CLINAL VARIATION IN WHITE-THROATED SWIFTS FROM UTAH AND THE ROCKY MOUNTAIN REGION

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THE White-throated Swift (Aeronautes saxatalis) was first described as Acanthylis saxatalis by Woodhouse (1853: 64) on the basis of a sight record, namely swifts that he saw in flight from the top of Inscription Rock, New Mexico. A short time later the species was again described by Baird (1854) as Cypselus melanoleucus with a type specimen this time, taken in the San Francisco Mountains, Arizona. Seemingly Baird (1858: 143) did not realize that the two were the same, for he commented "there is good reason to believe that additional species of Cypselidae will yet be discovered in the far west, (among them the one with white rump, Acanthylis saxatalis, seen by Dr. Woodhouse at Inscription rock, New Mexico." When it was realized that both descriptions and names applied to the same species, Woodhouse's name was rejected because no specimen was taken and the description given was not entirely accurate. In the course of nomenclatural history the generic name became Aeronautes. Finally Oberholser (1920) argued for the restitution of the trivial name saxatalis of Woodhouse on the grounds that the birds were without doubt identifiable as White-throated Swifts and "there is no rule of nomenclature that provides for the rejection of a name based on the printed description of an animal only seen in life, nor for the rejection of a name if certainly identifiable even though the description be partly inaccurate." His argument prevailed.

The White-throated Swift's breeding range reaches from British Columbia, southern Alberta (possibly), Montana and northwestern South Dakota, south to Guatemala and El Salvador. With such an extended range the species is migratory in its northern part but resident in the southern portion. The species winters from central California, central Arizona, and southwestern New Mexico southward. The species was regarded as monotypic until Dickey and van Rossem (1928) described the race A. s. nigrior from Central America, with a breeding range from "High mountains of El Salvador, northwest through Guatemala at least to Hidalgo, Mexico." This race was recognized by Peters (1940: 253) who added that it intergrades with A. s. saxatalis in central Mexico. Friedmann et al. (1950: 161) gave additional records of nigrior for Michoacan and Chiapas.

Rogers (1939) undertook a study of the variation of the species from the northern part of the range, the result being the description of a race that he called A. s. sclateri with type locality at Loveland, Larimer County, Colorado, and an attributed range of Colorado east of the Continental Divide, Nebraska, Wyoming, Montana, and South Dakota. Rogers detected no color differences in swifts from the ranges of *sclateri* and *saxatalis*, so his distinguishing characters pertained solely to size, *sclateri* being larger than *saxatalis*. Rogers was somewhat apologetic about his new race for he remarked (loc. cit.): "Aeronautes saxatalis sclateri is, therefore, just another 'millimeter race' which some ornithologists will not endorse, but this study has at least added to our knowledge of the geographic variation in the species, has shown the existence of two populations undeniably somewhat different, and provided a name, for the use of those who care to recognize such a difference, for the population hitherto undifferentiated [= undescribed]."

Peters (1940: 253) in his check-list did not recognize *sclateri* and Twomey (1942: 403) commented that it was not well-marked. Nevertheless, the latter employed the name *sclateri* for the specimens that he took from the Uinta Basin of northeastern Utah and northwestern Colorado. He gave the average wing measurements for males as 142.8 mm as compared to 144.3 for females and pointed out that his birds were larger than southern specimens from Sonora but not so large as those from Montana.

The fifth edition of the A.O.U. check-list of North American birds (A.O.U., 1957) recognized the two races and designated the range of saxatalis as follows: "Breeds from southern British Columbia (Vaseaux Lake and Okanagan Valley), Idaho, western Colorado, New Mexico, and western Texas (Davis and Chisos mountains) south to the Cape region of Baja California (including the Santa Barbara Islands and Guadalupe Island), Sinaloa, and Guanajuato. Winters from the San Francisco Bay region in central California, central Arizona (Big Sandy and Phoenix), and southwestern New Mexico (Hachita and Chloride) south to south-central Mexico." For sclateri it states: "Breeds from Montana (possibly from southern Alberta) and northwestern South Dakota south to eastern Colorado and western Nebraska. Winter range unknown but probably in Mexico." A distributional note adds that the race sclateri has been "recorded in migration in southwestern Texas (Davis Mountains)."

