EXTRAPAIR FERTILIZATIONS AND THE EVOLUTION OF COLONIAL BREEDING IN PURPLE MARTINS

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ABSTRACT.—We used DNA fingerprinting to show that, in Purple Martins (*Progne subis*), forced extrapair copulations (FEPC) result in age-biased extrapair fertilizations. Older males achieved 96% paternity of their broods and increased their fecundity at the expense of young males, which achieved only 29% paternity. Older males recruit young males and females to unused nesting cavities that they had previously defended against other older males. Each year, nearly half (45%) of the breeding martins were recruited young birds not born in the colony. Recruitments are individually timed and begin when each older male's mate has completed a nest. Adult males may have accrued an average of 3.6 fertilized eggs through forced extrapair copulations in addition to eggs produced by their mates (4.5 eggs) for an overall average of 8.1. Noncolonial males without the opportunity for FEPCs would suffer 44% lower lifetime fecundity. Thirty-six percent of the eggs in the nests of young males were the result of egg parasitism, the significance of which is unstudied. These findings support the hypothesis that colonial breeding evolved in Purple Martins to increase the opportunity for extrapair fertilizations. Martins may be an extreme example of a general trend in breeding systems where migration and temperate climate concentrate fertile females in time and space. *Received 26 May 1989, accepted 12 October 1989.*

COLONIAL breeding has evolved often in birds that do not defend feeding territories, a trait common in swallows (Birkhead 1979, Gladstone 1979, McKinney et al. 1984, Wittenberger and Hunt 1985, Emlen and Wrege 1986, Brown and Brown 1988a). Purple Martins (*Progne subis*) seem to gain none of the many suggested advantages for colonial breeding in swallows (reviewed in Shields and Crook 1987). Colonial breeding in Purple Martins is not explained by predator satiation (they do not nest synchronously and colony size is small). They capture large, dispersed food items to feed young (Walsh 1978), which precludes the use of information from colony-mates to locate prey concentrations, and they do not reduce predation by mobbing predators in large groups (Hoogland and Sherman 1976, Brown 1986, Brown and Brown 1987, Stutchbury 1988). Martins take little individual risk in mobbing, fitting the pattern found in other colonial swallows (Brown and Hoogland 1986). Purple Martins would seem to gain no advantage, yet still have the costs, of group living. Costs include increased intraspecific competition for critical resources and increased ectoparasite or disease transmission (Moss and Camin 1970, Alexander 1974).

The reason that Purple Martins nest colonially in forested regions may be related to constraints not found in smaller species of swallows or in other species of *Progne* that breed in the tropics. Monogamous pairing is standard in Purple Martins and the long breeding cycle (ca. 64 days) restricts them to one nesting per year (Allen and Nice 1952, Morton and Patterson 1983). Martins are the world's largest swallows (ca. 56 g; i.e. ca. 12 g heavier than other *Progne* species and the African Mosque Swallow [*Hirundo senegalensis*] Turner and Rose 1989). The young grow relatively slowly (Ricklefs 1968) and take 28 days to fledge after hatching. Both parents must feed for full-sized broods to survive, and males and females of older pairs share equally in provisioning young (Allen and Nice 1952, Morton 1987). Leffelaar and Robertson (1986) discuss this requirement in the Tree Swallow (*Tachycineta bicolor*). Thus, fecundity cannot be increased through multiple nesting or polygyny.

