Condor, 82:170–175

SLEEPING BEHAVIOR OF PURPLE MARTINS

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ABSTRACT.—I studied the behavior of Purple Martins (*Progne subis*) at nightfall and the birds' sleeping arrangements, each night, from spring arrival until premigratory flocking began. Martins slept in martin houses until about 15 June, after which they commonly slept in trees. Birds that were firmly established on a territory slept in a room of that territory. Some pairs of birds slept together in the same room and others did not. This behavior was determined by the males. Pairs that occupied their territories for a week or longer often slept together.

While building nests, pairs began to prefer certain rooms for sleeping. During egg laying and incubation, all females slept in the nest. They slept with the young and probably brooded them at night until the nestlings were 13–15 days old. Some females ceased sleeping with the nestlings after two weeks, and these females either slept in a tree or resumed sleeping with their mates. Many vagrant martins slept in martin houses, often on occupied territories. Martins frequently called from 03:00 until daybreak.

I hypothesize that Purple Martins copulate in martin house rooms at night, probably in the early morning. Pairs' sleeping together facilitates mating. Nocturnal copulation benefits males by minimizing cuckoldry and neighbor interference. Females benefit by being less vulnerable to gang rapes. Pairs also may sleep together to conserve heat on cool spring nights.

Despite recent studies of Purple Martins (*Progne subis*), primarily by Finlay (1971, 1976), Niles (1972), Brown (1978a–e, 1979), and E. J. Bitterbaum (pers. comm.), and earlier work by Allen and Nice (1952), Johnston and Hardy (1962) and Johnston (1966), little attention has been paid to sleeping behavior of martins after spring arrival and before premigratory flocking. In fact, sleeping behavior has not been well studied in any North American swallow.

A consideration of sleeping patterns in Purple Martins is important for three reasons. First, since martins are thought to copulate within the nesting cavity (Brown 1978a), any sleeping arrangement that uses this chamber could facilitate copulation. Copulation within the cavity may, among other functions, minimize male cuckoldry. Second, sleeping patterns are reliable indicators of an individual's colony residency, and thus are useful in censuses of Purple Martins. Third, additional knowledge of behavior in the genus *Progne* may be helpful in defining phylogenetic relationships among member species. I present here an investigation of sleeping behavior in Purple Martins.

STUDY SITE AND METHODS

I made all observations at a Purple Martin colony in Sherman, Grayson Co., north Texas, each year from 1968 to 1976. The colony grew from 2 pairs in 1968, to 3 in 1969–1970, 8 in 1971–1972, 19 in 1973, 20 in 1974, 25 in 1975, and 35 in 1976. A total of 123 pairs (246 individuals) was observed. Although some birds returned year after year, to simplify procedures I treated all birds each year as different individuals; thus the reported total is slightly inflated.

All individuals were recognized either by painted aluminum bands, colored plastic leg bands, behavior characteristics, or plumage features. Approximately half of the birds each year were banded or color-marked, and I could also recognize some individuals by their slight habits which became evident after careful observation. These traits included establishing ownership of certain perches on which no other birds were allowed, specific routes to and from the nesting houses, unusually strong aggression toward other martins in the colony and toward other species that came near, and individual patterns of the Claiming-Reclaiming (Johnston and Hardy 1962) display which, for many males early in the season, were uniquely characteristic.

Plumage differences were useful in identifying first-year males because the purple mottling on the head, breast, and belly is variable. Most females were also recognizable by the shading and patterning of gray on the head, breast, and belly. My techniques for capturing adults had a low yield and I could not capture all birds for banding. Only those that were individually recognizable were included in the study.

After the martins arrived and became established at the colony, I observed each pair daily and recorded sleeping behavior throughout the season. Toward the end of the season as the colony grew (especially in 1975–1976), it became difficult to observe the behavior of each pair every evening, but all birds were observed at least every other evening.

During 1968–76, I noted sleeping behavior on 1,392 nights (24,324 bird-nights). By month, there were 60 nights in February, 262 in March, 253 in April, 242 in May, 270 in June, 265 in July, and 40 in August. I distinguished five major stages during the nesting

cycle: I—arrival and pair formation, II—nest building, III—egg laying and incubation, IV—feeding young, and V—post-breeding nest defense. During these stages, there were 4,876, 4,744, 4,910, 7,786, and 2,008 bird-nights of observation, respectively. The stages overlapped among pairs, reflecting dissimilar spring arrival times and low synchronization of colony activities.

