GEOGRAPHIC VARIATION IN HIRUNDO PYRRHONOTA (CLIFF SWALLOW) FROM NORTHERN NORTH AMERICA

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The number of subspecies recognized in *Hirundo* pyrrhonota Vieillot (Cliff Swallow) from Alaska, Canada, and the northern contiguous United States ranges from one (Peters 1960) to three (e.g., Jewett et al. 1953, Oberholser 1974). Most sources (e.g., American Ornithologists' Union [A.O.U.] 1957, Behle 1976) recognize two subspecies: *hypopolia* Oberholser, 1920, breeding from central Alaska to the central Great Basin, and two disjunct populations of nominate *pyrrhonota*, breeding on the west coast and east of the Rocky Mountains. Although various authors have reported measurements of wing chord, they have not provided quantitative data for other plumage characters, and they disagree in the characterizations and ranges of the subspecies they recognize. Because of this, I reviewed the geographic variation among the northern populations.

My study is confined to specimens from Alaska, Canada, and the contiguous United States south to Merced County in California, both slopes of the Rocky Mountains from Montana to Colorado, and northern half of the eastern United States from Kansas east to Virginia (Figure 1). The A.O.U. (1957) gave the breeding range of hypopolia as extending from Alaska and Mackenzie to southeastern British Columbia, the eastern parts of Washington, Oregon, and central-eastern California, central Nevada, northern Utah, Montana, and northwestern Wyoming, and the range of nominate pyrhonota as from southwestern British Columbia, western Oregon and Washington to southern California, southern Nevada, southern and eastern Utah, and east of the Rocky Mountains. I excluded specimens of H. p. ganieri Phillips, 1986, a subspecies (Browning 1990) that breeds from at least west-central Tennessee to Texas, and H. p. tachina Oberholser, 1903 (sensu Phillips 1986), which breeds north to central California, Utah, Arizona, and New Mexico. I follow Phillips (1973) for the use of the generic name Hirundo for the Cliff Swallow, Hellmayr (1935) for the use of the specific name pyrrhonota.

TAXONOMIC HISTORY

Oberholser (1920) described *H. p. hypopolia* (type locality, Fort Norman, Mackenzie) as differing from nominate *pyrrhonota* (type locality, Paraguay) by its longer wing, whiter (less buffy) forehead extending farther back on the head, less rusty breast, grayer flanks, darker upper breast, and paler rump. He reported the breeding range of *hypopolia* as extending from central Alaska and Mackenzie District to central British Columbia and Montana. Oberholser (1932) later described *H. p. aprophata* (type locality, mouth of Twenty Mile Creek, Warner Valley, 9 miles south of Adel, Oregon) as differing from *hypopolia* by its more buffy (less clearly white) forehead and more extensively white lower parts. He gave the breeding range of

aprophata as the Warner Valley in central southern Oregon. Van Rossem (1936) synonymized aprophata with hypopolia and extended the range of the latter to east of the Cascades in the Pacific Northwest and Great Basin. Gabrielson and Jewett (1940), who did not discuss variation in the species. referred all specimens from Oregon to nominate pyrrhonota (sensu A.O.U. 1957). Miller (1941) referred to his series of topotypical aprophata from the Warner Valley, Oregon, as intermediate between the nominate subspecies and hypopolia. Aldrich (in Jewett et al. 1953) and Oberholser (1974) recognized both aprophata and hypopolia. The A.O.U. (1957) included the breeding range of aprophata within that of hypopolia, and Peters (1960), without comment, listed both approphata and hypopolia as synonyms of nominate pyrrhonota. Behle (1976) concluded, as did Miller (1941), that the Warner Valley birds are intermediate between hypopolia and nominate pyrrhonota. Browning (1979) synonymized aprophata with hypopolia, as did Phillips (1986), who recognized hypopolia tentatively. Turner (1989) commented briefly that it is unlikely that approphata is distinct from hypopolia.