Further doubt as to the validity of the race *sclateri* comes from the statements of Bailey and Niedrach (1965: 466) concerning specimens from Colorado in the Denver Museum of Natural History. After giving measurements of their birds they state: "It is evident that Colorado swifts in the Museum collection all fall within the size of the smaller birds, and except for the fact that the type locality of *A. s. sclateri* is Loveland, we would be inclined to consider the birds of the entire state as belonging to the smaller *saxatalis*."

TABLE 1									
Comparison	OF	\mathbf{M}_{ALE}	AND	FEMALE	AERONAUTES	SAXATALIS	IN	$\mathbf{F}_{\mathrm{OUR}}$	
Measurable Characters									

		Males			Females				Level of signifi-
Character	N	Mean	SD	N	Mean	SD	T Value D	DF	cance (Alpha)
Wing	81	140.4	4.573	83	138.5	14.67	1.054	161	0.15
Tail	77	56.84	3.004	80	55.67	6.212	1.500	155	0.07
Culmen	75	5.82	0.535	80	5.85	0.894	-0.1851	153	0.57
Tarsus	65	12.10	1.005	73	11.74	1.574	1.579	136	0.06

I became interested in the geographic variation in White-throated Swifts in connection with my work on the birds of Utah. Specimens from the southern part of the state were of small size, which suggested that they represented the race saxatalis (Behle, 1943: 41; Woodbury and Russell, 1945: 61; Behle et al., 1958: 53; Behle, 1960: 30). In contrast, examples from the northern part of the state were larger. Behle and Ghiselin (1958: 5) with a different sample of birds from northeastern Utah obtained about the same results as Twomey and following his lead referred them to sclateri. Behle (1958: 20) also listed a large male from the Raft River Mountains in northwestern Utah as sclateri although, according to the ranges as delineated in the A.O.U. check-list (1957), the population here should have represented saxatalis. Thus the twin problems shaped up of whether the United States portion of the range of the species indeed contains two races and if so the determination of a more appropriate designation of their ranges. The most important consideration was determining the basic pattern of geographic variation displayed by the species in the northern portion of its range. As opportunity arose in subsequent field work throughout the state additional swifts were taken, the result being that at present the collection at the University of Utah has 123 specimens, almost all from Utah. These, together with the loan of those swifts from the Rocky Mountain region in the National Museum of Natural History (through the courtesy of Richard L. Banks) made a total sample of 164 birds to analyze.

As regards variation with age, Ridgway (1911: 688) noted that young were similar to adults, but the white of the underparts in duller (more or less grayish or sooty) and the blackish of the sides is duller, especially anteriorly, where it is more sooty grayish and less strongly contrasted with the whitish of the throat. The birds assembled contained few such young, and these were eliminated so that the study dealt solely with adults. Concerning sexual variation, Ridgway's (1911)

TABLE 2
Wing Length (in mm) of Several Populations of Adult
Breeding White-throated Swifts

Population	Sample size	Range	Mean with SE	SD	Coeffi- cient of variation
Montana	17	134.2-150.1	143.24 ± 1.050	4.328	3.0
Colorado	7	139.5-147.3	143.71 ± 1.185	3.135	2.2
Northeastern Utah	39	131.8-146.4	141.19 ± 0.59	3.698	2.6
Central northern Utah	6	140.2-146.9	143.90 ± 0.96	2.358	1.6
Northwestern Utah	15	137.2-151.1	145.97 ± 0.896	3.470	2.4
Central Utah plateaus	9	132.2-146.9	139.48 ± 1.42	4.260	3.1
Central western Utah	8	137.3-145.5	140.46 ± 1.05	2.979	2.1
Central southern Utah	9	134.6-140.5	139.42 ± 0.771	2.311	1.7
Southwestern Utah	13	130.0-140.0	134.19 ± 0.793	2.868	2.1
Southeastern Utah	22	132.4-143.3	137.64 ± 0.760	3.563	2.6
Arizona, New Mexico	17	130.5-144.4	136.51 ± 0.998	4.113	3.0

