

THE TAXONOMY OF ROUGH-WINGED SWALLOWS (*STELGIDOPTERYX*; HIRUNDINIDAE) IN SOUTHERN CENTRAL AMERICA

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ABSTRACT.—Based on morphological and distributional information, it appears that two species of *Stelgidopteryx* swallows breed in Costa Rica: the northern and highland *serripennis* (represented by the race *fulvipennis*, if one recognizes subspecies at all), and the southern and lowland *ruficollis* (represented by *uropygialis* on the Caribbean versant and *decolor* on the Pacific). In general, the forms of *ruficollis* have larger bills, shorter wings, brighter throats, and paler rumps than do those of *serripennis*. Overlap without demonstrable hybridization occurs between *uropygialis* and *fulvipennis* locally along the northern and eastern foothills of the central highlands of Costa Rica. Previous accounts of hybrids, intergrades, etc. have failed to take into account the amount of individual variation and migratory behavior of all forms. Appropriate English vernaculars for the species *serripennis* and *ruficollis* would be Northern and Southern Rough-winged Swallow, respectively. Received 10 June 1980, accepted 24 September 1980.

THE Rough-winged Swallows of the genus *Stelgidopteryx* are fairly small (ca. 15 g), brownish swallows, adult males of which possess short, stiffened barbs with sharp recurved tips on the outer web of the outermost primary; these produce the "rough" or "saw-toothed" feel to the leading edge of the wing that gives the birds their English and Latin names. Virtually all recent systematic discussions (e.g. A.O.U. 1957, Mayr and Short 1970) consider the genus monotypic, the single species *S. ruficollis* being divided into numerous races distributed from southern Canada to Argentina. In the past, however, two to four species were often recognized (e.g. Ridgway 1904). The presence of two of these forms in Costa Rica, apparently breeding sympatrically (Skutch 1960 and pers. comm.) prompted me to reexamine the relationships of these birds. In the process, I have examined virtually all specimens of *Stelgidopteryx* from southern Middle America in major museums and investigated breeding distributions in the field. The major conclusion to emerge is that there do appear to be two species of Rough-winged Swallows breeding in Costa Rica, with only slight geographical overlap and no conclusive evidence of hybridization.

HISTORICAL REVIEW

Most of the forms of *Stelgidopteryx* discussed here were described within a short period: the North American breeding race *serripennis* from South Carolina by Audubon in 1838, the southern Mexico-northern Middle American *fulvipennis* from Jalapa, Veracruz by Sclater in 1859, and the southern Middle American-northern South American *uropygialis* from central Panamá by Lawrence in 1863 (original citations in Ridgway 1904). The fact that the original description of *fulvipennis* was based on a juvenal bird led to confusion: in 1904 Ridgway (1904) named what turned out to be the adult of this form as a new species, *salvini* (type locality Dueñas, in the central Guatemalan highlands), and in the process synonymized *fulvipennis* with *serripennis*. Ridgway considered "*salvini*" closest to *serripennis* (but distinct) and considered *uropygialis* to be a representative of the South American *S. ruficollis* complex. He distinguished "*salvini*" from *serripennis* on the basis of its darker crown, brighter throat (these characters showing some approach to the condition in

uropygialis), and white-tipped tertials (but had only four adult male specimens of "salvini" available), but noted that juvenals of the two forms were similar. *Uropygialis* was distinguished from both of the preceding by having a still blacker crown and brighter throat, a pale rump, yellowish belly, and boldly black-tipped under tail coverts; the juvenal plumage differed from that of *serripennis* and "salvini" but resembled that of *ruficollis* in most respects.

Bangs (1906) noted variability in several of the characters cited by Ridgway, particularly in a series of *Stelgidopteryx* taken by Underwood in southwestern Costa Rica. He questioned the distinctness of several forms and recommended that "salvini" be considered a subspecies of *serripennis* (a suggestion subsequently followed by virtually all authors).

The prevailing modern treatment of *Stelgidopteryx* took shape in a review by Griscom (1929). He too found that not all *uropygialis* had strongly black-tipped under tail coverts, whereas some *serripennis* and *fulvipennis* had dark crissal markings, and that very fresh-plumaged *serripennis* had buff-tinged throats. He noted that birds from southwestern Costa Rica and adjacent Chiriquí Province, western Panamá, were extremely variable but averaged paler than adjacent forms, and he described them as a new race, *decolor*. He also named a paler race of *serripennis* from southwestern U.S.A.-northwestern Mexico as *psammochrous*. In surveying the genus as a whole, he noted a general trend from darker, more brightly patterned birds in South America to progressively paler, more uniformly colored birds in North America. Hypothesizing that the eastern South American *ruficollis* was the ancestral form, he interpreted this pattern as a "progressive northwards dilution of ancestral characters" and recommended lumping all forms into *S. ruficollis*.

