MOLT CYCLES OF PURPLE MARTINS (*PROGNE SUBIS*)

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Interest in the adaptive aspects of avian molt cycles has recently engendered several studies of molt, relying, in part at least, upon a detailed comparative base. Comparative studies of avian molts including detailed comparisons between sexes and among juveniles, first-year birds, and adults of a single passerine species are rare; Foster's (1967) is the only one known to me. The Purple Martin (*Progne subis*) is a species in which juvenal, first-year, and adult plumages (the latter two strongly sexually dimorphic) can be distinguished (Ridgway 1904; Niles, unpubl.), and is thus an appropriate subject for the examination of intrapopulation variation in molt.

This paper describes certain aspects of the postnuptial and postjuvenal molts of Purple Martins, with emphasis on age-related or sex-related differences in timing and extent of the molts. The molts are also discussed relative to other major events of the species' annual cycle.

Purple Martins are locally common or abundant, colonially nesting summer inhabitants of much of the forested or wooded portion of temperate North America south of the trans-Canadian boreal forest (A.O.U. 1957).

The distribution of *P. subis* while on migration south of the United States is imprecisely known. Bond (1961) lists the species as a transient in the Antilles, and Purple Martins are a fairly common migrant on the Yucatan Peninsula (Paynter 1955; Russell 1964) and in coastal Honduras (Monroe 1968). In contrast to the relative abundance of records from these regions, Loetscher (1955) and Miller et al. (1957) report only two records of presumed migrant martins from eastern México north of the Yucatan Penninsula, implying that most birds from eastern North America adopt an at least partially overwater route to and from the wintering grounds. Lowery (1946) cites one shipboard observation of many Purple Martins over the Gulf of México. There is apparently virtually nothing known of the migratory distribution in Central America of *P. subis* from populations breeding in the western United States or México. The species' wintering range encompasses much of Brazil, Venezuela, and the Guianas (A.O.U. 1957).

METHODS

For the present study I have examined 327 museum skins of *P. subis*, 251 taken from 1 July onward in the eastern United States and Canada (thus excluding at least for the late summer period, consideration of the partly montane western populations), 21 autumn-taken skins from Central America and the Antilles, 44 "wintering" specimens from South America, and 11 spring-taken Central American birds. Almost half of the North American skins were obtained from "pest control" activities (random shooting) at two large nocturnal roosts; one sample of 80 specimens was collected on the night of 17 August 1965 at Lawrence, Douglas County, Kansas, the other, of 38 birds, on 21 August 1967 at Jefferson City, Cole County, Missouri. Both of these samples are preserved at the Museum of Natural History of the University of Kansas. The next largest temporally and geographically uniform sample available to me consisted of eight birds; most samples contained but one or two specimens.

I have not tried to examine geographic variation in the molts; late summer birds may already have begun migration (see beyond), and cannot be surely allocated to a definite breeding population.

Molt on the body was scored in five regions: *chin and throat* (the anterior, undivided portion of the ventral tract), *breast* (middle portion of the ventral tract immediately posterior to its bifurcation), *sides* (the dorsal edges of the postero-lateral branches of the ventral tract beneath the wings), *top of the head* (the capital tract), and *back* (roughly the anterior half of the dorsal tract). Feathers in each of these regions were pushed upward and forward with a dissecting needle, and the bared areas underneath were examined for papillae or ensheathed new feathers. An "active molt score" for each of the first four regions was assigned for each specimen on the basis of a "0" for no active feather replacement, a "1" for relatively small or moderate numbers of visible papillae or unfolding feathers, or a "2" for relatively heavy feather growth. I was unable satisfactorily to expose the back skin of most specimens, and could detect molt in that region only in the presence of (usually fairly well-grown) basally sheathed feathers. A score of 0 or 1, respectively indicating absence or presence of detectable new growth, was tallied for the back of each bird. Summing the scores from the above five regions gave each bird an active molt score within the range of zero (no molt) to nine (heavy molt in all regions).

Some birds were also assigned a value based upon the percentage of fresh feathering, relative to total plumage, touched by four transverse lines across the specimen's dorsum at the level of the eyes, 5 mm anterior to the junction of the nape and back, and 20 mm and 40 mm posterior to that junction. Adding the four percentages thus obtained gave birds with completely fresh emergent feathering at all four levels a score of 400, those in completely old feather, a zero. This score was applied only to first-year and adult specimens from the two large samples of roosting birds. Most of the smaller samples were unavailable to me when I attempted this scoring, and the difficulty of distinguishing "old" from "fresh" body feathers during the late summer portion of the postjuvenal molt precluded the analysis of young in this way.

Each primary on one (usually the left) wing of each bird was given one of three values: "0" for an old feather, missing feather, or new feather less than ¼ grown; "1" for a feather ¼ to ¾ grown; or "2" for a feather ¾ to fully grown. The nine values obtained from each bird were summed to provide a total "primary score." Thus a bird possessing completely renewed primaries would score 18, while a bird with primary 1 half-grown and primaries 2–9 old would be assigned a score of 1, etc. Molt of the secondaries and rectrices was treated descriptively only.

