AN HISTORICAL ANALYSIS OF SPRING ARRIVAL TIMES IN PURPLE MARTINS: A TEST OF TWO HYPOTHESES

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THE HYPOTHESES

The period between spring arrival and egg laying in adult Purple Martins (*Progne subis*) is normally about two months. This hiatus is caused by selection for a very early spring arrival, because nesting is usually associated with mild weather and the commencement of the growing season (Johnston and Hardy, 1962; Johnston, 1967; Allen and Nice, 1952). But selection for an early spring arrival is perplexing because many early-arriving adults sometimes starve in periods of cold, rainy weather (Bent, 1942; Steward, 1972). Johnston and Hardy (1962) attribute the exceedingly early arrival of martins to a shortage of nest holes. This interpretation is supported by the fact that Tree Swallows (*Iridoprocne bicolor*) and Violet-green Swallows (*Tachycineta thalassina*) are second only to martins in their early arrival times; in addition to martins, these are the only other North American swallows that typically nest in secondary cavities.

Rethinking the early arrival syndrome for Purple Martins suggests that Johnston and Hardy (1962) might have been partly incorrect. Unlike Tree and Violet-green swallows, Purple Martins exhibit an extreme sexual dichromatism. The causes of interspecific differences in the development of sexual dichromatism are poorly understood, but are perhaps best approached by asking what favors bright plumages in either sex. A recent summarization of arguments suggests that brightness evolves as an aggressive signal when resources are defensible and limiting (Rohwer et al., Ms.). Thus in many hole nesting species females are as brightly colored or boldly patterned as males. This is attributed to the severe intraspecific competition that commonly exists for nesting cavities, and suggests that females as well as males are limited by the number of satisfactory nest holes. That resource limitation favors bright female plumages is further confirmed by studies of two of some 20 species of hummingbirds that are both sexually monochromatic and brightly colored. In both, females as well as males defend feeding territories (Wolf, 1969, 1975). Thus brilliance in female plumages seems to be associated with selection for aggressive behavior, as also appears to be the case for brilliance in male plumages (see Peek, 1972; Smith, 1972; Morris, 1972; Lewis, 1972).

But these considerations concerning sexual monochromatism are incompatible with a hole-limitation hypothesis to explain the very early spring arrival of martins. This paradox may be resolved by a two-part speculation concerning summer competition in martins. The hypothesis is (1) that males are female limited and (2) that females are limited by opportunities to nest in large colonies of, for example, 5 to 10 or more pairs. What are the consequences of female and large colony limitation? In short, they mean

that males show a much greater variance in fitness than females. Since nest holes are highly defensible, this variance difference means that agonistic sexual selection favoring brightness operates far more strongly on male than on female Purple Martins. We assume males are female limited for the following reasons. (1) There is a shortage of females in some populations. In 1970 and 1971, in Lawrence, Kansas we found a wandering population of subadult males of unknown size; these were presumably males that were unmated despite an abundance of nest sites. Additionally in 1971, 10 of 40 subadults that held holes did not obtain females (Rohwer and Niles, Ms.). (2) All females appeared to breed in Lawrence in 1970 and 1971, and no other published studies of martins indicate nonbreeding females (Allen and Nice, 1952; Johnston and Hardy, 1962). (3) Male martins are sometimes polygynous (Southern, 1959; Brown, 1975). These points mean that the reproductive success of males can vary from 0 up to 2-times the average success for females in a summer, depending on whether males are unmated, monogamous, or polygynous.

Females and males are both presumed to be limited by large-colony nesting opportunities. By large colonies we mean the opportunity to nest either in colony-houses satisfactory for many pairs (Rohwer and Niles, Ms.) or in a cluster of small houses close enough for the presumed advantages of coloniality to obtain. Breeding success has not been measured in colonies of different sizes in the same year, so there is no direct proof of a large-colony nesting advantage. However, several points are suggestive. (1) Martins are colonial by preference rather than from a shortage of solitary nesting opportunities. Between 10 and 20 April 1971, in Lawrence all 8 of the large colonies we visited were occupied whereas only 3 of 7 small colonies had yet been settled (eventually sizes for large colonies were 5-21 adult males; for small, 1-2 adult males.) Furthermore many apparently satisfactory small nest boxes are unused in Lawrence. Indeed, there was great competition among box keepers to attract martins, and some were dismayed to lose their birds from one year to the next despite a continuing maintenance program. Jackson and Tate (1974) also report unused colony-houses in Mississippi. (2) In large colonies martins show a greater ability to resist intrusion by House Sparrows (Jackson and Tate, 1974; Rohwer and Niles, Ms.). Hoogland and Sherman (1976) have also shown mobbing of predators to be more effective in large colonies of Bank Swallows (*Riparia riparia*), and Allen and Nice (1952) suggest the same for martins. (3) Finally, colonial nesting should facilitate the reciprocal communication of the location of short-lived abundances of prey, although this has not been demonstrated for martins (Emlen and Demong, 1975).

Breeding in a large or small colony affects the reproductive success of males and females alike. But to this source of limitation must be added female-limitation for males. Consequently, agnostic sexual selection acts far more intensely on males than on females, meaning that females should leave competition for optimal nesting sites to males and choose mates on the basis of the quality of resources they hold. Thus we expect a bright plumage in males.

The cryptic plumage of females is rationalized by assuming (1) that holes were never limiting to females and (2) that the advantage of nesting in large colonies is not great enough to repay the cost of intense aggressive behavior and an associated brilliant plumage. The second point is reasonable because aggression and bright colors are less compatible with the female role in avian reproduction than with the male role.