Males might overcome this constraint through forced extrapair copulations (FEPC) (Brown 1978, Morton 1987), but no data are available on the success of FEPCs in achieving extrapair fertilizations. In 1984, females that were not
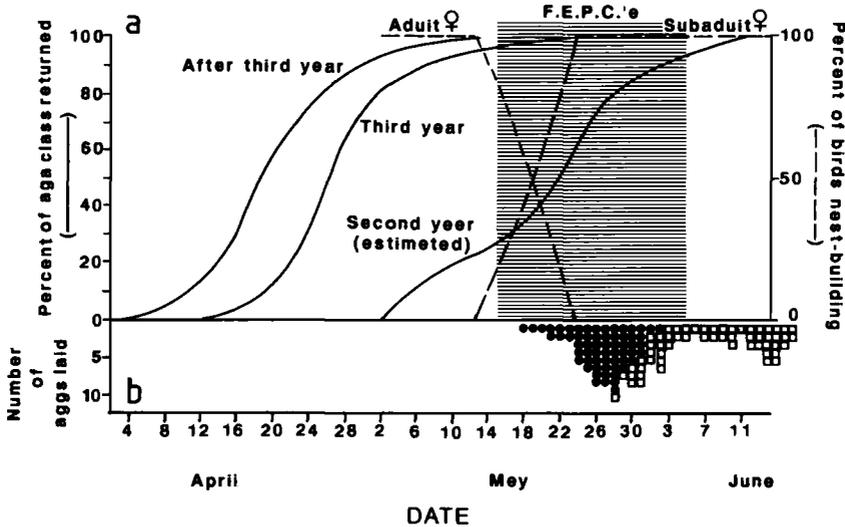
Fig. 1. (a) Percentage of final total breeding adults (after-third and third year) and subadult-plumaged (second year) Purple Martins by date (solid lines: average for 3 yr, arrivals summed over 3-day intervals). Percentage of all nest-building females (either adult or subadult by date) is shown by dashed lines. The shaded area shows dates of most intense forced extrapair copulation activity (FEPCs) and is also the time of most active dawnsinging by adult males. (b) Number of eggs/day layed by mates of adult males (filled circles) and subadult males (open squares) in 1987, in relation to the events in "a."

guarded by their mates suffered an average of 2.6 FEPCs per female in which cloacal contact by the male with the female was observed. Nevertheless, mate guarding was highly variable and its intensity was unrelated to the age of the male (birds in their second calendar year of life [SY] versus birds past the second calendar year [ASY]). Individual males mate-guarded from 0–100% during forays to the ground by females to collect nest material, the main situation in which FEPCs are observed. Furthermore, no correlation was found between mate-guarding intensity by males and their parental feeding effort (Morton 1987).

DNA fingerprinting (Jeffreys et al. 1985) provides reliable information on paternity and maternity. Knowledge of the genetic parentage of young can enhance understanding of behavior that otherwise appears enigmatic. Nocturnal, predawn singing (dawnsong) by male ASYs (Morton 1985) is one example. After-second-year males begin dawnsinging when their mates initiate egg laying (Morton pers. obs.). Because pairs are formed a month or more earlier, dawnsong does not function in this pair bonding. Second-year birds arrive at the colony in large numbers after dawnsinging begins (Fig. 1a). Morton (1988) hypothesized that male ASYs in-

crease their fecundity through FEPCs on newly recruited females, which pair with male SYs. If this is true, then male SYs should have lower paternity relative to male ASYs. We tested this hypothesis through the use of DNA fingerprinting.

We show that FEPC success is achieved by older males at the expense of young ones, and it provides a sufficient source of selection to favor colonial breeding and not favor nesting singly.

MATERIALS AND METHODS

Colonial breeding behavior in martins.—Six of the eight species in the New World genus *Progne* nest singly (includes *Phaeoprogne tapera*). However, the species limits in *Progne* are uncertain (AOU 1983). The Cuban Martin (*P. cryptoleuca*) and Caribbean Martin (*P. dominicensis*) may be colonial or noncolonial, depending upon nest-site availability (Wetmore and Swales 1931). Gray-breasted Martins (*P. chalybea*) nest as isolated pairs and do not tolerate proximity even when provided with a martin house (Beebe et al. 1917). Purple Martin males have a repertoire of song types acoustically designed to overcome masking in the "cocktail party" cacophony of colonial breeding. These songs, used chiefly by males perched near defended nest sites, have rhythmic syntax and end with a series of punctuated pulsed notes. These differ from its dawn-

song (Morton 1985). Brown (1984) termed these "croak songs" and Bitterbaum (1986) used "primary song," in a comparison of Purple, Gray-breasted, and Caribbean martins. Purple Martin songs are adapted acoustically for use in colonial breeding, whereas other *Progne* species use song for long-distance defense of isolated nesting sites. Volunteers, who wished to attract martins to unoccupied martin houses, played recorded dawnsong from early to mid-morning during SY arrival to attempt to attract SYs in the absence of live martins. A sample of unoccupied martin houses where playbacks were not performed were observed for comparison with those where they were performed.