Intersample differences in active body molt values and primary molt scores were tested with a Mann-Whitney *U*-test. I used Student's *t*-test to compare amounts of fresh body feathering. Proportional differences (for example, in molting vs. nonmolting birds) between two samples were tested via a chi square analysis of two-way contingency table. Linear regression analysis of primary score on data was obtained from the population of South American, wintering martins. Only birds in active molt were included in this analysis. Since the molt score data used to generate the regression probably do not fulfill the basic requirements of linear regression analysis (see Sokal and Rohlf 1969), the line here produced can be used only as a best available estimate of the progression of the molt; the statistics implicit in the regression equation cannot be meaningfully compared with statistics from other analyses. A general objection to the use of linear regression in examining primary molt (that a sigmoid curve might be expected to result from fewer than average numbers of feathers growing at the start and the end of molt, see Newton 1966) is mitigated in the present case by the tendency of martins to replace only one primary at a time throughout the South American portion of the cycle. Evans (1966), who used a similar primary molt scoring system (though more refined than mine), discusses the use of linear regression in molt studies.

MOLT IN NORTH AMERICA

Dwight's (1900) statement that the "first winter" (first-year) and "adult winter" (adult) plumages of *P. subis* are acquired after the southward fall departure is probably the basis for the somewhat misleading generalizations by Bent (1942) that "complete molt takes place after the birds have gone south," and by Allen and Nice (1952) that "molting occurs after the Martins have reached their winter quarters in Brazil." Dwight, however, mentioned two molting Purple Martins from the small sample available to him from late summer in the United States; and Johnston (1967) noted that adult martins in Kansas begin molting in August prior to fall migration.

The present study substantiates and expands the findings of Dwight and of Johnston, showing that there is a generally occurring, late summer component to the postnuptial and postjuvenal molts of *P. subis* in eastern North America.

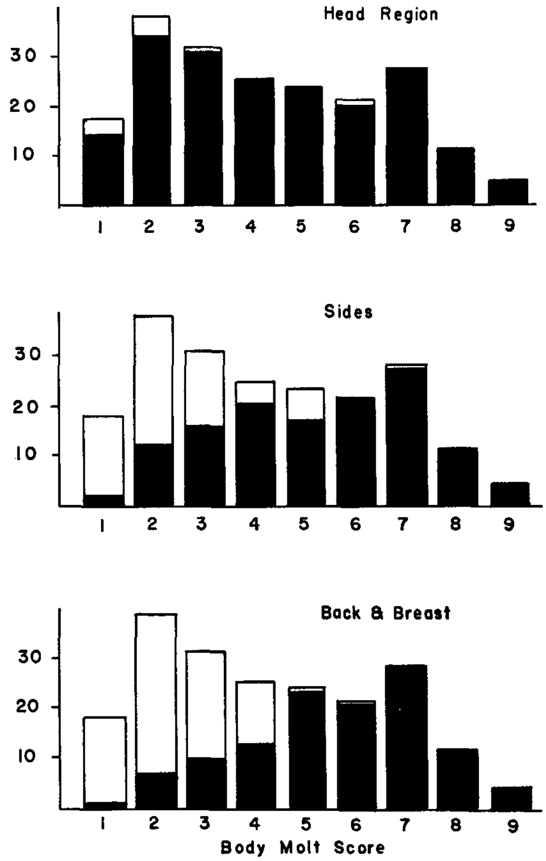

FIGURE 1. Comparison among three body regions (head, upper; sides, middle; back and breast, lower) of the proportion of the total North American sample of *Progne subis* in active molt at each of nine molt scores (see text). The height of the bars indicates sample size; the height of the darkened portion, the number of individuals in molt.

MOLT PATTERNS

Body molt. Judging from birds beginning the body molt (feathers being replaced in no more than two of the five regions examined) feathers are typically first lost from one or both of the regions on the head. Molt on the sides usually follows head molt fairly closely, and is in turn followed by molt on the upper back and/or breast. Figure 1 shows how, in birds with a low total active molt score, head molt (top of head and/or chin and throat) typically predominates. For scores of 1–3, the proportion of the total sample in head molt is significantly greater than the proportion molting on the sides or back-breast ($P < 0.05$). At a score of four the proportion in side molt no longer differs significantly from that in head molt,

TABLE 1. Numbers of North American Purple Martins in active postnuptial and postjuvenal body molt relative to the total sample in each of ten successive periods.

