

THE BIOLOGICAL SIGNIFICANCE OF AGE-SPECIFIC RETURN SCHEDULES IN BREEDING PURPLE MARTINS¹

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Abstract. We describe age-related differences in return dates in the colonial Purple Martin (*Progne subis*). Adults ≥ 4 years of age returned earlier than Age 3 adults which returned earlier than first-time breeders. Males tended to return slightly earlier than females in birds Age 3 and older. The arrival schedule results from competitive asymmetries over secondary cavity nest sites and predation pressure but not from the timing of reproduction. Older and earlier returning birds select higher nests. Nests located in higher levels suffer significantly less predation from climbing predators. The return dates of mates are not correlated but mated pairs do tend to be similar in age. Egg-laying date is not related to arrival date.

Greatly reduced certainty of paternity is correlated with a reduction in reproductive effort in first-time breeding males. The variable subadult plumage in Age 2 males provides for individual recognition, which benefits them in within age-class nest-site competition.

Key words: Purple Martin; arrival schedule; coloniality; mixed-reproductive strategy; subadult plumage; predation; *Progne subis*.

INTRODUCTION

In passerine birds, first-time breeders are well-known to arrive later and lay smaller clutches than older age classes (e.g., Hill 1989, Saether 1990). Hypotheses relating these patterns to life history strategy suggest that first-time breeders may be *constrained* because they lack skills associated with breeding and/or *restrained* because reduced reproductive effort in their initial breeding season will increase lifetime reproduction (Curio 1983). However, the theoretical underpinning of these hypotheses, that optimal life history is a balance between the allocation of resources to survival vs. reproduction (Williams 1966, Roughgarden 1979, Charlesworth 1980), is not well supported for short-lived species. Saether (1990) found only slight evidence that reproductive effort one year might influence reproductive performance at future ages.

We discuss age- and sex-related differences in return dates to breeding sites and nesting-cavity selection in the Purple Martin (*Progne subis*). Return dates are readily obtainable for martins because they nest colonially in human-provided "martin houses." Previous work on these life history traits did not consider age-specific dif-

ferences in paternity and maternity assurance. This omission is probably because the majority of bird species are socially monogamous (Lack 1968, Ford 1983). However, with new molecular techniques it is clear that social monogamy does not always coincide with parental assurance (Gowaty 1985, Westneat et al. 1990). Morton et al. (1990) showed in Purple Martins that paternity rates of first-time breeding males averaged only 29% whereas paternity rates of broods cared for by older males averaged 96%. Thus, an age-specific difference in paternity or maternity assurance may contribute to lowered reproductive effort in first-time breeders whether or not their lowered reproductive effort relates to lifetime reproductive success.

We describe the significance of arrival schedules at breeding sites for martins of known age in reference to both observed social behavior and genetic results of the male martin's mixed-reproductive strategy (Morton 1987). Arrival dates were analyzed for differences among age classes and between sexes, and arrival dates and ages of birds forming breeding pairs were compared. We also analyzed these data for differences among the tier heights (one of four levels in each house) used for nesting in relation to age, return date, and predation. We focus our attention on the return calendar to our study site but place this in the context of the continent-wide pattern of first arrival date at breeding sites.

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METHODS

Return dates were recorded at a breeding site in Severna Park, Maryland, consisting of three 24-compartment aluminum martin houses (Trio Manufacturing Co.) positioned 9 m from Morton's house. Each house contained four tiers with six compartments on each tier. Birds were observed with a 40-power telescope from a second-story window. Breeding adults had been individually color-banded since 1979, and all young banded since 1976, the year the colony was established. Additional data were collected at three smaller colonies, located 5–10 km from the main colony, and were included in the analyses when appropriate information was available.

We recorded the dates of arrival at the colony from 1982–1989 and consider these accurate to within 3 days for previously banded adults. Migrating martins rarely used the site for in-transit roosting, thus our data refer only to the arrival of breeding birds. Arrival dates of first-time breeders, most of which were new to the colony and unbanded, were recognized through their distinctive subadult plumage (Niles 1972); most subadult males could be individually identified due to distinctive plumage markings (Rohwer and Niles 1979). We restricted return date analyses to the more accurate data for subadults that were color-banded as fledglings in the main colony (returning to their natal colony to breed) or nearby colonies. Our data comprised birds from two (subadults in their second calendar year) to 10 years of age.

STATISTICAL ANALYSIS

Most analyses used the Statistical Analysis Systems (PC-SAS) package (SAS Institute 1985). The General Linear Model (GLM) procedure was used to examine variation in return date among different age classes, between sexes, among years, and among tiers, and variation in tier selection among age classes and between sexes. Ray (1982) recommended using GLM when the data are unbalanced (unequal cell sample sizes), which was the case in this study. Return dates were not normally distributed (entire data set; $W = 0.89$, $n = 205$, $P < 0.001$), however tests performed on all the age classes separately (except Age 2) could not be distinguished from a normal distribution. To be cautious, all parametric analyses of variance were done on both nontransformed and rank-transformed data (see Conover and

Iman 1981 for use of parametric tests on ranked data). For clarity, the results from the unranked data are presented. In all comparisons between these approaches, the results were nearly identical with insignificant changes in the F -values. In most instances, the proportion of the variance explained was greater when using ranked data. Thus, the reported values are probably conservative.

