Female and immature Rufous (Selasphorus rufus) and Allen (S. sasin) Hummingbirds frequently present problems of identification in California. The general appearance, behavior, and vocalizations of these two species are extremely similar, and only adult males can be safely distinguished in the field. The situation is further complicated by the fact that the fairly clear-cut mensural differences between rufus and the mainland population of sasin are largely bridged by the Channel Island population of sasin, S. s. sedentarius. The objective of this paper is to present a workable method for identification and age and sex determination of these three taxa, hereafter referred to as rufus, sasin, and sedentarius. The need for such a method is especially pressing at present, since several hummingbird banding studies have recently been initiated in southern California. Moreover, sedentarius has recently been found breeding on the mainland (Stiles and Wells, in prep.), and identification of females and immatures will be essential for documentation of possible further spread of this population.

Literature review. Ridgway’s (1911) descriptions of the adult plumages of rufus and sasin are reasonably complete and accurate, but the measurements are based upon very small samples that may not have been uniform with respect to molt, plumage wear, etc. However, sedentarius had not yet been described when Ridgway wrote. The only discussion of mensural differences between sasin and sedentarius is in Grinnell’s (1929) original description of the latter, which was based on a small and not entirely representative sample. The most detailed discussion of molt and plumage sequences in sasin and rufus is by Aldrich (1956) but certain of his conclusions were apparently based on specimens with faulty sex and age data and require correction. To date there is no adequate published reference for distinguishing immature plumages of these taxa.

Distribution and identification. A reasonably detailed discussion of breeding ranges and migrations of the three taxa is given by Grinnell and Miller (1944). I shall, however, briefly outline potential overlap situations and recent range extensions. Breeding ranges of the three taxa are essentially allopatric. Rufus breeds from Alaska south through the Cascade Mountains of Oregon; sasin breeds along the western slope of the coast ranges of California, from western Ventura County north to about the Oregon line. These two taxa may come in contact in extreme northern California. Although previously thought to be confined to the Channel Islands, sedentarius is now known to breed on the Palos Verdes Peninsula just south of Los Angeles (Stiles and Wells, in prep.). This is about 100 mi. SE of the nearest breeding population of sasin.

During January and February migrating sasin pass through at least the mainland part of the range of sedentarius. At this time the nonmigratory sedentarius may have been breeding for several months in some years, and immatures may be common. All migrating sasin should be in essentially adult plumage, thus reducing somewhat the difficulty of identification. In March and April large numbers of rufus pass northward through the breeding ranges of sedentarius (at least the mainland part) and sasin. Again all rufus should be in essentially adult plumage; adult and immature sasin and sedentarius should be present in their respective breeding ranges (cf. Aldrich 1956).

After breeding, adult and immature sasin and rufus move southward in the mountains and along the coastal slope. At favorable feeding areas, such as Nicotiana stands in coastal lowlands and Penstemon patches in mountain meadows, large numbers of individuals may congregate (see Stiles 1972, and included references). It appears that sasin moves south earlier, passing through southern California in June and July. By August and September, most or all of the birds in such feeding assemblages in the Los Angeles area are rufus (Stiles 1972). However, I also collected a young male sedentarius (along with 10 immature rufus) from a feeding assemblage in

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the central part of the Santa Monica Mountains, some 40 miles from the Palos Verdes population, in early August. Thus, in southern California at least, postbreeding distributions of all three taxa must be clarified. The relative scarcity of adults of both sexes in these late-summer assemblages suggests that they move south earlier and more quickly than do immatures.

METHODS

This paper grew out of a hummingbird banding program being carried out by Shirley Wells of San Pedro, California, and out of my own work on hummingbird ecology in the Santa Monica Mountains, California. Through handling numerous female and immature Selasphorus, I could distinguish several plumage types, each characterized by a series of color and mensural characteristics. Limited collecting confirmed that these plumage types corresponded to age and sex categories of the various taxa.

I then began a study of museum skins, and quickly concluded that either many specimens were misidentified as to age, sex, and/or species, or that these categories were not correlated with plumage type. Because of their small size, hummingbirds are frequently hard to sex. The small gonads of young birds (especially females) and the considerable amounts of fat in the abdominal cavities of many fall birds add to the difficulty of sex determination. Many collectors used plumage characters rather than gonads to sex birds; with no adequate descriptions of immature Selasphorus plumages, misidentifications would be inevitable. Therefore, museum skins had to be used with great care.