Purple Martins breed colonially in forested areas of North America. Historically, they colonized dead tree snags that had accumulated woodpecker holes (e.g. Wilson 1832). Most martins in western North America use such sites (Allen and Nice 1952, Richmond 1953). There are few historical reports of martins breeding as isolated pairs in single-cavity sites in forest biomes even though single-cavity sites are more common than multiple-cavity sites (*contra* Brown 1984). They rarely colonized cliff sites (Bent 1942). American Indians of the southeastern United States grew a variety of the gourd (*Lagenaria siceraria*) specifically for Purple Martins (Speck 1941) and passed the longstanding tradition on to European colonists. Currently, in eastern North America, martins nest almost exclusively in gourds or martin houses provided by humans. These are best viewed as supernormal stimuli for martins rather than as a cause of colonial nesting (see below). Purple Martins in the southwestern deserts of the United States, however, nest solitarily in woodpecker holes in saguaro cacti (*Carnegiea gigantea*) (Phillips et al. 1964). Martins may prefer the larger cavities made by Northern Flickers (*Colaptes auratus*), which kill the cactus stem and, therefore, do not accumulate to provide colony-nesting potential (McAuliffe and Hendricks 1988). Hereafter, we refer only to the colonial breeding populations of Purple Martins unless otherwise stated.

Demographic profile of the study colony.—We marked for individual identification breeding adults and their young in a colony located in Severna Park, Anne Arundel County, Maryland. The nearest colony is ca. 5 km away. All young fledged had been banded since the colony began (1976). Since 1979 (usually ca. 1 July), adults were captured in their nesting cavities at night by a specially designed martin-house trap (see Morton and Patterson 1983). A complete relationship matrix of the breeding adults was calculated by J. Ballou (Ballou 1983).

The colony is only 9 m from Morton's house, and the birds were observed and individuals identified with a 40× telescope from a second-story window. The dates when banded ASY individuals arrived in spring were recorded in 1986–1988. We estimated the numbers and arrival dates of SYs, most of which were

unbanded, by daily counts of individuals and by identification of male SYs through their individualistic speckling of dark feathers. The plumage of male ASYs is entirely purple, allowing easy distinction from that of SYs (Niles 1972a). The start of dawnsinging and nesting chronology were recorded daily. The colony was housed in three 24-compartment aluminum martin houses (Trio Manufacturing Company) that can be raised and lowered vertically on 4.3 m poles for easy access to the compartments.

We obtained data on mate guarding in 1984 and 1987 following methods used earlier (Morton 1987). If a female was followed by her mate when she left their compartment to collect nest material, this was tallied as one mate-guarded trip. Nest material was gathered within 40 m of the colony site. We studied 20 pairs daily from the initiation of nest building to nest completion (when the birds bring green leaves plucked from trees to line the nest cup).

DNA fingerprinting.—In 1987, we obtained blood samples from 12 complete families (7 with male SYs and 5 with male ASYs) of the 30 breeding pairs. Samples were obtained from some but not all family members of the remaining 18 families. In these cases, the male or female roosted outside of the nest box on the trapping night. Two more families were completed by the 1988 capture of one female and one male that escaped capture in 1987—for a final sample of 7 SY families and 7 ASY families. We had obtained mate-guarding data previously (during nest building) on 13 of the 14 pairs. The number of feeding trips by each pair member was recorded from two days of videotaped records (28 and 29 June 1987). Simultaneous analyses of feeding by all colony members controlled for weather effects on foraging conditions. To control for differences in age and number of young between nests, we compared feeding rates of mates.

