The Auk 114(2):249–262, 1997

MOLT AND MIGRATION IN THE NORTHERN ROUGH-WINGED SWALLOW

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ABSTRACT.—We describe the prebasic molt of Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) using museum specimens. Birds from eastern North America initiate their flight-feather molt about 40 days earlier than birds from west of the Rocky Mountains, suggesting that ecological differences between the two populations affect their molt schedules. In both populations, juveniles start their flight-feather molt 1 to 4 weeks later than adults, but the timing of body molt does not differ for adults and juveniles. Molt occurs simultaneously with the fall migration in both populations. However, eastern birds interrupt their migration when they reach the northern coast of the Gulf of Mexico. Here, they spend about two months finishing their flight-feather molt before crossing the Gulf in October and November. Molt and migration often are concurrent in diurnally migrating swallows, but the two activities do not occur simultaneously when migration must be sustained without interruption. *Received 15 May 1996, accepted 6 December 1996.*

MOLT IS AN ESSENTIAL COMPONENT in the annual cycle of birds because worn feathers detrimentally affect survival and reproduction (Jenni and Winkler 1994). Because the timing of molt rarely overlaps with other demanding activities, such as reproduction and migration, it is often considered energetically "expensive." However, efforts to measure the energetic costs of molt vary depending on study methods and the species studied (Perek and Sulman 1945, Wallgren 1954, Lustick 1970, Gavrilov 1974, Gavrilov and Dolnik 1974, Chilgren 1975, Wijnandts 1984, Dietz et al. 1992, Lindström et al. 1993). Murphy (1996) argues that the protein and energy requirements of molt do not appear to be great enough to pose significant nutritional challenges and suggests that the scheduling of molt in the annual cycle is a selective compromise associated with various non-nutritional demands.

The timing of molt relative to migration varies among species. This variation may be associated with the duration and physiological costs of molting and migrating, as well as with social and ecological requirements. In most north-temperate passerines, a complete postbreeding molt of body and flight feathers occurs on the breeding grounds just prior to fall migration, or on the wintering grounds following migration (Pyle et al. 1987). Less often, this molt begins on the breeding grounds, is suspended during migration, and is completed on the wintering grounds (Niles 1972). Finally, some passerines from western North America and some trans-Saharan migrants from Europe begin fall migration prior to molting, but interrupt migration to molt before continuing on to their wintering grounds (Rohwer and Manning 1990, Young 1991, Jenni and Winkler 1994). Common to these strategies is the temporal separation of molt and migration.

Molt and migration occur simultaneously in many species of swallows (Niles 1972, Cramp 1988, Jenni and Winkler 1994). However, because few North American species have been studied in detail (Niles 1972, Stutchbury and Rohwer 1990), it is difficult to make comparisons among swallows. Here, we report the timing of prebasic molt in the Northern Rough-winged Swallow (*Stelgidopteryx serripennis*) and the extent to which this molt overlaps with the fall migration. We also document differences in the scheduling of molt and migration in Northern Rough-winged Swallows breeding in eastern and western North America. Differences in the timing of molt and migration in these two populations elucidate factors that affect the scheduling of molt in the annual cycle.

METHODS

We examined 477 museum specimens of Northern Rough-winged Swallows collected from throughout their winter and summer ranges. Specimens were examined from all times of the year except late April and May, with an emphasis on specimens taken from late

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TABLE 1. Seasonal distribution of all specimens examined.

	Eastern population									Western population								
	Adult			Juvenile			Age ?			Adult			Juvenile			Age ?		
Date	M[a]	F	?	M	F	?	M	F	?	M	F	?	M	F	?	M	F	?
1–15 June	6	1		1						15	13		2	1				
16–30 June	3	1		1	1					8	5		3	3				
1–15 July	7	7		6	2	1				16	4		4	2				
16–31 July	4	3		6	3	4				13	4	1	5	9	3			
1–15 August	3	2		6	4	1				3	2		13	11	1			
16–31 August	1	2		6	3	1				6	1		23	12	2			
1–15 September	4	3		2	1		1				1		7	4	2			
16–30 September	1				1		1			3	1	1	2		1			
1–15 October				3			3	1										
16–31 October	1	1			1			4			1		1					
1–15 November					1		2	2					1			2	2	
16–30 November							1											
1–15 December								5										
16–31 December																3		
1–15 January							2	3	1							2	1	
16–31 January							4	5								1	1	
1–15 February							2	1	1							5	1	
16–28 February							2	2								5	1	
1–15 March							6	6								7	1	
16–31 March							4	1								21	7	
1–15 April							10	5								17	10	

[a] M = male; F = female; ? = sex unknown.

summer through early winter (Table 1). Our sample consisted of 60.2% males, 35.6% females, and 4.2% of unknown sex. Juveniles were identified by the cinnamon color on their upperparts and on the edges of their wing coverts and inner secondaries (Pyle et al. 1987). After the first prebasic molt, first-year birds become indistinguishable from adults; these birds, mostly taken in late winter, were of unknown age. In our specimens, 31% were adults, 35% were juveniles, and 34% were of unknown age. Birds taken in or west of Alberta, Montana, Wyoming, Colorado, and New Mexico, or west of Tabasco and Chiapas in Mexico, were defined as the western population; birds taken elsewhere in the United States or Canada were defined as the eastern population.

The two recognized species of Rough-winged Swallows (*Stelgidopteryx*) breed from southern Canada to Argentina (Stiles 1981) and are divided into numerous races. Southern Rough-winged Swallows (*S. ruficollis*) are resident from eastern Honduras to Argentina, and are distinguished from Northern Rough-winged Swallows by their blacker crowns, brighter throats, paler rumps, yellowish bellies, and boldly black-tipped undertail coverts. Southern races of the Northern Rough-winged Swallow that breed from Mexico to Costa Rica (e.g. *fulvipennis, stuarti,* and *ridgwayi*) are practically indistinguishable from populations north of Mexico. These races vary from resident to partly migratory and may have molt schedules that differ from races to the north. All populations of Northern Rough-winged Swallows that breed in northern Mexico, the United States, and Canada are migratory (Miller 1957). We excluded specimens collected south of the Mexican states of Sinaloa, Durango, and Coahuila from June through August (most of which would have been residents) but included those collected after August. We have assumed that including specimens from the resident races would be less harmful to our results than excluding migrants from North America, most of which should have arrived in these areas by the end of August.

