

COLONIALITY AND BREEDING BIOLOGY OF PURPLE MARTINS (*PROGNE SUBIS HESPERIA*) IN SAGUARO CACTI¹

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Abstract. Purple Martins (*Progne subis hesperia*) breeding in natural cavities in saguaro cacti did not form dense colonies, unlike martins (*Progne subis subis*) that breed in nest-houses in eastern North America. However, nests were clumped on a larger geographic scale. Birds in these groups of nests quickly formed mobs of up to 10 birds in response to a model crow at the nest. Males and females defended an area around their nest cavity with a radius of about 20–30 m, and often defended cavities other than the nesting cavity. Only 5–15% of breeding males were subadults and some subadult males defended cavities without a mate, indicating that many subadult males did not breed as one-year-olds. A literature review of martin colony sizes in natural cavities indicates that nest-house colonies fall within the range of breeding densities to which martins were exposed historically. The many similarities in breeding biology and social behavior between this desert subspecies and nest-house populations suggest that nest-houses are appropriate models of natural conditions.

Key words: Purple Martin; *Progne subis*; saguaro; coloniality; cavity-nester.

INTRODUCTION

Purple Martins (*Progne subis*) in eastern North America are highly colonial and have bred almost exclusively in man-made nesting houses for at least a century (Allen and Nice 1952, Morton 1988). Many studies of the breeding biology and behavior of martins in nest-houses have been conducted (e.g., Allen and Nice 1952; Johnston and Hardy 1962; Finlay 1971; Brown 1978a, 1979, 1980, 1984a; Morton 1987; Morton et al. 1990; Stutchbury, in press a, b), but there is very little known about natural populations. Recent studies on other secondary cavity-nesting species have revealed important differences in breeding biology between nest box and natural populations (Korpimäki 1984; Nilsson 1984a, 1984b; Rendell and Robertson 1989; Robertson and Rendell 1990). Although montane western populations of Purple Martins still breed primarily in natural cavities, they are widely scattered (Grinnell and Miller 1944, Gabrielson and Jewitt 1970). A subspecies of the Purple Martin (*Progne subis hesperia*) breeds in abandoned woodpecker cavities in saguaro cacti (*Cereus giganteus*) in the Lower Sonoran Desert (Cater 1944, Brandt 1951, Phillips et al. 1964). Birds of this subspecies have

slightly smaller bodies (Brandt 1951, Johnston 1966, Behle 1968) and females are paler in color (Johnston 1966) than *Progne subis subis*. Apart from their roosting habits (Cater 1944, Anderson and Anderson 1946), there is little information on the breeding biology of this subspecies (Brandt 1951, Phillips et al. 1964). The purpose of this study was to describe the breeding biology and social behavior of *Progne subis hesperia* and to compare this natural population with martins that nest in artificial houses.

Colony sizes in martin houses range from several to over 40 pairs (Allen and Nice 1952). In nest-houses, young males in subadult plumage arrive relatively late in the spring (Morton and Derrickson 1990), and compete with older males for a nesting cavity (Rohwer and Niles 1979; Stutchbury, in press a, b). Extra-pair copulations and intraspecific brood parasitism are common (Morton 1987, Morton et al. 1990). Dawn song by adult males may function to attract subadult males to the colony, so that adult males can gain opportunities to cuckold their subadult neighbors (Morton et al. 1990). To assess the evolutionary significance of such behavior, it is important to know to what extent natural populations of martins were colonial, because colony size can affect the nature and intensity of social interactions such as mate guarding (Hoogland and Sherman 1976, Moller 1987), cuckoldry (Brown and Brown 1988), intraspecific brood parasitism (Brown 1984b), and predator mob-

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bing (Brown and Brown 1987). To evaluate the extent to which ancestral populations of martins were colonial in natural cavities other than saguaros, I also conducted a literature review of colony sizes reported for naturally nesting martins.