Blood was collected by jugular venipuncture (0.25–1.0 ml) in a heparinized syringe on 3 July 1987. Whole blood was separated by centrifugation, and packed red cells were stored at −70°C. DNA extraction was accomplished by standard protocols that involve SDS/proteinase K digestion, phenol/chloroform extraction, and ethanol precipitation (Maniatus et al. 1982). We used ca. 10 μg of DNA in a 40 μl reaction mixture to which 80 U of *Hin*fI was added. The digests were incubated overnight at 37°C and electrophoresed in 0.7% agarose at 75 V for ca. 19 hours. Gels were depurinated in 0.25 M HCl, alkali denatured in 0.5 M NaOH/1.5 M NaCl, and neutralized in 0.5 M Tris/3 M NaCl before Southern transfer onto Amersham Hibond membrane. The 33.6 minisatellite hybridization probe (Jeffreys et al. 1985) was radioactively labeled by the primer extension method with alpha ^{32}P-dCTP to specific activities of greater than 5 × 10^8 cpm/μg. Membranes were hybridized overnight at 62°C in a buffer of 0.15 M NaCl, 0.015 M sodium citrate, 10% dextran sulphate, and 5 × 10^7 cpm/ml of probe. Wash stringencies followed Jeffreys et al. (1985). Filters were

exposed for 2–6 days at −70°C with one intensifying screen. Final DNA fingerprints were prepared by Cellmark Diagnostics, Germantown, Maryland. All comparisons reported were from DNA fingerprints on the same autoradiograph. Autoradiographs were visually scored for band sharing (following the methods of Wetton et al. 1987 and Burke and Bruford 1987).

RESULTS

Chronology and recruitment.—Colonies form when adults appear at their past breeding site and then immigrant SY breeders arrive. After-second-year martins migrate to traditional breeding sites a month or more before SY breeders (Allen and Nice 1952). At our site, adults arrived from 2 April until 11 May, and most were laying when SYs arrived (Fig. 1). Adults in their third year arrive later than older adults but before most SYs (Fig. 1a).

Adult males pair monogamously and nest in one cavity but defend extra nest holes in martin houses from other adult males (Allen and Nice 1952). We found 2–6 extra compartments were usual, with a maximum of 24 (an entire house) defended by one male. Brown (1979) reported that up to 36 cavities were defended by a single male. Subadult pairs began to occupy the extra nest cavities after ASY males began to line their nests with green leaves (Morton 1987) and their mates began to lay (Fig. 1b). Most SYs were new to the colony. Only 38 (25 males and 13 females) of 733 (5%) young fledged in 1976–1987 returned to breed in their natal colony. From 1979 to 1988, 236 of 527 (45%) breeding birds in the colony were new recruits. Most breeding ASYs are derived from birds first recruited as SY breeders (169 of 291, 58%).

The arrival of large numbers of SYs coincides with the beginning of dawnsinging by those male ASYs that are carrying green leaves to line nests (Fig. 1a). Dawnsinging is an individual performance from beginning to end and does not involve any cooperation (e.g. flying as a group, synchronizing departure from the colony houses). Dawnsong lasts from ca. 0415 until 0540 EDT. Singing commences in mid-May and ends in mid-June in Maryland. A few male SYs begin dawnsongs for a few days in mid- to late June, after their mates begin incubation. Playbacks attracted one to three SYs at 3 of 5 previously unused martin houses, whereas 0 of 10 houses where dawnsong was not played attracted martins. Playback significantly attracted

martins ($P = 0.02$, Fisher exact probability test, Siegel 1956). Additionally, male ASYs ceased defending "extra" nesting compartments against arriving male SYs (Rohwer and Niles 1979), although they continued to exclude male ASYs and vigorously defended the cavity that contained their nest against all males (pers. obs.). Finally, male ASYs began to attempt FEPCs with nest-building females (Fig. 1a).