Beginning about 1 April each year, I checked each nest in the colony every other day to determine laying dates, clutch size, incubation period, egg and young losses, and hatching and fledging dates. These data were important in relating sleeping behavior to stages of the nesting cycle. Aluminum martin houses were lowered on telescoping poles and doorpanels were raised to note nest contents; wooden martin houses were reached with ladders and nest contents were checked with a small dental mirror inserted through the entrance hole (see Brown 1978b).

All-purple male martins (i.e. at least two years old) were termed "adults," and one-year-old males with mottled purple feathering on the head, breast, and belly were termed "yearlings." Yearling females were distinguished from adult females primarily by banding records; I assumed that very pale-breasted and pale-bellied females with little purple on the mantle who arrived late in the season were yearlings.

Because the term "roost" for the Purple Martin often connotes premigratory flocking (which is well documented and not considered here), I use the term "sleep" in this paper. It might be incorrect to assume that martins in their nesting compartments sleep throughout the night, but I think "sleep" is preferable to ambiguous and awkward terms such as "house-roosting." The birds were not active enough after dark to speak of "nocturnal behavior" (as in owls). I was concerned with the birds' behavior at sleeping time and with their physical arrangements for spending each night, rather than with the physiological state of sleep. In this paper, whenever I state that a martin "slept" in a room, I mean only that the bird spent the entire night in that room and did not come out until daybreak.

RESULTS

I. ARRIVAL AND PAIR FORMATION

Upon arrival at a colony, Purple Martins established territories consisting of one or more martin house compartments. The birds slept in these rooms, behavior that I found to be a useful criterion for indicating whether a martin was established on a territory. Residents slept in a room on their territories 98.8% of the bird-nights during Stage I.

Resident birds behaved differently from nonresidents, who also slept in martin houses. Residents, after foraging away from the colony during the afternoons, returned to the colony about an hour before twilight. At that time they sat and preened on their territories or on wires, or they foraged in the immediate vicinity. Nonresidents behaved hesitantly; typically they arrived near twilight and darted into rooms with none of the "leisure" activities which residents engaged in before sleeping.

A resident's bond to its territory was tested at sleeping time, much as Johnston and Hardy (1962) suggested for pair-bonds. If a prospective resident failed to appear and sleep on a territory, that martin was not established there (though it may have appeared to be established earlier in the day). Of birds that became established as breeders and for those whose exact day of arrival at the colony was known (N = 202), 80.7% slept their first night at the colony on the territory which they were to hold that year. Most of the remaining birds slept as vagrants on various territories in the colony until they found a territory of their own. Both males and females followed these patterns.

The sleeping behavior of a female indicated the strength of a pair-bond. Some females visited several unmated males in the colony during the mornings, yet they typically slept in the room with their "favored" male. This bird was likely to be chosen by the female as her mate. Sixty-five females that had a choice of two or more males slept with the male they later chose as their mate on 71% of the nights. Some females associated with two or more males for several days, sleeping with a different one each night. These females did not appear to favor any one male, although they later left all except one. Rarely, a female slept with one male for several weeks and then left him, but once established, pairs of martins were remarkably stable.

Some males claimed only one room, and females shared it with them. Most males, however, claimed more than one room (Brown 1979), and such pairs slept either together or in separate rooms. Pairs that were established for less than a week were more likely to sleep apart than were pairs that had been together for more than a week. During the first week a pair was present at the study colony (N = 123), 61% slept together on four or more nights, while 39% slept separately. After the first week of residency, the respective percentages of pairs sleeping together and separately during Stage I were 78.1% and 21.9%. Although sleeping together was more prevalent than sleeping separately, I found no correlation between a pair's sleeping arrangement and reproductive success (Brown, unpubl. data).

