempo and mode of evolution (for reviews, see Wright 1978, Shields 1982).

Dispersal has been studied extensively in birds and many other taxa (for reviews, see Baker 1978, Greenwood 1980, Shields 1982). Among swallows, dispersal has been investigated in the Common House-Martin (*Delichon urbica*; see Rheinwald 1975, Bryant 1979), Purple Martin (*Progne subis*; Allen and Nice 1952), Tree Swallow (*Tachycineta bicolor*; Chapman 1955), Bank Swallow (*Riparia riparia*; Stoner 1936, Mead 1979, Freer 1979), Cliff Swallow (*Hirundo pyrrhonota*; Mayhew 1958), and Barn Swallow (*Hirundo rustica*; Davis and Davis 1936, Mason 1953, and in some European populations cited in Farner 1945). The general swallow pattern is that most adults manifest varying but low levels of breeding dispersal (defined as the distance moved between consecutive breeding sites). First-time breeders manifest greater but still varying degrees of natal dispersal (defined as distance between hatching and first breeding site). (For more detailed dispersal definitions and rationales, see Greenwood et al. 1979a, Shields 1983.)

As Freer (1979) noted, although reports about the degree of adult site tenacity and juvenile philopatry (i.e. the proportion of birds remaining in a previously used "area" and the actual distribution of dispersal distances) abound, there are few studies concerning the potential causes of the observed patterns in swallows. Studies of other bird groups indicate that age (e.g. Austin 1949), sex (e.g. Greenwood 1980, 1983), local habitat or nest-site stability (e.g. McNicholl 1975, Freer 1979), and prior breeding experience at a particular site or with a particular individual (e.g. Darley et al. 1977, Nolan 1978, Freer 1979, Coulson and Thomas, 1983, Dow and Fredga 1983, and, for review, see

Rowley 1983) could affect the degree and magnitude of dispersal.

Since 1979, my field associates and I have been studying the behavior and ecology of individually marked populations of the Barn Swallow. Because previous studies on this species (e.g. Davis and Davis 1936 and Mason 1953 versus the studies cited in Farner 1945) reported wide variation in dispersal patterns among their populations, we wished to document dispersal in our area in order to characterize sufficiently its local population structure as a basis for other ecological and behavioral studies (e.g. Shields 1984, Crook and Shields in press). In addition, we planned to explore the effects of sex, age, status, prior experience, and local environmental conditions on dispersal and mate and site fidelity in our population in order to test some of the generalizations about the proximate control of avian site fidelity (e.g. Baker 1978, Freer 1979, Greenwood 1980).

Study Area and Methods

We studied the Barn Swallow in the vicinity of the Cranberry Lake Biological Station of the State University of New York, College of Environmental Science and Forestry. The station and other study sites are located on and around Cranberry Lake, the third largest lake within the Adirondack State Park. The lake is large (>30 km^2 of surface area and >80 km of shoreline), relatively undeveloped (>80% of the shoreline is undeveloped), and surrounded by typical second-growth northern hardwood forest and associated habitat. Historically, Barn Swallows nested in and on cliffs and caves (Bent 1942) and may still be found in such natural sites (Speich pers. comm.). Today, the species typically nests on human artifacts like bridges and buildings (Bent 1942). Our region is analogous to an archipelago of suitable habitat islands surrounded by large expanses of unsuitable forest, not unlike the traditional distribution of suitable nest sites. Cranberry Lake and its inhabited environs are isolated from other inhabited areas (e.g. Star Lake 20 km to the west, Massawepie 17 km to the northeast, and Sabattis 12 km to the southeast) by even larger tracts of forest, designated as wilderness. Many, but not all, of the suitable inhabitated areas harbor swallow colonies.