First, I set up a reference series of adult females by choosing specimens taken early in the breeding season and within the breeding range of each taxon, thereby excluding migrants of other taxa and immatures, respectively. If Aldrich (1956) is correct in stating that the annual molt of adults occurs on the winter range, then summer and fall adults should have the same plumage characteristics as spring birds, allowing for greater wear. Conversely, any late-summer specimen in fresh plumage would likely be a bird of the year. I was thus able to segregate adult and immature birds taken during the post-breeding season. Because Aldrich (op. cit.) stated that adult females were molting on the throat all through the breeding season, I excluded throat color as a criterion for age determination.

With adult specimens excluded, I set up reference series of male and female immatures of rufus and sasin (there were too few immature sedentarius in the collections that I visited to set up a series). Skins with gonad data and put up by reliable collectors were chosen wherever possible. The great majority of specimens in each series so assembled were of a single plumage type; the remainder fitted neatly into another category (usually the opposite sex of the same species). In every case the plumage types of each age, sex, and species category so designated agreed with my earlier determinations derived from examination of live birds.

To establish criteria for sexing immature sedentarius, I utilized the data collected by Shirley Wells from her banding program on the Palos Verdes Peninsula population of sedentarius. These data included wing length, bill (exposed culmen) length, weight, color notes, and one or more rectrices plucked from each of the 80-plus birds she handled. I thereby determined that male and female plumages of sedentarius corresponded to those of rufus and sasin.

To test the sex and age criteria developed above, I collected 11 Selasphorus from a feeding assemblage of about 30 hummingbirds at a Nicotiana patch in Encinal Canyon, Santa Monica Mountains, Los Angeles County, California, on 8 August 1970. Before preparing specimens, I predicted the age and sex of each, using my plumage criteria. In every case, skull and gonad data confirmed my predictions. The specimens included six immature male and four immature female rufus, and one immature male sedentarius (to date the northernmost mainland record of this form), and are deposited with the Western Foundation of Vertebrate Zoology.

Although hummingbirds never attain the double-layered skull of most birds, one can distinguish adults from immatures in the fall, after the breeding season, by skull thickness. The skulls of adults are translucent and relatively thick; those of young birds are soft, thin, and quite transparent. By the following spring, the skulls of first-year individuals are no longer distinguishable from those of older birds.

PLUMAGE DESCRIPTIONS

In general, one can determine the age and sex of any given specimen using color characters; each age and sex class is characterized by a similar plumage in all three taxa. The most useful characters for sex and age determination are color pattern of the rectrices and throat color. To identify the taxon to which a given individual belongs, the following measurements are most useful: length of wing, length of exposed culmen, and widths of the first and the fifth rectrices. The shape of the tip of the second rectrix is also useful in species determination.

The following plumage descriptions emphasize the color characters useful in sex and age determinations; they are not complete descriptions of the plumage in any sense. The mensural characters useful in distinguishing taxa are summarized in table 1.

ADULT MALES

I include a discussion of adult male plumages largely for completeness, as identification is relatively simple. This is the only age-sex class that can be readily recognized in the field, and the only one in which distinct color differences between taxa occur. Adult male rufus have a rufous back; while sasin and sedentarius have green backs; however, there is often a considerable number of green feathers in the backs of some adult male rufus. Adult males of all taxa have the rectrices entirely rufous, except for varying amounts of black at the tips, especially along the shafts. The lateral rectrices of rufus are considerably broader than those of sasin or sedentarius. I can find no consistent color differences be-
### Table 1. Summary of measurements (mm) of *Selasphorus rufus*, *S. sasin* sasin, and *S. sasin* sedentarius.