Behle's (1976) review included measurements of wing chord and tail length and comparisons of the color and height of the pale frontal stripe (= forehead) and color of the abdomen, flanks, pectoral region (= upper breast), and rump. He did not quantify the extent of the pale portion of the forehead or discuss the frequency of color variants in other plumage characters. Behle concluded that variation in wing chord is clinal, with largest birds in Alaska and northwestern Canada. Although Behle concluded that the color of the upper breast and rump is not a useful taxonomic character, he described the abdomen and rump as paler and the chest and flanks as grayer in hypopolia than in nominate pyrrhonota. Behle also characterized hypopolia as differing from the nominate subspecies by its greater average wing and more "predominantly" white forehead. Phillips (1986:34), who excluded Alaska and central-southern Mackenzie from the range of hypopolia (contra Behle 1976), characterized hypopolia as differing from the nominate subspecies in its "usually somewhat paler" cheeks and throat and "average" paler rump, and he characterized some individuals of nominate pyrrhonota as having white foreheads. The minimum for wing length he gave for hypopolia (108 mm) was considerably less than that given by Phillips et al. (1964:100) ("about 112 millimeters or more"), and Phillips (pers. comm.) later concluded that wing chord is not a useful character for identifying the northern subspecies.

METHODS

I examined 222 specimens (breeding birds collected from late May to late July) for variation in size and forehead color, and 131 for variation in the color of the cheeks, rump, and lower parts. Except for six from Alberta, the specimens were grouped into eight geographic samples (Figure I) as follows (names of the samples used in the text are in capital letters):

- A. Interior ALASKA, Yukon, and Mackenzie District;
- B. Southeastern BRITISH COLUMBIA (majority from the Okanagan Valley);

- C. ADEL, Warner Valley, Lake County, central southern Oregon;
- D. IDAHO, western Montana;
- E. WEST COAST (west of Cascade/Sierra Nevada divide from southwestern British Columbia to Merced County, California);
- F. WEST SLOPE OF ROCKY MOUNTAINS (Wyoming and Colorado);
- G. EAST SLOPE OF ROCKY MOUNTAINS (Montana, Wyoming, and Colorado);
- H. NORTHEASTERN (NE United States and SE Canada).

Samples A–D and most of F represent *hypopolia*, and E, G, and H represent nominate *pyrrhonota* (sensu A.O.U. 1957). Phillips (1986) differed in placing most of A in the latter. Sample C is *aprophata* of Oberholser (1932) and Aldrich (in Jewett et al. 1953).

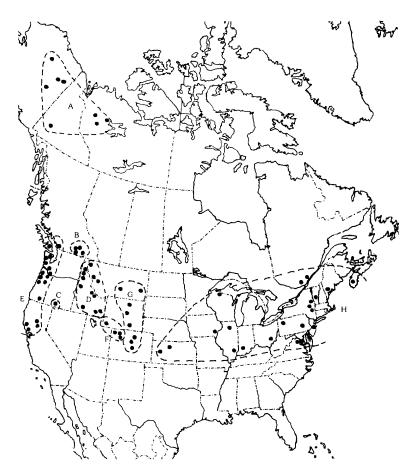


Figure 1. Approximate localities of specimens of *Hirundo pyrrhonota* examined. Dashed lines enclose the eight sample areas defined.

The sexes differed statistically (Student's *t* test) in mean wing length only in the samples from Alaska and Idaho. Because these differences were small, however, only 1.84 mm and 1.94 mm, respectively, and because wing measurements were not sexually dimorphic in other samples, data for males and females are pooled (Table 1). Sexual dimorphism was likewise not observed in other characters. I measured the height of the pale forehead (Table I) from the base of the exposed culmen to the point where the paler feathers meet the darker feathers near the top of the head. Some variation in that character is no doubt the result of specimen preparation. Preliminary data from measurements and other characters (e.g., tarsus length, bill size, throat color) revealed no geographic variation, and I did not consider them further.

I ranked the color of the forehead (Table 2) as pale (= white), dark (near Avellaneous of Ridgway [1912]), or intermediate. I ranked the cheeks as pale if near white, dark if near Bay of Ridgway and near Maroon (No. 31) of Smithe (1975). I ranked the color of the rump as pale if near white, dark if near Tawny of Ridgway, and near but redder than Robin Rufous (340) of Smithe. Because the gray color of the upper breast (Table 2) in most specimens is actually a combination of gray and Vinaceous Buff (Ridgway 1912), I considered the upper breast as gray when gray was the predominating color (= less buffy and not white). The color of the flanks (Behle 1976) is more individually variable than the other plumage characters and was not considered in this study. The term buff (= ochraceous of Behle 1976), used for characterizing the forehead, rump, and upper breast, refers to the color near Vinaceous Buff of Ridgway. Soiled, worn, damaged, and badly prepared specimens were excluded from my analysis.