Subsequent treatments of these forms have essentially followed Griscom's arrangement, adding distributional information as more specimens were collected (e.g. Brodkorb 1942, Miller 1957, A.O.U. 1957, Monroe 1968, Mayr and Short 1970, Wetmore MS). Hellmayr and Cory (1935) went a step further and sank *decolor*, in essence considering it a hybrid swarm between *fulvipennis* and *uropygialis*; its status has remained in doubt ever since (e.g. Slud 1964, Wetmore MS). In a discussion of the validity of *psammochrous*, Phillips et al. (1964) called attention to the great amount of variability in specimens of *Stelgidopteryx* due to plumage wear, *post mortem* foxing, and individual variation, a caution that I find applicable to *all* forms of *Stelgidopteryx*. In any case, no authors seriously questioned Griscom's basic premise, that there was but a single species of *Stelgidopteryx*. Skutch (1960 and pers. comm.) however, observed sympatric breeding of dark-rumped and light-rumped birds (= *fulvipennis* and *uropygialis*) in the Pejevalle Valley, Costa Rica, without apparent interbreeding; he found burrows of the two forms only a few meters apart. Slud (1964) noted that specimens of *fulvipennis* and *uropygialis* in breeding condition had been taken in the same areas, but, beyond adding some distributional information, he did not attempt a critical evaluation of the status of these forms and did not rigorously define breeding distributions. Therefore, the time seems ripe for a careful reexamination of the available specimens, and precise documentation of breeding distributions, in order better to evaluate the status of the various forms of Rough-winged Swallows in Costa Rica.

METHODS

The bulk of the data presented here derives from an examination of 296 museum specimens of *Stelgidopteryx*, many of them recently taken and thus not available to earlier revisers of the genus. It proved

surprisingly difficult to obtain adequate sample sizes for some forms, especially *fulvipennis*, *decolor*, and *serripennis* on their winter range: evidently collectors in the tropics prefer to collect more easily shot and "tropical" species than Rough-winged Swallows! For each specimen, measurements were taken with dial calipers of exposed culmen length (corrected insofar as possible for feather distortion) and wing chord; notes were taken on plumage coloration, wear, and molt; and gonad data were noted when available. For purposes of analysis I grouped specimens of the southern races into putatively "sympatric" and "allopatric" populations (i.e. separated specimens taken within and outside the known ranges of other forms) and also measured a sample of breeding *serripennis* from different parts of North America to compare with migrants of this form from southern Middle America. In all I examined 41 specimens of *decolor*, 89 of *uropygialis*, 55 of *fulvipennis*, and 111 of *serripennis*. In addition, on 11–12 April 1980 I mist-netted 17 *serripennis* during their northward migration at Chomes, Provincia de Puntarenas, Costa Rica and measured them as described above. Twelve of these birds were banded and released; five were collected and subsequently remeasured as specimens. Mean measurements of these netted birds were in close agreement with those of the sample of *serripennis* specimens from Costa Rica, and measurements of the five latter birds in the field and as specimens differed by no more than 0.2 mm (bill) or 1 mm (wing). Hence, I have included these mist-netted birds in the sample of *serripennis*, raising to over 300 the total number of birds included in the study.

Breeding distributions of the forms were examined in the course of my travels in Costa Rica between 1977 and 1980 and from specimen data; wherever possible the composition of breeding colonies was determined by observation or collecting. I have been unable to make long-term observations on particular pairs or colonies; hence, the present paper will deal mainly with specimen and broad distributional data.

PLUMAGE COLORATION

There appears to be considerable variability in plumage coloration in *all* populations of *Stelgidopteryx* (Table 1). Much of this is evidently due to age and plumage wear, but even subtracting these, a good deal of individual variation remains. Thus, there are practically no plumage characters that can in themselves distinguish all forms consistently (at least in museum specimens). It is virtually always possible, however, to distinguish *serripennis* or *fulvipennis* from *uropygialis* or *decolor* by color characters alone; within each of these pairs, some specimens are very difficult to assign to race without distributional data.

The most distinct form, in terms of coloration, is *uropygialis*, but a fair proportion of this race consists of rather pale-colored individuals virtually indistinguishable from many *decolor*. This has been taken as evidence for hybridization with *fulvipennis* by some, but because such pale birds have been taken during the putative breeding season (see below) in eastern Panamá, far from the range of *fulvipennis*, I think it more reasonable to consider this as simply individual variation. It could also be argued that this reflects widespread introgression of *fulvipennis* genes, but were this the case one should find a high frequency of hybridization and intermediate individuals in the zone of contact; in my experience, such is not the case (see below).

