

Light-breasted Purple Martins Dominate Dark-breasted Birds in a Roost: Implications for Female Mimicry

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Rohwer et al. (1980) proposed the Female Mimicry Hypothesis to account for subadult plumages in North American passerines. They argued that by mimicking a female's plumage, yearling males gain access to habitats of better quality where they are more likely to attract females. The basic premise of Rohwer et al. is that in direct competitive interactions deceptive plumage alters the competitive asymmetries between adults and yearlings, enabling a yearling to usurp part of an adult male's territory. In this paper I propose another hypothesis to explain why female mimicry may be advantageous to yearling males. My hypothesis is based on the idea of Smith (1980) that in many monogamous species of birds males are subordinate to females during parts of the nesting cycle. Presumably, it is advantageous for males to allow females access to critical resources that may be channeled into the production of eggs and young, in which males have genetic interest (Smith 1980). I suggest that yearling males may resemble females in order to deceive adult males into behaving submissively toward them, too, and that they thereby gain access to resources such as food or space normally reserved for females. If males, on average, are unable to breed their first year (as is the case in many North American passerines, Rohwer et al. 1980), yearling males cannot lose, and in fact can gain, by taking resources from females.

I conceived this hypothesis while studying dominance relationships of Purple Martins (*Progne subis*). The martin is the only North American swallow that is strongly age- and sexually dimorphic. Two-year-old and older males are easily distinguishable from females throughout North America (Johnston 1966), whereas yearling males are female-like to varying extents (Rohwer and Niles 1979). To test my hypothesis of female mimicry and that of Smith (1980), I examined displacements that occurred on perching sites as the birds competed (presumably for the best space) during a time (Smith 1980) when breeding males should defer to females.

My study was done in June 1981 at a roost of about 1,500 Purple Martins that congregated daily on utility wires along a dirt road north of a golf course and behind homes on Abrego Drive in Green Valley, Pima County, Arizona. In the eastern United States roosts are premigratory gatherings, but in Arizona Purple Martins roost throughout the nesting season (Cater 1944, Phillips et al. 1964). I observed no juveniles in this roost (identified by characteristics listed in Brown 1978a). In the roost there were many sexual chases (Brown 1978b), and the martins were uttering almost their full vocal repertoire, strongly suggesting that

these birds were actively nesting (in nearby saguaros) when I observed them. The martins arrived each afternoon about 90 min before sunset and remained until shortly after sunset (when they all flew southeast toward the Santa Rita Mountains, presumably to sleep). While in the roost, martins constantly arrived and left from the wires. Periodically, they would leave *en masse*, circle about for several minutes, and then gradually reassemble on the wires. Birds generally would approach the wire from the north (with a southerly wind) and then either glide along the wire to find an open space or actively displace a bird already sitting there.

On 12–15 June 1981, an assistant and I quantified the displacements that occurred on these perching sites. We easily distinguished dark-breasted Purple Martins (i.e. adult males) from light-breasted ones (i.e. females and yearling males). Many yearling males were present. They could be identified by their vocalizing, their pursuit of females in sexual chases, and the purple spots on their throats and breasts. Their appearance was noticeably more female-like than that of yearling males in northern Texas, however (Brown unpubl., see also Rohwer and Niles 1979); thus, it was not practical to identify yearling males consistently. This was unfortunate but not fatal to the testing of my hypothesis (for reasons discussed below).

Displacements were scored (a) when an incoming bird flew toward one sitting on the wire, displaced it, and perched in the vacated spot; (b) when an incoming bird landed near another bird and forced the incumbent to move away, usually by forcing it to sidle along the wire a few centimeters; and (c) when an incoming bird landed beside another bird and was subsequently pecked or lunged at by the incumbent and forced to fly away. Most of the displacements were of type a. Occasionally, in the course of a displacement, two birds would grapple briefly in flight or while hanging onto the wire, but a successful displacement was scored only if the incoming bird succeeded in perching on the disputed site while the incumbent flew away. The martins obviously preferred the uppermost wire; displaced birds sometimes flew to a lower wire, where far fewer birds perched, flew away entirely, or moved along the top wire to find another spot. Males (both adults and yearlings) often chased females that they encountered flying near the wires. These chases were accompanied by courtship songs (Brown unpubl. MS) and resembled Pair and Rape Chases (Brown 1978b). These chases, however, were not scored as displacements owing to their apparent sexual context and the fact

TABLE 1. Number of displacements among light- and dark-breasted Purple Martins in an Arizona roost.