METHODS

This study was conducted in the summers of 1988 and 1989 in the Saguaro National Monument (Tucson Mountain District) and Tucson Mountain Park, about 25 km west of Tucson, Arizona. Purple Martin nests were located by driving slowly, or walking, along roads in the study site. Martins were very conspicuous as they foraged or perched on saguaros 8–10 m above the ground. Alarm calls and male song were also used to identify areas in which martins were nesting. In 1989, each location where martins were nesting was searched for 1–2 hours for additional nests during late July, when most pairs were feeding young. The open landscape allowed for easy viewing of large areas of potential nesting habitat. Areas along roads between known locations of breeding martins were also searched thoroughly. In July 1989, I searched for breeding pairs over four days in a second population, located in the Rincon Mountain District of the Saguaro National Monument, about 50 km east of the main study area.

For each breeding pair, I noted whether the male had adult or subadult plumage coloration. One-year-old male Purple Martins are sexually mature, but have a distinctive subadult, female-like plumage (Niles 1972). Adult males have an entirely glossy dark blue plumage, whereas subadult males are mostly white on their undersides, with varying amounts of blue feathering. Where possible I made detailed sketches of subadult males to document the amount of blue feathering on their undersides. These drawings were transferred to a grid to estimate the actual area of blue feathering. When detailed sketches were not possible, I classified subadult males as dull or bright, based on the range in blue feathering found in eastern populations of martins (Rohwer and Niles 1979).

The height of nesting cavities was measured with a Suunto Clinometer (PM-5/100P). The width of cavity entrances was estimated by placing a ruler, attached to an extensible aluminum pole, over the nest hole. The depth of the nesting cavity was estimated by lowering a 20 g weight,

attached to fishing line running through two pulleys and down the length of the pole, into the nesting cavity. A ruler attached to the pole was used to measure how far the weight descended into the cavity. Depth measurements were taken only after the eggs had hatched.

The density of saguaros near the nest cavity was measured by counting the number of saguaros greater than 3 m tall within a 50 m × 50 m square. The grid was centered on the nest site, and ran on a north–south axis. For 15 breeding pairs in 1988, I identified all possible nesting cavities within this 2,500 m² area. Woodpeckers often abandon excavation of a cavity, leaving only a dead-end hole in the side of the saguaro (Kerpez and Smith 1990). If a cavity did not measure at least 5 cm in depth, the cavity was not included as a potential nesting cavity.

Since saguaros are unstable, ladders were not used to inspect nest contents. Instead, I used lighted mirrors attached to extensible poles to reflect the image of the nest contents inside the cavity toward the ground. A 5 cm round convex mirror, with two miniature flashlight bulbs attached in front, was mounted at the distal end of a narrow, thin aluminum bar. A larger (10 × 14 cm) flat mirror was mounted diagonally at the intersection of the bar and the extensible poles, so as to reflect the image from the lighted convex mirror inside the cavity toward the ground. An observer on the ground viewing the large mirror with 10× binoculars could see the image of the nest contents. Nest checks were done before dawn to obtain best visibility of nest contents. Many cavities were not oriented vertically inside the saguaro, so that the bottom of the cavity could not be seen. However, I obtained clutch size information on 11/23 nests attempted. Incubating females remain on their nests overnight, and in some cases clutches could not be viewed because the female would not leave the nest cavity. Although eggs were usually clearly visible, nestlings could not be counted.

I recorded breeding behavior during half-hour observations on 16 focal adult pairs over two years. Watches were done on each pair every 2–4 days, between 06:00–09:00, from mid-June through early August. Nesting behavior and the movements of the focal pair were noted, including their exact perch sites. Saguaros vary greatly in the number and shape of their branches, so I used sketches to identify perch sites. Measurements of distance and orientation of perch sites

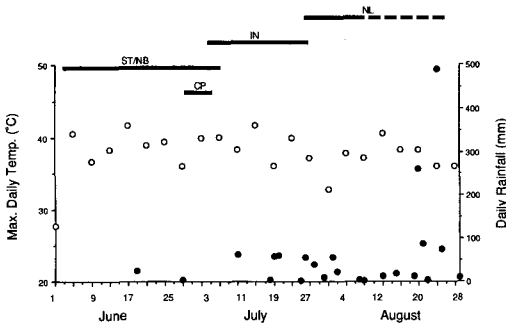


FIGURE 1. Timing of the settlement and nest building (ST/NB), copulation (CP), incubation (IN), and nestling (NL) stage of Purple Martins in relation to maximum daily temperature (open circles) and daily rainfall (closed circles) in 1988. The dashed line for the nestling period indicates the probable duration. Temperatures are plotted only for every fourth day, but every day on which rainfall was recorded is shown.