	Age-sex groups										
	Males				Females				Totals		
Period	AD[a]	FY	JUV	PJ	AD	FY	JUV	PJ	AD	FY	JUV
1–10 July	0–5[b]	0–2		0–7	1–3			1–3	1–8	0–2	
11–20 July	1–2	0–2	1–2	1–4	0–2	0–1	1–2	0–3	1–4	0–3	2–4
21–31 July	6–10	6–8	5–6	12–18	3–3	2–4	3–6	5–7	9–13	8–12	8–12
1–10 Aug.	2–2	6–6	3–6	8–8	1–2	2–2	1–2	3–4	3–4	8–8	4–8
11–20 Aug.	9–9	14–14	18–19	25–25	11–12	12–12	28–30	23–24	20–21	26–26	46–49
21–31 Aug.	9–9	7–7	14–16	16–16	9–9	5–5	17–19	14–14	18–18	12–12	31–35
1–10 Sept.			2–2				3–5				5–7
11–20 Sept.	1–1		1–1	1–1					1–1		1–1
21–30 Sept.											
1–10 Oct.							1–1				1–1

[a] AD = adult; FY = first-year; JUV = juvenile; PJ = adults and first-years combined.
[b] Number in molt-total sample.

and side as well as head values are now significantly greater than the back-breast value. At higher total scores there are no significant differences among the three proportions. Low total scores include some birds that have begun to cease molting prior to migrating; the head dominates the *last* stages, as well as the beginnings, of the summer molt. The pattern of feather replacement in the summer body molt does not appear to vary with sex or age.

Molt of flight feathers. The sequence of Purple Martin primary and secondary molt is, as in *Hirundo rustica* (de Bont 1962), typically passerine. Martin primary molt occurs in descending sequence (from the innermost primary, P1, distally); secondary molt begins at two loci, proceeding proximally from S1 in to S6, and radially from S8 out to S7 and in to S9. The centrifugal tail molt exhibited by *P. subis* is also like that of most passerines (Stresemann and Stresemann 1966).

TIMING OF THE MOLT

Table 1 details, for each of ten successive periods of the late summer and the fall, the numbers of eastern North American martins in each of the six age-sex classes undergoing active body molt. In summary, body molt in martins of the eastern United States and Canada is rarely begun prior to mid-July; but, over half of the individuals will have initiated such molt by the end of the month. Except for occasional juveniles, virtually all birds are in body molt by 10 August.

Table 2 similarly depicts primary and secondary molt of first-years and adults. Molt of the juvenal flight feathers occurs entirely on the wintering grounds. While renewal of

TABLE 2. Numbers of North American martins that had dropped at least one inner primary or secondary (format and symbols as in table 1).

		Age-sex groups							
		Males			Females			Total	
Period		AD	FY	All	AD	FY	All	AD	FY
1–10 July	P	0–4[a]	0–2	0–6	1–3		1–3	1–7	0–2
	S	0–4[a]	0–2	0–6	1–3		1–3	1–7	0–2
11–20 July	P	1–3	0–2	1–5	1–2	0–1	1–3	2–5	0–3
	S	1–3	0–2	1–5	0–2	0–1	0–3	1–5	0–3
21–31 July	P	4–10	3–8	7–18	3–3	1–4	4–7	7–13	4–12
	S	3–10	0–8	3–18	2–3	1–4	3–7	5–13	1–12
1–10 August	P	2–2	3–6	5–8	2–2	2–2	4–4	4–4	5–8
	S	0–2	0–6	0–8	1–1	1–2	2–3	1–3	1–8
11–20 August	P	8–9	14–15	22–24	10–12	5–7	15–19	18–21	19–22
	S	5–9	6–13	11–22	8–12	3–6	11–18	13–21	9–19
21–31 August	P	7–9	6–7	13–16	7–9	2–5	9–14	14–18	8–12
	S	3–9	1–7	4–16	7–9	2–5	9–14	10–18	3–12

[a] Several birds examined for primary molt were not susceptible to analysis of secondary molt.

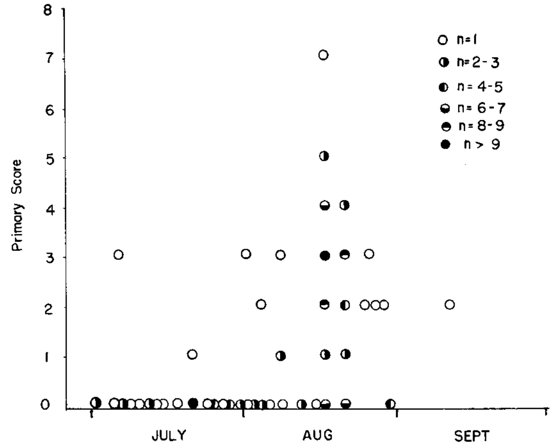

FIGURE 2. Distribution of primary molt scores (0–8) by date in late summer, eastern North American Purple Martins (see methods section of the text and table 2 for scoring system and values of *n*).

primaries, like that of body feathers, becomes relatively common during the period, 21–31 July, and is occurring in most individuals taken in later periods, there are some birds in which the onset of primary molt lags behind that of body molt. The same is true of secondary molt vs. both body and primary molt. Of the 111 first-year and adult birds examined that had begun molt in at least one area, 21 had undertaken body molt only, 34 had begun body and primary molt only, one was molting body and secondary feathers only, and only four showed molt of one or both kinds of remiges without renewal on the body.