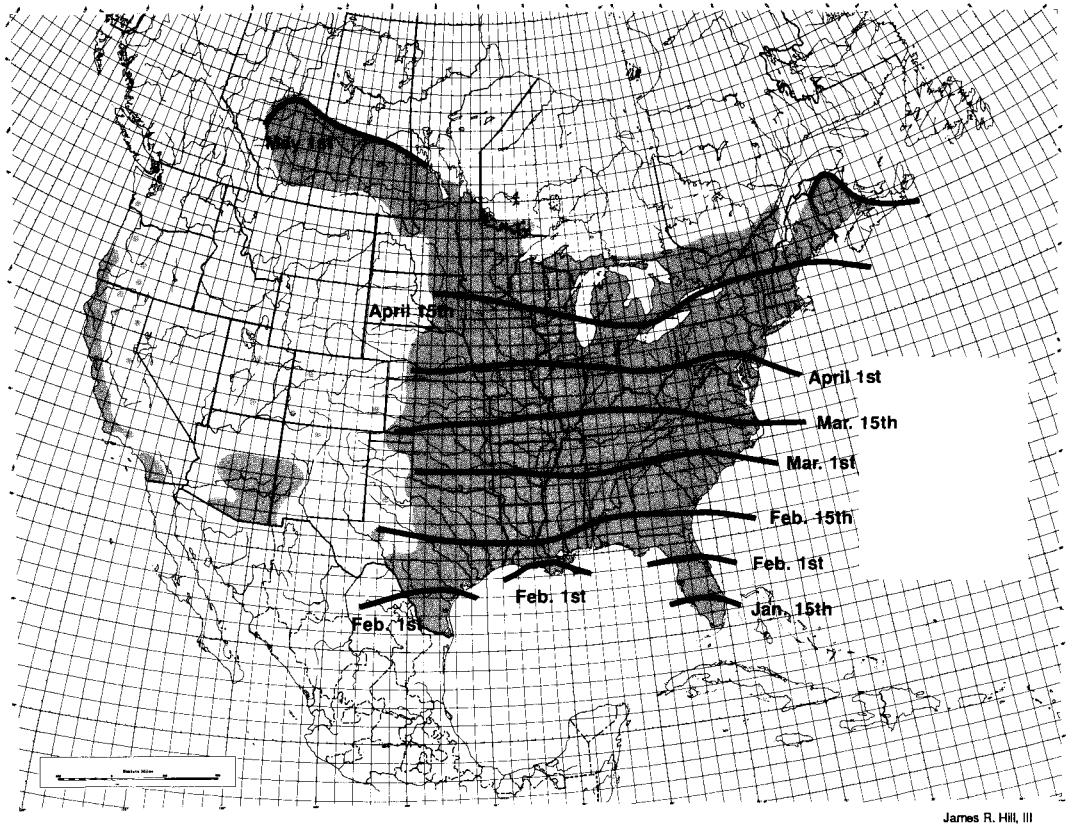
Tukey's studentized range test was used to compare means of return date or tier selection between the sexes, among age classes, or between years. The Tukey procedure in SAS is a powerful procedure and is recommended for analyses with unequal cell sizes (Ray 1982). As mentioned above, this procedure was done on both non-transformed and rank-transformed data with no differences in outcome. Contingency tables were analyzed using χ^2 or G -test for independence (Sokal and Rohlf 1969).

RESULTS

GENERAL PATTERN OF ARRIVAL

Purple Martins winter in South America largely east of the Andes, and are abundant in southeastern Brazil (AOU 1983, pers. observ.). Adults first appear at breeding colony sites in mid-January in southern Florida and progress northward ca. 3–5 degrees latitude (330–550 km) each half month until ca. 1 May, when they reach the northern limits of the current breeding range in North America (Fig. 1). Formerly they bred north to Great Bear Lake, Northwest Territories (65°N) and arrived there about 17 May while snow still partially covered the ground, and the rivers and lakes were still ice-covered (Wilson and Bonaparte 1832).

The first arrivals at a colony are males in adult plumage. These are followed closely by adult females, and often females first appear at the same time as males. Subadults of both sexes arrive several weeks later. This age-related pattern is typical throughout the breeding range (Allen and Nice 1952) except for martins breeding noncolonially in saguaro deserts in southwestern U.S. These noncolonial birds first arrive at breeding sites in early May (Phillips et al. 1964), 2½ months after martins arrive at colonies at the same latitude in the eastern U.S. Whether this arrival difference is due to the food limitation of the desert habitat or the difference in coloniality between the populations is unknown.



James R. Hill, III

FIGURE 1. Average first return dates to breeding colonies throughout the Purple Martin's breeding range, based on returns to four or five colonies per state or province having arrival dates covering 10–50 years. The isobars connect colonies with similar return dates.

Eastern birds arrive during normal or above normal temperatures but often suffer high mortality if cold and stormy weather ensues (Bent 1942, Allen and Nice 1952, Mayfield 1969, Steward 1972). We later discuss hypotheses offered to explain the dangerously early arrival of adults to northern latitudes but now focus on our study site at latitude 38°N in Maryland.

CORRELATES OF RETURN DATES TO A SINGLE COLONY

Return dates to our study site (Fig. 2) showed the common passerine pattern of first-time breeders (Age 2) returning significantly later than all older age classes. Additionally, Age 3 birds returned significantly earlier (27 days on average) than Age 2 birds, and significantly later (11 days on average) than all older age classes (Tukey's studentized range test). Return dates differed significantly among age classes (ANOVA; $F = 71.44$,

$P < 0.0001$) and age explained 75% of the variation in return date. Age 2 differed significantly from all other ages and Age 3 differed from Ages 2, 4, 5, 6, and 7 (Tukey's). Ages 4 and greater could not be distinguished statistically from one another and were pooled in some subsequent analyses. Return dates did not differ among years ($F = 0.98$, $P = 0.32$) or between the sexes ($F = 0.02$, $P > 0.9$) in one-way ANOVAs.