relative to the nesting saguaro were made later. In 1989 a Ranging 620 rangefinder was used to estimate distances, but in 1988 a tape measure was used. The martins were not individually color banded, so I assumed that individuals perched near or in the nesting cavity were actually the territory owners. Only rarely was there any confusion as to the identity of a bird in the territory.

During watches, I recorded all intrusions by other martins on the territory of the focal pair. Although intruders often flew through the territory, or briefly circled in the territory, I analyzed only those intrusions where the intruder perched. If possible, I noted whether the intruder was an adult male, subadult male, or female. The behavior of the intruder, duration of the intrusion, and response of the focal male and female were also noted.

In 1989, in early August when the nestlings were about 10 days old, I quantified the predator mobbing behavior of martins by erecting a plastic crow near a nesting cavity. The crow was mounted on the end of an extensible pole. One person quietly walked to the base of the nesting saguaro, and erected the pole so the crow was within 2 m and directly below the nesting cavity. A second person recorded the number of martins mobbing the model every 20 sec for 5 min.

From late June through early August, between 04:45–05:30, I noted the presence or absence of male dawn song (Morton 1988, Morton et al. 1990) in locations where I was conducting nest checks. Beginning sometime before 04:15, over

TABLE 1. Measurements (mean, standard deviation, sample size, and range) of martin nesting cavities in saguaros.

| Cavity characteristics | Mean | SD | <i>n</i> | Range |
|------------------------|------|-----|----------|----------|
| Cavity height (m) | 7.4 | 1.4 | 49 | 4.7–10.4 |
| Saguaro height (m) | 9.0 | 1.6 | 49 | 5.1–12.2 |
| Entrance diameter (cm) | 7.4 | 2.0 | 17 | 5.0–9.0 |
| Cavity depth (cm) | 15.5 | 8.4 | 17 | 7.0–24.0 |

an hour before dawn, males flew high in the air giving the distinctive dawn song.

Weather data were obtained from the Saguaro National Monument (Tucson Mountain District) weather station.

RESULTS

NEST MEASUREMENTS AND BREEDING BIOLOGY

Timing of breeding was determined from focal watches on 16 pairs over both years of the study. Nest building took place in late June and early July, incubation during early and mid-July, and nestlings hatched in late July (Fig. 1). Breeding did not appear to be timed according to daily temperature, but the nestling period did coincide with the late summer monsoon season (Fig. 1), when highly localized thunderstorms produced much rainfall.

The nesting cavities used by martins were generally at least 7 m above the ground (Table 1), but some nests were as low as 4.7 m. Entrance diameters ranged from 5–9 cm, and cavity depths from 7–24 cm. Most nesting cavities were within 3 m of the stem apex (35 of 40 cases where the saguaro was not broken or bent sharply near the top). The mean orientation (Batschelet 1965) of cavities ($n = 51$) was 233°, and 67% of the cavities faced a southerly or westerly direction (136–315°). Most nesting cavities (90%) were located in the main stem of the saguaro, as opposed to a branch. The density of saguaros (over 3 m tall) near the nesting cavity ranged from 5–26 per 2,500 m².

Nest building was done primarily by females (48/53 of all trips). I observed martins adding green leaves to their nest during the incubation period on only three occasions during 36 hr of observation. The leaves were from ocotillo (*Fouquieria splendens*) and jojoba (*Simmondsia chinensis*) plants. Clutch sizes obtained from 12–25