Beyond the middle of August, I can demonstrate no relationship between the primary score of North American martins and date (fig. 2). Birds in which the molt is begun relatively early or in which the primary molt progresses relatively rapidly may thus be migrating earlier than the relatively tardy molters; they apparently do not necessarily accomplish more late summer molt than do the slower birds.

Tail feathers are only uncommonly shed north of the wintering grounds. Of all North American first-years and adults examined from August or September, 17 per cent showed some tail molt, and of these birds, 80 per cent had lost or renewed only one of the innermost rectrices. Similar asymmetry may be manifest, though probably to a lesser degree (I have only scattered observations), in the initial stages of remex molt. There is no apparent relationship between the extent of body or wing molt and that of tail molt; for example, birds that had shed one tail feather had primary scores variously ranging from zero to seven.

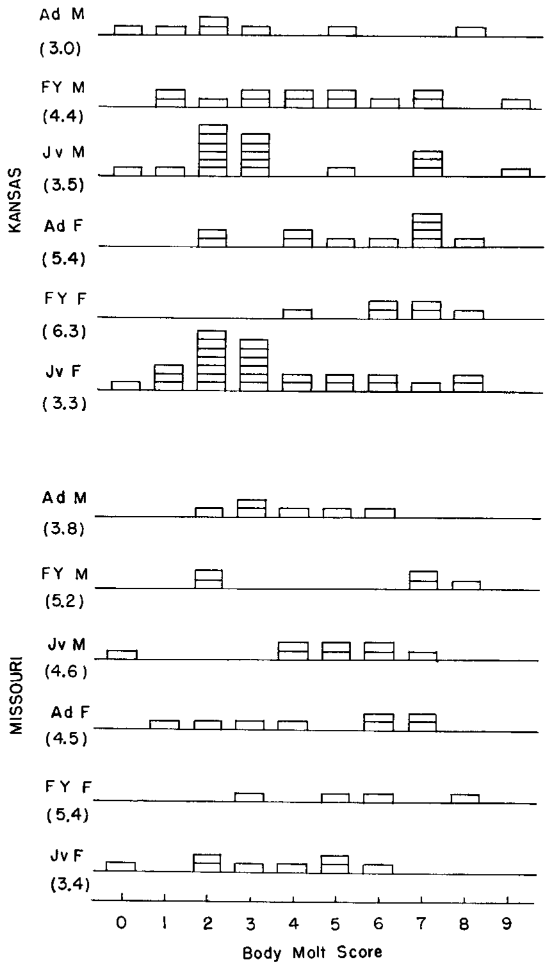

FIGURE 3. Distribution of active body molt scores within the age-sex classes of Purple Martins from the Lawrence, Kansas, and Jefferson City, Missouri, roost samples (Ad = adult; FY = first-year; Jv = juvenile; M = male; F = female; the number in parenthesis equals the mean value for the age-sex sample).

COMPARISONS AMONG AGE AND SEX CLASSES

Postjuvenal vs. postnuptial molt. As already mentioned, juvenile martins delay the replacement of flight feathers until they reach South America. They may also accomplish less body molt in the north than do older birds. Among females in the Lawrence, Kansas, roost sample, the intensity of postjuvenal body molt is lower ($P < 0.05$) than that of the postnuptial molt in each of the older age classes (fig. 3). A one-tailed test was used for these comparisons on the a priori assumption that inexperienced young birds will be less efficient than first-year or adult birds in meeting the energetic demands of the molt. Among males, while

TABLE 3. Amount of fresh feathering in dorsal plumage of Purple Martins from two mid-August samples from Kansas and Missouri.

	Age-sex	Fresh feathering[a] $\bar{x} \pm$ SE	*n*
Kansas			
	AD ♂[b]	122.00 ± 30.44	7
	FY ♂	110.58 ± 20.84	12
	AD ♀	56.13 ± 29.43	11
	FY ♀	83.33 ± 35.06	6
Missouri			
	AD ♂	98.67 ± 17.18	6
	FY ♂	90.00 ± 21.89	4
	AD ♀	8.75 ± 3.87	8
	FY ♀	28.75 ± 16.63	4
Combined			
	AD ♂	111.23 ± 17.82	13
	FY ♂	105.44 ± 16.37	16
	AD ♀	32.44 ± 15.59	19
	FY ♀	61.50 ± 22.94	10

[a] Value for each bird based on sum of percentages of four transverse lines intercepting fresh feathers; maximum possible score = 400 (see methods section).

[b] Symbols as in Table 1.