<table>
<thead>
<tr>
<th></th>
<th>Adult males</th>
<th>Adult females</th>
<th>Immature males</th>
<th>Immature females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n ± ± sd</td>
<td>n ± ± sd</td>
<td>n ± ± sd</td>
<td>n ± ± sd</td>
</tr>
<tr>
<td>Exposed culmen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sasin</em></td>
<td>30 15.92 ± 0.49</td>
<td>30 17.32 ± 0.64</td>
<td>30 15.62 ± 0.99</td>
<td>30 16.77 ± 0.97</td>
</tr>
<tr>
<td><em>sedentarius</em></td>
<td>20 18.28 ± 0.73</td>
<td>30 19.69 ± 1.01</td>
<td>30 17.75 ± 0.97</td>
<td>17 19.03 ± 1.53</td>
</tr>
<tr>
<td><em>rufus</em></td>
<td>30 16.07 ± 0.60</td>
<td>30 17.63 ± 0.64</td>
<td>30 16.01 ± 0.70</td>
<td>30 17.26 ± 0.81</td>
</tr>
<tr>
<td>Wing length (chord)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>sasin</em></td>
<td>30 38.08 ± 0.84</td>
<td>30 41.46 ± 0.80</td>
<td>30 40.29 ± 0.59</td>
<td>30 42.26 ± 0.74</td>
</tr>
<tr>
<td><em>sedentarius</em></td>
<td>20 38.45 ± 1.04</td>
<td>30 43.17 ± 1.06</td>
<td>30 40.93 ± 0.83</td>
<td>30 43.45 ± 0.96</td>
</tr>
<tr>
<td><em>rufus</em></td>
<td>30 40.32 ± 0.87</td>
<td>30 44.40 ± 0.81</td>
<td>30 41.98 ± 0.88</td>
<td>30 44.77 ± 0.87</td>
</tr>
<tr>
<td>Tail length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sasin</em></td>
<td>30 24.37 ± 0.74</td>
<td>30 23.89 ± 0.96</td>
<td>30 23.57 ± 0.65</td>
<td>30 24.10 ± 0.70</td>
</tr>
<tr>
<td><em>sedentarius</em></td>
<td>20 24.57 ± 0.95</td>
<td>30 25.19 ± 1.09</td>
<td>16 24.79 ± 1.02</td>
<td>23.0 - 25.0</td>
</tr>
<tr>
<td><em>rufus</em></td>
<td>30 27.36 ± 0.91</td>
<td>30 25.92 ± 1.03</td>
<td>30 24.67 ± 1.10</td>
<td>30 25.86 ± 0.89</td>
</tr>
<tr>
<td>Width of rectrix 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sasin</em></td>
<td>30 7.98 ± 0.42</td>
<td>30 7.45 ± 0.33</td>
<td>30 7.51 ± 0.34</td>
<td>6.0 - 7.8</td>
</tr>
<tr>
<td><em>sedentarius</em></td>
<td>30 7.18 ± 0.38</td>
<td>25 7.58 ± 0.43</td>
<td>17 7.92 ± 0.32</td>
<td>6.3 - 7.9</td>
</tr>
<tr>
<td><em>rufus</em></td>
<td>30 7.96 ± 0.29</td>
<td>30 8.13 ± 0.42</td>
<td>30 8.50 ± 0.41</td>
<td>7.5 - 8.7</td>
</tr>
<tr>
<td>Width of rectrix 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sasin</em></td>
<td>30 2.39 ± 0.21</td>
<td>30 2.06 ± 0.23</td>
<td>30 2.87 ± 0.22</td>
<td>2.0 - 2.7</td>
</tr>
<tr>
<td><em>sedentarius</em></td>
<td>30 2.60 ± 0.18</td>
<td>30 2.17 ± 0.22</td>
<td>23 3.00 ± 0.33</td>
<td>2.2 - 3.0</td>
</tr>
<tr>
<td><em>rufus</em></td>
<td>30 3.34 ± 0.31</td>
<td>30 3.18 ± 0.24</td>
<td>30 3.97 ± 0.36</td>
<td>2.8 - 4.0</td>
</tr>
</tbody>
</table>

Contrary to Aldrich (1956), throat color is the most useful character in distinguishing adult females from immatures in all three taxa. The amount and pattern of rufous and white in the rectrices can also be diagnostic.

**Plumage description.** Throat basically white; the interramal area usually immaculate, or with a very few bronze-green flecks; sometimes buffy or rufous wash over interramal area. Red feathers concentrated in center of throat; varying amounts of green spotting laterally. Red color occupies whole tip of feather, with, at most, a very narrow whitish edging; bronze-green spots usually towards tip of feather, not con-
FIGURE 1. Representative throat patterns of *Selasphorus*. \(a\) = adult female; \(b\) = immature male; \(c\) = immature female. Solid black = red; hatched = bronzy or greenish; light hatching = buffy. Note differences in shape and distribution of bronzy-green spots or streaks; also amount and distribution of red. Throat of some immature females so lightly marked as to be nearly immaculate. Amount of red in immatures varies with age.