Specimens were examined using a magnifying lamp lighted with an incandescent bulb. The molt of flight feathers was scored as described in Newton (1966). Each of the 18 primaries, 18 secondaries, and 12 rectrices was scored as: 0 (no molt), 1 (missing or small pin), 2 (large pin or brush), 3 (brush to one-half grown), 4 (one-half to three-quarters grown), or 5 (three-quarters to fully grown). Birds with a complete set of new flight feathers received a score of 240.

In summarizing molt progression, we compared the intensity of molt among molt series for specimens in which the outermost growing primary was the same. The intensity of flight-feather molt was assessed both as the average number of the feathers growing simultaneously and as the average amount of missing feathers in linear millimeters. We converted the raw molt scores to fractions of missing feather as follows: 1 = 100% missing, 2 = 87.5%, 3 = 62.5%, 4 = 37.5%, and 5 = 12.5%. The amount of each feather that was missing was calculated by multi-plying the fraction missing by the feather's aver-age length. The average length of each of the primaries, secondaries, and rectrices was obtained by measuring feathers from specimens (four of each sex) that contained a complete set of fully grown flight feathers.

Body molt was scored for six non-overlapping regions: crown, back, rump, chin, breast, and belly (see Rohwer 1986). Four to eight feathers were lifted with forceps at five to eight points in each region to check for pin feathers or for growing feathers with sheaths. Then, each region was scored on an ordinal scale of 0 to 4 for the proportion of actively molting feathers, where 0 = none, 1 = less than 25%, 2 = 25–50%, 3 = 50–75%, and 4 = more than 75%. The maximum body molt score for the total of the six regions was 24.

We analyzed frequency data using the G-test with Williams' correction (Sokal and Rohlf 1995). Collection dates were divided into half-month blocks (e.g. early and late September). For body molt data, we used log-linear models (Sokal and Rohlf 1995) to test the independence of four factors (population, age, sex, and body region) in a three-way interaction with time and frequency of molting birds. Also, using G-tests with log-linear models, we tested the independence of flight-feather molt stage (i.e. no molt, first half of molt, and second half of molt) in an interaction with latitude (divided into 5° blocks) and frequency of specimens.

We used linear regression to estimate the mean starting and completion dates, and the mean duration of flight-feather molt as described in Pimm (1976). This method treats molt score as the explanatory variable and date as the dependent variable so that mean starting and completion dates of molt are estimated for individuals rather than populations. Although this method has been criticized for violating assumptions of the linear regression model, it is computationally simple and used more often than the likelihood method developed by Underhill and Zucchini (1988). Moreover, we were not able to convert molt scores to percentage feather mass grown as described in Underhill and Zucchini (1988) because masses for individual flight feathers of Northern Rough-winged Swallows were not available.

To test for differences in flight-feather molt schedules between populations, and among age and sex groups within populations, we performed three-way analyses of covariance (ANCOVA). Regression analyses and ANCOVA were performed using Minitab 8.21 (Minitab Inc. 1991). In assessing the timing of molt, we included only birds replacing flight feathers and excluded birds for which locality, age, or sex were unknown. Significance level was set at $P < 0.05$ for all tests.

Specimens taken by various collectors over long time periods probably do not represent a random or systematic population sample. Collecting effort may be biased by sex or age class, time of year, plumage, molt stage, and geographic location. Indeed, we found few specimens in later stages of molt from the western population (Table 1). Therefore, in addition to statistical analyses, we relied extensively on graphical summarizations of our results.

Replacement Rules

A molt series is a set of remiges or rectrices that is replaced according to a single set of rules (Langston and Rohwer 1995). Because the direction of feather replacement may not reliably identify a molt series (e.g. inner secondary series of passerines; Jenni and Winkler 1994), attention to the temporal sequence of replacement is essential in defining a molt series. We treated primaries and secondaries together because the inner primaries and outer secondaries can be part of a single molt series (e.g. Langston and Rohwer 1995). Following Langston and Rohwer (1995), we categorized each growing primary, secondary, and rectrix according to the direction of molt, and whether it was the feather that starts or stops a molt series. This is done by placing each growing (or focal) feather into one of the four categories discussed below.

Proximal to distal replacement.—This occurs when the focal feather is less advanced in growth than the next proximal feather, and more advanced than the next distal feather. For P9 and S9, comparisons can be made only with a single adjacent feather. To avoid inferences about direction based on incomplete information, and to eliminate double tallying, such feathers are classified either as nodal or terminal (see below). For example, in many passerines P9 can only be compared with P8 (because P10 is not functional and much reduced in size), so it is assigned as the terminal feather if it is shorter than P8.

Distal to proximal replacement.—This occurs when the focal feather is more advanced in its growth than the next proximal feather and less advanced than the next distal feather. Again, at the beginning or end of a molt series, where comparisons can be made only with a single adjacent feather, feathers are classified either as nodal or terminal (see below).

Node of initiation.—Nodal feathers mark sites where molt is initiated in the present episode of molt. They are typically newer or more advanced in their growth than either of the adjacent feathers (e.g. P1). Nodes often mark the beginning of a molt series, but they fail to do so when molt within a single series is interrupted in one episode of molting and resumed in the next (see Langston and Rohwer 1995). When a focal feather has but one adjacent feather (e.g. P9 in many passerines), it is nodal if it is lost before its neighbor. Among passerines, this condition should only exist in *Muscicapa striata,* which replaces its primaries from outer to inner (Stresemann 1963). When two adjacent feathers are at the same stage of development, both should be tallied as nodes of initiation, even though one may not mark the beginning of a molt series. For example, P1 and P2 sometimes are lost nearly simultaneously in passerines, thus causing both to be

TABLE 2. Frequency of remiges in active molt. Remiges are identified as directional, nodal, and terminal, using replacement rules described in Methods.

	Focal feather																	
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9
Proximal-to-distal replacement			9								34	35	17	14	14	15	12	
Distal-to-proximal replacement					5	8	12	10	11									
Nodal feathers	6	32	1					1		44	13				1			
Terminal feathers	10			7					1					1				12

recorded as nodal in some individuals. This is a consequence of the loss of P2 following the loss of P1 closely in time. Other specimens, however, show that only P1 is a nodal feather, because it usually is lost before P2.