measurements suggested a slight difference in size. For wing length his 14 males averaged 145 (131-148) mm while 10 females averaged 142.5 (135.5-149). His averages for tail length, culmen, tarsus, and middle toe were about the same for both sexes. Rogers (1939) presented wing and tail measurements for swifts from several areas and concluded that very little if any sexual difference in size exists, even though various samples showed differences from one region to another. Twomey's (1942: 403) sample of nine specimens suggested that females were slightly longer in wing length with an average of 144.3 mm as compared to 142.8 for males. For the birds assembled for the present study, the mensurable data for four characters, namely lengths of wing, tail, culmen of bill, and tarsus, were subjected to a computerized statistical analysis, population by population. No significant differences associated with sex appeared in any of the characters in any of the 11 designated populations. The data for all the males were then pooled and compared with the total aggregate of all the females. The results for this last test appear in Table 1. As no significant differences were revealed between males and females in any of the characters studied, the data pertaining to males and females were henceforth lumped together to increase sample sizes for analysis of the geographic variation.

Pertaining to geographic variation in color characters, as indicated by the race *nigrior*, birds from the southern part of the species' range differ from those in the northern portion. Dickey and van Rossem (1928) noted as subspecific characters for the southern race the clear back color dorsally; the forehead, loral, and auricular regions being concolor with the head; the superciliary streak being nearly obsolete, indeed being indicated only by grayish edgings of the feathers; the white flank patches reduced in area; and the white median abdominal streak being reduced

TABLE 3
TAIL LENGTH (IN MM) OF SEVERAL POPULATIONS OF ADULT
BREEDING WHITE-THROATED SWIFTS

Population	Sample size	Range	Mean with SE	SD _	Coeffi- cient of variation
Montana	17	55.7-61.6	57.92 ± 0.449	1.853	3.2
Colorado	7	54.8-61.5	58.60 ± 0.876	2.317	4.0
Northeastern Utah	38	52.3-64.2	56.60 ± 0.445	2.745	4.8
Central northern Utah	6	53.961.0	57.66 ± 1.270	3.113	5.4
Northwestern Utah	14	54.4-62.7	58.55 ± 0.847	3.170	5.4
Central Utah plateaus	9	51.559.1	56.26 ± 0.748	2.244	4.0
Central western Utah	8	55.6-59.2	57.13 ± 0.466	1.317	2.3
Central southern Utah	9	53.6-56.9	55.38 ± 0.338	1.015	1.9
Southwestern Utah	13	53.5-57.0	55.07 ± 0.465	1.675	3.0
Southeastern Utah	21	46.5-59.2	54.73 ± 0.625	2.865	4.9
Arizona, New Mexico	15	49.9-64.0	56.44 ± 0.840	3.252	5.8

in width. Monroe (1968: 170) stated that his single Honduran specimen agreed with *nigrior* in the darker dorsum, in reduced white below, and in the obsolete superciliary streak.

Dickey and van Rossem (1928) prophesied that further geographic variation in color characters would be detected in the species and commented that examples from the Rocky Mountain region "average considerably whiter than do those from California and Lower California, but the differences are seemingly too inconstant to justify naming the California bird." Despite this prediction Rogers (1939) as previously noted, found no differences in color between populations within the northern part of the species' range. In the present study I detected no significant geographic variation in color in swifts from Utah and the Rocky Mountain region.

The size data show a clinal variation from large birds in the north to smaller specimens as one proceeds southward. This is best seen in wing length, the data for which are summarized in Table 2. The populations listed cover large regions outside of Utah but their extent is much smaller within the state both because of the more plentiful material and the isolation of the many mountain ranges and plateaus from which the swifts were taken. My sample from Montana does not show as large a size as did Rogers' who gave the figures 147 for 3 males and 146.2 for 10 females. Nevertheless my materials indicate a difference of 6.73 mm between Montana and the Arizona-New Mexico population. The Colorado birds that I examined average essentially the same as my Montana representatives. The large number of swifts from northeastern Utah average slightly smaller than the Montana and Colorado groups and are close to the results of Twomey based on a separate sample. The circumstance that the average of the lot from northeastern Utah, Twomey's

from the same general area, and Bailey and Neidrach's measurements are all smaller than the average Rogers gives for his Colorado birds, suggests that Rogers' sample was atypically large and hence misleading as to the actual size differential between Colorado and New Mexico birds or his measuring technique may have differed slightly.