FIGURE 2. Variation in pattern of rectrix 1, adult and immature *Selasphorus*. Row A = adult females; B = immature males; C = immature females; \(a\)-\(c\) = *rufus*; \(d\)-\(f\) = *sasin*; \(g\)-\(i\) = *sedentarius*. Solid color = black; heavy stipple = green; light stipple = rufous; hatching = dusky.
AGE AND SEX DETERMINATION IN RUFOUS AND ALLEN HUMMINGBIRDS

FIGURE 3. Variation in emargination at tip of rectrix 2, adult and immature Selasphorus. Row A = adult females; B = immature males; C = immature females. Left three figures in each row = rufus; right three figures = sasin and sedentarius. a = least emarginated condition; b = typical condition; c = most emarginated condition.

Plumage description. Entire throat more or less heavily spotted or streaked with dusky bronze or greenish-bronze, this color usually concentrated towards the shafts of the feathers, which have more or less concentrated along shaft (fig. 1). Dorsum green, the feathers with narrow rufous edgings when fresh. Feathers of rump and upper tail-coverts with variable amounts of rufous at base; occasionally most of feathers rufous, but green seldom lacking entirely. Below white on sides of neck and center of breast, and belly; varying amounts of cinnamon-buff laterally. Usually whiter, more clean-cut below than immatures. Central pair of rectrices mostly green, with varying amounts of rufous basally and black distally; no white or buffy edging at tip (fig. 2). Sometimes white spot at tip of outer web of rectrix 2 (most common in sedentarius). Tips of rectrices 3, 4, and 5 white, usually without tinge of rufous or buffy (fig. 4). Subterminal black areas of these rectrices little or not at all suffused with rufous.

Comparisons between taxa. Tip of rectrix 2 usually more or less conspicuously emarginated on inner and outer webs in rufus; little or no emargination in sasin and sedentarius (fig. 3). (Note: Aldrich's 1956 drawing of tail of female sasin actually depicts tail of female rufus.) Rectrices of sasin and sedentarius narrower than those of rufus, with slight overlap. Wing of sasin shorter than wing of rufus (very slight overlap) or sedentarius (extensive overlap). Bill of sedentarius longer than those of rufus or sasin, again with slight overlap (table 1).

IMMATURE MALES

The most useful characters for distinguishing immature males are throat color and the pattern of the central rectrices. The lateral rectrices of immature males of each taxon are broader than those of adult males, but narrower than those of adult females. The wing length of immature males in all three taxa is closer to that of the adult female than the adult male, probably reflecting the modifications in the primaries of the latter for sound production.
FIGURE 4. Variation in shape and pattern of rectrix 5, adult and immature Selasphorus. Row A = adult females; B = immature males; C = immature females. a-c = rufus; d-f = sasin; g-i = sedentarius. Stipple = rufous; solid color = black; blank = white. All drawn to same scale.

less broad buffy or cinnamon-buff edgings. Amount of red in throat highly variable depending on age; some late-summer individuals with more red in throat than adult females, sometimes a few rufous feathers as well. Red less concentrated in center of throat than in adult female (fig. 1). Dorsum green, the feathers with cinnamon-rufous edgings. Feathers of rump and upper tail-coverts with rufous bases; rufous edgings often broader than on back; often green is obscured, reduced, or lacking, especially on upper tail coverts. Below white medially, often with dusky tinge; cinnamon-buff laterally, this color often darker and more extensive than in adult females. Rectrix 1 with distinctive pattern: basal 50-54% rufous, tip green and black, and with the black concentrated proximally and along the shaft (fig. 2), recalling the adult male pattern. Both the white tips and black sub-terminal bands of lateral rectrices frequently more or less suffused with rufous, especially along the shaft. Little or no green in rectrix 2, none in 3, 4, or 5 (fig. 4).