If S1 and P1 are lost simultaneously (they are not in most passerines), recording both as nodal would be appropriate because each marks the beginning of a separate molt series. When the nodal feathers of separate molt series are adjacent (e.g. S1 and P1), then the second of these to be replaced will have a new feather on one side and an old (or less advanced) feather on the other side. In this case, the first feather of the second series to begin molting would incorrectly be categorized as directional. The node of the second series can be identified by examining the association in timing of replacement with nearby feathers. For example, P2 is replaced shortly after P1 in passerines, but S1 may be lost when any of several inner primaries are growing, indicating that it is nodal.

Terminal feathers.—When the focal feather is less advanced in its growth than adjacent feathers it is unambiguously terminal, unless feathers of a series are molted in a nonlinear sequence. When a focal feather has but one adjacent feather (e.g. P9 in many passerines), it may be identified as terminal if it is lost after its neighbor. When a focal feather shows one adjacent feather in a more advanced state of growth, and the other adjacent feather is fully grown, then the focal feather is terminal, and the growing feather is part of the molt series of the terminal feather. The new feather is usually the nodal or terminal feather of the adjacent molt series. When two molt series proceed in opposite directions to meet at a centrally located pair of feathers, only one of these two feathers can be identified as a terminal feather by this rule. The other must be identified using information on direction and timing of replacement (e.g. S7 in this data set).

RESULTS

Flight-feather molt.—The sequence of primary and secondary molt in Northern Rough-winged Swallows is typical of most passerines. The primaries form a single molt series and are replaced from the innermost (P1) outward (Table 2). P1 and P2 appear to be molted almost simultaneously, because the scores of these feathers were either the same (13 of 35 birds molting both P1 and P2) or differed by a score of only one. The secondaries are divided into two molt series, S1-S6 and S7-S9 (Table 2). Molt of the inner secondaries begins with S8, when the outermost growing primaries are P2-P4, and proceeds in the sequence S8-S9-S7. Of 22 birds with only one of these secondaries in molt, 21 were growing S8. In all eight of the birds where only two inner secondaries were in molt, the feathers were S8 and S9. Molt in the outer series of secondaries (S1-S6) begins with S1, after the molt of the inner secondaries has been initiated, and proceeds proximally (Table 2).

Molt of the rectrices is divided into an inner series (R1-R5) and an outer series (R6; Table 3). Rectrix molt begins with the loss of R1 (which occurs when either P3 or P4 is the outermost growing primary) and proceeds outward to R5. We included R5 in the inner series because in most cases R5 is lost after R4 (in two cases R5 was molted before R4 on one side but not on the other), whereas timing of the loss of R6 varied considerably. R6 was molted before R4 in three of seven cases, between R4 and R5 in three of seven cases, and after R5 in one of seven cases.

TABLE 3. Frequency of rectrices in active molt. Rectrices are identified as directional, nodal, and terminal, using replacement rules described in Methods.

	Focal feather					
	R1	R2	R3	R4	R5	R6
Proximal-to-distal replacement		12	9	7	2	
Distal-to-proximal replacement						
Nodal feathers	19	2				6
Terminal feathers	1				5	1

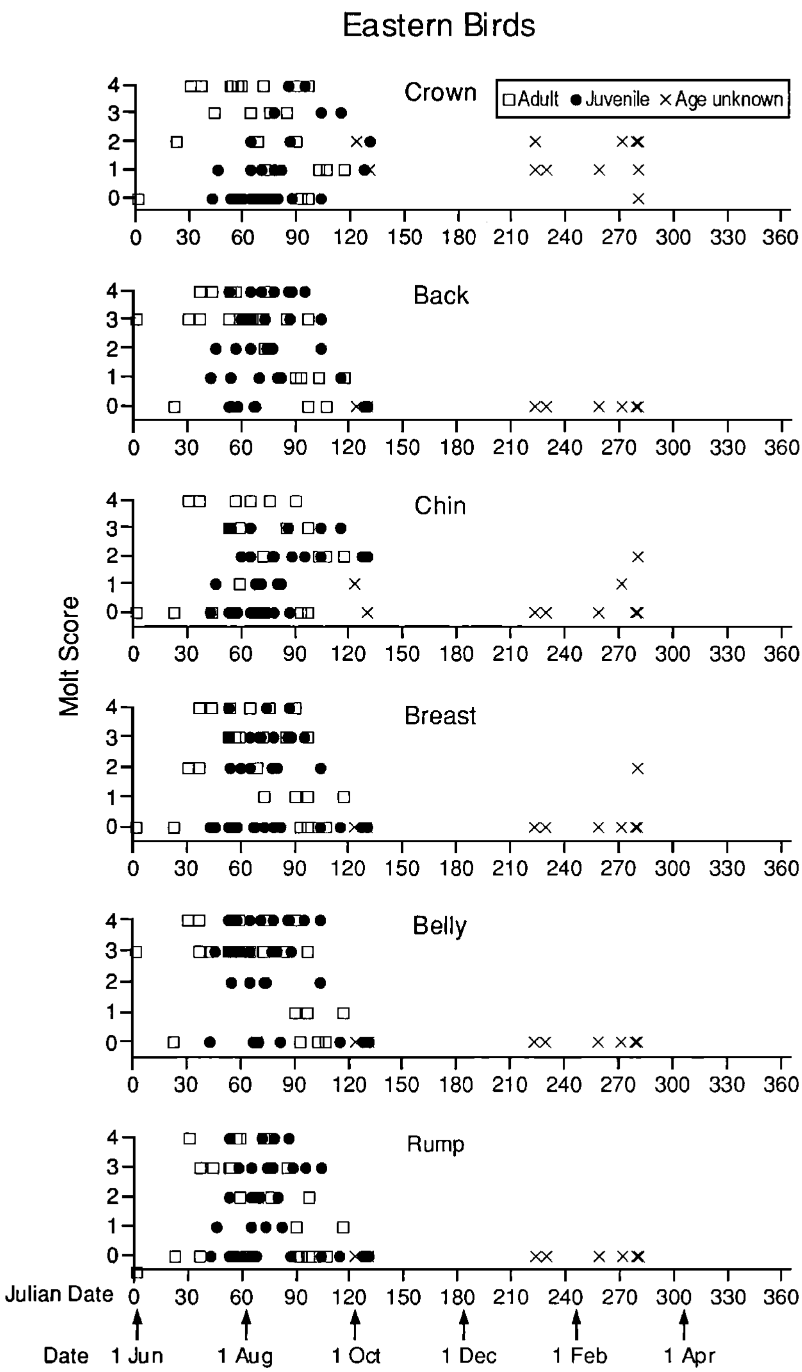

FIG. 1. Temporal distribution of body molt in crown, back, chin, breast, belly, and rump for eastern populations of Northern Rough-winged Swallows. Only data for specimens undergoing body molt are shown. Data for western populations not shown. See Methods for description of molt score. Julian (day 1 = 1 June) and calendar dates in bottom panel.