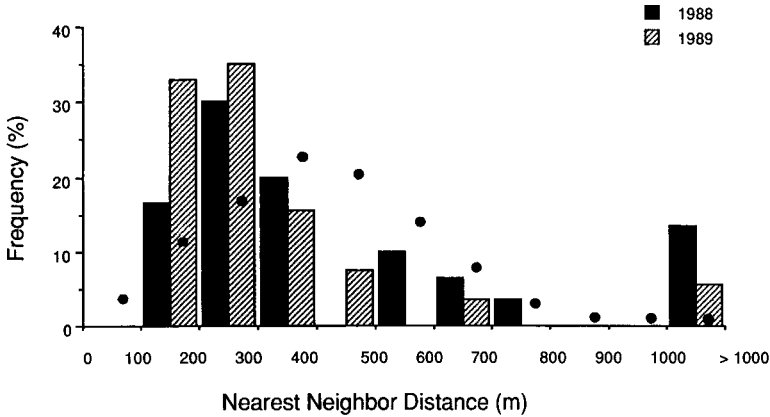


FIGURE 2. Frequency distribution of nearest neighbor distances in 1988 and 1989. Expected frequencies (solid circles) based on a random distribution of nests are shown for 1989.

July, when females were incubating, ranged from 3–5 eggs (mean = 3.9, SD = 0.70, $n = 11$). Of 16 nests where focal watches were done, 94% had at least one nestling hatch and survive to an age of 10 days, as indicated by parental feeding behavior. Both males and females fed the nestlings, with females making 115 of 205 (56%) feeding trips.

COLONIALITY AND SOCIAL BEHAVIOR

I located 30 breeding pairs in 1988 and 52 pairs in 1989. I never found more than one pair breeding in a single saguaro. The median nearest neighbor distance was 325 m in 1988, and 238 m in 1989 (Fig. 2), and no pairs nested less than 100 m apart. However, on a larger scale, breeding pairs formed distinct groups (Fig. 3). In 1989, areas within about 500 m of roads between breeding groups were searched for nests, and had similar densities of saguaros. The expected frequency of nearest neighbor distances was calculated for a randomly distributed population based on a nest density of 1.9/km² (total number of nests/total area searched) using the methods of Clark and Evans (1954). The observed distribution of nests in 1989 was significantly more clumped than the expected random distribution (Fig. 2; G -test, $G = 34.1$, $df = 5$, $P < 0.001$).

The predator mobbing response of martins gives a measure of the extent to which neighboring pairs function as a social unit. The number of martins mobbing the model crow ranged from 1 to 10 (Fig. 4), and was significantly correlated ($r_s = 0.71$, $n = 10$, $P < 0.05$) with the number of birds known to be breeding within

about 500 m of the focal nest. Mobs consisted of birds circling the model and alarm calling, sometimes repeatedly diving at the model (e.g., Brown and Hoogland 1986). In 7 of 13 trials, one or two birds (likely the owners of the nest) dove repeatedly at the model.

Only 2 of 30 breeding males (7%) were subadults in 1988, and only 8 of 52 (15%) in 1989. A similar proportion (4/23; 17%) of breeding males were subadults in the Rincon Mountain Unit population about 50 km east of the main study site. In both years, five subadult males defended cavities but did not have mates. Although these males were not color banded, their distinctive subadult plumage allowed reliable identification of individuals over successive days. The amount of time these males were known to defend a cavity alone ranged from 4–37 days.

Subadult males bred later in the summer than adult males. In 1988, I found 14 mated adult males between 8–28 June, but found no subadult males with territories and mates. Despite intensive searches for nests in 1989, only one mated subadult male was found before the end of June, but the seven other mated subadult males were found from 7–27 July. Three of these latter pairs were seen nest building from 7–11 July, which is when most adult pairs have already begun incubation (Fig. 1).