Within age classes, males and females differed significantly in return date for Ages 3, 5, and 7, with males arriving earlier than females (Fig. 2). The tendency for males to arrive earlier than females was found in all age classes except Age 2. On average females arrived 5.2 days earlier than males in Age 2, and males arrived 4.8, 2.5, 7.1, 2.6, and 8.8 days earlier than females in Ages 3 through 7, respectively.

A two-way ANOVA indicated that return dates were influenced by age and sex ($F = 65.44$, $P <$

0.0001, $r^2 = 0.75$), but sex was significant only after age had entered into the model ($F = 5.2$, $P < 0.024$); there was no significant age by sex interaction. As expected, when the analyses were repeated using grouped age classes (grouped as 2, 3, and ≥ 4 ; see above) both age and sex continued to affect return date ($F = 124.8$, $P < 0.0001$). However, the influence of females arriving earlier than males in Age 2 and later in the other two age-class groupings now produced a significant interaction ($F = 4.95$, $P < 0.008$).

AGES AND RETURN DATES OF MATES

There is a significant association between the ages of mates (Table 1; $\chi^2 = 170.7$, $df = 9$, $P < 0.0001$), with older females being paired with older males. In fact, 78% of Age 2 females were mated to Age 2 males, and less than 3% mated with males older than 3 years of age (Table 1). In contrast, none of the oldest (≥ 5 years) females mated with Age 2 males and 75% mated with males older than 3 years of age. Females of Ages 3 and 4 were intermediate, with 27% and 49% pairing with males greater than 3 years of age, respectively. This pattern occurred in all the colonies. Such a pattern could arise from pairs forming lifetime pair-bonds, but the same individual martins rarely remated. For example, of 15 pairs that were mated in 1984 and for which both members were present at the colony in 1985, only two pairs (13%) remated. It is also not simply an artifact of the correlation of arrival times between age classes because there is no correlation between the return dates of mates ($F = 1.39$, $P < 0.25$) for all birds ≥ 3 (Age 2 excluded from analyses because of the low sample size for accurate arrival time data). There was also no correlation between the return dates of Age 3 and Age ≥ 4 females and their mates when analyzed separately ($F = 0.38$, $P = 0.56$; $F = 1.13$, $P = 0.30$).

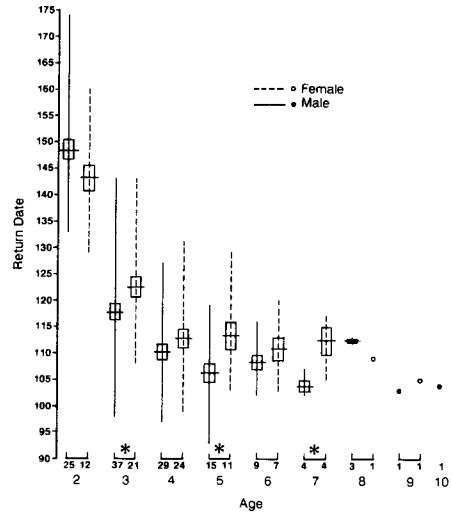


FIGURE 2. Return dates of males and females of different ages at the main study colony in Maryland (38°N). Day 90 = 31 March. Horizontal lines represent means, boxes SEs, and vertical lines the ranges. Ages in which the sexes differ significantly are denoted by *. Sample sizes recorded directly above the age classes for both males and females. Significant differences among age classes discussed in the text.

DIFFERENTIAL NEST-SITE SELECTION BY AGE CLASSES

The tiers selected for nesting did not differ among years ($F = 1.55$, $P = 0.13$) or between colony locations ($F = 1.25$, $P = 0.26$), and therefore, these data were pooled for subsequent analyses. Tier selection did differ significantly among the age classes ($F = 7.60$, $P < 0.0001$), but age explained only 7% of the variance (Fig. 3). Approximately 25% of the Age 2 birds managed to nest in the top tier (Fig. 3). The proportion of individuals nesting in the top tiers increased with age, with Age 3 birds displaying the population's

TABLE 1. Ages of females and their mates in four colonies in Maryland. The expected cell values (rounded) given in parentheses.

Age of female (years)	Age of mate (years)				Total
	2	3	4	≥ 5	
2	88 (42) ^a	22 (44) ^a	3 (17) ^a	0 (11) ^a	113
3	19 (45) ^a	71 (47) ^a	16 (19)	17 (11)	123
4	4 (15) ^a	17 (16)	15 (6) ^a	5 (4)	41
≥ 5	0 (9) ^a	6 (9)	12 (4) ^a	6 (2) ^a	24
Total	111	116	46	28	301

^a Observed cell value significantly higher or lower than expected.

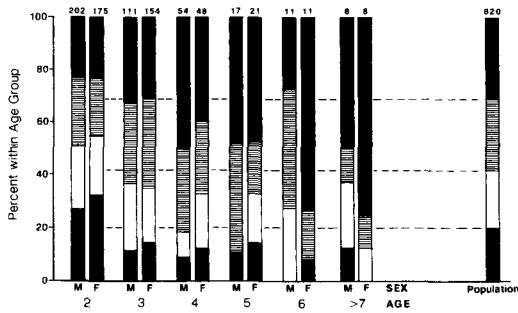


FIGURE 3. Percentage of males and females of different ages nesting in the four tiers. Tiers are arranged from top (black) to bottom (heavy horizontal lines). Sample sizes given at top of each bar.

average and older birds being over-represented, exceedingly so for the oldest age classes. Age 2 differed from Ages 3, 4, 5, and 6 (Fig. 3). All other ages could not be distinguished from one another, especially because individual peculiarities in a few older birds, especially males, increased the variance in age classes 6 and ≥ 7 .