But how does this hypothesis relate to martin arrival times? It means that female martins are not hole limited, per se, but limited by the availability of holes in large colonies. Thus we hypothesize that the very early spring arrival of males is to obtain and defend holes in large colonies where there is a high probability that females will settle. Females arrive nearly as early as males, but their dull coloration suggests that they do so only to form an early pair bond with males holding the best nest holes. This is supported by the fact that males are more aggressive than females (Allen and Nice, 1952).

THE TEST

To distinguish this female/colony-limitation hypothesis from the original hole limitation hypothesis we have taken advantage of a massive perturbation experiment. East of the Great Plains, Purple Martins now nest almost exclusively in man-made colony houses. If holes have been limiting in the past, such has surely not been the case in recent years. At the present there is an abundance of unused colony-houses and nest holes (Jackson and Tate, 1974; Mayfield, 1969; Allen and Nice, 1952; our data for Lawrence). By the hole limitation hypothesis of Johnston and Hardy (1962), this surplus of nest holes should have resulted in a recent shift toward a later spring arrival time. Selection for such a shift must be intense, for inclement spring weather often kills great numbers of adult martins (Bent, 1942; Allen and Nice, 1952; Steward, 1972; Rohwer and Niles, Ms.). Contrarywise, by the female/colony-limitation hypothesis we propose above, martins should still be arriving early. This is so because there appears still to be a great shortage of colony-houses with a large number of nest holes (see Table 7 in Jackson and Tate, 1974).

By the female/colony-limitation hypothesis one could even argue that the selective balance has shifted in favor of an even earlier spring arrival because man-made martin boxes sometimes contain many nest holes. The effect of these large colonies has been to increase the variance in colony size, and this increased variance may have caused a recent increase in the fitness difference caused by nesting in large and small colonies. Because of the overriding importance of female-limitation, it is unlikely that this would have affected the arrival times of males, but it may have caused females to return earlier.

To distinguish the female/colony-limitation hypothesis from the hypothesis of hole limitation per se we have summarized several time-series of arrival dates from the Fish and Wildlife Service Migratory Bird files at Laurel, Md. Our criteria for choosing a

locality were (1) that it be east of the Great Plains where martins nest almost exclusively in man-made colony-houses, and (2) that the time-series be a long one. Unfortunately these arrival dates are not recorded separately for males and females, but since the records were of "first arrivals" they may be assumed to pertain largely to males. We have summarized data for the state of Connecticut (1877-1968); Pensacola, Florida (1961-1967); Baltimore, Maryland (1878-1973); and for Ottawa (1885-1925), London (1885-1935) and Toronto (1895-1935), Ontario.

The data were consistent in showing no trend either for an earlier or a later arrival time. The long history of records available for Baltimore are presented in Figure 1 as a sample of the graphs obtained. There is considerable variance in these arrival dates caused largely by a lose scatter of first returns recorded in mid- and late April. These likely represent years when martins were not seen as soon as they returned, an interpretation supported by the much tighter clustering of points in late March and early April, the "normal" arrival time for Purple Martins at the Baltimore latitude. Note, however, that fitting a line through this tight cluster of early dates would still reveal no historic trend toward an earlier or later spring arrival.

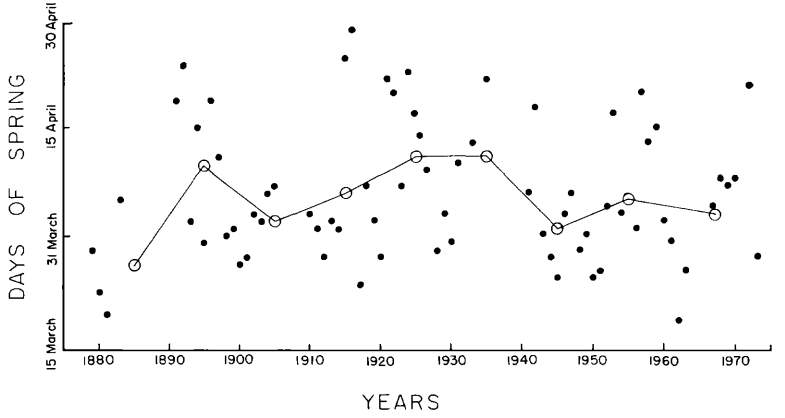

FIGURE 1. First arrival dates (closed circles) of Purple Martins through time for Baltimore, Maryland. Note the absence of a trend for a later spring arrival in recent decades; mean arrival dates for decades (open circles) are connected by straight lines.

We feel these data argue rather strongly against the hole limitation hypothesis as originally exposited (Johnston and Hardy, 1962). The argument is strong because of the frequency of disastrous spring kills which should select strongly for a later arrival. On the other hand, the data are consistent with the alternate hypothesis that, in summer, males are female-limited and females limited by colonial nesting opportunities. Some may argue that such an evolutionary test is not legitimate over 50- to 100-year time scales. However, the work of Johnston and Selander (1964;

1971) on rapid evolution in North American House Sparrows (*Passer domesticus*) should allay such skepticism. Furthermore, we have shown specifically that subadult martin males have experienced a recent rapid evolutionary response to the recent increases in nesting opportunities by becoming more female-like in appearance (Rohwer and Niles, Ms.). In short, rapid evolution seems to be a reasonable expectation. The regularity of spring kills should have generated a strong selection for later arrival but this has, apparently, been countered by the syndrome of female/colony-limitation in summer.

SUMMARY

Purple Martins return to their North American breeding grounds so early in spring that disastrous kills are common. If a shortage of nest holes had been the cause of this early return they should have begun returning later because of the proliferation of artificial nest boxes. However, the dullness of the female plumage suggests that the number of nest holes, per se, was never limiting. If, as hypothesized, a combination of female and colonial nesting opportunities has been limiting, then martins should not have commenced returning later in spring. A summary of several long time-series of arrival dates shows no recent change in spring arrival times.

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