MOLT, PLUMAGE, BODY MASS, AND MORPHOMETRICS OF A POPULATION OF THE WHITE-THROATED SWIFT IN SOUTHERN CALIFORNIA

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ABSTRACT: Over a 10-year period, I examined molt patterns, plumage, and body-mass changes in a population of White-throated Swifts in the Mecca Hills, Riverside County, California, by sampling birds at regular roosts in each month from February through November. The swifts used the roosts year round but numbers at them declined in March then increased in June and July, after breeding. As a result of plumage wear, the juvenal plumage can be categorized in three "phases": prior to fledging, after fledging, and prior to the first prebasic molt. I found no sexual dimorphism in wingspan, wing length, tarsus length, tail length, culmen length, or body mass. I found an average difference between the sexes in the depth of the tail fork, but because of much overlap it cannot be used to determine the sex of individuals. The maximum difference between highest and lowest body mass was 28.7%, less than reported for other species. Testis size began to increase in March, reaching a peak in April. Primary molt lasted 6–7 months, from May through November. Tail molt lasted about 2.5-3 months, from June through August. Breeding began at this desert site one to two months earlier than at a coastal site. The overlap of breeding and molt in this desert population appears to be less than reported for other species of swifts.

The White-throated Swift (*Aeronautes saxatalis*) is a medium-sized swift widely distributed in North America, from British Columbia, Canada, south through mountainous terrain to Honduras (AOU 1998). It is the most common and only resident swift in southern California (Garrett and Dunn 1981, Unitt 1984).

Despite the species' wide distribution, most of what is known about the White-throated Swift is distribution and taxonomy (Bent 1940, Behle 1973, Navarro et al. 1991, Ryan and Collins 2000), breeding sites (Bradbury 1918, Pitelka 1943, Dobkin et al. 1986), and physiology (Bartholomew et al. 1957). The goal of this study was to describe the patterns of molt and variation in body mass in a single population of White-throated Swifts over an annual cycle.

STUDY AREA AND METHODS

From 1990 through 2000, I collected 112 specimens of the White-throated Swift from a single large roost in Painted Canyon, Riverside Co., California (33° 30′ N, 116° 00′ W; elevation 125 m). The roost was a crack in a large boulder about 15–18 m above the ground and located in a sandy cliff about 60–80 m in height, along a desert wash in the Mecca Hills. I collected a minimum of ten adult specimens per month from February through November. Most specimens were collected within the middle third of each month and are deposited at the Natural History Museum of Los

Angeles County (LACM), Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ), and the Western Foundation of Vertebrate Zoology, Camarillo (WFVZ).

Swifts have ten primaries. Molt is generally bilaterally symmetrical, so I scored it for one wing only. The molt score of each primary ranged from 0 to 1: a feather with a score of 0.5 would be about 50% grown, while a feather with a score of 1 would be 100% grown, or new. A bird with all new primaries received a score of 10. Swifts have five pairs of rectrices, and I scored their molt with the same system; thus birds with all new rectrices had a score of 5. The increase in the average molt score by month tracks the progress of the molt. For more details on this method see Stiles and Wolf (1974) and Marin and Stiles (1992). The plumage nomenclature follows Humphrey and Parkes (1959), and color nomenclature follows Smithe (1975, 1981), giving the number and name (e.g., 219 Sepia) of the color of closest match for that plumage. Since I followed no nests at Painted Canyon, I supplemented observations of the plumage sequence with descriptions of chicks ready to fledge at a coastal site in Ventura County.

I measured body mass to the nearest 0.1 g with an Avinet spring balance with a 50-g capacity. I measured wing length (flattened) and tail length to 0.5 mm by using a stopped ruler. I measured wingspan, tarsus, exposed culmen, and tail fork by following the techniques described by Baldwin et al. (1931). To quantify the seasonality of breeding I multiplied the length and width of the larger testis of each male, using this result as an index. Juvenal-plumaged birds were excluded from all morphometric analyses.

RESULTS

Roost Usage and Population Size

The Painted Canyon roost was used year round; judged by the large accumulation of fecal matter at the base of the cliff, it had been in use long before its discovery in 1987. The population varied in number from a low of 25–30 birds in March to more than 400 from July through mid-winter. The most dramatic change in the population size occurred between February and March, when numbers at the roost dropped from about 350 birds to only 25–30. In the latter month local dispersal was obvious, as I found many nest sites elsewhere in the canyon.