DNA fingerprinting.—We tested the effectiveness of FEPC in fertilizing extra eggs through DNA fingerprinting (Jeffreys et al. 1985, Wetton et al. 1987, Burke and Bruford 1987). Purple Martin minisatellite phenotypes were extremely variable. In one comparison of eight unrelated adults, we distinguished a total of 65 bands, of which each averaged (±SE) 21.90 ± 0.398. Comparing these eight individuals in pairs, the probability that a band present in one is also present in another was 0.089. The probability that all bands present in one individual are present in another is $0.089^{21.9}$ ($<10^{-24}$).

We made pairwise comparisons of banding patterns with the similarity coefficient D, which varies from 0 (when no bands are shared) to 1 (when all bands are identical) (Wetton et al. 1987). Parents and offspring would be expected to have D values ca. 0.500. We considered D values <0.400 as genetic mismatches between putative parent and offspring. This is a conservative value because the average D ($\bar{D}$) value for unrelated adults was 0.187 ± 0.013 ($n = 40$ pairwise comparisons between birds represented on the same autoradiograph). After-second-year and second-year males differed strikingly in paternity, regardless of their mates' ages or the intensity of mate guarding (Fig. 2). In male ASYs, $\bar{D} = 0.538 \pm 0.016$, and only 1 of 28 young was genetically mismatched with its putative father (Table 1). Second-year males fathered few of the young (7 of 24, 29%) in their nests ($\bar{D} = 0.288 \pm 0.032$). In contrast, female SYs and ASYs did not differ as greatly in maternity, but 36% of the young in female SY nests ($n = 28$) may have resulted from egg parasitism (Table 1). In after-second-year females, $\bar{D} = 0.536 \pm 0.025$; in second-year females, $\bar{D} = 0.420 \pm 0.019$.

The DNA fingerprints were also examined for band mismatches (Burke and Bruford 1987). Each band in an offspring not also represented in one or both of the parents is due to a mutation or an extrapair fertilization. Single mismatched bands were found in 2 of 28 young raised by male ASYs. An average of 4.95 ± 0.481 mis-
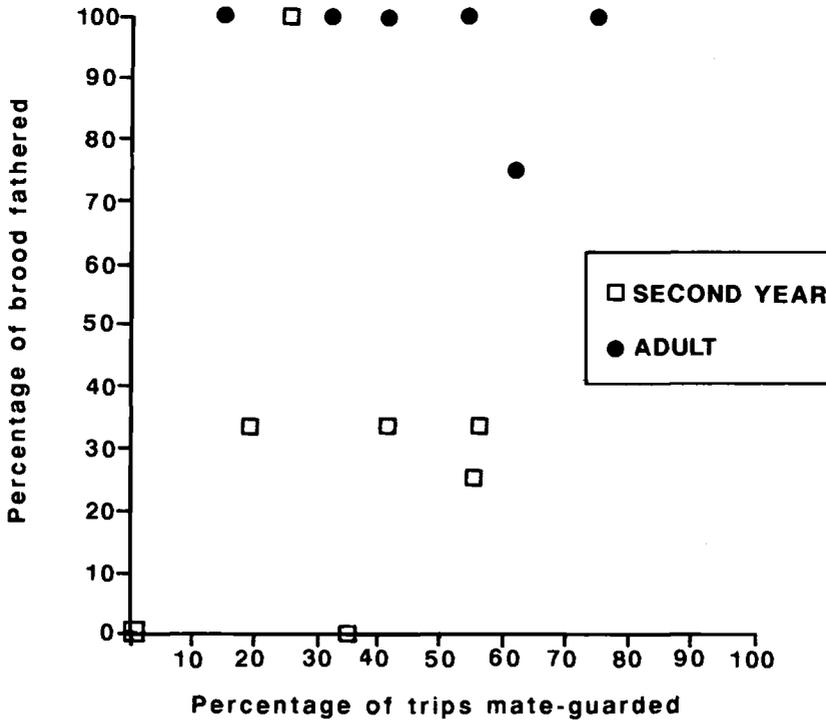
Fig. 2. Percentage of nest material gathering trips that a male guarded his mate against forced extrapair copulations versus percentage of brood fathered as determined by DNA fingerprinting.

matched bands per young was found in 19 of 24 young cared for by male SYs (Table 1). The mate of the only uncuckolded male SY in our sample (see Fig. 2) began to lay on 14 June, after the time of abundant FEPCs (Fig. 1a).