Date	Observation time (min)	Light displaces light	Light displaces dark	Dark displaces light	Dark displaces dark
12 June	31	12	26	2	4
13 June	90	26	57	5	10
14 June	90	21	55	5	3
15 June ^a	65	12	33	2	1
	65	20	30	1	2
Total	341	91	201	15	20
Expected ^b	—	96	81	81	69

^a Two observers.

^b If displacements are random.

that they did not usually originate on the wires. When scoring displacements, we concentrated on sections of wires containing 30–100 birds at a time. We made observations from parked cars and were close enough to the birds that binoculars were not needed to determine coloration of the birds involved. To determine the approximate ratio of dark- to light-breasted birds in the roost, on 15 June I photographed the half of the roost where we concentrated our observations and later counted birds in the photos.

The displacements are recorded in Table 1. The photographs indicated that the roost contained approximately 46% dark-breasted birds (284 of 618 total birds). I used this figure to calculate the expected number of displacements for the purpose of Chi-square analyses, assuming displacements were random (Table 1). Light-breasted birds displaced dark-breasted birds much more frequently than they would if displacements were random ($\chi^2 = 61.0$, $P < 0.001$), but light-breasted birds displaced other light-breasted birds at random. Light-breasted birds as a class displaced all other birds considerably more than did dark-breasted birds as a class ($\chi^2 = 161.5$, $P < 0.001$).

These data show that when a light-breasted bird approached a wire, it was clearly dominant over the dark-breasted birds and could displace them. It could displace some light-breasted martins, but at a rate approximately one-half the displacement rate of dark-breasted birds. Dark-breasted martins were essentially submissive on the perching sites, and, when they approached a wire, they were not likely to displace any birds. Instead, they attempted to find an unoccupied space.

In this roost, yearling male Purple Martins realize two advantages by being female-like (i.e. light) in plumage. First, by mimicking a female's appearance, they are not displaced by females as often as they would be if they were dark. Second and perhaps more important, they may also deceive adult males and thereby dominate dark-breasted birds to gain access to preferred perching space, such as uppermost wires.

Uppermost wires may be optimal, because they presumably afford a better view of predators (and possibly also passing insect prey items) and may allow martins to launch into flight and gain altitude quickly, adaptive behavior for avoiding aerial predators. My photographs of this roost showed about 59% of the birds on upper wires ($n = 558$) were light-breasted, whereas about 8% of the birds on lower wires ($n = 60$) were light-breasted, suggesting that light-breasted birds do indeed gain preferential access to the upper wires. Birds also may try to perch in the center of groups to maximize selfish herd effects, and light-breasted birds may get the center positions more readily as a result of their dominance. In this Arizona roost, the resource at stake was undoubtedly perching space, not greater access to females perching there (Rohwer et al. 1980), because no copulations occurred in this roost. Advantages of space acquisition for yearling males may represent selective pressures for maintaining the female-like plumage, at least in the southwestern United States where martin roosting behavior is pronounced. Once male Purple Martins attain breeding age (≥ 2 yr), sexual selection for dark plumage (Johnston 1966) presumably overrides the advantages of female mimicry.

A possible criticism of my interpretation is that I could not distinguish yearling males from females in the light-breasted class. Even if the displacements of dark-breasted birds recorded in Table 1 were all by females, however, a yearling male still gains by being less susceptible to displacement than an adult male. On the other hand, if the displacements of dark-breasted birds were all by yearling males, a yearling male gains by being clearly dominant over adult males. Either way the yearling male has an advantage.

Adult males in this roost were submissive and rarely displaced any birds, whether dark- or light-breasted. There appeared to be no differences in general behavior of adult males and light-breasted birds that might account for these results; adult males in all other respects acted like light-breasted birds in the roost. While one would predict that adult males should defer to light-breasted birds if female mimicry is to work, the fact that adult males are also submissive to each other and rarely displace each other is unexplainable at present.