Plumage and Age Classes

The juvenal plumage can be subdivided into three "phases" resulting from wear. In the first phase, when nestlings are ready to fledge, both sexes are dark sooty brown (between Dark Brownish Olive 129 and Vandyke Brown 121) and have the primary feathers tipped white with contrasting white edging on both sides of the vane. The forehead is pale sooty-brown (close to Smoke Gray 45), finely edged paler brown, and contrasting with the darker body. The feathers from the upper back to the upper tail coverts and the vent and crissum are finely edged with white. The tertials, particularly the middle ones, are margined with white, as in the adult plumage. Within a month or two after fledging (June–July) the plumage moves into its second phase, in which the fine white edges to the feathers of the back and upper tail coverts

have worn off. The third phase of the juvenal plumage is seen from February through June in the birds' second calendar year. At this time the white edges on the primaries are also gone and the tertials are very worn with some individuals having hardly any white edging remaining. The fine white edges on the feathers of the vent and crissum, however, persist.

The body feathers of the juvenal plumage wear rapidly, and by February they become pale sooty brown (close to Dark Brownish Olive 129) with some areas such as the rump and middle of the back slightly darker. The body color is similar to that of the head. This plumage phase is found just prior to the onset of their first complete molt of primary and body feathers and just before the arrival at the roost of recently fledged birds. The pale body coloration of the juvenal-plumaged birds distinguishes them easily from birds in the definitive adult plumage. Thus, using these plumage characteristics, I could distinguish two age classes throughout the fall (hatching year, HY, and after hatching year, AHY) and the following spring (second year, SY, and older, after second year, ASY). The amount of white on the tertials varies by sex and age class. In general, however, most of the older juvenal-plumaged birds have the tertials more worn than do birds in definitive plumage.

In the first basic plumage the forehead, nape, and body are dark sooty brown (close to Sepia 119) with a slight greenish gloss to the body feathers. The fresh primaries have a narrow white edge along the inner web but lack the well-defined white edge on the tip and outer web of the primaries of juveniles. The fresh feathers of the undertail coverts, particularly the more posterior ones, have a very fine white edging, which wears off quickly. The fresh feathers of the definitive adult plumage are similar to those of the first basic plumage except that the undertail coverts are fully dark sooty brown, lacking white edging. Because of the rapid wear of the fine white edges, the first basic plumage can be distinguished from the definitive adult plumage for only a short period, in August and September.

Primary Feather and Rectrix Molt

Although some swifts in the Mecca Hills initiated their primary molt by late April or early May (by 8 May 1992 growth of the innermost primary was evident), most individuals initiated this molt by late May or early June. By 17 June 1990, all specimens had some growing primaries with molt scores ranging from 0.9 to 2.55. On 26 June 1993 the molt score ranged from 3.25 to 4.3, further suggesting that some individuals started their molt as early as late April. The sequence was centrifugal (from the innermost to the outermost primary) and was usually symmetrical in both wings. During the first half of primary molt up to three feathers could be found molting simultaneously (e.g., two growing and one dropped or three growing at different stages). During the second half, however, usually only one or two primary feathers per wing were molting simultaneously. From May through November the molt progressed steadily, as indicated by the increase in molt score (Figure 1). Some individuals completed their primary molt as early as late September, and by November all specimens had completed their primary molt (Figure 1). Overall for this population, primary molt lasted about 6–7 months, typically from May through November. Although I