Considerable color variation occurs in *decolor*, especially in the rump, throat, and crissum: the more strongly-marked individuals are scarcely distinguishable from many *uropygialis*. The often less contrasting rump, less heavily marked crissum, and/or paler throat of many *decolor* have also been interpreted as evidence of hybridization with *fulvipennis*, but again these variants occur commonly throughout the range of *decolor*, including populations far from the range of *fulvipennis* (see below). For instance, a series of 6 birds that I collected from a breeding colony on the Río Tigre, Península de Osa included 4 with boldly black-tipped crissum feathers, 1 with bold dusky subterminal spots in each web, and 1 with only faint dusky smudges. All *decolor* in fresh plumage that I have seen have a distinct contrast

between rump and back, although the pale area of the former may consist of feather-edgings that nearly or quite wear away in the course of a year (particularly due to abrasion in the nest burrow). Also, all *decolor* have the throat distinctly rusty to pale cinnamon, the chest and sides distinctly brownish. Overall, the color scheme of *decolor* resembles that of *uropygialis*, bleached or washed out to a varying extent. This is sufficiently consistent that I have no hesitation in recognizing this race; I fail to find any evidence of hybridization with *fulvipennis*. The two forms are apparently not even in contact at the present time. Of course, the coloration of *decolor* could represent the residue of extensive contact and hybridization between *fulvipennis* and *uropygialis* (?) sometime in the past. Measurements fail to disclose any indication of the intermediacy of *decolor*, however (see below).

The two most similar forms of *Stelgidopteryx* in Costa Rica are undoubtedly *fulvipennis* and *serripennis*. The former is, on the average, more heavily pigmented and contrastingly colored, but these differences become exceedingly difficult to discern in birds with worn plumage or in some old specimens. Many worn *fulvipennis*, including a nesting pair I collected near Turrialba in April 1977, have, at most, a faint buff tinge on the throat, less than many fresh *serripennis* (including one of the five collected at Chomes in April 1980). One of these latter also has distinct dusky smudges on the longest under tail coverts, a condition much more frequent in *fulvipennis* (Table 1). Without taking molting season into account (July–October for *fulvipennis*, evidently later for *serripennis*, as the migrants netted at Chomes were all in fresh plumage), it would be very difficult to assign many specimens to race.

The fairly bright throats and dark-spotted crissa of some *fulvipennis* might again be taken as evidence for introgression of *uropygialis* genes (although I have never seen a *fulvipennis* with a distinctly pale rump). Among the very brightest-throated *fulvipennis* I have seen, however, are the type series of “*salvini*” from Guatemala; in my experience, Costa Rican *fulvipennis* are, if anything, duller-throated than those of northern Middle America; they also tend to have very poorly defined dark caps. Were introgression the cause of this variation, one would expect the reverse tendency, with the southern birds the most brightly colored. I can see no clear-cut trend whatever in the extent of dark spotting on the crissum: this feature seems to be highly variable in all populations of *fulvipennis*.

A further factor to consider is the possible presence in Costa Rica of wintering birds of the pale form *psammochrous*, as Wetmore (MS) and Phillips (MS) cite specimens from central Panamá. I consider *psammochrous* to be a poorly marked race at best, however: I am unable to distinguish many breeding specimens of *psammochrous* from paler individuals of *serripennis* or, for that matter, of *fulvipennis*, as *psammochrous* tends to have a brighter throat than *serripennis*, approaching that of *fulvipennis* in the southern part of its range (Phillips MS). Most available data suggest that *psammochrous* winters north of Costa Rica. I have yet to see a definite Costa Rican specimen of this form and suspect that the Panamanian *psammochrous* may be merely a very pale *serripennis*, or at best a stray. In measurements, *psammochrous* appears similar to *serripennis* and *fulvipennis* (cf. Griscom 1929, Brodkorb 1942, Phillips et al. 1964); even if it were subsequently shown to winter in Costa Rica, this would not affect the major conclusions drawn here.

I have examined too few juvenals of any of the forms to evaluate the degree of individual variation in this plumage. There appear to be two basic types of juvenal plumage, however, one shared by *fulvipennis* and *serripennis*, the other by *uro-*

TABLE 1. Plumage description of four races of *Stelgidopteryx* swallows found in southern Middle America.