The payoff to adult males by nesting in sites with "extra" nesting cavities is enormous. If 3 or more band mismatches define a young genetically unrelated to its male "parent," then 83% of the 1987 young are unrelated to the male SYs that attended them. Because 57 eggs were laid in nests controlled by male SYs (Fig. 1b), potentially 47.3 eggs total—or 3.6 eggs per male ASY ($n = 13$ male ASYs in the colony)—were gained by FEPCs. If male ASYs did not have the opportunity for FEPCs, they would suffer 44% lower lifetime reproductive success than those in the study colony. Obviously, this is an average and some male ASYs undoubtedly are more successful in FEPCs than others.

Second-year males adjusted to their low paternity and fed young significantly less frequently than their mates did (51 vs. 67 feedings per day, $n = 10$ pairs, $T = 6.5$, $P < 0.05$, Wilcoxin matched-pairs signed-rank test). After-second-

year males and their mates do not differ (78 vs. 87 feedings per day, $n = 11$, $T = 21.5$, $P > 0.05$).

DISCUSSION

Forced extrapair fertilizations and the evolution of coloniality.—Although the lack of territorial food defense allows colonial breeding to evolve easily in swallows and other groups (Wittenberger and Hunt 1985), colonial breeding in Purple Martins is less easily explained. Members of one Purple Martin population and of all the other species of *Progne* are noncolonial breeders. Coloniality in Purple Martins is not simply an ancestral breeding system. We believe that Purple Martins breed colonially in forested portions of their range because of a combination of ecological and genetic factors. Multicavitied tree snags are a necessary ecological background. The restricted breeding season of the Temperate Zone climate and slow growth of young produce breeding constraints. Forced extrapair copulation is the only way for males to increase fecundity, and this may be enhanced by a cli-

TABLE 1. D values from paired comparisons of Purple Martin young with each of their putative parents, and the number of bands (in parentheses) not found in one or both parents, calculated from DNA fingerprints using Jeffrey's Probe 33.6. Broods are separated with a space and arranged according to the age of the male parent.

Broods with male ASYs[a]		Broods with male SYs[a]	
0.519 (0) 0.436*	0.526 (0) 0.632*	0.156 (3)0.563	0.418 (0) 0.540*
0.644 (0) 0.500	0.691 (0) 0.618	0.182 (4) 0.484	0.262 (3) 0.561
0.436 (0) 0.436	0.602 (0) 0.792	0.035 (5) 0.344	0.137 (5) 0.551
0.581 (0) 0.452	0.632 (0) 0.597	0.129 (9) 0.522	
0.500 (0) 0.557	0.483 (0) 0.621	0.111 (4) 0.131	0.509 (0) 0.340
		0.122 (3) 0.357	0.100 (4) 0.517
0.444 (0) 0.545*	0.615 (0) 0.582*		0.271 (6) 0.456
0.367 (1) 0.720	0.577 (0) 0.509	0.308 (7) 0.500	
0.400 (1) 0.714	0.509 (0) 0.448	0.308 (6) 0.411	0.333 (6) 0.340
0.464 (0) 0.702	0.423 (0) 0.436	0.286 (4) 0.515	0.146 (5) 0.250
		0.576 (0) 0.435	0.244 (9) 0.250
0.472 (0) 0.409	0.586 (0) 0.531		
0.542 (0) 0.375	0.679 (0) 0.475	0.444 (0) 0.525	0.523 (3) 0.576*
0.689 (0) 0.320	0.537 (0) 0.511	0.459 (0) 0.475	0.514 (1) 0.427
0.486 (0) 0.441			0.333 (7) 0.438
	0.554 (0) 0.375		
	0.548 (0) 0.429		
	0.546 (0) 0.487		

[a] Female ASYs are marked with an asterisk; for each young, male D value is on left, female D value to the right of the number of band mismatches (in parentheses).

matically restricted fertile period in females. The difference in breeding chronology between SYs and ASYs is also important to enhance fecundity for ASYs through forced extrapair copulations.