Of 11 territorial subadult males that were sketched in detail, the average of blue feathering on the underside was 1.4 ± 0.8 cm². An additional 10 territorial subadults for whom detailed sketches were not made were classified as having a dull plumage score, falling within the range

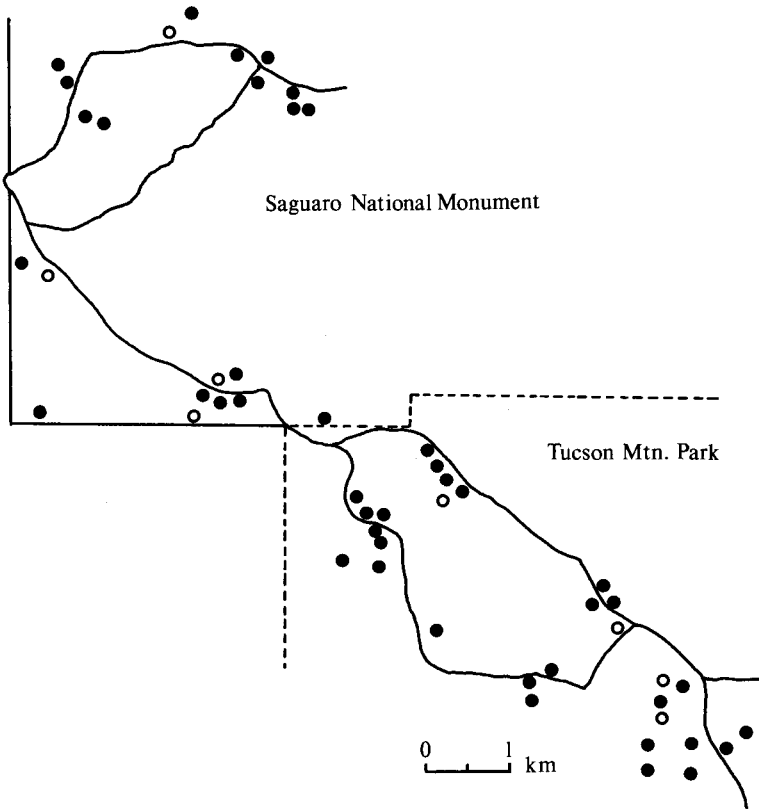


FIGURE 3. Location of martin nests in 1989. Adult male pairs (solid circles) and subadult male pairs (open circles) are indicated. Roads are shown with solid lines, park boundaries with dashed lines.

observed for the 11 detailed drawings. All subadult males had tan colored foreheads and napes, as did all females.

Although breeding pairs were spaced over 100 m apart, there were cavities within this area that were within the range of cavity depth and height above ground of cavities actually used for nesting (Table 1). Of 15 territories where I searched for extra cavities within a 2,500 m² area centered around the nesting cavity, six territories had no other cavities, four had one other cavity, two had two other cavities, and three had three other cavities. In 6 of 15 territories, there were one or two other cavities in the same saguaro as the breeding pair. Cavities used by other species were not included in this analysis, but martins were found nesting in the same saguaro as Brown-crested Flycatchers (*Myiarchus tyrannulus*) and Gila Woodpeckers (*Melanerpes uropygialis*), and within 15 m of Northern Flickers (*Colaptes auratus*).

Of the 30 cavities used in 1988, 40% were used by martins again in 1989, 14% had a pair nesting in a nearby cavity, 7% were occupied by Gila Woodpeckers or Northern Flickers, 10% were not available because the saguaro had fallen down, and 29% were apparently vacant.

Breeding pairs frequently defended cavities other than their actual nesting cavity, by perching on or in the cavity, usually during intrusions by other martins. Both males and females were seen participating in multiple nest site defense. Of 16 focal pairs where watches were conducted, nine pairs defended one or more additional cavities. Extra cavities ranged from 0–115 m from the nesting saguaro (mean = 29.1 m, SD = 33.4 $n = 12$).

Territorial boundaries were difficult to define, so I used the location of perch sites observed during half hour watches as a measure of territory size. The distance of perch sites (including the nesting saguaro, but not the cavity itself) from

the nesting saguaro was weighted for each bird according to the amount of time spent perching at that location, over all watches. The weighted average perching distance for males was 27.5 m (SD = 14.1, $n = 16$), and 17.8 m (SD = 10.6, $n = 16$) for females.

Although some territorial pairs had greater than three intrusions during a 30 min watch, there were no intrusions during 133 of 183 watches (72.6%). Since subadult males had so little blue feathering, it was sometimes not possible for me to distinguish them from females during brief intrusions. For all intrusions by males, 32 of 39 were subadult as opposed to adult males. Territory owners were often not aggressive toward intruders, but in 17.7% of the intrusions one of the territory owners displaced, chased, or fought with the intruder. All three fights observed involved birds grappling in the air; I never observed birds fighting inside a cavity or on the ground.