	<i>serripennis</i>	<i>fulvifrenis</i>	<i>urophygialis</i>	<i>decolor</i>
Adults				
Back	Medium greyish-brown	Medium greyish-brown	Medium to dark greyish brown	Medium to fairly dark greyish brown
Crown	± concolor with back	Concolor to distinctly darker than back	Blackish; usually distinctly darker than back	Slightly to definitely darker than back
Tertials (fresh plumage)	Edged pale greyish	More broadly edged greyish white	Sharply edged whitish	Edged pale greyish to greyish white
Throat	Very pale grey-brown, tinged buff (faint; most strongly on chin) when <i>very fresh</i>	Pale greyish brown, usually strongly tinged cinnamon to buff <i>when fresh</i>	Cinnamon-rufous to pale cinnamon, fading with wear	Fairly bright to pale cinnamon; fading to rusty-buff with wear
Chest and sides	Very pale grey-brown; sides sometimes browner with dark shaft-streaks	Pale greyish brown, usually with dark shaft-streaks	Medium grey-brown; feathers of center of chest often with dark centers and shaft-streaks	Pale grey-brown, usually with dark shaft-streaks; feathers sometimes with dark centers on chest
Belly	Dull whitish to creamy white	Dull whitish to creamy white	Yellowish white to pale yellow	Whitish, usually tinged yellow, sometimes strongly so
Crissum	White, fairly often with dark shaft-streaks, occasionally with indistinct dusky subterminal spots or smudges	White, usually with dark shaft-streaks; fairly frequently with dusky subterminal spots in each web; these usually faint, sometimes large and bold	White, with faint dark shaft-streaks; usually with central feathers boldly tipped black or dusky, narrowly edged white; sometimes with large dusky subterminal spots in each web	White, with faint darker shaft-streaks; usually with central feathers boldly tipped black or dusky, narrowly edged white; sometimes with large dusky subterminal spots in each web; rarely with small, faint spots

TABLE 1. Continued.

	<i>serripennis</i>	<i>fulvipennis</i>	<i>uropygialis</i>	<i>decolor</i>
Rump	Concolor with back; feathers very narrowly edged paler, so in very fresh plumage may appear slightly paler and greyer than back	Concolor with back; feathers narrowly edged paler, so in very fresh plumage may appear slightly paler or greyer	Usually whitish, contrasting sharply with back feathers edged/tipped broadly whitish; contrast reduced with wear	Usually greyish white to pale greyish, slightly to distinctly paler than back; feathers less broadly edged paler; occasionally no contrast in worn birds
Juvenals				
Dorsum	Dull grey-brown, feathers broadly and indistinctly edged or suffused dull cinnamon or tawny; tertials broadly edged dull buff, greater coverts dull cinnamon	Dull grey-brown feathers, broadly and indistinctly edged cinnamon to tawny; tertials broadly edged dull buff, greater coverts dull cinnamon-rufous	Dull dark grey-brown; feathers of back and especially wing-coverts distinctly edged cinnamon to buffy; tertials broadly and sharply edged buffy white to pale buff; rump pale brown to white	Dull grey-brown; feathers of back and wing-coverts distinctly edged dull buff; tertials sharply edged dull buffy to whitish; rump pale grey-brown to whitish
Venter	Throat and chest pale grey-brown, more or less washed with cinnamon; belly creamy white, crissum white, immaculate	Throat and chest grey-brown usually strongly washed cinnamon; belly dull creamy white; crissum white, immaculate to (rarely) faintly spotted	Throat and chest pale dull rufous to cinnamon, sides browner; belly dull white with slight yellowish wash; crissum white less heavily spotted than adult, sometimes nearly immaculate	Throat and chest pale to fairly bright cinnamon to cinnamon-buff; belly dull white with (sometimes) faint yellowish wash; crissum usually indistinctly spotted, often nearly immaculate

TABLE 2. Summary of measurements of *Stelgidopteryx* swallows from Middle and North America.