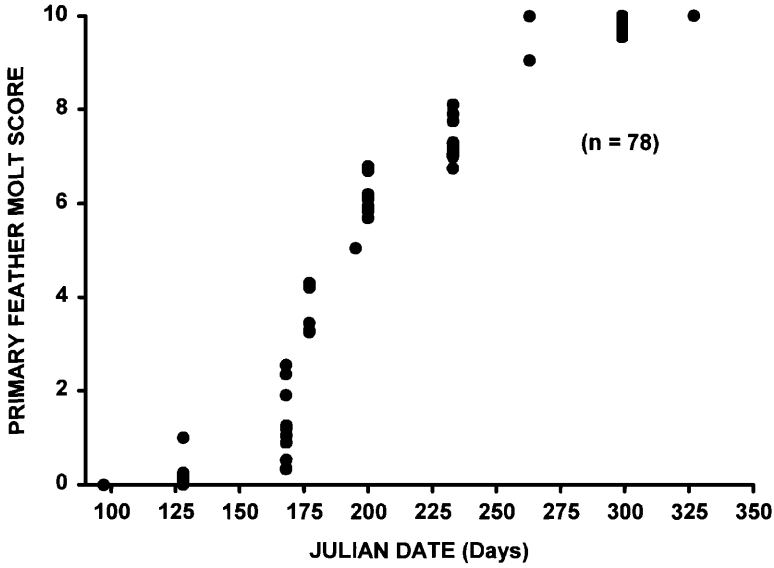

Figure 1. Primary molt score by Julian date in the Painted Canyon population of White-throated Swifts. Julian day 100 = 9 April; day 150 = 29 May; day 200 = 18 July; day 250 = 6 September; day 300 = 26 October. For protocol for determining molt scores, see Methods.

collected these monthly data over 10 years, skipping some months in any given year, the correlation between molt score and date was high ($r^2 = 0.91$, $P < 0.001$), suggesting little year-to-year variation in the molt pattern.

Rectrix molt lasted about 2.5 to 3 months and began about 1 to 1.5 months after the beginning of primary molt. Rectrix molt proceeded centripetally, from the outermost pair to the innermost. As for the primaries, rectrix molt was symmetrical. Usually two pairs of feathers from each side were in molt simultaneously. With the exception of the first (outermost) and last (central) pairs of retrices, each rectrix was molted when the preceding one was almost fully regrown. A few birds began their rectrix molt by late June, but most did so in July. Some finished by August, and all had completed this molt by September (Figure 2).

The molt of the body feathers began by mid August and usually finished by October or November, with some probably continuing into December.

Biometry, Body Mass, and Gonad Size

Depth of the tail fork was the only measured variable in which I found sexual dimorphism. Comparison of wing span, wing length, tail length, tarsus length, exposed culmen, and body mass yielded no significant differences. In males, the depth of tail fork averaged 12.7 mm (range 11–17 mm, $n = 34$), while in females it averaged 10.7 mm (range 5–13 mm, $n =$

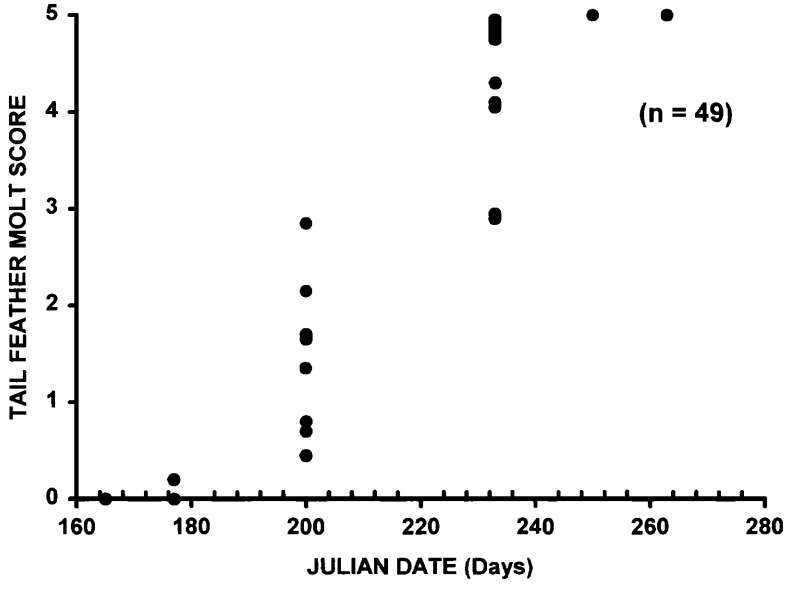

Figure 2. Tail molt score by Julian date in the Painted Canyon population of White-throated Swifts. Julian day 120 = 29 April; day 180 = 28 June; day 220 = 7 August; day 280 = 6 October.

17). This difference was statistically significant (t = 2.80, df = 49, P = 0.007). Measurements of both sexes are summarized in Table 1.

The average body mass by month was similar over the study period. The lowest individual values from June (27.3 g) and July (26.5 g) were only 2–3 g less than minima in all other months (Figure 3). The highest body masses were recorded in April (37.2 g) and October (34.8 g). The overall mean body mass was about the same for males (31.7 g, standard deviation 2.36, n = 51) and females (31.2 g, standard deviation 1.77, n = 32).