From 29 June–5 July, I observed five instances of pairs copulating outside the nesting cavity. I never observed forced copulations by males. No males were seen closely guarding their mates during the presumed fertile period. During the period of 27 June–5 July, when most females would be fertile (Fig. 1), females were guarded (male departed with female) on only 7% (3/45) of nest building trips, not guarded (male present but did not follow) on 40% of trips, and females were alone (male absent from area) on 53% of trips.

Over both years, I heard males dawn-singing on all 37 days that I was in the study area before 05:30 from 30 June–8 August. Many different males participated in dawn-singing, as I heard dawn-singing at 12 different breeding groups in the study area. The minimum number of males estimated to be singing at one location on a given morning ranged from 1–7.

DISCUSSION

NEST SITE CHARACTERISTICS AND BREEDING BIOLOGY

Purple Martins in this study area bred fairly late in the summer. Other cavity-nesting species including Gila Woodpeckers, Northern Flickers, and Brown-crested Flycatchers were feeding young when the martins began nest building. The nestling period coincided with the rainy season (Fig. 1), suggesting that martins may delay breeding so that aerial insects are abundant during the time they feed nestlings. The race of Cliff Swal-



FIGURE 4. Maximum number of martins mobbing the model crow, in relation to the number of birds breeding within about 500 m.

lows native to southern Arizona, *Hirundo pyrrhonota melanogaster*, also breeds later in the summer than more northern races (Phillips et al. 1964; C. R. Brown, pers. comm.).

Martins are dependent on Gila Woodpecker and Northern Flicker cavities for nesting sites. Purple Martins nested in cavities with entrance diameters covering the range of both woodpecker species (McAuliffe and Hendricks 1988). Flickers almost always excavate cavities within 3 m of the stem apex, but over half of Gila Woodpecker cavities are closer to the ground than this (McAuliffe and Hendricks 1988). Most cavities used by Purple Martins were within 3 m of the stem apex, suggesting that martins were avoiding available lower cavities.

Females made the majority of nest building trips and about 50% of the feeding trips, as is found in nest-house populations (Allen and Nice 1952). Although males and females were seen adding green leaves to their nests during incubation, it occurred at a much lower frequency than in eastern populations (Allen and Nice 1952). This is likely because most plants in the study area did not have fresh green leaves during early July.

Several studies on secondary cavity-nesting species have shown that populations using natural cavities have smaller clutch sizes than those using nest boxes (Korpimäki 1984, Nilsson 1984a, Robertson and Rendell 1990), a pattern which may be due to the smaller floor area in natural cavities (Karlsson and Nilsson 1977, Robertson and Rendell 1990). The average clutch size in this natural population (mean = 3.9 eggs, SD = 0.70, $n = 11$) was significantly (t -test; $t = 5.88$, $df = 273$, $P < 0.001$) smaller than the av-

TABLE 2. Reports in the literature of colony size (number of pairs) of Purple Martins breeding in natural cavities for eastern and western populations (not including the Sonoran Desert). The number of reports is a measure of the frequency of occurrence of that colony size.

| Location | Colony size | No. reports | References |
|----------------|-----------------------------------|-------------|--------------------------------------|
| Eastern states | 1 | 4 | 4, 11, 20, 29 |
| | 2-6 | 5 | 3, 8, 16, 20, 23 |
| | "colony" | 1 | 1 |
| | 50, ^a 300 ^a | 2 | 20 |
| Western states | 1 | 11 | 6, 7, 10, 13, 14, 17, 18, 26, 28, 30 |
| | 2-7 | 5 | 5, 12, 14, 15, 22 |
| | "numerous" | 1 | 2 |
| | 12-20, 25 ^a | 4 | 9, 25, 27, 29 |
| | 40 | 1 | 21 |

^a Colonies nesting under boulders or in rock crevices.