Strong evidence in favor of this hypothesis comes from the enormous genetic payoff accrued by male ASYs through FEPCs. If extrapair fertilization success was not related to age, then the proximate factors (discussed below) that underlie our hypothesis of colonial breeding in martins would remain only loosely related to reproductive success. The genetic payoff is the ultimate reason in favor of colonial breeding. The importance of breeding gregariously is highlighted by the fact that all FEPCs observed were initiated by colony members (Morton 1987, this study). There were no extracolony males engaging in FEPCs. Furthermore, from the vantage of its territory, a male is able to observe favorite spots where females gather nest material. Males prone to attempt FEPCs often wait at these sites for the appearance of unguarded females (See Morton 1987 for a description of FEPC behavior).

The genetic data illustrate the importance of many different factors that range from communication to arrival chronology, to enhance the payoff for male ASYs. The timing of these events suggested that male ASYs, with their

own nests secure, attracted SYs to the colony expressly to increase their fecundity. An attempting polygyny hypothesis seems unlikely as polygyny is virtually unknown in the species (Brown 1975) and has not occurred in our study colony in its 12-year history. An attempting polygyny hypothesis also fails to explain male SY recruitment. Early arrival of male and female ASYs to colony sites might result from competition for nest sites in a secondary cavity-nesting species (e.g. Stutchbury and Robertson 1987). Martins in the noncolonial southwestern populations, however, return a month or more later than more northerly colonial populations (Cater 1944, Phillips et al. 1964). This suggests that nest-site competition alone does not explain the early arrival of colonial populations.

Delayed return of third-year birds (TYs), especially males (Fig. 1a), may also be related to the competition for FEPCs they encounter for the first time. Third-year birds are in adult plumage, and most have nested before (as SYs) in the colony. We note that male SYs have undergone a complete, not a partial, molt (Rohwer and Butcher 1988), by the time they breed (Niles 1972b, Klimkiewicz and Hill unpubl. data). Thus the only difference between TYs and other age classes is that TYs are in adult plumage for the first time. As SYs, they "gave up" eggs in return for a chance to nest without

adult competition for nest sites. Now in adult plumage, TYs are in competition with older birds for both nest sites and extrapair fertilizations and must compete for nest-site dominance.

This hypothesis can be tested by comparing nest sites used between the second-year to third-year nesting with those between the third and fourth year of age. A sample of 18 male SYs from 1984 to 1988 that returned to breed as ASYs supports the difference in site dominance suggested. Of 18 males, 17 changed nest boxes or compartments within the same nest box between their second- and third-year nestings. The change between nest sites in TYs and the same individuals as 4-year-olds was significantly less: only 6 of 11 changed location ($\chi^2 = 4.4899$, df $= 1$, $P < 0.05$). Most of these changes were to compartments adjacent to their third-year sites. Nest sites held as a breeding male SY did not translate into dominance at that nest site upon return to the colony as a TY. We speculate that the timing of arrival is a balance between increased vulnerability to starvation from early spring cold weather (Mayfield 1969) and the genetic payoff accrued by having a completed nest and extra nest sites by the time SYs arrive and are available for recruitment. We believe that TYs, which do not have site dominance, avoid assymetrical contests for nesting compartments by delaying arrival at colonies until after-third-year birds (ATYs) have settled their contests. The middle arrival time of TYs represents an adaptive balance (feeding conditions are adequate to support the increased aggression necessary to fit into established male ATY territories) and is early enough to establish a nest and to be ready for FEPCs on the later arriving SYs.