Comparisons between taxa. As in adult females, the tip of rectrix 2 emarginated more or less strongly in rufus, weakly or not at all in sasin and sedentarius. Width of rectrix 5 distinguishes rufus from sasin and sedentarius. Wing of sasin shorter than rufus; sedentarius overlaps broadly with both. Bill of sedentarius longer than rufus and sasin; some overlap in both characters. One should note that bills of immature hummingbirds are highly variable, probably depending on age. Very young birds may have bills much shorter than those of adults of the same sex. By late summer or early fall, most immatures have bills essentially the same length as bills of adults. Rufus averages paler below, less rufous in rump than others. By late summer, sedentarius usually has more red in throat; many individuals are well into postjuvenal body molt, and are recognizable by rufous sides of head and deeper rufous color below (like adult male). Measurements are summarized in table 1.

IMMATURE FEMALES

Throat color distinguishes adult from immature females. The latter differ from immature males in having less red on the throat and in the pattern of rectrix 1. In general, immature females have broader lateral rectrices than do adult females or immature males.

Plumage description. Throat similar in pattern to immature male, but with little or no red; buffy feather edgings average broader and paler, sometimes restricting the dusky-brown color to the shaft itself, giving the effect of very fine streaking on an otherwise unmarked buffy or whitish throat (fig. 1). Dorsum similar to immature male, but cinnamon-rufous edgings and feather bases not usually obscuring green on rump and upper tail coverts. Below like immature male but cinnamon-rufous or buff of sides usually paler and less extensive. Pattern of rectrix 1 most like that of adult female, but averaging less rufous, often more dusky at base (fig. 2). Usually a narrow buffy edging to tip of rectrix 1, not seen in adult; often white or buffy at tip of rectrix 2 as well. Rectrices 3, 4, 5
with white tips and black subterminal band usually more or less suffused or obscured by rufous, especially along shaft (cf. fig. 4).

Comparisons between taxa. Few consistent color differences; rufus generally has most green, least rufous in rectrix 1; sedentarius sometimes has large amounts of black on this rectrix, largely obscuring the green. Wing length of sasin shorter than rufus, sedentarius overlaps both widely. Lateral rectrices of rufus broader than sasin or sedentarius; bill of sedentarius longer than rufus or sasin. Some overlap in all mensural categories (table 1). Emargination at tip of rectrix 2 greatest in rufus but very variable, usually less pronounced than in adult females or immature males.

DISCUSSION

The three taxa under discussion are extremely closely related, and form a monophyletic unit within the genus Selasphorus. The two most closely related forms are sasin and sedentarius, which differ almost entirely by mensural characters. Some birds, especially immatures, are intermediate and cannot safely be referred to either taxon. This is to be expected if some gene flow still occurs between them, and justifies their status as subspecies. Rufus differs from sasin and sedentarius in the color of the adult male and in the shape and width of the rectrices. Although there is overlap between taxa in nearly all measurements, by using two or three measurements one can virtually always separate rufus from sasin and sedentarius, and usually sasin from sedentarius. The relative scarcity of intermediates suggests that rufus is indeed reproductively isolated from sasin and sedentarius. Moreover, as will be discussed elsewhere, the displays of sasin and sedentarius are virtually identical, but differ from those of rufus in a number of respects.

A good procedure for identifying birds in the hand is first to determine sex and age, using color characters of the throat and rectrices. Then the length of bill (exposed culmen) and of wing should be measured as accurately as possible using calipers or a millimeter rule. The amount of emargination at the tip of the second rectrix should be noted, and the widths of rectrices 1 and 5 should be measured to the nearest 0.1 mm. This is most easily done if the rectrices 1 and 5 on one side are plucked, and measured after the bird is released. The plucked rectrices should be saved as in a labeled glassine envelope stapled to a 4 x 6 card upon which can be kept color notes, recapture data, measurements, etc.

The methods I propose for identification, age, and sex determination of Rufous and Allen Hummingbirds are summarized in the following dichotomous key. This method, being derived largely through the study of museum skins, should be regarded as tentative at this stage. The definitive test will come as birds banded in immature plumage are recaptured as adults.