As in previous studies (e.g. Bent 1942, Snapp 1976), our studies indicated that the "colonies" varied in size from a single nest to as many as 25 nests on or in single structures, usually boathouses or boatslips. These colony sizes are probably similar to those found in traditional sites and are the same as those found in such sites today (nest densities ranging from 1 to 15; Speich pers. comm.). We have no way of knowing how much this recent change in breeding dispersion affects the behavior we observe. By direct count and estimation, Cranberry Lake itself hosts 300–500 breeding pairs from year to year. We have concentrated on four major and many smaller colonies over the years. In the main study area at the biological station (hereafter CLBS), there were 17 pairs in 1979, 18 in 1980, 11 in 1981, 10 in 1982, and 15 in 1983, scattered around the campus. The secondary area at the biological station marina (hereafter Bay City or BC) hosted 20 pairs in 1980, 16 in 1981, 22 in 1982, and 16 in 1983, all under the roof of a single boat slip. We also worked in other large and small colonies around the lake.

We defined as colonies any group of nesting swallows that was likely to interact socially, especially at common grounds (e.g. sunning areas, mud puddles during nest building, common foraging grounds), more than occasionally during the breeding season. During incubation and nestling stages, we never observed breeders visiting other colonies. Within the spatially larger colonies, nests were significantly clumped (for CLBS the coefficient of dispersion for nests = 2.09; $\chi^2 = 125.7$, $P < 0.001$; Pielou 1969, see also Ball 1983). From data indicating that mobbing groups were recruited from nests within 25 m of a focal nest (Shields 1984), we defined as a cluster all nests within a circle 25 m in diameter around each focal nest. Birds within clusters interacted on a daily basis rather than occasionally. As defined, a nest could belong to more than one cluster, and clusters ranged in size from single isolated nests to as many as 25 nests on or in single buildings. From these definitions, we identified CLBS as a multicluster colony, whereas the BC colony consisted of a single cluster in every year.

Through 1983, we banded 264 adult, 130 juvenile, and 453 nestling swallows. Since 1980, this has included all unmated birds and all but one breeder at CLBS, and about 50% of the Bay City breeders (about 10% in 1980–1981, 85% in 1982, and 100% in 1983). We banded all CLBS and BC nestlings, a sample of nestlings from other colonies around the lake, and many free-flying juveniles (known to have hatched elsewhere, but captured in our colonies in July and August). All adults, since 1980, were given unique combinations of permanent plastic color bands and temporary tail colors, in addition to U.S. Fish and Wildlife service aluminum bands, in every year. The birds' white tail spots were painted with Testors airplane dope, one color on each side, after capture or recapture each year. The paint faded over the breeding season but could still be read 3–4 months after application. Nestlings were given single color bands indicative of hatching year and clutch membership (CLBS nestlings only), membership in other colonies (other nestlings), or "foreigner" status (origin unknown, including all juveniles). We captured most birds with mist nets at common grounds and flyways,