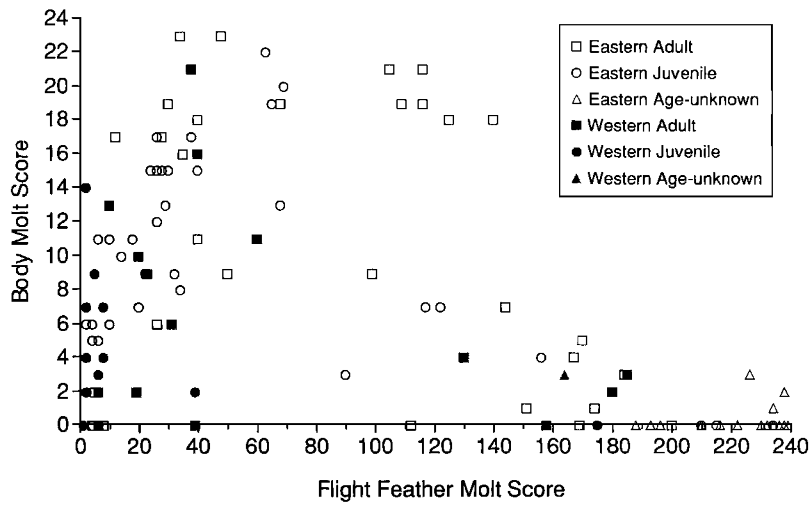

FIG. 2. Timing of body molt compared with flight-feather molt for Northern Rough-winged Swallow undergoing flight-feather molt.

Body molt.—Molt of non-flight contour feathers occurs at about the same time in each of the six body regions (Fig. 1). The timing of molt is not significantly different among body regions for all birds examined, or for the western and eastern populations analyzed separately (G-tests, $P > 0.30$ in all cases). For this reason, we present the data only for eastern birds; the relationship between molt and timing for western birds is similar in all respects, except that western birds initiate molt later (see below). In juveniles, crown and chin feathers tend to molt later and with less intensity than in adults. Spring specimens of unknown age showed light molt on their crowns (10 of 11) and occasionally on their chins (2 of 11). Among adults, body and flight-feather molt begins at about the same time, but the body molt is completed before all flight feathers have been replaced (Fig. 2). Out of 27 adults with flight-feather molt scores of more than 160, 17 had already finished their body molt. Juveniles begin their body molt before the onset of their flight-feather molt and, like adults, complete it well before replacing all flight feathers.

Intensity and relative scheduling of molt.—When molt intensity is measured as the mean number of feathers growing simultaneously, the intensity of the primary molt peaks at P5 (Table 4). However, when measured as the mean length of missing feather(s), molt intensity is more scattered, and the overall trend is a decline in intensity from P2 to P9. This pattern may result in smaller gaps in the total surface of the primaries when the longer and more important feathers of the wing are replaced. The most intense periods of inner and outer secondary molt do not overlap (Table 4). Body molt is most intense during the time that P3 to P6 are being grown, and is mostly completed by the time that P8 is growing.

Timing of molt.—On average, eastern birds initiate flight-feather molt in early July and complete it by late December (Fig. 3). Western birds initiate flight-feather molt in mid-August and complete it by early January. Analyses of the effects of population (western or eastern), age, and sex on the timing of molt, with the stage of the flight-feather molt held constant as a covariate, revealed that population and age, but not sex, affect the timing of flight-feather molt significantly (population: $F = 25.7$, $P < 0.001$; age: $F = 10.9$, $P < 0.01$; sex: $F = 0.62$, $P > 0.4$; df = 1 and 84 in each case). However, when only western populations were examined, no significant difference in flight-feather molt schedules was found between age classes ($F = 0.61$, df = 1 and 25, $P > 0.4$), but a significant difference was found between sex classes ($F = 4.45$, df = 1 and 25, $P < 0.05$). This difference is not apparent when observed graphically, and the results for western populations may be due to small sample sizes and the potentially spurious effects of outliers.

Eastern adults begin molting flight feathers in early July, about 26 days earlier than eastern ju-

TABLE 4. Summary of the intensity and scheduling of molt in different feather tracts.

	Outermost growing primary								
	1	2	3	4	5	6	7	8	9
Sample size	8	26	21	11	7	8	11	8	12
	Mean no. of feathers growing per side								
Primaries	1.00	1.96	2.24	2.36	2.43	1.75	1.82	1.38	1.25
Inner secondaries (7–9)		0.31	0.95	1.36	1.43	1.00			
Outer secondaries (1–6)			0.05		0.86	1.00	1.82	1.00	0.75
Inner rectrices (1–5)	0.13		0.24	0.64	1.57	2.00	2.56	0.63	
Outer rectrices (6)							0.64	0.13	
Totals	1.13	2.27	3.48	4.36	6.29	5.75	6.82	3.13	2.00
	Mean mm of feathers missing per side								
Primaries	44.6	79.6	66.3	100.4	85.2	67.9	74.2	72.5	56.7
Inner secondaries (7–9)		8.1	23.2	28.6	25.4	20.9			
Outer secondaries (1–6)			2.2		31.6	33.6	57.3	17.9	15.4
Inner rectrices (1–5)	5.9		11.0	29.3	56.0	48.4	70.3	18.9	
Outer rectrices (6)							19.7	6.4	
Totals	50.6	87.8	102.8	158.3	198.1	170.7	221.6	115.7	72.1
Mean body-molt score	5.25	4.46	11.52	15.73	17.86	10.63	5.82	0.75	0.33

veniles (Fig. 4A, Table 5) and about 40 days earlier than western adults (Table 5). The data indicate that western juveniles initiate flight-feather molt about 10 days later than western adults (Fig. 4B, Table 5), although the difference is not significant. Estimates of the mean duration of flight-feather molt are 94 and 105 days for eastern adults and juveniles, respectively. The estimates for western populations are not discussed because of the large variability in the data.