	Exposed Culmen				Wing chord			
	<i>n</i>	Mean	SD	Range	<i>n</i>	Mean	SD	Range
Males								
<i>serripennis</i>								
Central and eastern U.S.A.	21	6.78	0.34	6.2-7.5	23	108.87	2.83	103.8-112.4
Western and northwestern U.S.A.	25	6.75	0.42	6.1-7.6	25	110.22	2.88	105.0-116.4
Costa Rica-Panamá	13	6.74	0.25	6.3-7.3	14	109.38	2.73	104.6-113.3
Total	59	6.76	0.35	6.1-7.6	62	109.55	2.79	103.8-116.4
<i>fulvipennis</i>								
Northern Middle America	18	6.72	0.26	6.3-7.1	17	110.87	3.51	105.2-116.3
Costa Rica-Panamá	15	6.67	0.28	6.3-7.2	15	110.84	3.55	105.5-116.7
Total	33	6.70	0.27	6.3-7.2	32	110.86	3.53	105.2-116.7
<i>uropygialis</i>								
Honduras-Costa Rica	26	7.26	0.37	6.6-8.0	26	107.88	2.22	102.4-111.6
Panamá	24	7.27	0.32	6.7-8.1	22	106.47	2.28	103.2-111.8
Total	50	7.26	0.35	6.6-8.1	48	106.80	2.24	102.4-111.8
<i>decolor</i>								
Southwestern Costa Rica	12	7.50	0.38	6.9-8.3	12	106.85	3.00	100.6-110.7
Chiriqui-Veraguas	8	7.40	0.45	6.9-8.2	8	106.96	2.65	103.0-110.6
Total	20	7.46	0.41	6.9-8.3	20	106.89	2.82	100.6-110.7
Females								
<i>serripennis</i>								
Central and eastern U.S.A.	17	6.75	0.36	6.2-7.4	17	102.33	3.16	98.2-108.4
Western and northwestern U.S.A.	22	6.85	0.38	6.3-7.7	22	104.58	2.67	99.7-110.6
Costa Rica-Panamá	23	6.85	0.34	6.3-7.6	23	102.77	2.20	99.2-107.2
Total	62	6.83	0.35	6.2-7.7	62	103.32	2.81	98.2-110.6
<i>fulvipennis</i>								
Northern Middle America	14	6.71	0.31	6.3-7.2	13	102.92	2.64	99.2-107.7
Costa Rica-Panamá	10	6.75	0.37	6.2-7.4	10	104.93	3.11	98.7-109.3
Total	24	6.73	0.33	6.2-7.4	23	103.76	2.96	98.7-109.3
<i>uropygialis</i>								
Honduras-Costa Rica	19	7.38	0.39	6.7-7.9	19	99.58	2.80	93.4-103.8
Panamá	21	7.23	0.28	6.7-7.8	22	99.36	2.38	95.7-103.7
Total	40	7.30	0.33	6.7-7.9	41	99.46	2.55	93.4-103.8
<i>decolor</i>								
Southwestern Costa Rica	12	7.51	0.55	6.6-8.4	12	99.59	3.04	93.5-103.3
Chiriqui-Veraguas	8	7.29	0.39	6.8-8.0	9	99.79	2.47	95.7-102.6
Total	20	7.41	0.48	6.6-8.4	21	99.67	2.76	93.5-103.3

pygialis and *decolor* (Table 1). These types were first clearly described by Ridgway (1904). In general, young birds have the crissum less heavily and/or less frequently marked with dusky or black than do adults; whether this holds for birds in first basic plumage is conjectural.

MEASUREMENTS

All forms of *Stelgidopteryx* considered here are sexually dimorphic in wing length, with males averaging very significantly larger than females ($P < 0.01$ in all cases by *t*-test). In no form is there significant dimorphism in bill (exposed culmen) length. Thus, given the possibility of mis-sexed specimens, bill length is probably a better measure with which to compare forms. On this basis, the four races break into two

TABLE 3. Results of *t*-tests of differences in measurements of four races of *Stelgidopteryx* swallows.^a

SPECIMENS FROM COSTA RICA AND ADJACENT AREAS					
A. Exposed culmen					
		Males			
		<i>serripennis</i>	<i>fulvipennis</i>	<i>uropygialis</i>	<i>decolor</i>
Females	<i>serripennis</i>		0.189	3.429**	4.097***
	<i>fulvipennis</i>	0.742		5.370***	6.153***
	<i>uropygialis</i>	3.196**	4.184***		1.750
	<i>decolor</i>	2.761*	3.440**	0.720	
B. Wing chord					
		Males			
		<i>serripennis</i>	<i>fulvipennis</i>	<i>uropygialis</i>	<i>decolor</i>
Females	<i>serripennis</i>		1.135	2.750*	2.109*
	<i>fulvipennis</i>	2.287*		4.182***	3.206**
	<i>uropygialis</i>	4.128***	4.601***		0.269
	<i>decolor</i>	3.545**	3.870***	0.171	
GEOGRAPHIC VARIATION WITHIN FORMS OF <i>STELGIDOPTERYX</i>					
		Exposed culmen		Wing chord	
		Males	Females	Males	Females
Costa Rica-Honduras vs. Panamá <i>uropygialis</i>		0.096	0.670	0.934	0.487
Costa Rica vs. Panamá <i>decolor</i>		0.551	0.693	0.179	0.103
C.R.-Panamá vs. Northern Middle America <i>fulvipennis</i>		0.592	0.271	0.095	1.830
C.R.-Panamá vs. Eastern + Central U.S.A. <i>serripennis</i>		0.340	0.903	0.493	0.515
C.R.-Panamá vs. Northwestern + Western U.S.A. <i>serripennis</i>			0.020	0.011	0.821
Eastern + Central U.S.A. vs. Northwestern + Western U.S.A. <i>serripennis</i>		0.072	0.652	1.653	2.410*