It appeared that males mostly determined whether pairs slept together or separately. When martins returned to their respective rooms at twilight, a male often entered and remained briefly in several rooms of his territory. His female followed him into each

room. If the pair were to share a room, the male either remained in the room or came out and then re-entered the room. If they were to sleep separately, the male went into another room. The female often followed him into this room, but then he exited again. A pair frequently moved between rooms for five minutes or more until the female ceased following, and they slept separately. Occasionally in newly established pairs, the female flew away and did not sleep at the colony after the male repeatedly refused to sleep with her. She was likely to return on following days, and the procedure was often repeated. Inclination to sleep with a female seemed to vary among males, but after a pair had been established for six or more days the male invariably was willing to sleep with the female. Other males readily slept with a female the first day she arrived. Although most males apparently were willing to sleep with their mates after six days of residency, they sometimes still slept separately, especially after egg laying began. Some pairs holding large territories (e.g. eight rooms or more) were so preoccupied with territorial defense at sleeping time that they were forced to sleep separately as it became dark while they were chasing away intruders, and the female could not find the male.

Females seemed to strongly desire to sleep with males during Stage I and they took the initiative in this behavior. A female on a large territory often sought out her mate by peering into all rooms until she found him. Most other interactions between members of a pair seemed to be initiated by the male. Sleeping with a male was an apparent means by which females indicated mate choice, yet some males initially refused to sleep with females.

Behavior described for this and following Stages applied equally to adult and yearling martins, although yearling females sometimes showed less initiative than did adults in seeking to sleep with a male.

II. NEST BUILDING

Sleeping behavior during this stage was similar to that in Stage I. Pairs were well established by the time nest building began, and pairs commonly slept together although they sometimes slept apart. During this stage pairs showed sleeping preferances for certain rooms; these were the rooms (or room) where the female had been doing most of her nest construction. Sleeping occurred 79.6% of the nights in rooms where the nest was or where the nest was to be built.

III. EGG LAYING AND INCUBATION

After laying their first egg, female martins slept in the nest room each night. I never recorded a female sleeping anywhere other than the nest once egg laying began. At that time most males (61.6%), if accustomed to sleeping with their mate prior to egg laying, continued to sleep with her then and during incubation. The fact that a pair spent the night in the nest room during egg laying probably was responsible for slightly staggered hatching of martin clutches, indicating that some embryonic development occurred in the heated nest at night before incubation began (Allen and Nice 1952). The remaining males (38.4%) regularly slept in other rooms of the territory during incubation.

IV. FEEDING YOUNG

In Stage IV established sleeping patterns began to dissolve. All female martins slept in the nest with their young until the nestlings were two weeks old, after which some females ceased sleeping with them.

Prior to 15 June in Sherman, most females (89.2%) with broods over two weeks old continued sleeping with the young. After 15 June, females (68.4%), especially yearlings, with broods over two weeks old slept elsewhere. Regardless of date, however, all females slept with the young until they were 13–15 days old, suggesting that young Purple Martins may require night-brooding for at least two weeks. (My studies show that nestlings are brooded during the daytime until they are 10 days old.)

Although time of year influenced when a female ceased sleeping with the young, brood size was important also. No quantitative data are available, but for broods of five to seven young, female parents seemed less likely to sleep with the young after the two-week period than were female parents of smaller broods. In large broods, which probably raise the temperature inside the nest slightly, the young may stay warmer than do young in small broods, thus large broods require less night-brooding.

Date and brood size also influenced the sleeping behavior of males. In broods of one to four young, a male was likely to sleep with the female and the young throughout the four-week nestling period, especially prior to 15 June. In broods of five to seven young, males frequently ceased sleeping in

the nest even before the young were two weeks old. Generally, if a male slept in the nest with the female during incubation, he continued to do so for a time after the young hatched. If a male slept separately during incubation, he continued to do so after the young hatched.

When parents did not sleep with their young, they occupied another room of the territory (often a pair resumed sleeping together at that time), especially prior to 15 June. After 15 June parental martins either continued using another room, or they slept in trees, a prelude to premigratory roosting. Sleeping in trees was infrequent before 15 June but rapidly became common after that date. If the parents slept in a tree, they normally left the colony at twilight and returned at daybreak to feed the young. Martins from one to six different colonies repeatedly slept at a communal tree or grove within one km of the colonies. If a pair claimed only one room—the nest—as their territory, sometimes they quietly entered rooms on another pair's territory to sleep in during Stage IV.

V. POST-BREEDING NEST DEFENSE

Martins rarely slept in their houses during this stage although pairs spent much time there during the day. Only 6.5% of the resident birds slept in the colony during this stage. Martins mainly slept in trees during Stage V, and premigratory flocking and roosting began then.