The results changed slightly when age classes were grouped into Ages 2, 3, and ≥ 4 . Tier selection still differed among the three age categories ($F = 29.31, P < 0.0001$), but now all three age categories differed from one another (Tu-

key's) with Age 3 being intermediate. Each sex showed the same pattern, with a larger proportion of Age 2 individuals nesting in lower tiers (females, $n = 417, \chi^2 = 34.3, df = 6, P < 0.0001$; males, $n = 403, \chi^2 = 33.52, df = 6, P < 0.0001$). Because older birds return earlier than young birds and older birds select compartments in the upper tiers we assume that nesting cavities in the upper tiers are favored.

RETURN DATE AND NEST-SITE SELECTION

The return dates of individuals nesting in different tiers differ (Fig. 4; $F = 9.10, P < 0.0001$) and tier level explains 15% of the variance in return date. The four levels differed significantly from each other in mean return date (Tukey's), with the earlier returning birds, on average, securing nesting cavities in the upper tiers. This is expected because age is correlated with both return date and tier choice. The sexes do not differ in their return dates within a tier (Fig. 4; $P \geq 0.23$ for all tiers) and the return dates of mates were not correlated within tiers (top two tiers and bottom two tiers combined to maintain adequate sample sizes).

NEST-SITE QUALITY

Differential predation among nests situated in the different tiers is one possible explanation for

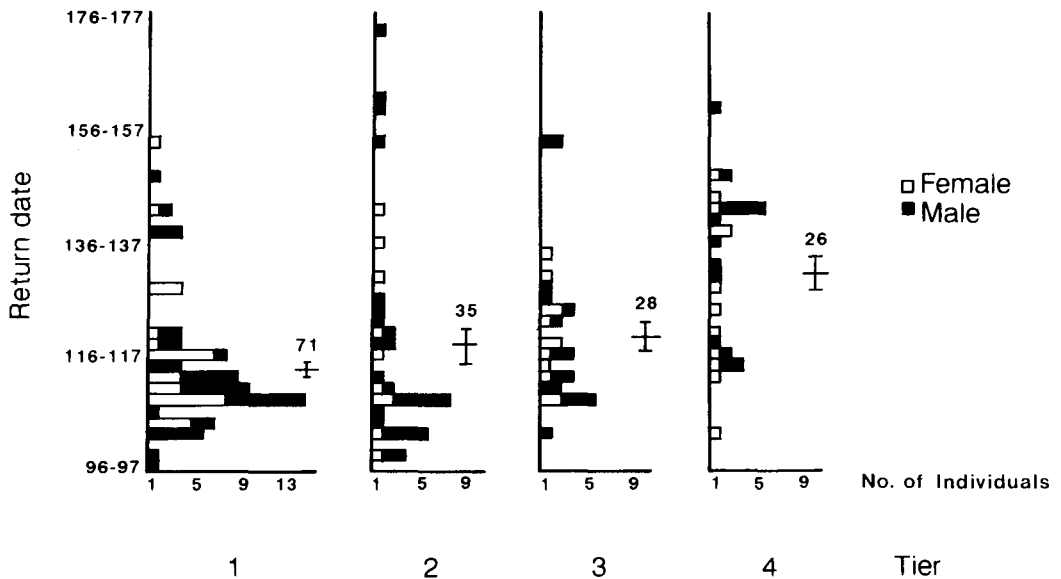


FIGURE 4. Histograms of the return dates for males and females in each tier (1 = top tier, 4 = bottom tier). Mean and SE are given to the right of each histogram. Total sample sizes given above mean and SE.

why adults prefer to nest in compartments in the top tiers. The proportion of nests taken by predators, including the deaths of three adults, decreased significantly from top to bottom ($G_{adj} = 26.1$, $df = 3$, $P < 0.0001$). Predation by raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*) on nesting martins was recorded in 1981 and 1982, before guards against climbing predators were installed. None of the 22 nests in tier 1 (the highest tier) were taken, while one (5.9%) of 17 nests in tier 2, three (20%) of 15 nests in tier 3, and 13 (54%) of 24 nests in the lowest tier were destroyed by these predators. Climbing predators appear to start at the bottom and continue to search horizontally among other compartments in the lower tier. Occasionally, predators will proceed to higher levels by moving vertically up a column of compartments. A single occurrence of this latter pattern accounted for the only depredated nest in tier 2 and one of the three nests taken in tier 3.

EARLY RETURN DATES OF OLDER FEMALES: TIER SELECTION OR EARLY EGG LAYING?

We asked if tier selection or date of laying the first egg was influenced by return date or age of female, and whether this differed among years. These analyses were restricted to females older than Age 2 for which all of the above variables were known ($n = 55$). As expected age affected tier selection, even in this restricted subsample (Ages 3, 4–5, ≥ 6 ; Tiers 1–2, 3–4; $\chi^2 = 15.02$, $P < 0.001$). Tier selection did not differ among years (1984–1986, 1987–1988, 1989; Tiers 1–2, 3–4; $\chi^2 = 1.66$, $P > 0.15$). Return date, in a one-way ANOVA, was correlated with tier selection ($F = 4.70$, $P < 0.035$), but this result is highly influenced by age.