Testis size began to increase in March, peaked in April, and declined from May onward. The greatest change occurred between March and April (an increase) and between June and July (a decrease); from July onward testis size was nearly uniform (Figure 4).

White-throated Swifts in the Painted Canyon area appeared to begin breeding in March. On a visit from 17 to 19 March 2000, I found five active nests along the canyon. From the swifts' behavior they probably contained eggs, although I was not able to check nest contents.

DISCUSSION

From February to June, two distinct patterns of plumage wear and color were apparent among the White-throated Swifts in Painted Canyon. The plumage of the birds hatched the previous year was worn and a pale sooty

Table 1 Measurements of White-throated Swifts from Painted Canyon, Riverside County, California[a]

Feature	Mean	SD	Range	*n*
Wing length (mm)	138.1	3.96	127.0–148.0	73
Wing span (mm)	330.1	9.17	310.0–355.0	80
Tarsus length (mm)	11.5	0.57	10.0–12.8	82
Exposed culmen (mm)	5.5	0.32	4.9–6.5	83
Tail length (mm)	55.3	3.61	44.5–64.0	77
Mass (g)	31.7	2.15	26.5–37.2	89

[a]Sexes combined, as they do not differ significantly.

brown; these birds retained some faint white edging on the under-tail coverts. In contrast the plumage color of older birds was dark sooty brown and lacked any white edging on these coverts. It appears that the juvenal plumage wears more rapidly than do post-juvenal plumages.

White-throated Swifts cannot be sexed on basis of plumage color and pattern. While it is possible to identify the sex of some individuals on the basis of length of tail fork, this character should be used with caution, as there is much overlap. Because there is a great deal of variation among both sexes and ages in the amount of white on the longest tertials, with juveniles of both sexes having the extent of white similar to that of adults in definitive plumage, this character can not be used to age or sex White-throated Swifts,

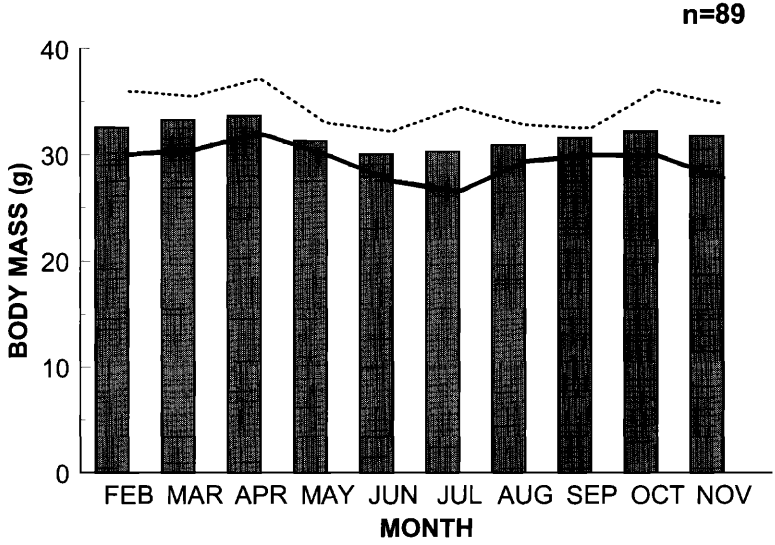

Figure 3. Mean (bars) and range (minimum, solid line; maximum, dotted line) of body mass in grams by month in the Painted Canyon population of White-throated Swifts.

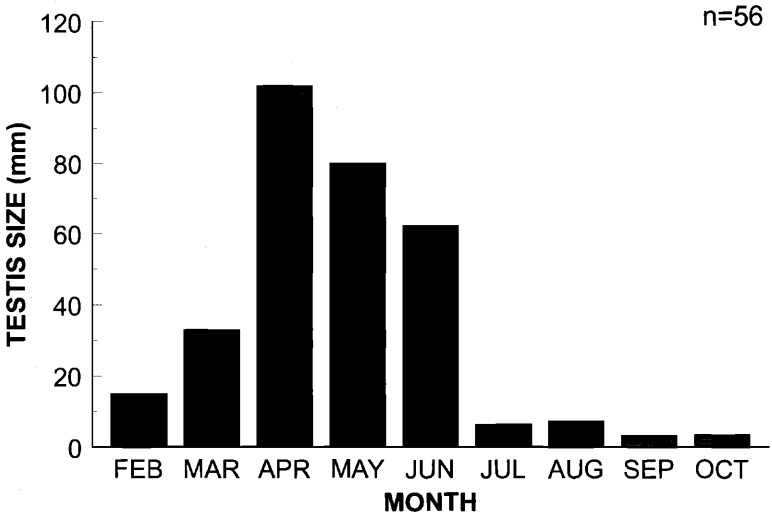

Figure 4. Mean testis size (mm) by month in the Painted Canyon population of White-throated Swifts. No males were captured in November.