Table 1 Measurements of Wing Chord and Height of the Forehead in Various Populations of *Hirundo pyrrhonota*

		Wing C	hord	Height of Forehead				
Sample ^a	n	Range	Mean ± SD ^b	n	Range	Mean ± SD		
A B C D E F G	19 19 29 25 46 11 38 29	108.4-114.9 101.4-114.4 107.0-114.4 107.0-115.2 102.1-112.6 106.6-113.6 100.1-117.0 101.1-112.6	112.3 ± 1.70 109.2 ± 3.00 109.9 ± 2.22 110.3 ± 2.11 107.5 ± 2.64 110.9 ± 1.97 109.4 ± 3.47 107.6 ± 2.83	19 16 27 25 24 10 34 18	4.5-7.7 4.4-7.0 3.8-7.7 4.2-8.0 3.8-7.1 4.5-7.0 3.9-8.2 3.3-7.8	6.11 ± 0.82 5.69 ± 0.65 5.51 ± 0.99 5.84 ± 1.12 5.51 ± 0.95 5.99 ± 0.83 5.77 ± 1.10 5.81 ± 1.16		

^aA, Alaska B, British Columbia; C, Adel (Oregon); D, Idaho; E, west coast; F, west slope of the Rocky Mountains; G, east slope of the Rocky Mountains; H, northeastern. For furter detail, see Figure 1.

bSD, standard deviation.

Table 2 Percentages of Plumage Character States in Various Populations of *Hirundo pyrrhonota*

	$Sample^a$								
Character	Α	В	С	D	Е	F	G	Н	
Forehead (n)	(17)	(19)	(27)	(25)	(46)	(10)	(38)	(34)	
Pale	76	37	52	72	26	20	45	12	
Interm e diate	12	58	37	16	63	70	29	26	
Dark	12	5	11	12	11	10	26	62	
Cheeks (n)	(19)	(11)	(12)	(27)	(19)	(6)	(12)	(18)	
Pale	37	64	40	63	17	50	33	33	
Rump (n)	(19)	(11)	(12)	(27)	(16)	(6)	(12)	(18)	
Pale	32	36	38	37	32	33	25	28	
Upper breast (n)	(18)	(11)	(12)	(27)	(19)	(6)	(12)	(18)	
Gray	66	45	42	30	25	17	25	61	
Lower parts (n)	(18)	(11)	(12)	(27)	(19)	(6)	(12)	(18)	
Buffy	39	45	58	30	42	33	33	72	

^aA, Alaska; B, British Columbia; C, Adel (Oregon); D, Idaho; E, west coast; F, west slope of the Rocky Mountains; G, east slope of the Rocky Mountains; H, northeastern. For further detail, see Figure 1.

GEOGRAPHIC VARIATION

Wing chord. Although the Student's t test revealed statistically significant differences between the means in wing chord of some of the geographic samples (e.g., Alaska and British Columbia; east slope of the Rocky Mountains and the northeastern sample), the more conservative nonparametric Kruskal-Wallis one-way analysis of variance revealed no statistical difference between the means of the same samples. The mean of six birds from Alberta (not in a sample) is similar (111.9 mm) to that of the Alaska sample (see also Rand 1948). Measurements of individual specimens revealed that 41% of the birds from the west coast, which averaged the smallest, and 48% from the northeast, which averaged next to the smallest, are within the range of birds from Alaska, which averaged the largest (Figure 2). All specimens from the west coast and from the northeast are within the range of variation of birds from British Columbia. The ranges in wing chords of specimens from Adel, Idaho, and from the west slope of the Rocky Mountains are generally similar, with means larger than those of the samples from British Columbia, the west coast, east slope of the Rockies, and the northeast (Table 1). The degree of overlap precludes wing length as a useful taxonomic character.

Height of forehead. The height of the forehead (Table 1) averages slightly greater for birds from Alaska and the west slope of the Rockies, and slightly less for birds from the west coast and the northeast, than for specimens from the other localities. There is virtually complete overlap among all samples in this character.