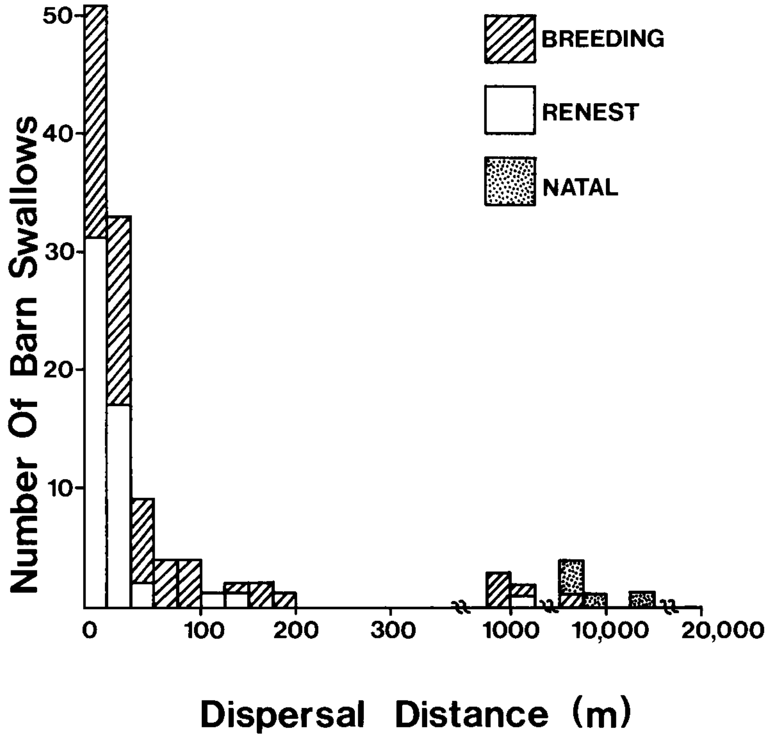

Fig. 1. Distribution of Barn Swallow natal, breeding, and renest dispersal distances in meters, 1979-1983. In our study area, individuals moving more than 300 m changed colonies, more than 25 m changed clusters, and more than 0 m changed nests.

and there was no evidence that our operations induced any birds to desert the study area.

Birds were sexed by tail lengths (Samuel 1971a) or, after marking, by behavior (e.g. only males sing complete songs; females do the majority of incubating; Bent 1942, Ball 1983). Unmarked adults occasionally could be classed as yearlings or older by skulling. When skulling was equivocal, they were classed as yearlings. Throughout the study, complete life histories were taken of as many nests as our resources allowed (all nests at CLBS in 1980-1983 and at BC in 1982-1983). Data included the identity of breeders, the location of the nest with respect to colony and cluster within colony, the fate of the nest, the causes of nest failure, and whether it was a first attempt in a season or a renest.

Dispersal data were obtained as a result of recapture or resighting of breeding birds that had been identified as individuals or as members of specific clutches, clusters, or colonies during previous years. Dispersal distances were measured between natal nests and the first known breeding site of a bird (natal dispersal) or between consecutive nests, clusters, and colonies of experienced adults both within (renest dispersal) and between seasons (breeding dispersal). Distances were measured with a 30-m tape within colonies and estimated from U.S.G.S. topographic maps between colonies. From 1980 through 1983, 111 nests attempts including 74 known first nests and 37 known renests (including those following successful and failed first nests) provided the dispersal data base. Because we could not document every variable for every attempt, all analyses report on some subset of this total.

RESULTS

Natal dispersal.—Of the 331 nestlings banded through 1982 that could have returned to breed through 1983, we have recaptured or resighted 7 (2%), but only 5 of these were documented to be breeding. The other two (both males) were recaptured at CLBS in May but disappeared before nest building had begun. None of our nestlings bred in their natal colonies (Fig. 1). Owing to the wide spacing of colonies, their median dispersal was 6,375 m, with one unsexed bird being recovered dead during the breeding season by a camper about 15,000 m

TABLE 1. Returns of adult Barn Swallows across breeding seasons, 1979-1983.

Year	Newly banded	Prior returns	Total marked	Total returns[a]	Percentage returns
1979	24	—	24	10	42.0
1980	48	10	58	22	38.0
1981	31	22	53	21	39.6
1982	60	21	81	37	45.6
Total	—	—	216	90	41.6

[a] Returns are from the year after marking, i.e. 1980 returns are counted in 1981 and include birds marked before or during 1980.

from its hatching site. Three of the four known-sex returns were males, and of the sexed birds, the lone female dispersed the farthest (8,125 m, Fig. 1).

Breeding dispersal.—About 40% of the marked adults breeding in our colonies in any year returned to breed in the study area in the next year (Table 1). Given the 50-70% annual adult mortality expected of migratory passerines (e.g. Lack 1954) and the Barn Swallow (e.g. Lack 1949, Mason 1953), this is consistent with strong adult site tenacity. Only 7% of the adults were ever documented changing colonies between breeding seasons: 36% of the colony-faithful reused the same nest, and an additional 29% remained in the same cluster, usually on the same building, for their first attempts in consecutive breeding seasons. Three of the four colony switches between seasons were due to females and two of these were due to a single female that bred at CLBS in 1980 and 1981, then switched to an island colony 600 m away in 1982, only to return to CLBS in 1983.