Certain generalities pertain to Stages I–IV when martins always slept in their houses. Only once did I observe a martin sleep outside on the porch of a house. This individual was an intruder who was backed into the corner of a porch and was unable to move because the defending resident sat in the entrance of a room nearby and pecked the intruder vigorously whenever he tried to move. Males in particular often perched in the entrance of a room or on a porch until it was quite dark, but in my study they invariably retired inside the room to sleep. However, J. C. Finlay (pers. comm.) found that martins in Alberta, Canada, occasionally left their rooms at night, to return at daybreak.

I installed one martin house with reflecting interiors so that I could observe the martins sleeping inside the room in silhouette whenever a light was flashed onto the house. This showed that a pair, when sleeping together, frequently changed position during the night. Typically, the birds slept on either side of the entrance, but they were active during the night and moved often. I do not think that the light, which was flashed from the ground, influenced their behavior. While capturing Purple Martins at night for banding in Gainesville, Florida, E. J. Bitterbaum (pers. comm.) found males resting on top of females; the birds possibly slept in this position (and copulated?).

Intruders began appearing at the colony about an hour before twilight, but they were driven from occupied territories by residents. As twilight neared, the "homeless" vagrants tried vigorously to find a place to sleep. They would enter a room very quickly, in contrast to their slow, cautious behavior during the day. Rapid entry sometimes enabled them to escape detection by the residents, and the vagrants were then able to sleep in that room. Residents tenaciously defended their territories until dark, and vagrants found sleeping rooms only with great difficulty. Vagrants sometimes entered a room containing other vagrants, residents, or House Sparrows (*Passer domesticus*), and the intruders were quickly repulsed. Rarely a male and a female vagrant entered the same room and slept there together. Vagrants often flew from one martin house to another trying to find a room. I did not find out where room-less martins slept, but they probably used trees. The vagrants sleeping in rooms departed at daybreak. When the study colony was relatively large (1973–76), varying numbers of vagrants used the colony *each* night throughout Stages I–III and during much of Stage IV. Often at least 15 vagrants slept at the colony per night.

All martins in my study seemed reluctant to fly or move outside their rooms after dark. I never observed them change rooms during the night, and whenever martins flew after dark owing to major disturbances (e.g. jarring or lowering a martin house), they appeared nervous, disoriented, and uncoordinated in flight. However, Southern's (1959) homing experiments showed that Purple Martins indeed are able to see and successfully orient at night.

Purple Martins characteristically call at night (Sprunt *in* Bent 1942, Oberholser 1974). The birds at my colony typically began calling about 03:00 and continued until sunrise. Apparently the vocalizations were given while the birds were inside the martin houses, although limited evidence suggested that martins occasionally left their houses shortly before daybreak and called. Nocturnal calls consisted of typical martin

contentment notes and songs, including the guttural trill used by males when courting females.

DISCUSSION

Since Purple Martins have rarely been seen copulating during the day, I (1978a) suggested that copulation probably occurs inside the rooms. Martins do not move between rooms at night, so frequent sleeping together likely facilitates copulation by bringing the sexes together.

From the standpoint of a male, copulating at night could be a habit that ensures that his sperm and not that of a competitor are transferred to his mate (and see Hoogland and Sherman 1976 on Bank Swallows, *Riparia riparia*). Attempts at forced copulation ("rape") are frequent in Purple Martins (Brown 1978a) and also are known in Gray-breasted Martins (*Progne chalybea*; Bitterbaum, pers. comm.). Conspicuous diurnal copulations elicit massive interference and attempted rapes by nearby males (Allen and Nice 1952; Brown, unpubl. data). It is therefore almost impossible for martins to mate during the daytime near a colony; if they do so at all, they must be away from the colony. It seems to me more likely that they copulate in rooms at night, when interference from other males is nil. Copulation probably takes place in conjunction with the nocturnal calls. Similar calls and songs accompanied 10 observed diurnal copulations (Brown, unpubl. data).

From the standpoint of a female, by copulating at night, she is not subjected to frequent and intense rapes. These are potentially dangerous to her because she abruptly plunges into tree branches and onto martin houses in efforts to escape (Brown 1978a), and attacking males are aggressive toward her. Owing to the contagiousness of such behavior (Brown 1978a), a receptive female would probably be raped if she flew about the colony in daylight soliciting either her mate or other males. Even though rapes occur somewhat regularly in Purple Martin colonies (Brown 1978a), more might be attempted if martins often copulated diurnally. The apparent eagerness of females to sleep with males is consistent with the hypothesis of nocturnal copulation.