Mate guarding.—Mate guarding has little to do with assurance of paternity (Fig. 2). Mate guarding and its variability in martins most likely permit the female to complete nest building (Gladstone 1979, Morton 1987). The earlier a male completes a nest to assure its monogamously based annual fecundity, the more time it can devote to FEPCs. Purple Martins carry green leaves to line the completed nest. This behavior is performed mainly by the male and may function as a precoitial display to induce frequent copulation with its mate during the female's most fertile period (Morton 1987). In the tropical Gray-breasted Martin, males neither guard mates nor use green leaves in the nest (Morton unpubl. data, but see Dyrcz

1984). This supports the precoitial display hypothesis but does not exclude an antiectoparasite function for green leaf use in nests by Purple Martins (Wimberger 1984).

Response of male SYs to lowered paternity.—Male SYs respond to lowered paternity levels by feeding nestlings at a lower rate than their mates. Male SYs will attempt to colonize a new nesting site away from male ASYs, but single male SYs are not successful in attracting mates. New colonies begin with a minimum of two nesting pairs because females will not nest alone with an isolated male (Morton, pers. obs. of the unsuccessful attempts of 3 isolated male SYs to attract mates vs. the successful "founding" of 8 new colonies by 2 or 3 male SYs). Females constrain second-year male options by avoiding noncolonial breeding, which eliminates this option for male SYs. The male SYs that join established colonies forfeit ca. 70% paternity but gain a nest compartment (one previously defended by a male ASY) and the presence of multiple nesting pairs that attract potential mates. At the Maryland colony, male SYs that did not attract a female by ca. 10 June did not nest. Although males do not gain site dominance until nesting for the second time as TYs, most SYs returned to our breeding colony for their entire lives. The loss of paternity in breeding the first year may be balanced by a higher lifetime genetic payoff through FEPCs.

Egg parasitism.—We were surprised to find that 36% of the young cared for by female SYs resulted from egg parasitism. This rate is similar to the 22–43% of parasitized nests found in Cliff Swallows (*Hirundo pyrrhonota*) (Brown and Brown 1989). Unlike Cliff Swallows, however, martins have not been observed to remove eggs (Brown and Brown 1988a, b). Egg parasites are likely to be other female SYs rather than female ASYs, as ASYs are incubating clutches when parasitism occurs and are unlikely to be laying eggs simultaneously (Fig. 1b). Perhaps the female SYs become egg parasites in part from the lack of parental effort from SY mates. However, the dynamics of this aspect of martin nesting biology remain unknown.

Cuckoldry potential relative to latitude.—The high rate of cuckoldry we found in Purple Martins may not be associated entirely with the colonial breeding system. Recently, other studies of migratory, Temperate Zone passerines showed higher than expected rates of cuckoldry in monogamous species that defend large, all-

purpose territories. For example, 30–40% of Indigo Buntings (*Passerina cyanea*) (Westneat 1987) and 34–38% in migratory populations of White-crowned Sparrow (*Zonotrichia leucophrys*) (Sherman and Morton 1988) were conceived via FEPCs. Indeed, Quay (1989) documented sperm transfer to females *during* migration in the Tennessee Warbler (*Vermivora peregrina*). In contrast, in nonmigratory Dunnocks (*Prunella modularis*), extrapair fertilizations were rare in monogamous pairs (Burke et al. 1989). In contrast, females should avoid FEPCs for several reasons (Burke et al. 1989, Westneat et al. 1990), not the least of which is injury. Cryptogamy is one predicted mechanism used by females to avoid FEPCs. One way to be relatively cryptogamous is for females to look like males, but this mechanism will be stable only if nest building is not correlated closely with fertility. In the Gray-breasted Martin, for example, nest building is highly synchronous in the late dry season in central Panama (Morton unpubl. data), but egg laying is delayed and highly asynchronous. Wetmore et al. (1984) report nesting almost throughout the year. Significantly, the sexes are alike in plumage as opposed to the extremely sexually dichromatic Purple Martin. Tropical- vs. temperate-breeding species of orioles (*Icterus* spp.) provide another example. The Purple Martin breeding system may, therefore, be an extreme case of a common system in the Temperate Zone. The pursuit of FEPCs may have more influence on avian biology, and with differing latitudinal consequences, than is currently appreciated.

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