References: (1) Scott 1872, (2) Coues 1878, (3) Roberts and Benner 1880, (4) Scott 1881, (5) Mearns 1890, (6) Sharp 1907, (7) Edwards 1914, (8) Phelps 1914, (9) Van Rossem 1914, (10) Dawson 1916, (11) Evermann and Clark 1920, (12) Dawson 1923, (13) Bryant 1924, (14) Finley and Finley 1924, (15) Bailey 1928, (16) Howell 1932, (17) Lumley 1932, (18) Kitchen 1934, (19) Huey 1936, (20) Roberts 1936, (21) Huey 1939, (22) Hayward 1941, (23) Bent 1942, (24) Grinnell and Miller 1944, (25) Richmond 1953, (26) Bunch 1964, (27) Banks and Orr 1965, (28) Svoboda et al. 1980, (29) Wade 1987, (30) C. R. Brown, pers. comm.

erage clutch size (mean = 4.97 eggs, SD = 0.58, $n = 214$) in a nest-house population in Texas (Brown 1978a). The smaller clutch sizes in this natural population could be due to the use of natural cavities, the smaller size and weight of females (Brandt 1951, Johnston 1966, Behle 1968), or some other factor such as food availability.

COLONIALITY AND SOCIAL BEHAVIOR

Although martins were not highly colonial in this natural population compared with martin colonies in nest-houses, nests were grouped on a larger geographic scale (Fig. 3). This clumping of nests was not due solely to physical factors since areas along roads without martin nests had similar densities of mature saguaros, and appeared to have an abundance of nesting cavities. Despite the relatively large nearest neighbor distances in these groups (100-400 m), martins quickly formed mobs of 6-10 birds in response to a model crow predator at the nest (Fig. 4). These breeding groups were focal points for many social interactions, including dawn-singing, intruder activity, and predator mobbing.

The distribution of nesting cavities in the Sonoran Desert is not necessarily similar to the distribution of natural cavities in other parts of the Purple Martin's range. Thus, the Sonoran Desert population cannot be used as a direct model of ancestral eastern populations. A review of reports in the literature of colony sizes of martins nesting in natural cavities in tree snags or rock crevices (Table 2) gives an indication of common colony sizes for the eastern and mon-

tane western race, *Progne subis subis*. Reports of colonies (2 or more pairs) are as common as reports of solitary nests, and large colonies have been reported in both eastern and western populations (Table 2). Colony size ranged from 1-300 pairs, with an average of 6.6 pairs (SD = 11.6, $n = 29$) excluding the extremely large colony. Allen and Nice (1952) report a similar range in colony size for house-nesting martins in eastern North America, and an average colony size of 8.7 pairs in Michigan ($n = 22$ nest-house colonies) and 7.9 pairs in Illinois ($n = 29-40$ nest-house colonies). In ancestral natural populations, solitary nesting likely occurred more frequently than it does today in nest-houses. However, nest-house colonies clearly fall within the range of breeding densities to which martins were exposed historically.

Brown and Hoogland (1986) suggest that diving at predators is a high risk behavior associated with solitary (colonial) nesting in swallows. Purple Martins in this study dove at the predator model in 54% of trials, and similar predator presentation trials at martin houses in Oklahoma resulted in diving behavior in 9 of 10 trials at different colonies (Stutchbury, unpubl. data). However, this does not indicate that historically Purple Martins were solitary-nesters. The dichotomy between solitary and colonial nesting overlooks those species whose nests are loosely clumped and have a high degree of social interactions. Tree Swallow (*Tachycineta bicolor*), also secondary cavity-nesters, are not colonial (Muldal et al. 1985) but often nest at densities of 4-12 pr/ha (Robertson and Rendell 1990). Similar

to the Purple Martin, this species commonly dives at predators (Stutchbury, pers. obs.).