Body molt occurs from late June through early October. Peaks are late July in eastern adults and mid-August in western adults (Fig. 5), a seasonal difference that is highly significant ($G_{adj} = 23.3$, df = 4, $P < 0.001$). Eastern birds show no significant differences between age and sex groups in the timing of body molt (age: $G_{adj} = 2.29$, df = 4, $P > 0.65$; sex: $G_{adj} = 6.73$, df = 5, $P > 0.2$). Sample sizes for the western population are too small for analysis.

Molt and migration.—Non-molting birds tend to be found in the north, whereas birds in the later stages of flight-feather molt are concen-

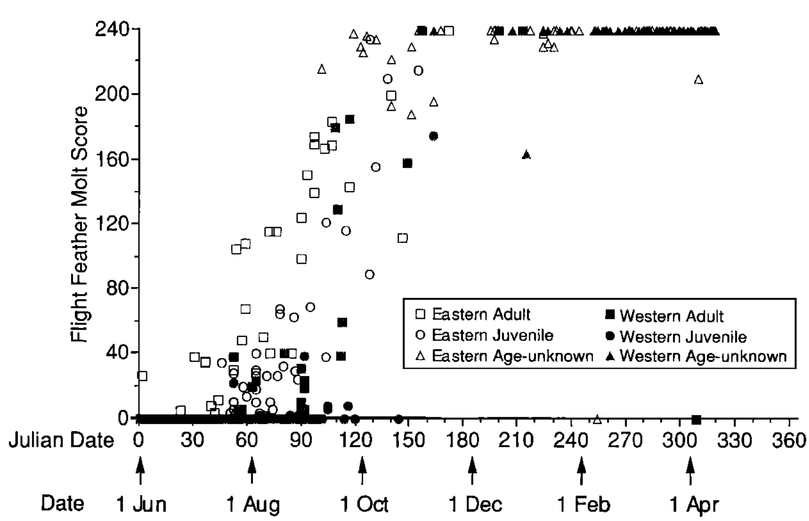

FIG. 3. Progression of flight-feather molt for adult and juvenile Northern Rough-winged Swallows in eastern and western populations. Molt score of 0 indicates no molt, and 240 indicates completion of molt. Note the general temporal order (eastern adults, eastern juveniles, western adults, and western juveniles).

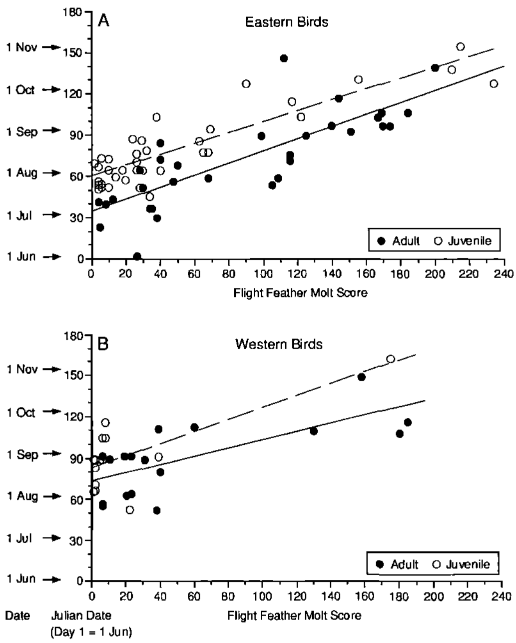

FIG. 4. Least-squares linear regressions of collection dates against total flight-feather molt score for adult and juvenile Northern Rough-winged Swallows separated by region of collection. Birds collected in winter are of unknown age and therefore excluded. Eastern adults: y = $0.439x + 34.0$ ($F = 55.6$, df = 1 and 29, $P < 0.001$, $R^2 = 0.657$); eastern juveniles: y = $0.393x + 60.0$ ($F = 125$, df = 1 and 34, $P < 0.001$, $R^2 = 0.786$); western adults: y = $0.294x + 73.8$ ($F = 15.0$, df = 1 and 15, $P < 0.01$, $R^2 = 0.499$); eastern juveniles: y = $0.432x + 83.3$ ($F = 16.2$, df = 1 and 13, $P < 0.01$, $R^2 = 0.555$). Only specimens undergoing flight-feather molt are analyzed. Solid regression lines are for adults, dashed lines for juveniles.

trated in the south (Figs. 6–8). There is a significant difference in the latitudinal distribution of locations where specimens were collected among different molt stages ($G_{adj} = 108.1$, df = 10, $P < 0.001$). Clearly, Northern Rough-winged Swallows are migrating southward at the same time that they are molting. Map summaries indicate that western birds probably migrate continuously through the western United States and Mexico while they are molting (Figs. 6–8). By contrast, eastern birds move southward while they are molting only until they reach the Gulf of Mexico (Fig. 8).

DISCUSSION

Sequence of flight-feather molt.—The sequence of flight-feather molt in Northern Rough-winged Swallows is typical of most passerines except for the outermost rectrices (R6). R6 is molted before R5, and often before R4, a pattern also found in several other passerines (e.g. European Barn Swallow [*Hirundo rustica*], Eurasian Crag-Martin [*Hirundo rupestris*], and Meadow Pipit [*Anthus pratensis*]; Jenni and Winkler 1994). Several species of Motacillidae also feature an early loss of R6 (Jenni and Winkler 1994). We suspect that closer attention to establishing the rules of flight-feather replacement may reveal that the rectrices are typically organized into two molt series, as we have documented for Northern Rough-winged Swallows.

The intensity of molt is relatively constant throughout much of the molt, which may reflect the fact that these swallows are under pressure to maintain high flight efficiency. Intensity of the primary molt peaks early and then steadily declines as the molt proceeds towards the longest and most important primaries. This phenomenon is much more evident when molt intensity is measured as the mean length of missing feathers, rather than as the mean number of growing feathers, which suggests the importance of the former measurement of intensity.