The mean date of first egg laid did not differ among the age classes ($F = 0.95$, $P < 0.47$). It did differ significantly among years ($F = 3.91$, $P < 0.005$), with the mean first egg appearing significantly earlier in 1987, than in 1985 and 1986 (Tukey's). In a one-way ANOVA return date did not affect the mean date of first egg ($F = 2.50$, $P < 0.12$). However, in an analysis of covariance in which year effects were controlled, return date was a significant factor ($F = 9.69$, $P < 0.003$). The regression between return date and the date of first egg laid was positive in all 6 years and significantly different ($P < 0.05$) from a slope of zero in two (1986, 1988) of the six (1984, slope

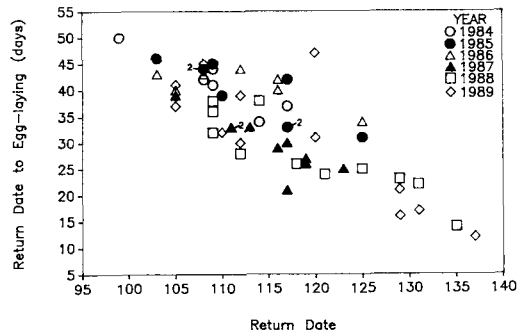


FIGURE 5. The interval between return date and first egg date vs. return date for age ≥ 3 females. Day 95 = 5 April. Points with two observations so labeled. All regressions were significant ($P < 0.009$), except for 1986 ($P < 0.07$) [1984, slope = -0.84 , $F = 23.78$, $n = 6$; 1985, slope = -0.74 , $F = 15.84$, $n = 8$; 1986, slope = -0.32 , $F = 5.11$, $n = 7$; 1987, slope = -0.86 , $F = 23.16$, $n = 10$; 1988, slope = -0.70 , $F = 34.01$, $n = 11$; 1989, slope = -0.90 , $F = 25.12$, $n = 13$].

= 0.162 , $F = 0.89$, $n = 6$; 1985, slope = 0.264 , $F = 2.04$, $n = 8$; 1986, slope = 0.68 , $F = 23.77$, $n = 7$; 1987, slope = 0.14 , $F = 0.64$, $n = 10$; 1988, slope = 0.30 , $F = 6.28$, $n = 11$; 1989, slope = 0.10 , $F = 0.29$, $n = 13$). There was much variation around the regression line, such that in most years it was not uncommon for a female that returned late to lay her first egg at the same time as the majority of other birds or for a female that returned early to lay her first egg at the same time as the majority of other birds.

If the relationship between return date and date of first egg laid is robust, then we would expect that the number of days between arrival and first egg laid (delay period) and return date would be independent of one another and the regression should have a slope of zero. In contrast, if the date of first egg was determined by extrinsic factors, which vary from year to year, we would expect a negative correlation between delay period and return date. This would occur because the earliest arriving females would wait until the extrinsic conditions were favorable whereas females arriving closer to this environmentally determined date would have to wait for a shorter period for appropriate conditions. Females arriving after this date should begin laying eggs as soon as possible. The latter scenario appears to be the case (Fig. 5). The duration of the delay period differed among years ($F = 5.07$, $P < 0.0008$), with the delay period in 1988 being significantly shorter than 1984, 1985, and 1986

(Tukey's). In an analysis of covariance, year effects ($df = 5$, sum of squares = 1,544, $F = 15.97$, $P < 0.0001$) and return date ($df = 1$, sum of squares = 2,054, $F = 106.26$, $P < 0.0001$) both significantly affected the duration of the delay period and together explained 79.5% of the variation. Further, there was much less variation around the regression lines calculated for each year. All regressions were significant ($P < 0.009$), except for 1986 ($P < 0.07$).

In sum, the mean date of first egg laid fluctuates from year to year and is relatively independent of return date. In contrast, the early return date of older females seems to be related to securing a nest site in a high tier which is correlated with a reduced likelihood of predation, and mating with an older male.

DISCUSSION

EARLY ARRIVAL BY OLD ADULTS

Dangerously early spring arrival has been noted in several secondary cavity-nesting species. That early arrival may be driven by competition for limited nesting sites is a viable hypothesis (Johnston and Hardy 1962, Brown 1978a), and often there is no direct relationship between settlement and egg-laying date (Stutchbury and Robertson 1987, this study). However, this does not adequately explain early arrival patterns in martins. Adults Age 4 and older arrived at breeding sites before Age 3 adults, even though the latter had bred at the colony previously. Age 3 males, in adult plumage for the first time, did not reclaim the nesting cavity they used when breeding in subadult plumage at Age 2 (Morton et al. 1990). Therefore, Age 3 males lack dominance over a particular cavity and are at a disadvantage when competing against older males, which reclaim cavities. Arrival after older birds have settled would enable Age 3 birds to identify undefended cavities, particularly because older males initially defend many cavities in addition to their nesting cavity (Brown 1979a, Rohwer and Niles 1979). Milder weather with higher food availability (Finlay 1976) and longer day length might also support the likely higher energetic cost of initial nest-site acquisition. Thus, we view the intermediate arrival of Age 3 birds as a consequence of severe nest-site competition in a secondary cavity-nesting species with the additional factors that the species is colonial and older birds have site dominance.