We gathered dispersal data on 1-, 2-, 3-, and 4-year-old breeders. Fidelity to mate, nest, cluster, and colony was not influenced significantly by adult age either across or within (e.g. renest fidelity, see below) breeding seasons (Table 2). Across breeding seasons, fidelity to mate, nest, cluster, and colony and the distance dispersers moved were influenced significantly by sex and prior breeding experience. More males (48%) than females (24%) manifested nest fidelity (i.e. reused the same nest in consecutive breeding seasons), although the sexual difference was only marginally significant ($\chi^2 = 3.12$, 1 df, $P = 0.077$). When the sexes were pooled, previous experience (i.e. whether or not the individual successfully reproduced with that mate, at that nest, in that cluster and colony in the previous season) had no effect on nest fidelity (37% of the successful and 33% of the failures stayed, $\chi^2 = 0.06$, 1 df, $P = 0.80$, Table 3). Failure, however, was associated with a significant reduction in mate fidelity (42% of the successful pairs, but none of the failures main-

TABLE 2. Probability of nest, cluster, and colony fidelity[a] within and between breeding seasons as a function of age and sex in the Barn Swallow.[b]

Sex and type of fidelity	Age in years[c]			
	1	2	3	4
Male				
Nest	0.69 (13)	0.42 (24)	0.53 (18)	0.75 (8)
Cluster	1.00 (13)	0.75 (24)	0.67 (18)	1.00 (8)
Colony	1.00 (13)	0.96 (24)	1.00 (18)	1.00 (8)
Female				
Nest	0.56 (16)	0.32 (22)	0.22 (9)	0.33 (6)
Cluster	0.88 (16)	0.64 (22)	0.44 (9)	0.67 (6)
Colony	0.94 (16)	0.91 (22)	0.89 (9)	0.83 (6)

[a] The proportion of birds that returned to colony or to a cluster within a colony or reused a nest they had used in previous seasons.

[b] The differences between nest, cluster, and colony fidelity within seasons were significant ($\chi^2 = 34.0$, 2 df, $P < 0.001$); the age differences in fidelity were not.

[c] Breeding data reflect the proportion of individuals that are faithful between first and second (2), or second and third (3), etc., breeding seasons. The renest data reflect the proportion of individuals that remained faithful to nests, etc., during their first (1), second (2), etc., breeding season. Breeding and renest data were pooled for older birds, but only renest data were available for 1 yr olds.

TABLE 3. Probability of mate, nest, cluster, and colony fidelity between seasons and the breeding dispersal distance [mean ± SE (n)] in meters as a function of sex and previous breeding experience in the Barn Swallow.

Sex	Prior success	Fidelity[a]				Dispersal distance (m)
		Mate (n)	Nest (n)	Cluster (n)	Colony (n)	
Male	Success	0.41 (17)	0.58 (19)	0.74 (19)	1.00 (19)	25 ± 8.4 (19)
	Failed	0.00 (9)	0.67 (9)	0.67 (9)	0.89 (9)	820 ± 798.2 (9)
Female	Success	0.41 (17)	0.35 (17)	0.53 (17)	0.94 (17)	95 ± 55.1 (17)
	Failed	0.00 (8)	0.00 (8)	0.38 (8)	0.63 (8)	1,155 ± 777.5 (8)

[a] The proportion of birds that returned to same mate, to reused nest, or to their previously used cluster or colony across seasons.

tained their bonds, $\chi^2 = 6.48$, 1 df, $P = 0.01$; for more on divorce, see Crook and Shields in press). The latter effect probably was due to females tending significantly to change nests and mates after a failure [100% of the female failures changed nests and mates, whereas successful females only changed nests 65% ($\chi^2 = 3.71$, 1 df, $P = 0.053$), and mates 57% of the time ($\chi^2 = 4.94$, 1 df, $P = 0.03$); Table 3]. In contrast, 39% of the successful and only 29% of the unsuccessful males changed nests ($\chi^2 = 2.13$, 1 df, $P = 0.14$), although the trend in mate fidelity was necessarily the same for both sexes (Table 3).