Timing of molt in adults relative to breeding.—Adults begin replacing body and flight feathers about 40 days later in the west than they do in the east (Table 5, Fig. 5). Breeding schedules also differ between western and eastern populations; egg dates for northwestern breeding localities range from early June to early July, with young fledging in late July (Weydemeyer 1933, Bent 1942, Jewett et al. 1953, Burleigh 1972, Cannings et al. 1987). In contrast, egg dates for northeastern birds range from mid-May to mid-June, with young fledging in early July (Bent 1942, Lunk 1962, Mumford and Keller 1984, Bull 1985, Bohlen 1989). The initiation of molt coincides with the fledging of young in both populations, beginning in early July in eastern adults and early August in western adults. Both male and female Northern Rough-winged Swallows provision their young, which may explain why the sexes are similar in their molt schedules.

Tree Swallows (*Tachycineta bicolor*) also initiate flight-feather and body molt when their young are fledging (Stutchbury and Rohwer 1990). However, Tree Swallows complete their flight-feather and body molt at about the same time, whereas Northern Rough-winged Swallows complete their body molt well before their flight-feather molt is finished (Fig. 2). This is due

TABLE 5. Estimates of starting and completion dates, and duration of flight-feather molt ± 95% confidence interval using the least-squares linear regression model. Dates are in Julian date (Day 1 = 1 June), with calender dates in parentheses.

	Starting date	Completion date	Duration (days)
	Eastern populations		
Adults	34 (4 Jul) ± 13	139 (17 Oct) ± 20	105 ± 29
Juveniles	60 (30 Jul) ± 6	154 (1 Nov) ± 14	94 ± 17
	Western populations		
Adults	74 (13 Aug) ± 14	144 (22 Oct) ± 31	71 ± 39
Juveniles	83 (22 Aug) ± 11	187 (4 Dec) ± 52	104 ± 56

to the shorter duration of body molt in Northern Rough-winged Swallows (about three months; see Fig. 5) compared with Tree Swallows (about four months).

Timing of molt in juveniles.—Juvenile Northern Rough-winged Swallows delay flight-feather molt but replace body feathers at the same time as do adults. Juvenile European Barn Swallows also delay the initiation of flight-feather molt (Cramp 1988). Adult Northern Rough-winged Swallows initiate flight-feather molt when juveniles are only a few weeks old and may still be growing their juvenal flight feathers (three early juveniles from Utah were still growing outer primaries). Juveniles may delay their flight-feather molt until they become experienced at foraging and escaping predators. Body molt may start earlier because it has less influence on flight performance. Fewer juveniles are molting crown and chin feathers than in other body regions, and the molt scores for crown and chin in juveniles generally are low. Interestingly, the limited spring molt is restricted almost entirely to feathers of the crown and chin, suggesting that birds molting in spring may be second-year birds.

Timing of molt relative to migration.—Northern Rough-winged Swallows molt during much of their fall migration, which occurs from July to October in eastern populations and from August to November in western populations (Bent 1942). Two recoveries of banded birds (Bird Banding Laboratory) indicate the timing of postbreeding migration: one was banded on 3 July 1950 in Michigan and recaptured on 13 August 1950 in Tennessee, and the other was banded on 24 June 1945 in Ontario, Canada and shot on 29 August 1945 in Louisiana.

Many other swallows molt during migration (Purple Martins [*Progne subis*], Niles 1972; Crag Martins, Elkins and Etheridge 1977; European

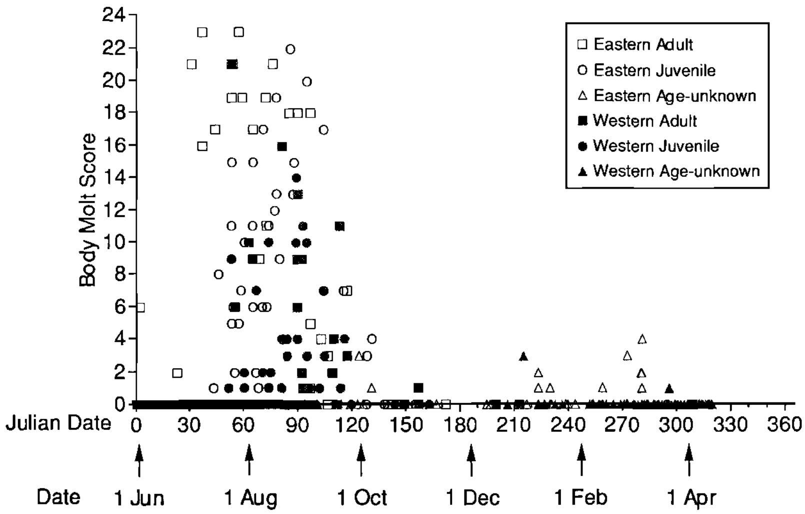

FIG. 5. Progression of body molt for adults and juveniles in eastern and western populations of Northern Rough-winged Swallows. Body-molt score of 0 indicates no molt or completion of molt. On average, eastern adults and juveniles undergo molt before western adults and juveniles.

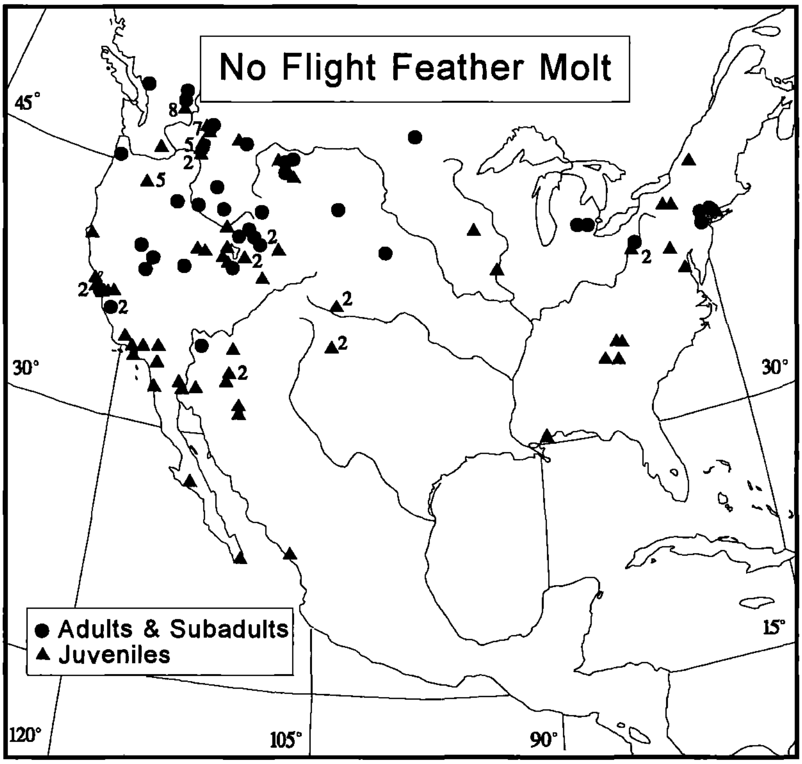

FIG. 6. Geographical distribution of Northern Rough-winged Swallow specimens collected before flight-feather molt. Only specimens collected between July and November are included. Numbers represent the number of specimens collected at the same locality.