The extreme early arrival of Age 4 and older birds may, in turn, be viewed as escape from competition with Age 3 birds for cavities in the higher tiers, which are safer from predators that climb, especially if lower nest sites are occupied. A relatively high nest cavity was undoubtedly important to escape predation in natural nest sites as well (Rendell and Robertson 1989, discuss this factor for Tree Swallows, *Tachycineta bicolor*). Tier levels in martin houses are a feature shared with natural cavity arrays, in which the age-related separation evolved. In fact, vertical separation in natural cavities is even greater than in artificial martin houses and might have provided more safety from predators than do the closely packed compartments of martin houses. However, compartments in martin houses are identical in such qualities as cavity size whereas natural cavities were likely to differ in these aspects. Thus, at times, quality differences in natural cavities may override the single advantage of height as we documented in martin houses. But, on average, a higher nesting cavity within a colony should be preferred and early arrival may be related to competition to procure them. Early arrival was correlated with relatively safe burrow sites in Bank Swallows (*Riparia riparia*), with higher burrows suffering less predation from climbing Beech Martens (*Martes foina*) (Sieber 1980, Jones 1987). This shows that, even without competition for secondary cavities, predation can cause selection that favors early arrival in colonial species.

Early arrival was not consistently correlated with early egg-laying date in females nor were the arrival dates of mates correlated in Ages ≥ 3 . As in Tree Swallows (Stutchbury and Robertson 1987), later arriving female martins began nesting more quickly after arrival than did early arriving females (Fig. 5). Nest building begins in early May for both Age 3 and older females, even though most older females have arrived by 22 April and some as early as 10 April. Egg laying in Age 3 and older females peaks on 28 May (range 16 May–2 June) and for Age 2 females is evenly distributed between 28 May and 14 June (Morton et al. 1990). This separation between the egg-laying periods of Age 2 and older females is important to the mixed reproductive strategy employed by adult male martins (Morton 1987, Morton et al. 1990).

To sum up, extreme early arrival by Age 4 and older males and females is favored due to com-

petition for safe (high tier) nest sites. Age 3 males and females arrive between 25 April and 5 May to avoid competition with older birds with site dominance and to take advantage of greater and more predictable food availability while also avoiding competition for mates and nest sites with Age 2 birds.

Although this general schedule underlies the concordance of mate ages (Table 1), the lack of correlation in arrival dates of mates suggests mate choice mechanisms are important, perhaps based on a nesting resource: in this case, high tier level. Lyon and Montgomerie (1986) list the Purple Martin in their category B species, territories are nest sites only, and predict that mate choice is based on plumage color rather than territory quality. However, predation pressure may introduce a quality difference in territories, even in B-type territoriality, in a colonial species.

LATE ARRIVAL BY AGE 2 MARTINS

Age 2, the largest breeding age class (45% on average, Morton et al. 1990), arrives from mid-May until ca. 7 June. While wintering in Brazil, Age 2 martins lag behind older birds in molt (Hill, Levy, Morton, and Stutchbury, pers. observ.). It is doubtful that Age 2 birds would begin migration until the molt is complete, because it involves flight feathers and contour feathers (i.e., it is a complete prenuptial molt, *contra* Rohwer and Butcher 1988, table 1). However, we prefer the hypothesis that the later molt is a result of, rather than a cause of, late arrival at breeding sites.

Age 2 birds likely return later than older birds, including Age 3 birds, for two reasons. First, by returning later they avoid the intense competition for nest sites. The reasoning here is identical to that posited above for Age 3 birds. However, because Age 2 males are newcomers they would lose in contests with Age 3 males, which have gained dominance over nesting cavities by early May. Age 2 males avoid competition with the older males and Age 3 males, by returning later than all older age classes. Second, by returning late, Age 2 males may secure a high tier compartment and/or an older female due to spring mortality of adults (Age 3 and older males). The reasoning for this possible advantage is given below.

Two factors explain why adults should tolerate and even actively attract Age 2 birds to nest in martin "houses" and, previously, in the wood-

pecker hole-ridden snag colony sites. First, adult males gain a large genetic advantage by the presence of Age 2 males. On average, each adult male gained 3.6 additional offspring through forced extra-pair copulations with Age 2 females paired with Age 2 males (Morton et al. 1990). Second, because Age 2 nests are in lower nesting cavities, adult pairs gain additional protection against climbing predators by having active nests below their nests.

SIGNIFICANCE OF AGE 2 MALE PLUMAGE

The presence of mostly femalelike ventral feathers grown in the spring molt by Age 2 males, and the recognizable Age 2 plumage in most females (Anonymous 1977), suggests that their subadult plumage is specifically adapted to their first breeding season (Rohwer and Butcher 1988). The Status Signaling Hypothesis (Lyon and Montgomerie 1986) might explain this for colonial martins because adult martins recognize Age 2 males and do not confuse them with females, even momentarily. Recognition is easily tested by observing adult males waiting at favorite nest material collecting sites to attempt forced extra-pair copulations (Morton 1987, Morton et al. 1990). Single or mate-guarding Age 2 males that land at such sites are ignored by adult males, which focus forced copulation attempts only on females.

However, the advantage of a subadult plumage in Age 2 males is that they are recognized as subadults rather than as both subadult and subordinate in the sense implied by the Lyon and Montgomerie (1986) hypothesis. Nor does the subadult plumage of males reduce their probability of obtaining a mate (Table 1). The identification through plumage and the timing of Age 2 arrival are simultaneously advantageous in increasing their chances for breeding. First, adult males whose mates are egg laying advertise the presence of unoccupied nesting cavities through dawn singing (Morton et al. 1990). This begins ca. 15 May at our Maryland colony and is highly correlated with an influx of Age 2 males and females. It is important for Age 2 birds to find a nest site within a colony and pair quickly, because the 64-day nesting cycle and early migration departure constrain martins to a single annual breeding attempt. Age 2 males that have not paired before 10 June rarely have bred successfully at our site. Second, defense of nesting cavities by adult males may decrease once their

mates begin incubation. Females are the same size as males and defend the nest site during the 16-day incubation period. We suggest that Age 2 arrival time and their recognizable appearance contribute to their success in settling after the peak in male intrasexual aggression. Hill (1989) has shown a similar pattern in the Black-headed Grosbeak (*Pheucticus melanocephalus*).

