

IMPLICATIONS OF JUVENILE HARASSMENT IN PURPLE MARTINS

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Juvenile Purple Martins (*Progne subis*) are frequently harassed by mature martins, both before fledging and afterwards. On their initial flights juveniles are chased and pecked by nonparental birds in the colony, and if nonparental birds encounter a fledged brood in a grouping area (see Brown 1978a), they continue to harass the juveniles and chase them away. Birds engaging in this behavior were termed "raiders" by Brown (1978a). Parents have never been seen harassing their own young.

Brown (1978a) suggested that harassment could improve juveniles' awareness and reflexes and make them more noticeable to parents during brood assembly. But these possible advantages do not seem selectively important enough to maintain this behavior, which appears maladaptive at first glance. In this paper we offer a new hypothesis to explain juvenile harassment, report certain observations that have important bearing on our hypothesis and discuss the implications of harassment.

METHODS

Studies of Purple Martin nesting biology and breeding behavior were conducted by CRB at a maximum of 36 colony locations in Sherman, Grayson Co., Texas, from 1968-1979 (Brown 1978a,b; 1979). During 1974-1979, all juveniles and 30-50% adults per year at 1 main study colony were marked with color-painted aluminum bands and colored plastic bands. The number of martin pairs occupying this study colony averaged 26 each year, with a similar average number of broods annually. Birds were captured as nestlings or (with more limited success) as adults using the technique of Klimkiewicz and Jung (1976). EJB made observations on martin behavior at 3 colony locations in Gainesville, Alachua Co., Florida, in 1977 and 1978. All adult birds in Florida (14 pairs in 1977 and 16 in 1978) were color-banded and marked with paints as they entered cavities; no juveniles were marked in Florida. Studies in both Texas and Florida emphasized direct observation of birds.

THE HYPOTHESIS

Purple Martins are specialized secondary hole nesters and face severe intraspecific (Nice 1957, Johnston and Hardy 1962) and interspecific (Brown 1977, 1978c) nest-site competition. We hypothesize that juvenile harassment is a strategy of breeding birds to reduce potential nest-site competition in subsequent years. Nesting birds chase juveniles away from colonies to insure that the juveniles will not become imprinted upon these sites, lessening the probability that juveniles will return there the following year to compete with the raiders.

RESULTS

Our hypothesis is based, in part, on the presumed ability of juvenile Purple Martins to learn the location of nest-sites. Observations at a Sherman martin colony indicate that juveniles may possess the ability to learn site locations in late summer. At this colony in 1977–1979, Purple Martins raised 3 second broods and an unusually late first brood. It now appears that double broods in martins are somewhat rare, but regular in Grayson County colonies, and are not always associated with unusual population increases (see Brown 1978d). Table 1 contains the dates on which these broods fledged. At these late dates other martins in the colony had completed breeding. Few, if any, nonparental birds were present to act as raiders.

In these cases, the juveniles returned to sleep in the nest for an extended period (Table 1). The female parents of all 4 broods led the juveniles to the nest for the first 6–7 days on which they returned, but after that time the juveniles had apparently learned the location of their nest-site within the colony and often appeared there in the late afternoons before their parents arrived. In Brood A's and Brood D's case, the female parent disappeared during the time of returning, but by then the juveniles had learned the location of their nests and returned in each case an additional 6 days without parental accompaniment. No male parents were associated with these late first and second broods in 1977–1979 after the juveniles fledged (unlike in 1976, see Brown 1978d). In addition, Brown (1978e) reported post-breeding nest defense by juveniles that had been out of the nest no more than 6–7 weeks. These individuals also learned the location of nest-sites and returned there repeatedly each day. Finlay (1971) and Brown (1978a,e) suggested that post-breeding nest defense might imprint the location of future nest-sites. These observations suggest to us that juveniles, if given perhaps a 10–15 day period, can learn the location of sites, implying that raiders may indeed realize an advantage by harassing and chasing them away.

In contrast to the late broods of 1977–1979, Purple Martin broods that fledge in late May and early June in Sherman, Texas, return to sleep in the nest a mean of only 4.85 days after fledging (Brown 1978a). We think that 4.85 days is insufficient time for juveniles to learn the location of sites, because the juveniles of Broods A–D never appeared to be capable of finding their nest on their own until at least the sixth or seventh day of returning. Since most Purple Martins in Sherman, Texas, fledge young prior to 15 July (Brown, unpubl.), it is likely that only a few (very late) broods ever learn the location of their nest-sites.

How effective are raiders at reducing, through harassment, possible

TABLE 1
TIME LATE PURPLE MARTIN BROODS IN SHERMAN, TEXAS RETURNED TO SLEEP IN
NESTS, 1977-1979

	Late broods			
	A ¹	B ¹	C ²	D ¹
Year	1977	1977	1978	1979
Total number of martin pairs in colony	13	13	29	39
Size of colony in rooms	42	42	66	90
Size of brood	4	3	2	5
Date brood fledged	19 July	10 Aug.	9 Aug.	4 Aug.
Date brood returned to sleep last time	28 July	28 Aug.	23 Aug.	19 Aug.
No. of days returned to nest	10	19	15	16

¹ Second broods.