^a * = significant at $P < 0.05$; ** = significant at $P < 0.01$; *** = significant at $P < 0.001$.

well-defined groups: short-billed *serripennis* and *fulvipennis*, and long-billed *uropygialis* and *decolor* (Table 2). The two in each group are similar in bill length, but all intergroup comparisons give highly significant differences (Table 3A).

The same breakdown occurs with respect to wing length, but the picture is slightly less clear-cut (perhaps due to occasional mis-sexed specimens). In general, *serripennis* and *fulvipennis* are long-winged; *uropygialis* and *decolor* are short-winged. Geographic variation within *serripennis* complicates the picture: birds from the western and northwestern U.S.A. are longer-winged than those of the eastern and central regions (Table 2). This difference is significant in females, but not in males. The Costa Rican-Panamá sample of *serripennis* is intermediate in wing length but closer to the eastern-central group, especially in the females (Table 3). Thus the *serripennis* that migrate through southern Middle America probably breed in the central U.S.A. and adjacent south-central Canada. There is no appreciable geographic variation in any other form (Tables 2, 3). Particularly pertinent here is a series of *decolor* taken by Wetmore in Chiriquí; evidently following Hellmayr and Cory (1935), he considered them hybrids or intergrades between *fulvipennis* and *uropygialis* (Wetmore MS). In both plumage and measurements, however, these specimens agree perfectly with the series of *decolor* from southwestern Costa Rica (Tables 2, 3) and actually provide strong support for the validity of this form.

DISTRIBUTION

The distributional picture in *Stelgidopteryx* is complicated by the fact that *all* the forms considered here are migratory to some degree. Following breeding, part or all of most populations desert the breeding grounds; I have repeatedly visited breeding sites of *uropygalis*, *decolor*, or *fulvipennis* 1–6 months after the young fledged, to find no *Stelgidopteryx* present or to find a different form from that known to breed there. Thus, it becomes critical to distinguish between breeding and nonbreeding distributions of the forms in question.

I have used two procedures in delimiting breeding distributions: noting the locations of all nests or colonies at which I was able to identify the form(s) in question, and considering specimens taken during the months of the observed breeding season, especially those with gonad data indicating breeding. Skutch (1960) noted egg-laying in March virtually throughout Middle America. My own observations indicate a wider span, roughly from early March through mid- to late May. As stated by Skutch, however, all populations appear to be single-brooded. Thus, specimens taken between March and June should represent breeding birds, with two possible exceptions: early breeders may have left the nesting area by June, and it is often difficult to distinguish many worn, faded *fulvipennis* from many individuals of *serripennis*. Because the latter have been taken as late as mid-May in Costa Rica, and I have observed Rough-wings presumably of this race migrating north with other swallows in early May, I have excluded from the sample any doubtful birds without gonad data.

The resulting list of breeding localities for the three forms is plotted in Fig. 1. The conclusions are clear-cut: *fulvipennis* is a montane form breeding as low as 300–400 m locally, but mostly above 600 m, occasionally as high as 1,800 m; it does *not* breed south of the central highlands of Costa Rica. *Uropygalis* is essentially confined to the Atlantic lowlands, but on the northern and eastern slopes of the central highlands it may breed up to at least 1,000 m locally, thus overlapping with *fulvipennis*. The southwestern form *decolor* breeds north to near the Golfo de Nicoya; it may overlap with *fulvipennis* in the hills above Parrita, but I presently lack data from this area. Certainly at numerous localities in the far southwest, typical *decolor* breed at elevations that would be occupied by *fulvipennis* farther north, e.g. a breeding pair I collected at Las Alturas (1,600 m) in April 1980.

Outside the breeding season I have seen occasional pale-rumped birds (presumably *uropygalis*) in Guanacaste and around San José, Costa Rica, although most birds in both areas are dark-rumped. Dark-rumped birds are also common in the Caribbean lowlands of Costa Rica during the nonbreeding season, and I have seen dark-rumped, pale-throated birds in the southwestern lowlands on several occasions between August and March.