Barn Swallows, Cramp 1988; Tree Swallows, Stutchbury and Rohwer 1990). Niles (1972) argues that swallows can meet the energy demands of molt during migration by migrating during daytime with frequent interludes for foraging. This pattern contrasts with most other passerine migrants, which migrate at night. For many swallows, the instantaneous cost of flight-feather molt is further reduced by its long duration (four to eight months; Niles 1972, Pyle 1987, Stutchbury and Rohwer 1990).

The 40-day difference in timing of flight-feather molt between eastern and western populations cannot be fully explained by differences in breeding schedules, because eastern birds fledge their young less than a month earlier than western birds. Western birds may delay initiating their molt until they have passed through the northern parts of their breeding range where late-summer conditions are dry and unproductive. The mean starting date of flight-feather molt for western populations of Northern Rough-winged Swallows is mid-August, and many individuals are probably well into migration by that time (cf. Figs. 6 and 7). Northern populations of Bullock's Orioles (*Icterus bullockii*) also migrate to the southwestern United States before they begin prebasic molt and are thought to do so to escape the dry late-summer conditions of the breeding grounds (Rohwer and Manning 1990, Rohwer and Johnson 1992). In contrast, Baltimore Orioles (*I. galbula*) undergo the prebasic molt on the breeding grounds prior to migration.

Eastern birds may initiate flight-feather molt early because of their need to complete it before the trans-Gulf migration. Most eastern specimens taken in later stages of flight-feather molt were collected in southern Alabama, Mississippi, and Louisiana (Fig. 8). Burleigh (1944:407) documented the early departure of Northern Rough-winged Swallows from the breeding range in the eastern United States and their concentration along the Gulf coast of Mississippi for over two months. He noted that flocks of Northern Rough-winged Swallows assemble along the

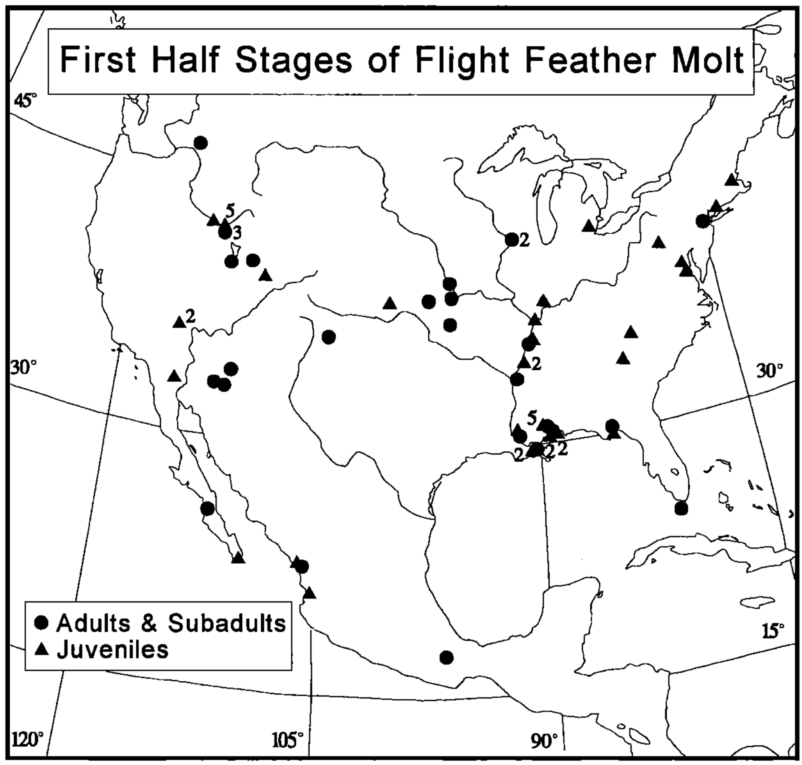

FIG. 7. Geographical distribution of Northern Rough-winged Swallow specimens collected during the first half of flight-feather molt. Only specimens collected between July and November are included. Numbers represent the number of specimens collected at the same locality.

Gulf coast from the middle of July through early August, gradually disappearing only after the first of October. The timing of their disappearance coincides with the completion of their flight-feather molt. Thus, eastern populations of Northern Rough-winged Swallows may initiate their molt earlier to accommodate their trans-Gulf migration, which they apparently do not undertake until flight-feather molt is completed.

We found no published documentation of a trans-Gulf migration in Northern Rough-winged Swallows, but there is indirect evidence for such a migration, including several winter records for the West Indies (Bond 1956, Faaborg and Terborgh 1980, Voous 1983) and Guatemala (Griscom 1932). Northern Rough-winged Swallows arrive in Yucatan in mid-October (Howell 1989). Northern Rough-winged Swallows are not recorded in any of the published accounts of trans-Gulf migrants dating from late August through early September (e.g. Paynter 1953). One specimen was collected in Quintana Roo, Mexico on 29 October 1952, an adult female who apparently had interrupted her flight-feather molt just before its completion, as P9 had not been replaced on either wing. We found no specimen collected along the Gulf coast of Texas and northeastern Mexico (Figs. 6–8).

In summary, evidence suggests that early fall arrivals of eastern Northern Rough-winged Swallows gather at the northern Gulf coast to complete their flight-feather molt before continuing their southward migration. A late trans-Gulf migration apparently follows the completion of this molt. Able (1972) suggests that optimum conditions for direct bird flight from the northern Gulf coast to the tropics (i.e. following the passage of a cold front far into the Gulf) occur in early to mid-October. Thus, weather conditions and the late completion of the flight-feather molt could favor a late migration of Northern Rough-winged Swallows over the Gulf.