Cluster and colony fidelity were similar to nest fidelity, but, as the distance scale increased, there was a greater tendency for birds to remain faithful to previously used sites (44% nest, 60% cluster,and 93% colony fidelity, $\chi^2 = 28.7$, 2 df, $P < 0.001$). The few birds that changed colonies had failed to raise young during the previous breeding season (Table 3). In sum, successful breeders of both sexes tended to return to their previous colonies, clusters within colonies, nests, and even mates, if the latter were still available. Unsuccessful birds of both sexes, and females in general, tended to disperse more frequently and moved the farthest when dispersing (Table 3).

Renest dispersal.—Barn Swallows were more sedentary and more faithful to mates for the purpose of renesting than they were across breeding seasons (nest fidelity: 53% reused nests within vs. 44% across seasons, $\chi^2 = 0.93$, 1 df, $P = 0.33$; cluster: 88% vs. 60% fidelity, $\chi^2 = 11.1$, 1 df, $P < 0.001$; colony: 98% vs. 93% fidelity, $\chi^2 = 2.91$, 1 df, $P = 0.087$; and mate: 78% vs. 27% fidelity, $\chi^2 = 27.4$, 1 df, $P < 0.001$). Those that did disperse tended to move shorter distances before renesting (compare Tables 3 and 4). The percentage of nests reused did not differ within and between seasons, but the statistical equality resulted from a reversal of the effects of prior experience at the two stages of the breeding cycle. Within seasons, successful nesters were more likely to change nests (22% vs. 68% fidelity for unsuccessful birds, $\chi^2 = 10.22$, 1 df, $P < 0.001$, Table 4), whereas the reverse was true between seasons (47% of successful vs. 33% of failures reused previous year's nests, Table 3). The difference between the stages was significant ($\chi^2 = 5.07$, 1 df, $P = 0.024$) and appeared to be due to a decreased probability that unsuccessful females would change nests and an increased probability that successful breeders of both sexes would change nests before attempting a second brood (Tables 3 and 4). Finally, both sex and prior experience appeared to affect mate and site fidelity during renesting. Unsuccessful birds, and particularly females, had a higher probability of changing mates, clusters, and colonies, although the differences were not as great as between seasons and only one approached statistical significance (27% of unsuccessful and 7% of the successful divorced, $\chi^2 = 2.77$, 1 df, $P = 0.09$, Table 4).

Case histories.—The quantitative analysis presented above provides information on how the "average" swallow is likely to behave. Consideration of the finer behavioral details and the lifetime movements of individual birds would provide more information and perhaps necessitate different conclusions. To conserve space, I will briefly discuss representative histories of individual birds and nests. I hope that they will illustrate how the general pattern has been derived from the behavior of those individuals.

Because the tables include only recovered birds, they provide no data on disappearances.

TABLE 4. Probability of mate, nest, cluster, and colony fidelity within seasons and the renesting dispersal distance [mean ± SE (n)] in meters as a function of sex and previous breeding experience in the Barn Swallow.