Most of the martins in this roost were probably still in stages of pair formation and nest building, as Cater (1944) reported that Purple Martins in southern Arizona began laying in late June and Phillips et al. (1964) indicated that martins do not arrive in south central Arizona until early May. The deferment of males to females during this period is consistent with the hypothesis of Smith (1980) and, by extension, with the function of female mimicry I propose here. Another possible reason that adult males are submissive to females is that breeding males are selected to reduce their aggressiveness toward fe-

males when pair formation and courtship occur (e.g. Tinbergen 1959), facilitating copulation. Whether adult males are submissive for this reason or for the reason proposed by Smith (1980), yearling males still are able to exploit the system and gain access to space.

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LITERATURE CITED

- BROWN, C. R. 1978a. Juvenile Purple Martins: field identification and post-fledging nest defense. *Bull. Texas Ornithol. Soc.* 11: 25-27.
- . 1978b. Sexual chase in Purple Martins. *Auk* 95: 588-590.
- CATER, M. B. 1944. Roosting habits of martins at Tucson, Arizona. *Condor* 46: 15-18.
- JOHNSTON, R. F. 1966. The adaptive basis of geographic variation in color of the Purple Martin. *Condor* 68: 219-228.
- PHILLIPS, A. R., J. MARSHALL, & G. MONSON. 1964. *The birds of Arizona*. Tucson, Arizona, Univ. Arizona Press.
- ROHWER, S., & D. M. NILES. 1979. The subadult plumage of male Purple Martins: variability, female mimicry, and recent evolution. *Z. Tierpsychol.* 51: 282-300.
- , S. D. FRETWELL, & D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Amer. Natur.* 115: 400-437.
- SMITH, S. M. 1980. Henpecked males: the general pattern in monogamy? *J. Field Ornithol.* 51: 55-63.
- TINBERGEN, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour* 15: 1-70.

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Dietary Sulfur Amino Acid Availability and Molt Dynamics in White-crowned Sparrows

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Although pitifully little is known about how the patterns of avian molt are controlled (Payne 1972), it is at least arguable on reasonable grounds that the rate and sequence of feather replacement are dominated by a genetic program. In the first place, molt patterns (ordination of replacement within pterygiae, coordination among pterygiae) are nearly invariant within major phyletic lines (Stresemann and Stresemann 1966), which implies that they are conservative traits that were fixed early in evolution. In the second place, the experimental investigations by Mewaldt and King (1978) of 12 populations of White-crowned Sparrows (*Zonotrichia leucophrys*) from various latitudes (35-49°N) showed that the duration of the postnuptial molt was progressively shorter northward, even though the birds from all populations were kept during molt in the same environmental conditions at an intermediate latitude. This implies a strong genetic component. Nevertheless, it is evident also that the genome that controls molt is sensitive to extrinsic influences, no doubt mediated by the neuroendocrine system, within a moderate range of plasticity. For instance, the postnuptial molt may be temporarily suspended by a late nesting cycle (King 1972), may be abbreviated in birds whose nesting season was prolonged by re-nesting following predation (Wingfield and Farner 1979), and, in experimental situations, may be modified in duration

within a relatively narrow range by air temperature or photoperiod (Gavrillov and Dolnik 1974, Chilgren 1978). Finally, the availability of nutrients has been frequently invoked as an actual or potential modifier of the course of molt. The amino acid cystine, because of its relative abundance in feathers (Murphy and King 1982a) and its importance in the structure of keratin, has frequently been cited as a potentially limiting nutrient in the growth of plumage (Hanson 1962, Newton 1968, Ward 1969, Gavrillov and Dolnik 1974). Although it has been found in some investigations that the rate of wool growth in domestic sheep (Reis and Schinckel 1963, Reis 1965) and of hair growth in the laboratory rat (Smuts et al. 1932) is enhanced by increased dietary sulfur amino acid (SAA) intake, the correlation of the rate of feather growth with SAA intake by domestic fowl is equivocal [Ackerson et al. 1928 (and references cited therein); Taylor and Russell 1943, Brake et al. 1979].

To test the foregoing hypotheses and speculations, we measured the rates of feather elongation, the shedding interval between remiges, the temporal coordination between remigial tracts, the duration of the molt, and the renewed feather mass in groups of White-crowned Sparrows that were fed diets differing in cystine and methionine content. The main purpose of these experiments was to characterize energy expenditure and nitrogen and sulfur balance