SYSTEMATICS OF THE SOUTHERN FORMS OF *SELASPHORUS* (TROCHILIDAE)

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Abstract.—Based upon evidence from morphology, behavior, and ecology, I propose that the taxonomy of the southern *Selasphorus* hummingbirds be set forth as follows:
Selasphorus flammula Salvin: Volcano Hummingbird
    S. f. flammula Salvin, 1864 (Volcán Irazú, Volcán Turrialba, Costa Rica)
    S. f. torridus Salvin, 1870 (Cordillera de Talamanca, Costa Rica-Panama)
    S. f. simoni Carriker, 1910 (Volcán Poás, Volcán Barba, Costa Rica)
Selasphorus scintilla Gould, 1850: Scintillant Hummingbird (Cordillera de Tilarán, Costa Rica south and east to Volcán Chiriquí, Panama, at lower elevations than populations of the preceding species).
Selasphorus ardens Salvin, 1870: Glow-throated Hummingbird (Serranía de Tabasará, Panama).
S. scintilla and *S. ardens* may comprise a superspecies. *S. "underwoodii"* is a hybrid between *S. scintilla* and *S. f. flammula.*

The breeding distributions of *flammula, simoni,* and *torridus* are entirely allopatric, but the birds may occur together in the nonbreeding season. In particular, a pronounced post-breeding movement may carry many *torridus* into the breeding areas of *flammula* and even *simoni.* A possible evolutionary history of these forms is proposed in relation to post-Pleistocene climatic changes, ecological requirements, and probable populations sizes. *Received 7 June 1982, accepted 2 December 1982.*

THE genus *Selasphorus,* as presently defined by most authors, includes 6 or 7 species of small (2–3½ g) hummingbirds with at least some rufous in the body plumage and tail; males have orange, red, or purple gorgets. Geographically, the genus comprises two groups of species: a northern group, whose three members breed in western North America, with one species extending south in the mountains to Guatemala; and a southern group in the mountains of Costa Rica and Panama.

Most of the North American populations of the northern species *rufus* (Rufous Hummingbird), *sasin* (Allen's Hummingbird), and *platycercus* (Broad-tailed Hummingbird) are migratory, wintering mainly in western and central Mexico; the population of the latter species breeding in Mexico and Guatemala, however, is evidently resident. There is thus a gap of several hundred kilometers between the southernmost population of *platycercus* and the nearest populations of the southern group, which is not bridged by migration. The southern forms *scintilla* (Scintillant Hummingbird), *simoni* ("Cerise-throated Hummingbird"), *flammula* (Volcano Hummingbird), *torridus* ("Heliotrope-throated Hummingbird"), and *ardens* (Glow-throated Hummingbird) are also

resident, although, as we shall see, they engage in regular altitudinal movements.

Due to the great similarity between some species and the variability of others, the genus *Selasphorus* has a long history of taxonomic problems. Even in a relatively well-studied area like California, Allen's and Rufous hummingbirds were not recognized as distinct species until 1877. The southern group presents an even more complex picture, with the status of *torridus* and the affinities of *simoni* in particular still being debated. In this paper I hope to clarify the taxonomic and geographic relationships of the various southern forms of *Selasphorus,* based upon a detailed examination of their plumages and information on their breeding distribution, annual cycles, and altitudinal movements.

TAXONOMIC HISTORY

The nomenclatural history of the southern *Selasphorus* hummingbirds began with the description of the orange-gorgeted *scintilla* by Gould in 1850 (type locality Volcán de Chiriquí). In 1864, the purple-gorgeted *flammula* was described by Salvin from specimens collected by Arcé on Volcán Irazú, Costa Rica. Other Arcé

specimens from Volcán Chiriquí provided the basis for Salvin's description of yet another putative species, the steely-purple to greenish-gorgeted torridus, in 1870. In the same paper he described the red-gorgeted ardens from a Salvin and Godman specimen taken at Castillo, Veraguas. Salvin finally bowed out of Selasphorus taxonomy in 1897 with the description of a form with a reddish-orange gorget, underwoodii, from a bird collected by Underwood on Volcán Irazú. (For the original descriptions, see the citations in Ridgway 1911.)

The first critical analysis of the southern Selasphorus was made by Carriker (1910), in consultation with the French hummingbird expert, Eugene Simon. Carriker strongly suggested that underwoodii represented merely an extreme variant of scintilla but did not actually reduce it to synonymy, as he had not seen Salvin's type. (Subsequent authors have considered underwoodii to be a synonym of scintilla.) More important, following a suggestion by Simon, Carriker recognized that the red-gorgeted birds that had been taken on Volcán Barba in Costa Rica were different from ardens of Panama in the color of the tail and crissum and in bill length; accordingly, he named the Costa Rican birds a new species, simoni. He was puzzled by the status of flammula and torridus, stating that the only difference between them was in the color of the males' gorgets. Following Simon, he reduced torridus to a subspecies of S. flammula but noted that the two had been taken together at several localities, which, in view of their supposed subspecific status, he found "rather difficult to explain." He hypothesized that the torridus in question were in reality just worn or faded flammula and that true torridus was found only in Chiriquí. Ridgway (1911) accepted most of Carriker's conclusions but raised torridus to species rank based upon supposed differences in the color of the rectrices of female flammula and torridus.