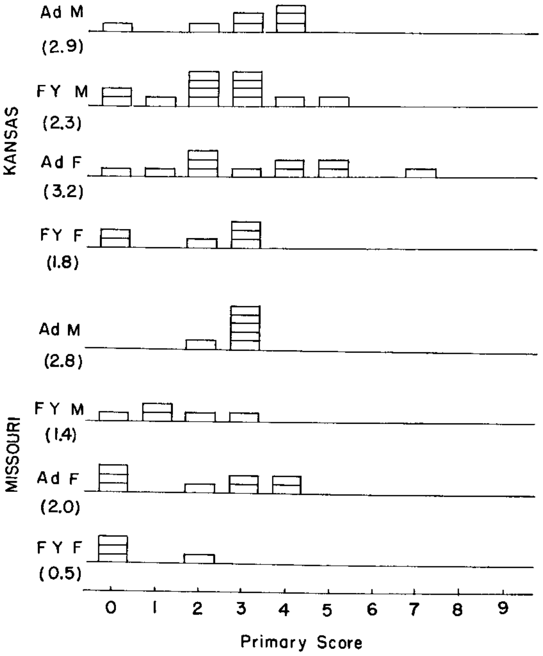

FIGURE 4. Distribution of primary molt scores within age-sex classes of Purple Martins from the Lawrence, Kansas, and Jefferson City, Missouri, roost samples (abbreviations and format as in fig. 3).

the active molt scores of juveniles are again lower on the average than those of first-years, the juvenile score is actually a bit higher than that of adults, and none of the sample differences is significant. There is reason to believe, however, that the relatively low active molt values of older males is due to their having already substantially finished the summer molt, older males having by this time replaced relatively large amounts of their dorsal body feathering. That such is probably not also true for juvenile males is intimated in table 1 where the proportion of North American juveniles in body molt during the first period of generally widespread molt, 1–10 August (which contains neither of the roost samples), is lower than that proportion for older birds ($P < 0.05$). The summer component of the postjuvenal body molt thus seemingly occurs later and (at least among females) is less intense than the summer body molt of older birds. Within the sexes of the smaller Jefferson City, Missouri, sample the ranking of the age classes *inter se* is the same as that within the Kansas sample, though none of the differences is significant.

The age-related differences in body molt described here appear similar to those found by Hoffman (1957) for the autumn "premigratory" component of the molt of Wood Sandpipers, *Tringa glareola*.

Older males vs. older females. There are no significant differences among the active body molt scores of the four older age-sex classes; in both the Lawrence and Jefferson City samples, however, the average values for females are somewhat higher than those of males (fig. 3). Conversely, males have replaced more of the dorsal body feathering than have females ($P < 0.001$ for first-years and adults combined, from the Kansas and Missouri samples combined; see table 3). Adult and first-year males thus apparently accomplish more late summer body molt, or complete the molt earlier, than do females, and males in the two samples may have begun slowing or ceasing the molt prior to migrating. There are no significant intersexual differences in primary molt values.

First-years vs. adults. Primary molt scores of first-years (sexes combined, from the Lawrence and Jefferson City samples combined) are less ($P < 0.02$) than those of adults (fig. 4). Additionally, a greater ($P < 0.05$) proportion of first-years than of adults from the total molting North American sample (thus including, but not limited to, the specimens from the above two samples) were growing only body feathers when collected. The North American element of the primary molt of first-years, then, is apparently retarded in timing or rate, relative to that of adults. There are no significant differences between first-years and adults in either of the body molt values analyzed.

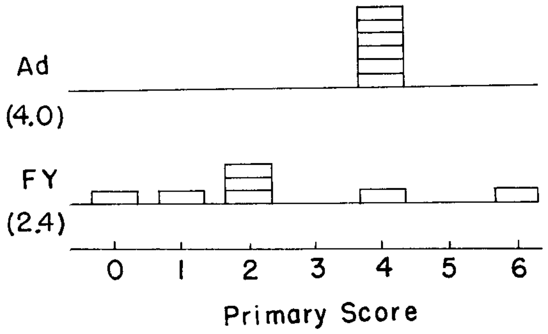

FIGURE 5. Distribution of primary molt scores from autumn-taken, Central American and Antillean, migrant Purple Martins (abbreviations and format as in fig. 3).

FALL MIGRATION SOUTH OF THE UNITED STATES

The 23 specimens allocated to this period for analysis were variously collected on the Yucatan Penninsula (18), in Honduras (1), Nicaragua (1), Cuba (1), and Brazil (2). The latter pair, one taken on 22 September, the other on 18 October, lack any sign of active molt, and are thus assumed to possess the plumage condition maintained during migration. Dates for the Central American and Antillean specimens encompass the period of 25 July (an adult male) to 8 October (also an adult male). Of the 21 migrants, fifteen were collected in the last three weeks of September; Russell (1964), Monroe (1968), and E. Eisenmann (in litt.), however, indicate that *P. subis* are common in Central America through most of August as well.

The postjuvenal and postnuptial molts have generally been interrupted by the time martins arrive in Middle America during the fall migration. Four of the 11 adult and first-year specimens from this region retained at least a trace of active molt in the form of basally sheathed feathers on the chin and throat. In one of these birds, a first-year female collected on 14 August in Quintana Roo, many of the ventral head feathers are still incompletely grown and one P1 is short. None of the remaining old birds and none of the 10 migrant juveniles examined were in active molt. With the exception of a single missing outermost secondary on one bird, and the just-mentioned short P1, all birds possessed a full complement of flight feathers.