Swifts taken in Utah also show clinal variation in length of wing. Furthermore, some surprising differences in size within the state suggest a mosaic pattern of variation accompanying many semi-isolated populations. The best example of this is seen in the Raft River Mountain population in extreme northwestern Utah. Here we have the largest swifts in the state (wing average 145.97 mm). These Great Basin birds are larger than those from central northern or northeastern Utah or Colorado and are similar to the large-sized Montana birds. In contrast, Swifts having the shortest wing length are from the Beaver Dam Wash of extreme southwestern Utah (wing 134.19). These from the lower Sonoran or Mohave Desert are smaller than those from central southern and southeastern Utah and even smaller than the Arizona-New Mexico sample. They are more like those from Sonora Rogers reported as 134.3 mm. Yet Monroe (1968) gave the wing length of his specimen as 140.3 mm. These extreme Utah populations differ by 11.8 mm, which is greater than the difference between Montana and Arizona-New Mexico birds (6.73 mm). Incidentally the measurements for California (139.5) and Lower California (139) birds as given by Rogers are about the same as those from central Utah. The circumstance that northern birds in general have longer wings than their southern relatives is probably correlated with the northern swifts being migratory, in contrast to the sedentary nature of southern swifts.

Tail length (Table 3) is more conservative than wing length and varies less from one region to another. Whereas a cline from longer-tailed birds in the north to shorter-tailed birds in the south is indicated, it is less marked than in the wing length. Bill (culmen) length is still less variable. Indeed the averages are essentially the same in all populations, the smallest and largest averages being 5.56 and 6.42 mm. The latter is the average for the swifts from the Raft River Mountains and is seemingly correlated with their longer wings and tails. Tarsal length likewise shows no significant variation between the several samples and the averages reveal no consistent pattern. They vary from a low of 11.45 mm to a high of 13.56. Unfortunately few weight data are at hand to correlate with size data, and none that will allow comparison of birds from the northern and southern extremes of the cline. Those weights available pertain to specimens from central and southern Utah; 22 males have an average weight of 34.2 g, while 18 females average 32.3 g.

The mensural data, then, demonstrate that geographic variation in size does indeed occur in the northern part of the breeding range of the species. The question is how this fits in with our present taxonomic system. If two races are to be recognized the ranges as given in the A.O.U. check-list (1957) are incorrect, as the larger northern birds occur not only in Montana, Wyoming, Nebraska, and northern Colorado, but extend westward into northern Utah and probably Nevada as well. The smaller southern swifts, as indicated in the check-list, are distributed through the area of New Mexico and Arizona and westward through Utah and south into Mexico, but they do not extend to the north. Birds from central Utah and central Colorado are of intermediate size. Thus if both sclateri and saxatalis are to be recognized an arbitrary dividing line would have to be established in central Colorado and Utah along some east-west axis to separate the ranges of the two races. The data presented here of clinal variation with only swifts from the two extremes of the cline being separable by size, the long span of intermediates with the type locality of sclateri being at midpoint in the cline, the absence of a step in the cline to separate two populations, all suggest the recognition of two races to be inappropriate.

The alternative to recognizing two races, sclateri and saxatalis is simply to conceive of one race north of the range of A. s. nigrior and to recognize that as part of the makeup of the taxon, the geographic variation is clinal and that much infra-subspecific variation exists. Designation of the variant local populations as well as the extremes of the clines can be done simply by commentary on birds from the geographic localities involved. I conclude from this study that sclateri should be placed in synonymy under saxatalis.

SUMMARY

A study of the geographic variation of 164 breeding specimens of White-throated Swifts from the Rocky Mountain region of western North America revealed a general pattern of clinal variation from large size in the north to small size in the south. This is most evident in wing length, less so in tail length, but scarcely shows up in culmen and tarsal lengths. The longer wing length in northern swifts is probably correlated with migratory habits whereas southern populations are more sedentary. In addition, a mosaic pattern of variation accompanies semi-isolated populations in different mountain ranges. No significant differences were found between males and females in the characters studied. Two races, A. s. saxatalis and A. s. sclateri, are presently assigned to the region but neither the characters ascribed to these nor their ranges are in con-

formance with the variation found. It is proposed, therefore, that A. s. sclateri be synonymized under A. s. saxatalis.

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