as was suggested by Pyle (1997). It is possible to separate juvenal-plumaged birds from those in their first basic and definitive adult plumages through the fall and winter by the presence of white-edged feathers on the vent and crissum. By spring birds in worn juvenal plumage tend to show more wear of the tertials than do adults. This characteristic, when combined with the overall paler color of the worn juvenal feathers, may allow age determination to be made at this time of the year.

Swifts, like many species of birds, molt their flight feathers once a year, taking from between five and seven months to complete this molt. Replacement of the primaries is symmetrical in both wings and sequential from the innermost to the outermost feather (Naik and Shivanarayan 1969a, Zhitong 1982, Marin and Stiles 1992, Bull and Collins 1993, Quang 1994). The Painted Canyon population of White-throated Swifts shows this pattern also. The centripetal tail molt observed in my study population is also similar to that of other swifts (Naik and Shivanarayan 1969b, Bull and Collins 1993). The tail molt, beginning when primaries 4–6 are being replaced, is also similar to the pattern shown by Vaux's Swift (*Chaetura vauxi*; Bull and Collins 1993).

The body mass for both sexes combined (32.1 g; Table 1) is similar to that previously reported from coastal southern California (31.7 g; Dunning 1993). Body mass fluctuates little seasonally (Figure 3) with a maximum difference of 28.7% between the highest and lowest values recorded. This variation in body mass is less than reported for most species of swifts (Naik and Naik 1996). The two most comprehensive studies of body-mass variation in swifts, for the temperate-zone Common Swift (*Apus apus*, Gladwin and Nau 1964) and a subtropical population of the House or Little

Swift (*Apus affinis*, Naik and Naik 1966), showed changes of 79% and 43%, respectively. Both studies concluded that this mass fluctuation is correlated with seasonal variation in weather. The relatively small seasonal variation in body mass I found in this population of the White-throated Swift might be related to Painted Canyon having more uniformly warm daytime temperatures throughout the year.

The White-throated Swift is not colonial per se, although it may nest in loose aggregations depending on nest-site availability. The Painted Canyon roost appeared to be active year round with numbers using the site declining at the time of breeding and gradually increasing again with the arrival of recently fledged birds and postbreeding adults.

In Painted Canyon White-throated Swifts seem to breed one to two months earlier than in parts of coastal southern California. In Ventura County they have fresh eggs from mid May to mid June (WFVZ egg data cards; $n = 60$; pers. obs.) and fledge young from late June to late August (pers. obs.). Thus the breeding and molting schedules of White-throated Swifts vary with local environmental conditions.

Many species of swifts have molt and breeding seasons that overlap broadly (Marin and Stiles 1992, Bull and Collins 1993). The Painted Canyon population of White-throated Swifts does not follow this pattern. The earliest date on which I collected fledglings at the Painted Canyon roost is 16 June. Given that the incubation period lasts about 24 days (H. Richardson in Ryan and Collins 2000) and the nestling period lasts 41–43 days (C. Collins pers. comm.), at least some individuals began laying eggs in early April. Nest building would have begun up to several weeks earlier, and I observed birds at nest sites in Painted Canyon as early as 17 March. In this population some individuals began to molt their primaries in late April and early May, but most did not do so until late May or early June, meaning only partial overlap between the period of incubation and chick rearing and flight-feather molt. Four adult swifts captured while feeding well-grown young near Camarillo, Ventura County, California, in July and August 1999 did not show primary molt, supporting the separation of breeding and molt. In contrast, observations of White-throated Swifts at another site in the coastal zone, in Los Angeles County, showed a broad overlap of breeding and molt (C. T. Collins unpubl. data). Additional study is required to clarify the amount of overlap of breeding and molt periods in this species.

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