Sex	Prior success	Fidelity[a]				Dispersal distance (m)
		Mate (n)	Nest (n)	Cluster (n)	Colony (n)	
Male	Success	0.88 (8)	0.22 (9)	0.89 (9)	1.00 (9)	7.7 ± 6.2 (7)
	Failed	0.79 (19)	0.74 (19)	0.95 (19)	1.00 (19)	8.8 ± 8.3 (19)
Female	Success	0.88 (8)	0.22 (9)	0.89 (9)	1.0 (9)	7.8 ± 5.4 (8)
	Failed	0.67 (21)	0.62 (21)	0.81 (21)	0.95 (21)	105 ± 86.2 (21)

[a] Proportion of birds that remained with same mate, reused nest, or remained in their previously used cluster or colony for renest.

More individuals (2 males and 6 females) disappeared during the breeding season after an unsuccessful first nest than after successful nests (1 male and 2 females). Although the sample is too small for rigorous statistical analysis, it appears to be likely that some of the within-season disappearances (and by implication some between-season as well) were colony desertions rather than deaths. This implies that, although site fidelity may be strong, it is less perfect than the documented returns alone imply.

Histories of individual birds indicated that they were not "innate" or continuous wanderers and that after changing colonies they would settle permanently after nesting successfully (2 cases) or return to a previously used area if they had failed in a new colony (1 case). It appears that swallows in our population were sedentary unless poor or changing conditions "forced" them to move. This was supported by the fact that all of the colony shifts ($n = 6$) and most of the cluster shifts (80%, $n = 20$) we observed were associated with previous nest failures or the disappearance or death of previous mates with whom the dispersers had bred successfully.

Individual nest histories suggested that favored nests might be used in every year, even if owner identities changed from year to year (2 nests used for 4 yr, 4 nests for 3 yr, and 6 for 2 yr). In addition, some individuals appear to have nest traditions (5 birds), with favored nests for first attempts in a season and different favored nests for renest attempts. We also have documented individuals using a nest in one year, using a different one the next, only to return to the original in the third year (4 cases).

Over time, individuals appear to develop personal preferences for favored nest sites. When two individuals with different nesting histories begin courting (e.g. because both of their previous mates have died or disappeared), there is at least the possibility of a conflict over where to nest. We have observed possible nest-site conflicts in four pairs. In those pairs, males attempted to defend two nest sites, the one that their female "preferred" (as evidence by her nest-building activities) and a nest that the male had used previously. In every case the pair ended up nesting at the site chosen (and in 3 of the 4 cases, previously used) by the female.

DISCUSSION

Natal dispersal.—In the Adirondacks, as in other North American populations (e.g. Mason 1953, Ball 1983), juvenile Barn Swallows usually disperse from their natal colonies before breeding for the first time. Large expanses of unsuitable habitat and long distances do separate suitable colony sites in our region. Like Mason's (1953), however, our data are consistent with the generalization that juvenile female passerines are more likely to disperse and move farther than males (Greenwood 1980). Whether the sexual bias functions to avoid too intense inbreeding (Greenwood 1980) or results from differences in intrasexual competition for mating resources (Greenwood 1980, Moore and Ali 1984) remains problematic. Until more natal returns are available, answers to such questions would be speculative.

Unless juveniles from the same nests or colonies disperse and immigrate into breeding colonies together (for which there is no evidence), it is likely that the breeding adults within a colony in our population are not particularly close kin. This implies that, unlike many colonial or even territorial bird species, in which close kin are probably social interactants [e.g. some cooperative breeders, Emlen 1978; the Great Tit (*Parus major*), Greenwood et al. 1979b], the primary forms of social interaction among breeding Barn Swallows should tend to be more selfish, competitive, or even disruptive than cooperative or altruistic (Greenwood et al. 1979b, Gadgil et al. 1983).

Breeding dispersal.—Once a Barn Swallow has bred, it tends to return to the same colony, cluster within a colony, building, nest (or set of nests), and even mate for as long as it lives (Tables 3 and 4). This fidelity may be favored by a number of environmental factors (reviewed in Baker 1978, Shields 1982). Returning to the same colony assures that a bird will be familiar with local resource distribution, including foraging areas and predator refuges, and so need not waste time in exploration early in every breeding season. For example, our swallows often forage at sheltered beaver ponds during cool windy weather. These ponds are surrounded by forest and occur at varying distances from the breeding areas (1-6 km). It probably saves time and energy to learn the location of such alternative foraging sites once in a lifetime rather than to learn it anew every year, and the savings are likely to benefit both sexes.