Emlen (1954) similarly reported that Cliff Swallows (*Petrochelidon pyrrhonota*) copulate within the nest, and, because of interference from neighbors, copulations were rarely successful unless the nest was substantial enough to screen the pair from other Cliff Swallows. Lunk (1962) suggested that Rough-winged Swallows (*Stelgidopteryx ruficollis*) copulate within the nest cavity (possibly at night?), and Petersen (1955) made a similar suggestion for Bank Swallows. Concealed copulation could be a common habit in the Hirundinidae, but additional studies are needed.

Since male Purple Martins choose the sleeping arrangement, the seeming indifference of some males as to whether they sleep with a female, especially early in the season, is puzzling. If martins copulate at night, males would be expected to encourage females to sleep with them. Yet, although some pairs (21.9%) slept separately more often than not (primarily because of the male's choice), *all* pairs were found to sleep together at least once during Stages I and II, the periods when fertilization was most likely. Theoretically, a pair needs to sleep together on only one night to achieve fertilization. Also, perhaps the male's option of sleeping with a female or not could indicate a degree of male choice of mates. All previous interpretations of pair formation in Purple Martins have implied female choice only (Allen and Nice 1952, Gaunt 1959, Johnston and Hardy 1962).

Bitterbaum (pers. comm.) found diurnal copulations more frequent in Gray-breasted Martins of Trinidad than in the Purple Martins he studied in Florida. He rarely heard Gray-breasted Martins calling at night. If they copulate during the day, they might not do so at night which could explain their lack of nocturnal vocalizations. Although rape occurs in Gray-breasted Martins, there is less interference from neighbors when mating than in Purple Martins (Bitterbaum, pers. comm.), so perhaps nocturnal copulation has not been selected for in Gray-breasted Martins.

On three occasions in Sherman, I saw more than two martins share a room for sleeping, and T. Dellinger (pers. comm.) noted the same on three occasions at a colony in Duncanville, Dallas Co., Texas. More than two birds (sometimes up to 12) sleep together only during periods of severely cold weather when food is scarce (Brown 1976). Martins abandon usual territory defense during cold weather, and many huddle and sleep together, evidently to conserve heat. In the early part of the nesting cycle in Sherman (i.e. February and March), nightly temperatures frequently range from $-1°$ to 10°C. Even when starvation is not imminent, single pairs may sleep together apparently to keep warm on cool spring nights.

My observations suggest two important points for Purple Martin researchers. First, those who use the banding technique of Klimkiewicz and Jung (1976) (involving lowering the martin house at night to band sleeping birds) are likely to capture a number of vagrants sleeping in the houses. These nonresidents should be taken into account when calculating survival rates and site tenacity of banded birds. Nonresidents usually depart immediately after banding and rarely reappear at the colony of capture. I know of no reliable way, short of observing the birds entering the rooms, to determine if a captured bird is a resident or a vagrant, although birds that are caught as pairs using the same room are likely to be residents who are sleeping together.

Second, proprietors of Purple Martin houses who wish to estimate populations in their colonies should use sleeping behavior to determine residency status of birds. Daytime counts of birds on wires and even of birds perched on martin houses are not adequate to determine population size. During the early, often cool part of the nesting cycle, the birds spend much time feeding away from the colony during the day. Unless one observes the martins at sleeping time when all residents appear, one is likely to underestimate population size. At other times of the year, site-seeking vagrants, juveniles, and post-breeding vagrants visit the colonies. At such times one may overestimate population size unless observations are made at sleeping time when residents can be recognized by their behavior.

Detailed observations of sleeping patterns in Purple Martins, such as those presented here, are valuable for an ethological comparison of this species with other members of the genus *Progne* and with other hirundinids. Bitterbaum's (pers. comm.) observations on the Gray-breasted Martin indicate differences in sleeping patterns between these congeners. Knowledge of sleeping behavior may prove useful in understanding the ecology and relationships of swallows and other birds.

ACKNOWLEDGMENTS

Erik J. Bitterbaum discussed martins with me and criticized the manuscript. Janet Hinshaw of the Josselyn Van Tyne Memorial Library was helpful in providing references. My martin studies have been supported largely by my parents.

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