Adult primary scores are not quite significantly $(0.05 < P < 0.10)$ greater than the scores from first-years (fig. 5). A significantly greater proportion of adults than of first-years $(P < 0.01)$ had renewed at least one secondary. These statistics substantiate the idea that the late summer remex molt occurring in North America is not as extensive in first-years as in adults.

MOLT IN SOUTH AMERICA

The relatively small total sample size available has dictated a largely qualitative treatment of body molt in South American Purple Martins. Further, once most of the body plumage has been replaced, it becomes difficult or impossible to distinguish females (and, in some cases, males) in their second winter from older birds. For these reasons I have not differentiated among postjuvenile age-sex classes from the winter period.

The South American portion of the postnuptial molt of *P. subis* evidently begins with renewal of the primary molt, followed closely by secondary and rectrix replacement. Four specimens from late September to mid-October had dropped P3 on each wing, but were not otherwise molting. I assume that these birds had just reinitiated molt when collected, rather than that they had come south with a pair of primaries missing. Three other birds, taken within the same period, though still without body molt, had dropped P4 and were growing or had grown P3; they were also molting part of the inner secondary (S7, 8, 9) sequence and the inner rectrices. Unfortunately I have seen no specimens from between 20 October and 23 December (by which time molt is well underway), and thus lack any further direct information on the initial stages of molt in the South American birds.

Among the five body regions examined, molt on the sides seems to be completed first and molt upon the head (either top of head or chin and throat) typically persists latest. Only five of 27 South American specimens in body molt were renewing feathers on the sides; perhaps the major portion of the molt in that region is accomplished before migrating. The progressively increasing importance of head molt, relative to that on other body regions, may be crudely depicted by totaling the body molt scores for all molting individuals from each of several successive time periods, and dividing each total by the summed head score from the particular period. Only 26 per cent $(n = 7)$ of the December total was obtained from the head, versus 60 per cent $(n = 12)$ of the January–February total and 89 per cent $(n = 8)$ of the March–April total. An increased absolute amount of head molt may also characterize the later months of the wintering period, though differences are not significant.

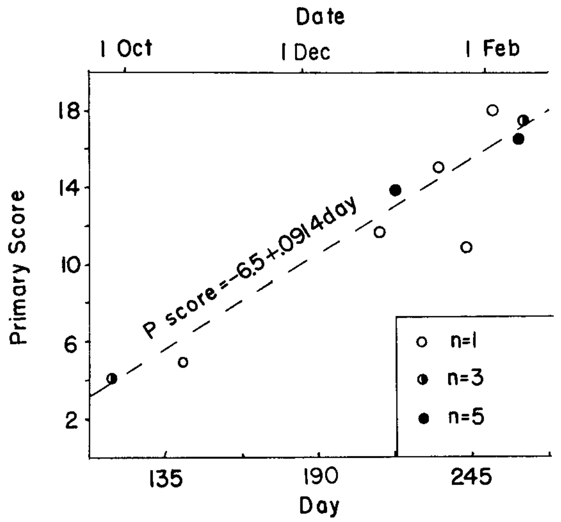

FIGURE 6. Regression of primary molt score on date for adult and first-year South American *Progne subis* in active molt (day 1 = 1 June).

Of a maximum possible head total of 4.0, the December birds averaged 1.1, the January–February birds, 2.3, and the March–April birds, 2.0.

Linear regression of primary molt on date estimates the progression of *P. subis* postnuptial primary renewal throughout the winter (fig. 6). Birds in postjuvenal molt were not included in this analysis. The regression indicates that, on the average, a primary score of 3.2 (the average value obtained from all first-year and adult Central American fall migrants) occurs about mid-September. The average time of completion of the primary molt is in late February. The earliest date for an adult (second winter or older) specimen in wholly fresh plumage is 31 January; the latest date for an adult still in molt is 2 April (traces of body molt only). The few specimens finishing the primary molt indicate that completion of secondary and tail molt is roughly coincidental with the end of primary molt, but that some feather renewal on the head may occur after the flight feathers are all grown.

Completion of the postjuvenal molt apparently lags behind that of the postnuptial molt. Extrapolation of primary scores from birds taken throughout the winter to the completed value (18), using the estimated postnuptial primary growth rate of 0.09 scoring units per day (fig. 6), shows a median completion date of 1 March for old birds and 13 April for juveniles. The accuracy of the latter figure depends upon how similar the rate of postjuvenal primary molt is to that of adults. I have no data for martins, but de Bont (1962) found year to year variation in the relative rates of postnuptial and postjuvenal primary molts of *Hirundo rustica*: juveniles gained on adults in some years and lost ground in others. Eisenmann (1959) states that juvenile Purple Martins complete primary renewal "a month or more later than older birds." My data are in accord with this statement.

SPRING MIGRATION

I have seen only ten adults and one first-year from the northward flight; eight of these birds were taken on the Yucatan Peninsula. Dates for the adults range from 18 February to 14 April; the first-year was collected on 17 April. Since, for the present study, I only sought to borrow and examine specimens collected up to early April, it is likely that I missed some birds collected late in the spring migration period. I presume that I missed most northbound first-years in this way. Monroe (1968) lists observations of *P. subis* from Honduras, 29 January–8 May. None of the spring migrants was molting when collected.