Eastern juveniles complete the flight-feather molt in late November. If juveniles migrate across the Gulf with adults in late October, then

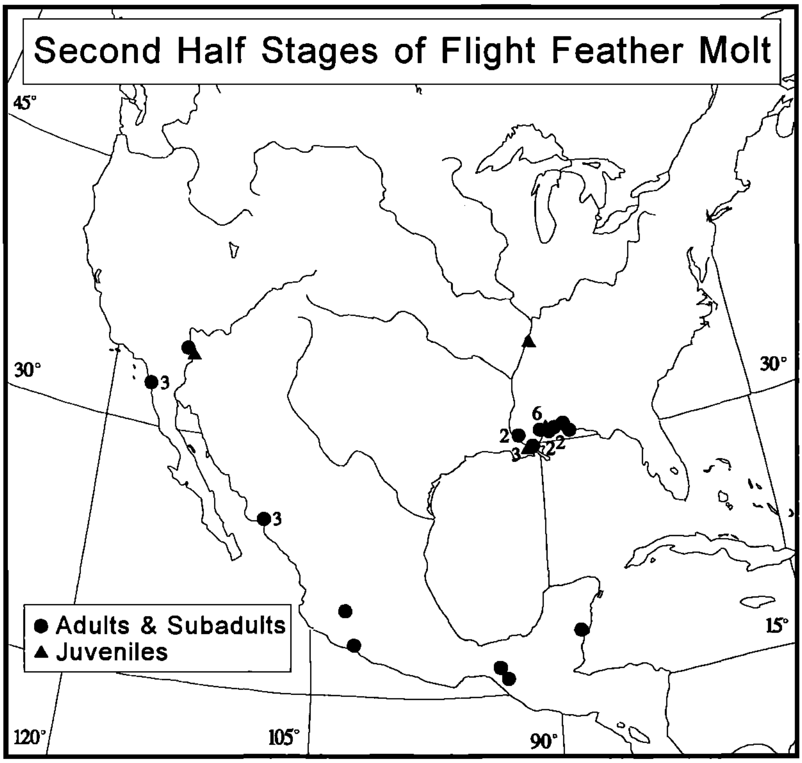

FIG. 8. Geographical distribution of Northern Rough-winged Swallow specimens collected during the second half of flight-feather molt. Only specimens collected between July and November are included. Numbers represent the number of specimens collected at the same locality. In comparing figures 6–8, note that specimens in more advanced stages of molt are collected farther south.

they would still be growing flight feathers during their trans-Gulf migration. The frequency of northerly, post-frontal winds, and particularly those penetrating to Yucatan and beyond, is greater in November than in September or October (Buskirk 1980). Thus, weather conditions are suitable for a late trans-Gulf migration in juveniles. However, such a late-fall passage may result in young-of-the-year being confronted with wintering habitats that are already filled with earlier migrants. For this reason, we suspect it will prove to be late-molting young birds that make up the flocks of Rough-winged Swallows wintering near the Sabine National Wildlife Refuge on the Louisiana-Texas border (Root 1988). Investigations of: (1) the progression of flight-feather molt in adults and juveniles along the Gulf Coast, (2) seasonal changes in age ratios of fall birds taken along the Gulf, and (3) the age classes of individuals wintering on the United States side of the Gulf of Mexico will further elucidate the relationships between molting and migration in Northern Rough-winged Swallows.

Conclusions.—Because temperate swallows are both diurnal migrants and aerial foragers, they have less need to separate molt and migration than do other passerines. When swallows migrate across deserts and large bodies of ocean unsuitable for foraging and obtaining water, they have different ways of avoiding the conflicts of simultaneously molting and migrating. North American Barn Swallows and Purple Martins interrupt their prebasic molt for the trans-Gulf migration (Niles 1972). Similarly, European populations of Barn Swallows, which are trans-Saharan migrants, interrupt their prebasic molt during the passage from southern Europe to tropical Africa (Cramp 1988). In contrast, eastern breeding populations of Northern Rough-winged Swallows interrupt their migration in order to complete molt before making their fall passage over the Gulf of Mexico.

Why should Northern Rough-winged Swallows have opted for delaying their migration while they finish molting? Barn Swallows, Cliff Swallows (*Hirundo pyrrhonota*), Bank Swallows (*Riparia riparia*), and Purple Martins winter in South America, where they occupy a relatively large land area. All of these species molt most of their flight feathers after arriving in their winter quarters (Pyle et al. 1987). In contrast, Northern Rough-winged Swallows, Tree Swallows, and Violet-green Swallows (*Tachycineta thalassina*) winter in the southern United States, Mexico, and Central America, where they are concentrated into a much smaller and perhaps less productive land area. These species complete their annual molt by late fall, either on the breeding grounds or during southward migration in North America. Similar patterns are also found in many European species; those wintering in southern Europe molt on their breeding grounds, whereas many trans-Saharan migrants molt in southern Africa (Jenni and Winkler 1994).

If a winter molt is energetically or nutritionally difficult for swallows that winter in the Northern Hemisphere on a relatively small land area, then one would expect that Northern Rough-winged Swallows from western North America also should pause in the southwestern United States to complete their molt (or at least migrate very slowly through the southwest) before migrating to their wintering grounds in southern Mexico and Central America. Unfortunately, we could not evaluate this prediction because of the dearth of specimens taken in western North America during the later stages of primary molt.

Acknowledgments

We are very grateful to the following institutions and their curators for access to specimens: Museum of Northern Arizona, University of Arizona, California Academy of Sciences, Los Angeles County Museum of Natural History, San Diego Natural History Museum, University of California at Los Angeles, University of California Museum of Vertebrate Zoology, Western Foundation of Vertebrate Zoology, Denver Museum of natural History, University of Colorado, Field Museum of Natural History, University of Kansas Museum of Natural History, Louisiana State University Museum of Natural Sciences, Museum of Comparative Zoology, University of Michigan Museum of Zoology, American Museum of Natural History, Carnegie Museum of Natural History, Philadelphia Academy of Natural Sciences, University of Utah, University of Washington Burke Museum, Washington State University Conner Museum, U.S. National Museum of Natural History. Banding recovery data were kindly supplied by the Bird Banding Laboratory, National Biological Survey. D. M. Niles scored many of the specimens for molt. R. B. Payne, J. S. Albert, and J. M. Swales provided valuable comments on the early draft of this manuscript. C. Thompson helped with references on the trans-Gulf migration.

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Associate Editor: J. S. Marks