A second resource affected by familiarity is potential mates. When both members of a previously mated pair of Barn Swallows return to the same colony, they can and often do remate (Tables 3 and 4; Crook and Shields in press). Colony fidelity is likely to facilitate mate fidelity, and the latter might generate additional savings in time and energy. An experienced pair may have to court less and should be more compatible than experienced but newly paired birds (older birds whose previous mates have died or disappeared) or, especially, than newly paired yearlings. Such familiarity could, as it has in other monogamous species, result in increased reproductive success (for reviews, see Rowley 1983, Coulson and Thomas 1983).

Male fidelity.—Because the primary benefits of colony and mate fidelity would accrue regardless of whether a bird used the same nest or returned to the same cluster, the less intense, but still significant, fidelity observed at these levels (Table 3) requires additional explanation. Such precise tradition is significantly stronger in males than in females. This sex bias could result from more intense intramale competition for a place in the breeding population. Once females have begun breeding, they appear to have a higher mortality than males (Mason 1953, Shields unpubl. data). The result is a male-biased sex ratio among breeding birds (Emlen and Oring 1977), with some male Barn Swallows remaining unmated in every year in each major colony (Crook and Shields in press). In such circumstances, males are expected to compete intensely for mating opportunities despite the monogamous mating system characterizing the species (for discussion of greater male competition in another monogamous swallow, the Purple Martin, see Brown and Bitterbaum 1980).

As Greenwood (1980) noted, because males of most bird species compete for territories (and nest sites) needed by females, it is males that would be expected to show greater site fidelity, and in the Barn Swallow they do (Table 3). Once a male has competed successfully with a specific set of male neighbors and gained control of a site that attracts a female, it may pay him to remain faithful to that cluster and its familiar social environment. On a speculative note, the value of male tradition could stem from a number of factors. Moving to a new cluster would require another round of competitive interactions with relative strangers. This could entail a greater likelihood of failure than would settling in a familiar cluster with familiar individuals with which a male has already competed successfully. It is even conceivable that the familiarity and repeated interactions of cluster members, both within and across years, might facilitate less intense aggression among neighbors as a form of reciprocity (Trivers 1971). Reduced aggression among familiar neighbors relative to that displayed towards strangers has frequently been documented in territorial songbirds (e.g. Weeden and Falls 1959, Emlen 1971).

Regardless of the value of cluster fidelity, each cluster contains a variable number of suitable nest sites and old nests. Assuming that nest sites vary in intrinsic quality, it would pay a male to use and advertise the highest quality nest site available. If a male does return to a colony, and to a specific cluster within that colony, it may be that it contains one best nest site, in terms of safety, shelter, or defensibility. If a site is better, it is also likely to have been used in previous years by the same or other males. In fact, the presence of an old nest may actually add to a site's quality, as it takes much less time and energy to refurbish an old nest than to build one from scratch (Bent 1942, Samuel 1971b). Once he has returned to a particular colony, a male might be forced to return to a previous cluster by social competition and then reuses the same nest because it is repairable and is located in the best site. In addition to offering potential explanations for an individual male's nest fidelity, such factors might help explain the observations of traditional nest sites and nests used by different individuals in different years.

Female fidelity.—Once females have returned to a colony, probably gaining the same advantages as males, their pattern of within-colony fidelity is similar but not nearly as intense as that of the males (Table 3). If a female wished to remate, she might be "forced" to return to the same cluster because of her mate's cluster fidelity. She would then be likely to use the previously used nest at the highest-quality nest site for the same reasons as her mate (e.g. earlier breeding, safer or more sheltered nest). In contrast, if for any reason she wished to move (e.g. availability of a better mate, nest site, or territory), she would not have to compete with unfamiliar local males before settling in a new cluster, even if she were forced to compete with local females for a nest site or male. If female competition were less intense than male, the costs of moving would probably be less for females, and they might choose to move more readily.