DISCUSSION

DO PURPLE MARTINS UNDERTAKE TWO ANNUAL MOLTS?

The relative tardiness of head molt within the winter body molt sequence contrasts with head molt's predominance within the earliest portions of the late summer body molt. This suggests the possibility of there being two separate annual molts at some or all of the feather follicles on the head. On birds that have recently completed the body molt, however (most April specimens, etc.), there are usually two color classes (and by inference, age classes) of body feathers visible. In adult males, for example, there is a somewhat faded, violet component to the body plumage, and a brighter, blue portion. The "older" feathers are typically grouped on the chin and throat, the frontal region, and on the nape and occiput, areas of predominant molt in the late summer. I thus infer that the late winter-early spring head molt of *P. subis* involves only feathers not replaced during the preceding late summer, and that individual follicles do not experience separate post- and prenuptial molts. Feather replacement on the head of Purple Martins then should be said to involve an interrupted postnuptial molt only.

There are at least two reasonable, if conjectural, explanatory hypotheses for the temporal pattern of head molt of *P. subis*. Johnston and Hardy (1962) noted the importance of the anterior plumage (especially that of the head) in threat display among male martins at breeding colonies. If there is continued, similar use of the anterior plumage (perhaps in ordering dominance relationships at roosts or within foraging flocks) throughout the year, it may be to a bird's advantage to have the overall brightness of the head plumage renewed biannually. Conder's (1949) and Emlen's (1952) observations on *Hirundo rustica* and *Petrochelidon pyrrhonota*, respectively, imply that spacial separation among individuals and perhaps a hierarchical social structure are in fact maintained among some swallows outside the realm of breeding and territorial defense.

The immediately premigratory refurbishment of some of the head plumage in both late summer and late winter probably also increases the aerodynamic (streamlining) effectiveness of the anterior end of the bird during each of its two annual long-distance migratory forays.

INTRAPOPULATION DIFFERENCES IN MOLT

Among the six age-sex classes of Purple Martins, the most striking differences in the timing of the annual molt are those between juveniles and older birds. That most juveniles apparently neither begin nor complete the molt until after most older birds have done so is not surprising, either in terms of current evidence on the relative foraging effectiveness and general survivorship of the two age groups in many bird species (see Lack 1954; 1968), or with reference to studies of molt in other species (Witherby et al. 1938; Hoffman 1957; de Bont 1962). Of more interest is the discovery that there are age and sex related differences in the molt among older martins.

There is no direct evidence to explain the average retardation of the late summer body molt of first-year and adult females vs. that of males. Widmann (table in Allen and Nice 1952), however, showed that when feeding nestlings, female parents make significantly more trips to the nest than do males. Presumably, therefore, males experience somewhat less average energy drain from reproductive activities than do females during the latter portions of the breeding seasons, and males may as a result be able to undertake the molt earlier or more rapidly than females.

The lack of similar intersexual variation in *primary* molt may, as postulated by Holmes (1966) for *Erolia alpina*, reflect the primaries' relative aerodynamic importance during the southward migratory journey. Female Purple Martins, then, may sacrifice an increment of late summer body feather renewal in order to replace the oldest inner primaries before migrating.

Data from other portions of the annual cycle are generally inadequate for discerning any later ramifications of this initial differential in molt timing. The observation by Phillips et al. (1964) that adult male martins depart Arizona in the fall about 10 days before females and young leave may be pertinent here, however. Johnston and Hardy (1962) found that nearly all of the first spring arrivals at a breeding colony were paired, males and females arriving simultaneously. Allen and Nice (1952), in apparent contrast, noted that first arrivals were usually adult males. Even assuming a slightly delayed average northward migration by females, however, there seems no reason to believe that their arrival time is anything but optimally suited to placing them at a colony when the unmated males have secured a nest site and have become receptive to pairing. I thus infer that the late summer intersexual molt difference, even if it persists through the winter molt period, results in no more than suitable coordination of the breeding activities of the two sexes.

Late summer molt in first-year martins features a delayed primary and secondary molt, relative to that of adults. This may reflect less efficient use or procurement of available energy during the preceding months by the younger birds; certainly first-year martins in Kansas produce, on the average, smaller clutches than do older birds (Johnston 1964). That first-years delay the remex molt, rather than the body molt, is in contrast to the pattern of intersexual difference. The inner primaries (and S8) of first-years, however, were grown during the postjuvenal molt on the wintering areas, probably over a month later than were those of adults, which mainly stem from molt of the previous summer in North America. First-years in late summer are thus probably under less than adult-level selection intensities for immediate remex renewal. Further, if a hierarchical arrangement exists within migrating or wintering flocks of martins, there may be extra impetus to first-years assuming adult *body* plumage as rapidly as possible. At least among breeding male Purple Martins, birds in adult plumage are dominant to those in first-year plumage (Johnston and Hardy 1962). If plumage and dominance are similarly related outside the breeding season, and among females as well as males, the relationship would provide a strong adaptive rationale for first-year martins emphasizing body plumage replacement during the early stages of their postnuptial molt.