The present distributional picture seems to indicate that these forms are essentially allopatric in their breeding ranges but that widespread mixing occurs outside the breeding season. In the narrow zone of overlap between *fulvipennis* and *uropygalis* occasional hybridization might not be unexpected, but I can find no entirely conclusive evidence for its occurrence. I have yet to see a specimen that is not clearly one form or the other. My own observations in the zone of overlap are limited but tend to support the hypothesis that assortative mating exists and that hybridization is rare if it occurs at all. In April 1979 I traveled most of the roads in a zone of overlap in the Sarapiquí drainage in north-central Costa Rica, between Virgen del

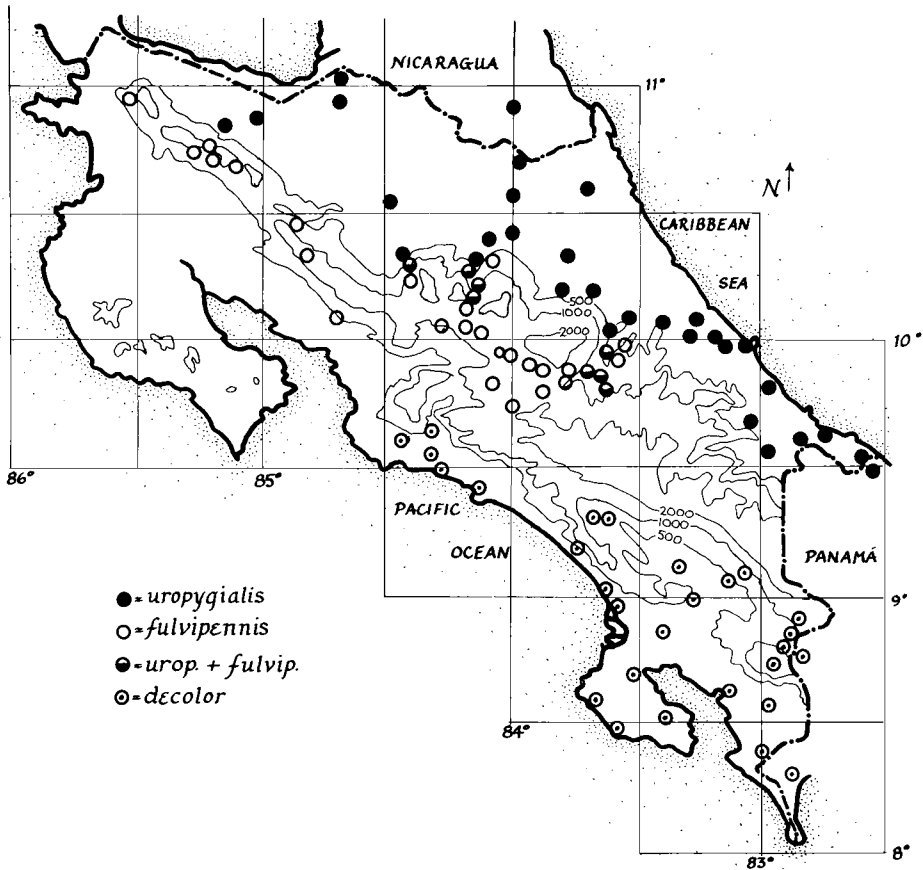


Fig. 1. Known breeding distributions of three races of *Stelgidopteryx* swallows in Costa Rica.

Socorro and Cariblanco (ca. 1,000 m) and San Miguel and Colonia Carvajal (300–400 m). In this area *fulvipennis* and *uropygialis* tend to form loose “pure” nesting colonies in roadbanks, rather than mixed colonies (although isolated pairs are not uncommon). Above about 700 m most birds seen were *fulvipennis*; below this elevation most were *uropygialis*. In all I found 37 “pure” *fulvipennis* pairs, 2 “pure” *uropygialis* pairs, and 2 possible mixed pairs (in both cases, involving the only *uropygialis* individuals I saw around the respective colonies of *fulvipennis*) in the higher parts of this area. Between San Miguel and Carvajal, I counted 18 “pure” *uropygialis* pairs, 4 “pure” *fulvipennis* pairs, and at most 1 possible mixed pair. In several cases I found pairs of the two forms breeding within 50–100 m. On a visit to Virgen del Socorro a month later, I was unable to find either putative mixed pair, though most “pure” pairs were located with young; the mixed pairbonds might not have persisted through egg laying. As colony locations tend to shift somewhat from year to year, such mixed pairs might include one bird whose previous nest site was now closer to or within the area occupied by a colony of the other form. More observations are clearly needed from this overlap zone to quantify the frequency and success of mixed pairs and to obtain comparative behavioral and ecological data.