Many breeding pairs in this study had extra nesting cavities within 25 m of their own cavity, even in the same saguaro, thus the availability of cavities did not prevent martins from nesting closer together. However, breeding pairs occupied an area around their nesting site with an average radius of 20–30 m, and defended extra cavities up to 115 m away. In nest-houses, martins defend a much smaller area (usually less than 1 m²), but they also defend multiple cavities (Brown 1979). The potential benefits of defending multiple nesting cavities include having an alternate nesting site in case the original site is destroyed, reducing interference from neighboring pairs (Robertson and Gibbs 1982), increasing the potential for polygyny (Brown 1979, Quinney 1985), and gaining opportunities for extra-pair copulations if neighbors are allowed to settle in those cavities (Morton et al. 1990). In early July 1988, I discovered one adult male with two females nest building in cavities only 0.5 m apart in the same saguaro. This saguaro blew over in a storm a few days later, and a pair (presumably the male and one female) immediately re-nested in a third cavity only 15 m away.

In this study, intrusions occurred during only 30% of the half hour observation periods, but owners repelled intruders in 18% of all intrusions. Intense fights, where birds peck and grapple with each other on the ground or inside a cavity, were not observed. In an Oklahoma nest-house population early in the season (Stutchbury 1990), the intrusion rate was much higher (60% of all watches) but the attack rate of male intruders was similar (20%). The relatively low frequency of intrusions may be representative of low-density martin populations, and correspondingly high availability of cavities.

Based on an annual post-juvenile survival rate of 0.45 from returns of banded adults (Stutchbury, unpubl. data), and assuming a similar survival rate for the Sonoran Desert population, the expected ratio of subadults to adults in the population (Robertson and Rendell 1990) is about 1 subadult to 0.82 adults, or 55% subadults in the population. Since only 5–17% of breeding males were subadults, many subadults were not breeding in their first summer. Subadult males were often seen intruding on territories, whereas adult male intruders were rarely observed. Since there were five instances of subadult males de-

fending cavities without a mate (for 24 and 37 days, in two cases), and not all cavities were re-used in subsequent years, there may be a lack of females, rather than nesting cavities. Non-breeding subadults are typical of many passerines with delayed plumage maturation (e.g., Flood 1984, Stutchbury and Robertson 1985, Hill 1988, Bjorklund 1989). Although some subadult males in nest-house populations are floaters (Brown 1978b) or remain unmated after obtaining a territory (Rohwer and Niles 1979), a high proportion (36–55%) of breeding males are subadults (Brown 1978a, Morton 1987) in contrast with this natural population.

Subadult males had little blue feathering on their undersides; all 21 breeding subadults had an area of 0–2.7 cm² of blue feathering (dull rank). This contrasts sharply with eastern populations of martins, where subadults can have extensive blue feathering on their undersides, ranging above 5 cm² (Rohwer and Niles 1979, Stutchbury, in press b). In addition, many subadult males from eastern populations have extensive blue feathering on the forehead (Rohwer and Niles 1979), whereas all subadults from this population had tan-colored foreheads (as do all females). Rohwer and Niles (1979) found that subadult males from western populations, which also use natural cavities, tended to have less blue on their throat and breast than eastern populations. If the dull subadult plumage plays some role in reducing the costs to floaters of searching for breeding opportunities (Studd and Robertson 1985), then the selection pressure to maintain a dull plumage may be stronger in natural populations where fewer subadult males are able to breed in their first year. However, since females are also paler in coloration in these western populations (Johnston 1966, Behle 1968), this geographic variation in coloration may be due to ecological or non-adaptive factors, rather than the use of natural cavities.

The close mate guarding and high frequency of forced copulations by males documented in nest-house populations (Morton 1987) were not observed in this population. The low density of breeding pairs, and the defense of relatively large territories around the nest cavity, likely limits the opportunities for extra-pair copulations, and hence reduces the benefits of mate guarding. Morton et al. (1990) proposed that male dawn-song functions to attract subadult males to the colony, so that older males can gain forced extra-

pair copulations with the mates of the younger males. However, in this natural population where mate guarding and forced copulations were not observed, dawnsong was widespread. Dawnsong in this population must have some benefit other than increasing opportunities for extra-pair copulations. The benefits of grouping nests (as opposed to nesting solitarily) are not known for Purple Martins, but dawnsong could function to increase local colony size, possibly increasing an individual's ability to detect predators and locate ephemeral food resources (e.g., Brown and Brown 1987, Brown 1988).

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