The highly variable Age 2 male plumage patterns suggest they may play a role in individual recognition, especially among competing Age 2 birds, as well as permitting age-class recognition during settlement. Indeed, highly variable Age 2 plumage in male martins may benefit individual winners in contests over nest sites. Age 2 males differ from older males in having no previous site dominance or breeding experience. Adult males have experience with each other and have asymmetries in site dominance easily recognized by site position and, possibly, through individual vocal recognition. In contrast, Age 2 males have no previous experience with one another and are not returning to a specific site. Thus, the variation in Age 2 male plumage may facilitate rapid recognition of asymmetries during the development of site dominance within this age class. This hypothesis, which we call the "individual recognition in subadults hypothesis" (IRISH) produces a functional explanation for the highly variable plumage in Age 2 males. It is identical to the Individual Recognition Hypothesis presented by Shields (1977) and Whitfield (1986), but is restricted to subadults in martins. IRISH explains the enigmatic complete prenuptial molt and incorporates those attributes peculiar to the life cycle of Age 2: severe within age-class competition combined with an initial symmetry in site dominance. Whitfield (1986) documented extensive plumage variation among territorial Ruddy Turnstones (*Arenaria interpres*), a long-lived shorebird with strong year-to-year site fidelity. He rejected the Status Signaling Hypothesis through several correlative tests and, using model-presentation experiments, found supporting evidence consistent with the Individual Recognition Hypothesis.

ARRIVAL TIMES BY LATITUDE

How does the arrival timing at our site relate to continentwide patterns (Fig. 1)? The question of late arrival by Age 2 birds at this scale is particularly important to the points made above. Adults with previous breeding experience that return to their colonies gain advantages as discussed above.

In contrast, the relationship between natal colony latitude and the latitude of their first breeding attempt of most Age 2 birds is unknown. There is evidence suggesting that Age 2 birds do not search for nesting sites before or during their first migration south (Morton and Patterson 1983), although this remains a possibility (Brown and Bitterbaum 1980). Thus, the latitudinal breeding "target" of Age 2 birds may be more plastic compared to adults. Because they represent the largest breeding age class, nest-site competition among Age 2 birds may lead to wide latitudinal dispersal relative to their natal latitude. Possibly, northward dispersal from the natal latitude prevails because early spring mortality of adults is more likely in the north and thus more likely to free up extra nest sites at colonies. Therefore, an additional benefit of late Age 2 arrival is the increased likelihood of nesting cavities freed up by adult weather-related deaths. Late arrival allows them to "test" potential nest-site availability at colonies along a generally northward latitudinal transect after weather-related deaths have occurred in adults. Age 2 females may obtain an older male, whose mate has died. This would be advantageous because adult males provision young more than Age 2 males (Morton et al. 1990). Late arrival by Age 2 males may gain them an older, "widowed" female for a mate (Table 1). Older females afford higher fecundity because they lay a larger clutch than Age 2 females (Allen and Nice 1952), although the paternity of those eggs is not guaranteed for an Age 2 male (Morton et al. 1990). One way to test this hypothesis would be by comparing colony age-class composition and arrival times by latitude.

AGE-RELATED PATERNITY ASSURANCE: CONSTRAINTS AND RESTRAINTS

Age-related differences in paternity assurance may be widespread but have been, to date, little studied. Extra-pair copulations (EPC) in Barn Swallows (*Hirundo rustica*) are most frequent between early nesting, older males and late nesting, first-time breeding females (Moller 1985). EPC success in fertilizing eggs is highly skewed in favor of older males in the Purple Martin (Morton et al. 1990). This asymmetry apparently cannot be overcome by earlier arrival in Age 2 males for reasons discussed above.

Are Age 2 males able to assess their paternity rate and respond to lowered paternity by reducing parental effort (a proximate adjustment) or

has selection fashioned a lower parental effort as a result of their lower average probability of paternity (in an ultimate sense)? Proximate adjustment of parental care to paternity probability has been suggested for the Barn Swallow, a facultatively colonial species (Moller 1988). In the obligate colonial-nesting Purple Martin, the Age 2 male population is regularly subjected to lost parentage via EPCs. Mate-guarding intensity by Age 2 males does not reflect parental assurance and their parental effort is not related to mate-guarding intensity (Morton 1987, Morton et al. 1990). Age 2 males may have only two options, adjust parental effort to their average paternity rate, and use behaviors to increase paternity assurance. One such behavior is to mate frequently with their females. Age 2 males that follow mates to nest material-gathering sites, apparently guarding them against EPCs (Brown 1978b), also force copulations upon their mates as they return with nesting material (Morton and S. Beissinger, pers. observ.). The females attempt to escape by flying upwards, often dropping the nest material they were carrying. We have not observed adult males forcing copulations upon their females. Adjustment away from the average paternity rate could be made if males could recognize their genetic offspring and nourish them preferentially. However, this appears not to occur in martins (Brown 1979b).

Age 2 females lay fewer eggs than older females, perhaps as a response to lowered Age 2 male parental effort. There is little difference in egg-laying periods between the age classes and food may increase throughout the summer (Johnston 1967). Thus the reduced reproductive effort by both sexes during their first breeding attempt can be related to the decreased paternity assurance for Age 2 males. Moller's (1988) proximate adjustment hypothesis, whereby parental effort is adjusted to EPC frequency, seems an unlikely mechanism for many species. For example, Age 2 males defending all-purpose territories in dense habitat may not have the opportunity to observe EPCs (Westneat et al. 1990). The extent to which lowered paternity assurance in other species may be related to constraints and/or restraints in reproductive effort deserves further study.