Outside of Costa Rica, *fulvipennis* breeds north and west through Middle America, principally in the highlands, to the Petén in Guatemala and Veracruz and Chiapas in México. *Uropygialis* breeds north on the Atlantic slope of Middle America to southeastern Honduras; whether it overlaps with *fulvipennis* outside of Costa Rica is unknown. Southeastwards, *urophygialis* breeds on the Atlantic versant of western Panamá and on both slopes of eastern Panamá; it also ranges across northern South America from Ecuador to Venezuela and Trinidad; at least in Middle America, it is essentially a lowland bird in all areas. The breeding range of *decolor* extends eastward on the Pacific slope of Panamá at least into Veraguas; little is known regarding the situation further east, especially with respect to possible intergradation with *urophygialis*.

DISCUSSION

Data on morphology and distribution convince me that there are two breeding species of Rough-winged Swallows in Costa Rica. The northern/highland species, *serripennis*, is represented by the race *fulvipennis*, the southern/lowland species, *ruficollis*, by the races *urophygialis* and *decolor* on the Atlantic and Pacific slopes, respectively. Appropriate English vernacular names for the species *serripennis* and *ruficollis* would be Northern and Southern Rough-winged Swallow, respectively.

Geographical variation within the genus *Stelgidopteryx* as a whole must be reassessed in the light of this conclusion. In general, variation within the species *serripennis* is not great and is basically clinal in nature, making strict delimitation of subspecies difficult. A weak cline of increasingly contrasting markings exists from *serripennis* (*sensu stricto*) through *psammochrous* to *fulvipennis*; superimposed upon this cline is a tendency towards paleness in the hotter, drier areas of the southwestern U.S.A. and northwestern Mexico (*psammochrous*). A cline in size exists across North America, with wing length increasing toward the northwest, doubtfully justifying recognition of the race *aphractus*; size also increases slightly from north to south. Given the gradual nature of this variation, the broad areas of intergradation, and the considerable individual variation in all forms, I feel that no great violence would be done to the facts by considering the species *serripennis* to be monotypic. I should note in passing that two very large, dark races of Rough-wings, *ridgwayi* and *stuarti*, found from Yucután to Chiapas and Veracruz, will not be considered here, as they do not occur in Costa Rica; based upon sympatric breeding (with *fulvipennis*) and clear-cut size differences, they probably constitute a third species of *Stelgidopteryx* (A. R. Phillips pers. comm.).

In *S. ruficollis*, the same tendency toward a paler form in a (seasonally) drier area is seen in comparing the Pacific *decolor* with the Caribbean *urophygialis*; in Central America the dry season is more pronounced on the Pacific slope. Both forms have pale rumps, a feature not found in nominate *ruficollis*. Thus, although certain kinds of variation recur in both *serripennis* and *ruficollis*, I can find little justification for considering variation in the complex as a whole to represent simply a "progressive northward dilution of ancestral characters." In fact, if Phillips et al. (1964) are correct in considering *Stelgidopteryx* to be closely allied to *Riparia* (regardless of whether one wishes to lump the two genera or not), there is good reason for questioning the supposedly ancestral status of *ruficollis* on geographical grounds.

With regard to possible isolating mechanisms between *urophygialis* and *fulvipennis*, the differences in throat, crown, and especially rump color could certainly serve as visual features promoting assortative mating. In addition, I found that with

practice I was able to distinguish the voices of the two forms. Although the vocal repertoires seem fairly similar overall, the calls of *uropygialis* seem lower-pitched, mellower, more rolling and liquid than do the harsher, drier corresponding ones of *fulvipennis*. In February 1977, prior to the actual breeding season, I repeatedly noted "pure" groups of both forms gathering in dead trees or on other conspicuous perches at Virgen del Socorro. Birds in these groups vocalized loudly and persistently. It is not unlikely that such groups function in pair formation, in which case the aforementioned vocal differences may be important as isolating mechanisms.

The difference in bill size between *S. serripennis* and *S. ruficollis* could indicate an ecological difference, perhaps in size of preferred prey. This would make an interesting study, as the question of ecological compatibility is a dynamic one. Distributions of birds like *Stelgidopteryx* swallows are very likely in a state of flux at present due to man and his roadbuilding and deforestation activities, which tend to produce new nesting and foraging habitat, respectively, in areas where neither existed before. Rough-winged Swallows are probably more numerous and evenly distributed in Middle America at present than ever before, and this seems a good point in time to undertake a detailed study of their ecology.

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