KEY TO PLUMAGES OF RUFOUS AND ALLEN HUMMINGBIRDS

1a. Entire throat metallic red to reddish orange (adult males) .......... 2

1b. Throat whitish with flecks of red, green and/or bronz (females and immatures) ................. 4

2a. Back rufous, sometimes with scattered green feathers; tip of second rectrix deeply emarginated (S. rufus) ............... 3

2b. Back green, contrasting sharply with rufous tail-coverts and tail; tip of second rectrix not deeply emarginated (S. sasin) ....... S. rufus

3a. Exposed culmen less than 17 mm .......... S. s. sasin

3b. Exposed culmen greater than 17 mm .......... S. s. sedentarius

4a. Rectrix 1 with basal % to % rufous; tip green and black, the black concentrated proximally and toward the shaft (immature males; fig. 2B) ...................... 5

4b. Rectrix 1 not as above; usually mostly green, with varying amounts of rufous basally and black distally, the black concentrated towards the tip of the feather (females; fig. 2A, C) ...................... 7

5a. Rectrix 5 2.7 mm wide or more; distinct emargination of tip of rectrix S. rufus

5b. Rectrix 5 2.6 mm wide or less; slight or no emargination at tip of rectrix 2 (S. sasin) ............... 6

6a. Exposed culmen greater than 17 mm and/or wing greater than 41.5 mm .......... S. s. sedentarius

6b. Exposed culmen less than 16 mm and/or wing less than 40 mm .......... S. s. sasin

(Note: if culmen 16–17 mm and wing 40–41.5 mm, cannot safely distinguish race.)

7a. Rectrix 1 without dusky tinge basally or whitish-buffy edging at tip; tips of lateral rectrices slightly or not at all tinged with buffy; throat basically white, spotted with red medially and green laterally, the color concentrated towards the tips of the feathers (adult females) ....... 8
7b. Rectrix 1 with dusky tinge basally and narrow whitish-buff edging at tip; tips of lateral rectrices with strong buffy or rufous tinge; throat feathers with broad, buffy-white edgings, flecks of bronzy towards shafts; sometimes throat nearly immaculate (immature females) .......... 10

8a. Rectrix 5 3 mm wide or more and/or rectrix 1 7.9 mm wide or more; tip of rectrix 2 emarginated on both inner and outer webs .......... S. rufus

8b. Rectrix 5 2.7 mm wide or less and/or rectrix 1 7.5 mm wide or less; tip of rectrix 2 with little or no emargination, and then only on outer web (S. sasin) .......... 9

9a. Exposed culmen greater than 18.6 mm and/or wing greater than 43 mm and/or tail greater than 26 mm ..................... S. s. sedentarius

9b. Exposed culmen less than 18.3 mm and/or wing less than 41 mm and/or tail less than 23.5 mm .... S. s. sasin

(Note: if exposed culmen is between 18.3 and 18.6 mm, wing is between 41 and 43 mm, and tail is between 23.5 and 26 mm, cannot safely assign to race.)

10a. Rectrix 5 3.4 mm wide or more and/or rectrix 1 8.5 mm wide or more ........................................ S. rufus

10b. Rectrix 5 3.2 mm wide or less and/or rectrix 1 7.7 mm wide or less (S. sasin) ..................................... 11

(Note: overlap at 3.3 mm for rectrix 5 and 7.8–8.4 mm for rectrix 1).

11a. Exposed culmen greater than 18 mm and/or wing greater than 43.5 mm .......... S. s. sedentarius

11b. Exposed culmen less than 16 mm and/or wing less than 42 mm ........................................ S. s. sasin

(Note: if culmen 17–18 mm and wing 42–43.5 mm, cannot safely distinguish race.)

ACKNOWLEDGMENTS

Much of my experience with sedentarius was gained through the banding program carried on by Shirley Wells, who also gave me access to her extensive data on mist-netted birds. Lloyd F. Kiff helped in collecting and preparing many of the specimens used in this study. Fernando Ortiz-Crespo and Frank A. Pitelka made helpful comments on the manuscript. The following museum curators allowed me to examine and measure specimens under their care: J. G. Miller (UCLA—Dickey collection); Ed N. Harrison and L. F. Kiff (Western Foundation of Vertebrate Zoology); K. E. Stager and J. R. Northern (Los Angeles County Museum); O. F. Pearson (Museum of Vertebrate Zoology, Berkeley); and S. M. Smith (University of British Columbia). I am grateful to Allan R. Phillips for helpful discussions of migration and distribution of rufus and sasin. L. L. Wolf provided calculating facilities. Much of this study was done while I held a Frank M. Chapman Memorial Fellowship at the American Museum of Natural History. It is a pleasure to acknowledge my great debt to the staff and collections of the Department of Ornithology there.

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