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LITERATURE CITED

- ALLEN, R. W., AND M. M. NICE. 1952. A study of the breeding biology of the Purple Martin (*Progne subis*). *Am. Midl. Nat.* 47:606-665.
- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds. 6th ed. American Ornithologists' Union, Washington, DC.
- ANONYMOUS. 1977. North American bird banding manual. Vol. 2. Canadian Wildlife Service, Ottawa.
- BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. National Mus. Bull. 179.
- BROWN, C. R. 1978a. On early spring arrival in Purple Martins. *Bird-Banding* 49:130-133.
- BROWN, C. R. 1978b. Sexual chase in Purple Martins. *Auk* 95:588-590.
- BROWN, C. R. 1979a. Territoriality in the Purple Martin. *Wilson Bull.* 91:583-591.
- BROWN, C. R. 1979b. Chick recognition in Purple Martins (Passeriformes: Hirundinidae). *Southwest. Nat.* 24:683-685.
- BROWN, C. R., AND E. J. BITTERBAUM. 1980. Implications of juvenile harassment in Purple Martins. *Wilson Bull.* 92:452-457.
- CHARLESWORTH, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.
- CONOVER, W. J., AND R. L. IMAN. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35:124-129.
- CURIO, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400-404.
- FINLAY, J. C. 1976. Some effects of weather on Purple Martin activity. *Auk* 93:231-244.
- FORD, N. L. 1983. Variation in mate fidelity in monogamous birds, p. 329-356. *In* R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- GOWATY, P. A. 1985. Multiple parentage and apparent monogamy in birds, p. 11-21. *In* P. A. Gowaty and D. W. Mock [eds.], *Avian monogamy*. Ornithol. Monogr. No. 37. American Ornithologists' Union, Washington, DC.
- HILL, G. E. 1989. Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? *Anim. Behav.* 37:665-673.
- JOHNSTON, R. F. 1967. Seasonal variation in the food of the Purple Martin *Progne subis* in Kansas. *Ibis* 109:8-13.

- JOHNSTON, R. F., AND J. W. HARDY. 1962. Behavior of the Purple Martin. *Wilson Bull.* 74:243-262.
- JONES, G. 1987. Colonization patterns in Sand Martins *Riparia riparia*. *Bird Study* 34:20-25.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LYON, B. E., AND R. D. MONTGOMERIE. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution* 35:605-615.
- MAYFIELD, H. F. 1969. Purple Martin population changes over fifteen years. *Auk* 86:522-528.
- MOLLER, A. P. 1985. Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* 17:401-408.
- MOLLER, A. P. 1988. Paternity and parental care in the swallow, *Hirundo rustica*. *Anim. Behav.* 36:996-1005.
- MORTON, E. S. 1987. Variation in mate guarding intensity by male Purple Martins. *Behaviour* 101:211-224.
- MORTON, E. S., L. FORMAN, AND M. BRAUN. 1990. Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* 107:275-283.
- MORTON, E. S., AND R. L. PATTERSON. 1983. Kin association, spacing, and composition of a post-fledging roost of Purple Martins. *J. Field Ornithol.* 54:36-41.
- NILES, D. M. 1972. Determining age and sex of Purple Martins. *Bird-Banding* 43:137-138.
- PHILLIPS, A. R., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. of Arizona Press, Tucson.
- RAY, A. A. 1982. SAS user's guide: statistics. 1982 ed. SAS Institute, Cary, NC.
- RENDELL, W. B., AND R. J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for Tree Swallows breeding in natural cavities. *Condor* 91:875-885.
- ROHWER, S., AND G. S. BUTCHER. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *Am. Nat.* 131:556-572.
- ROHWER, S., AND D. M. NILES. 1979. The subadult plumage of male Purple Martins: variability, female mimicry, and recent evolution. *Z. Tierpsychol.* 51:282-300.
- ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology. Macmillan, New York.
- SAETHER, B.-E. 1990. Age-specific variation in reproductive performance of birds, p. 251-283. In D. M. Power [ed.], *Current ornithology*. Vol. 7. Plenum Press, New York.
- SAS INSTITUTE. 1985. SAS/STAT guide for personal computers. Version 6 ed. SAS Institute, Cary, NC.
- SHIELDS, W. M. 1977. The social significance of avian winter plumage variability: a comment. *Evolution* 31:905-907.
- SIEBER, O. V. 1980. Kausale und funktionale Aspekte der Verteilung von Uferschwalbruten (*Riparia riparia* L.). *Z. Tierpsychol.* 52:19-56.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman, San Francisco.
- STEWART, P. A. 1972. Mortality of Purple Martins from adverse weather. *Condor* 74:480.
- STUTCHBURY, B. J., AND R. J. ROBERTSON. 1987. Do nest building and first egg dates reflect settlement patterns of females? *Condor* 89:587-593.
- WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON. 1990. The ecology and evolution of extra-pair copulations in birds, p. 331-369. In D. M. Power [ed.], *Current ornithology*. Vol. 7. Plenum Press, New York.
- WHITFIELD, D. P. 1986. Plumage variability and territoriality in breeding turnstones *Arenaria interpres*: status signalling or individual recognition? *Anim. Behav.* 34:1471-1482.
- WILLIAMS, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100:687-690.
- WILSON, A., AND C. L. BONAPARTE. 1832. *American ornithology*. Whittaker, Treacher, & Arnot, London.