MOLT IN RELATION TO BREEDING AND MIGRATION

Practically all (235 of 251 specimens) of the molt data from the late summer premigratory period were obtained from birds collected north of 37° N. Hence, where the following discussion relates the timing of the summer molt to breeding and autumnal departure it will consider these latter events as they occur in the northern half of Purple Martin range in eastern North America. Published egg dates (e.g., Johnston 1964; Knight 1908; Stewart and Robbins 1958; Wood 1951; Allen and Nice 1952; Roberts 1932; Stone 1937) imply a normal peak laying period for northeastern *P. subis* of about 25 May–15 June, with some average retardation at higher latitudes. Figuring an average period of about 55 days for parental responsibility toward eggs and young (derived from Allen and Nice 1952), one can predict that the majority of young martins in this region become independent, roughly, 19 July–9 August, a period which is coincidental with the major onset of molt in northeastern Purple Martin populations. While individual exceptions may occur (these data being only broadly indicative), it seems that the period of breeding and of molt are basically mutually exclusive. Other species of aerial foragers, for which there is comparable information, include Chuck-wills-widows, *Caprimulgus carolinensis* (Rohwer 1971), and White-throated Swifts, *Aeronautes saxatalis* (Rohwer, unpubl.), both of which commonly begin the molt while still caring for young, and complete the molt before the fall migration, and Common Nighthawks, *Chordeiles minor* (Selander 1954), which usually molt following migration. Eisenmann (1959), noting that migratory forms of *Progne* apparently temporally segregate the molt and breeding, reported that sedentary, equatorial *P. m. modesta* breed while actively molting.

At least part of the late summer North American Purple Martin population is comprised of birds that are in fact already moving southward. Phillips et al. (1964), for example, reported migrants from northern populations joining late summer and fall roosts at Tucson, Arizona, and in Chiapas, México; and Stone (1937) noted that the thousands of Purple Martins occupying a great nocturnal roost from late July through early September on Cape May, New Jersey, could not possibly all have been from the few local breeding colonies. Further, virtually all martins collected after early August, and thus most of these continental "migrants," are in molt. The simultaneous occurrence of the molt and the southward passage, while unusual among long-distance migrants generally, is typical of migrant hirundinids (de Roo 1966; Rohwer and Niles, unpubl.). Swallows, it is assumed, are able to meet the energetic demands of concurrent molt and autumn migration by virtue of the latter being restricted to a slow, daytime movement containing frequent foraging interludes (de Roo 1966; Broekhysen 1956). The usual hirundinine migratory mode thus differs from that typical of the majority of migrants which undertake relatively direct and sustained, usually nocturnal, movement. I know of no detailed, published observations of migrating *P. subis*, but I would speculate that much of the continental portion of their autumn passage fits the typical swallow pattern of slowly drifting southward while in molt. At some time, perhaps on nearing or reaching the gulf coast of the United States, Purple Martins then adopt the generally inactive molt status which characterizes them by the time they reach Central America. Interruption of the molt at this time presumably reflects the necessity for sustained, relatively long-distance flight, with few foraging opportunities, during the overwater portion of their journey.

Pimm (1970) has suggested that European *Hirundo rustica* may similarly interrupt their molt during passage between southern Europe and their African wintering areas. Wood Sandpipers (Hoffman 1957), which show several parallels with martins in their molt and migratory regime, molt while crossing Europe on their way southward, but interrupt the molt before venturing across the Mediterranean toward Africa.

Comparison of the average completion date of the postnuptial primary molt in South America (late February) with the average mass arrival dates of adults at middle latitudes in North America of about 15 March (Johnston and Hardy 1962) indicates a period of roughly two to three weeks following the molt for premigratory physiological preparation and the northward flight.

SUMMARY

The physical pattern of the molts of Purple Martins is briefly described. Postnuptial and postjuvenal molts begin in late July to early August in northeastern North America, are largely or entirely interrupted during the over-

water portions of the autumn migration, and are resumed and completed on the South American wintering grounds.

The late summer, northeastern North American portion of the postjuvenal body molt is less intensive and/or temporally retarded relative to the postnuptial body molt of older birds. Unlike first-year birds and adults, juveniles do not renew any remiges or rectrices during the late summer period.

First-year and adult males complete the late summer body molt earlier than do first-year and adult females. Remex molt of first-year martins is less extensive than that of adults during the late summer period.

In South America molt by first-years and adults is resumed, on the average, in late September and completed about the end of February. Specimens completing the molt span the period of late January to early April. The postjuvenal molt is probably not completed, on the average, until mid-April.

Breeding and molt by Purple Martins do not appear to overlap in time. Though the occurrence of overwater migration and molt appear to be largely mutually exclusive, at least part of the continental portion of the southward flight may be taken while molting.

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