² First brood.

nest-site competition from juveniles in subsequent years? Indirect evidence comes from banding studies by CRB and S. D. Wolfe (unpubl.), who banded 2016 Purple Martins, primarily nestlings, in Grayson County, Texas colonies 1974-1979. The results of this work suggest that raiders may be remarkably efficient at reducing potential competition. Fewer than 1% of nestlings banded have been recovered (dead, recaptured, or via sight records) the following year in their natal colony, and only about 8% of the juveniles have returned to any colony within the 6 km² area where most of the martin colonies and banding efforts were concentrated. We suspect that the 1% which returned the following year to their natal colony did so by accident. In contrast, among nesting mature birds (which, of course, are not subjected to harassment), approximately 35% of the residents exhibited site tenacity between years (Brown and Wolfe, unpubl.).

DISCUSSION

Other, though less direct, evidence supports our hypothesis. First, yearling males are most often raiders (Brown 1978a; Bitterbaum, pers. obs.). Since male Purple Martins generally return to colonies before females and establish territories, it is to their advantage to minimize future competition. Females search for territories with attending males and rarely establish territories where no male is present, seeking male-site combinations (Johnston and Hardy 1962, pers. obs.). There may be less selective pressure for females to be raiders because, unlike males, they do not engage in strict nest-site competition. Furthermore, Rohwer and Niles (1977) suggested that all females in a population breed, whereas not all males do.

If this suggestion is true, it supports our idea that selective pressures for males to be raiders are greater than similar pressures for females.

Second, it is likely that yearling males have more to gain by being raiders than do adult birds. As an adult male becomes older, there is less potential competition from juveniles since old males arrive earlier when cavities are relatively easy to obtain. A yearling conceivably could face appreciable competition from juveniles the following year. CRB observed approximately 15 instances in which a banded second-year bird (the preceding year's yearling) and unbanded yearlings (the preceding year's juveniles) arrived essentially simultaneously in the spring. Although these yearlings were not raised the preceding year at the main study colony, they nevertheless competed with the second-year birds for nest-sites.

A reduced time of returning to the nest to sleep for May and June Purple Martin broods as opposed to August broods is related, we believe, to increased juvenile harassment in the early part of the nesting cycle. Broods that fledge in late June and early July frequently do not return to sleep at all (Brown 1978a), possibly because at that time large numbers of post-breeding male raiders loaf near colonies. When raiders depart for the premigratory roosts in late July and August, broods that fledge and return to sleep then do so without harassment. Because raiders contribute to a scattering of broods (Brown 1978a), it is possible, though unproven, that survival rates of unharassed late broods before migration may be greater than similar survival rates of earlier broods.

Presumably it is advantageous for broods to return to the nest to sleep, and presumably harassment by raiders is disadvantageous to juveniles. Thus, it might seem that selection would favor late nesting to counteract raider effects. By nesting late, as these double-brooded birds did, their young were able to return to sleep for longer periods than were early broods. Furthermore, the late broods were not scattered by raiders, and the juveniles likely learned the location of potential future nest-sites.

However, Purple Martins in north Texas begin migration in early to mid-August, and late broods may not have the time available to early broods for increasing fat reserves and becoming proficient at foraging before migration. Given the probable rigorous stresses in migration, the advantages in early broods of having an extended period to accumulate fat during summer outweigh the advantages in late broods of having no juvenile harassment. And although we have no proof, late second broods probably suffer high mortality in migration, and thus double-broodedness is not selected for in populations (despite the lack of juvenile harassment of double broods). Conflicting energetic requirements of parents who raise second broods at a time when molt is initiated also may limit double-

broodedness, probably by causing greater mortality of these parents during migration.

To test our hypothesis further, it would be desirable to compare return rates to the natal colony of unharassed late broods and harassed early broods. If late broods learn the location of nest-sites, as we believe, they would be expected to return the following spring more often than would early broods. This test would be feasible if one could find and band enough late first and second broods for adequate returns, but unfortunately, in Texas and Florida, we were unable to locate very many. Comparison of return rates for late- and early-reared broods would also be useful in elucidating whether or not late broods suffer heavy mortality in migration as we hypothesize.

SUMMARY

We suggest that nonparental Purple Martins (i.e., raiders) harass unrelated juveniles to disperse them, thus preventing juveniles from learning the location of nest-sites. Observations indicate that if given a period of perhaps 10–15 days post fledging, juvenile martins can learn site locations. Harassment prevents site learning in all broods except late-reared ones that fledge after most other martins have left the nesting colonies. Juvenile harassment, brought about by intense intraspecific and interspecific nest-site competition, is selectively advantageous (especially for males) in that it minimizes future potential competition from juveniles. Late first and second broods suffer little harassment from raiders, but selection still does not favor second broods, possibly because of high mortality of late-reared juveniles in migration.

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