Most female dispersal follows nest failure with a particular male at a particular site (Table 3). If nest failure can be attributed to site- or mate-specific factors, then a female might gain by deserting her mate and his breeding territory and trying elsewhere. For example, if her current nest failed because her mate failed to defend it adequately or because he was in some way behaviorally incompatible with her (e.g. see Coulson and Thomas 1983), then she would probably do better with a new mate. If a female chose to desert her mate, his cluster and nest fidelity would force her to desert his territory and nest as well, regardless of their intrinsic suitability. Alternatively, if the nest or site itself were unsuitable (e.g. it were heavily parasitized or vulnerable to rain or wind), then she would probably do better by choosing a new nest site. If a female chose to change nest sites, her mate's site fidelity would usually insure that she deserted him as well, regardless of his intrinsic suitability. In either case, a female would have a greater probability of improving her reproductive success by dispersing away from her previously used nest and cluster than would a male. An unsuccessful male could also benefit by changing mates and nest sites, and some few actually do disperse (Table 3). More males than females, however, are apparently forced by intrasexual social competition to maintain the status quo with respect to breeding sites, even after breeding unsuccessfully (Table 3).

Renest dispersal.—All factors favoring mate and site fidelity across breeding seasons are likely to operate within breeding seasons as well. There are also additional reasons for expecting the even stronger fidelity observed (Table 4). In many passerines, including the Barn Swallow, first nests are likely to fledge more young than are renests (for the swallow, see Mason 1953; for reviews, see Lack 1954, 1966). In addition, whether an attempt is the first of a season or a renest, for many passerines the earlier a pair breeds, the higher the reproductive success it can expect (Lack 1966). This implies that for many species breeding conditions might deteriorate during the breeding season. If this were true, time would be a limiting resource and could constrain an individuals's decisions about renest dispersal. Even if a nest has failed and a bird could "blame" its mate or its nest site, it might not have the time to desert, search out a new mate and area, and have as high a probability of success as if it had remained faithful. The increased tendency to change nests after successful first nests (Table 4) might be a response to those factors (e.g. ectoparasites) that can reduce the quality of an active nest over the course of a breeding season.

CONCLUSIONS

The Barn Swallow, like most of the other swallows (e.g. Freer 1979) and passerine birds in general (for reviews, see Baker 1978, Shields 1982), manifests high levels of adult site tenacity coupled with significant natal dispersal. The greater natal dispersal could be an adaptation limiting the possibility of intense inbreeding (e.g. Greenwood 1980) or could be a fortuitous result of the greater social subordinance of younger birds (e.g. Murray 1967, Gauthreaux

1978). The sexual bias in dispersal, with greater male than female site fidelity (Table 3), is similar to the pattern observed in a majority of passerines (Greenwood 1980, 1983). Because the Barn Swallow's natal dispersal eliminates the possibility of close inbreeding, the sexual bias in breeding dispersal cannot be an adaptation to prevent inbreeding. Rather, it appears to result from sexual differences in the kinds and levels of intrasexual competition characterizing the swallow. Greenwood (1980, 1983) also suggested and Moore and Ali (1984) emphasized such competitive explanations of sex-biased dispersal. Finally, like many other bird species (e.g. Darley et al. 1977, MacDonald 1977, Nolan 1978, Coulson and Thomas 1983, Dow and Fredga 1983, reviewed in Rowley 1983), the breeding dispersal of adult swallows that are usually site tenacious is associated primarily with nest failure. The observation of a reversal in renest dispersal, nest desertion more often following successful attempts, is apparently unique to the Barn Swallow and remains to be explained.

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