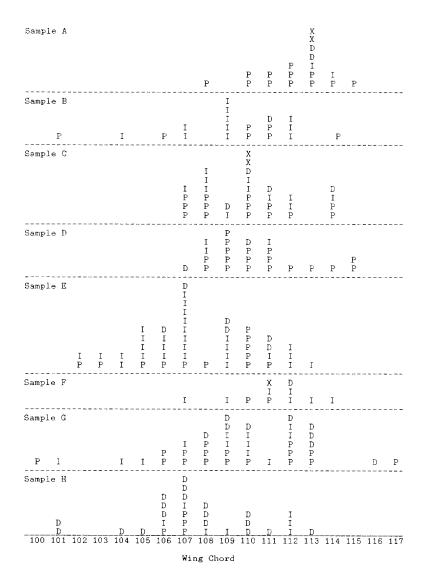


Figure 2. Frequency distribution of wing chord and forehead color (P, pale; I, intermediate; D, dark; x, specimen with forehead color indeterminable) in eight samples of *Hirundo pyrrhonota*. Wing measurements are rounded to nearest whole millimeter. A, Alaska; B, British Columbia; C, Adel (Oregon); D, Idaho; E, West Coast; F, west slope of the Rocky Mountains; H, northeastern. For further detail, see Figure 1.

Forehead color. The only sample with the forehead pale in 75% or more of the specimens is from Alaska. Sixty-two percent of the birds from the northeast have dark foreheads. More birds from west of the Rocky Mountains have either pale or intermediate foreheads (e.g., Alaska, 88%; west coast, 89%), whereas 88% of the specimens from the northeast have dark or intermediate foreheads. However, individuals with pale, intermediate, and dark foreheads were found in each of the samples (Table 2).

Cheek color. More specimens from British Columbia and Idaho have pale cheeks (Table 2) than do birds from elsewhere. About the same percentage of specimens from Alaska, Adel, the east slope of the Rockies, and the northeast have pale cheeks. More birds from the west coast have dark cheeks. Several authors (e.g., Behle 1976, Phillips 1986, Godfrey 1986) characterized the cheeks and rumps in hypopolia as "usually" pale. This study indicates somewhat the opposite conclusion, and may be the result of use of different specimens by different investigators. Cheek color is individually variable within populations, and geographic variation in this character is minor.

Rump color. About one-fourth of the birds from the east slope of the Rocky Mountains and about one-third of those in the remaining samples have pale rumps (Table 2). One half (n = 6) of the specimens from south-central Alberta (not a sample) have pale rumps. The color of the rump is subject to considerable individual variation.

Upper breast. The upper breast is gray in 66% of the specimens from Alaska (Table 2); 41% of the 66% are pure gray (no buff). The upper breast is gray in 42% of the specimens from Adel; the breast of the remaining specimens is buffy (26%) or white (33%). The upper breast is more buffy than gray in 75% of the specimens from the west coast and from both slopes of the Rockies. The upper breast among all populations varies from white to buffy, gray, and buffy-gray.

Lower parts. More specimens from the northeast than from elsewhere have buffy lower parts (Table 2). Although the buffy color is slightly darker in more specimens from east of the Rockies than from west of the Rockies, the darkest individuals are from Adel, British Columbia, and the west coast.

DISCUSSION AND TAXONOMIC CONCLUSIONS

Designations of specimens as resident breeding birds is complicated because some populations are breeding while some other populations are still migrating. Cliff Swallows breed as early as 5 April in California (Mayhew 1958), from early May to early August in British Columbia (Munro and Cowan 1947, Butler et al. 1986), and from June to early August in Alaska, where migrants arrive in mid-May (Kessel and Gibson 1978). Phillips (in Phillips et al. 1964) believed that migrants may visit local breeding colonies. Mayhew (1958) attributed additional birds at a breeding colony to late arrivals from the winter range.

I concede that some of the specimens I examined from the southerly localities may represent migrants from northern populations. However, whether migrants can be identified as *hypopolia* or *aprophata* is dependent on the amount of variation within those taxa and in nominate *pyrrhonota*.

Specimens from Alaska ("hypopolia") were most likely breeding birds. Only 18% of the Alaska sample with pale to intermediate foreheads did not overlap specimens from the northeast in wing chord. Specimens from other populations also overlap in all characters, whether compared separately (Tables 1 and 2) or in combination (Figure 2). I conclude that individual variation in the northern populations of H. pyrrhonota is too extensive to permit recognizing more than one subspecies. The names hypopolia and aprophata should be synonymized with H. p. pyrrhonota.

SUMMARY

Individual variation and extensive overlap among populations in wing length and several plumage characters precludes recognition of more than one subspecies of *Hirundo pyrrhonota* in northern North America. Cliff Swallows from this area belong to the nominate subspecies. The names *hypopolia* and *H.p. aprophata* are synonyms of *H. p. pyrrhonota*.

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Cliff Swallows collecting mud

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