The status of torridus and flammula was investigated by Berlioz (1949), who collected series of both forms. He ostensibly found such variability in torridus on Volcán Chiriquí that he considered it to be a color phase or morph of S. flammula. This conclusion was endorsed by Slud (1964), who noted that torridus and flammula "evidently coexist in Central Costa Rica" but did not provide a detailed analysis. He asserted that simoni differed from ardens in color characters only, not in measurements, and

suggested that it might be only subspecifically distinct from the latter (but he evidently did not examine their morphology in detail). He also stated that simoni and flammula were "partly sympatric" but did not specify whether or not this referred to breeding distributions. Wetmore (1968) restored torridus to subspecific status, considering that the Volcán Chiriquí birds, while variable, were clearly distinct from nominate flammula, which he found had not been collected by Berlioz on Volcán Chiriquí. Although noting specifically a specimen of torridus taken by Slud on Volcán Turrialba, however, he failed to account for the presence of both torridus and flammula on the Irazú-Turrialba massif and implied that the Chiriquí and Irazú-Turrialba populations were virtual disjuncts, with birds of the flammula-torridus complex being rare at best along the main Cordillera de Talamanca (despite Slud's statement to the contrary). Wetmore did not comment on the possible relationship of simoni to ardens.

It is worth noting that virtually all the taxonomic work on the southern Selasphorus hummingbirds to date has been based on color characters, especially of the males' gorgets and central rectrices. Other aspects of plumage morphology have gone almost entirely unappreciated, and measurements have been used haphazardly, without attention to sample sizes. In addition, reliable age and sex criteria, which allow one to compare birds of the same sex and age class of different forms, have not yet been derived from identifying birds not in adult male plumage. The distributions of the various forms have previously been delimited without regard to distinguishing the breeding distribution from postbreeding altitudinal and local movements; this, in turn, requires some knowledge of what months constitute the breeding and molting seasons.

METHODS

This study derives principally from an examination of museum specimens, supplemented by fieldwork with all of the forms concerned except ardens. Measurements of exposed culmen, wing chord, and tail length were taken with dial calipers of each specimen, and various morphological details were noted, especially the form and coloration of all the rectrices, which I had found very helpful for establishing sex, age, and species criteria among the northern group of Selasphorus (Stiles 1972). I visited nearly all the high mountains and major mountain ranges of Costa

Rica, where I was able to observe numbers of *simoni, scintilla, flammula,* and *torridus* in the field. I mist-netted at least some individuals of *torridus, scintilla,* and *simoni* and weighed them to the nearest 0.1 or 0.05 g with Pesola spring balances. The form most intensively studied has been *torridus* (cf. Wolf et al. 1976), for which I have been able to determine breeding and molting seasons and to document some altitudinal movements directly. This, in turn, has proved most helpful in evaluating seasonality and distribution of the other forms, based in part on plumage data from museum specimens. The southern *Selasphorus* have dive displays, just as their northern congeners do (Banks and Johnson 1961, Ortiz-Crespo 1980), and I have been able to observe the form of these displays, with their associated sounds, for *torridus, flammula, simoni,* and *scintilla.*

PLUMAGE CHARACTERISTICS

General aspects.—All of the forms of *Selasphorus* are quite similar in general aspect, which has undoubtedly contributed to the problems with their systematics. All are bronzy-green above and white below, with varying amounts of buffy or rufous suffusion on the sides, flanks, and crissum; males in particular tend to have considerable bronze-green spangling on the sides. Adult males have bright iridescent gorgets; the throats of females and immatures are varyingly speckled with dusky and tinged with buff. In all forms the front and sides of the neck are immaculate white, giving the birds a conspicuously "collared" look in the field that is not always evident in museum specimens. Overall, *scintilla* is much the most rufescent, often with only the center of the breast and belly white; *ardens* is intermediate between *scintilla* and the other forms in this respect, although its under tail-coverts are usually whiter than those of *simoni* and, sometimes, *flammula.* The form with the whitest underparts is *torridus,* on the whole; only the crissum is consistently tinged buffy. The outer three pairs of rectrices of females and immatures are tipped more or less broadly with white to cinnamon-buff. Immatures are recognizable as such for several months after fledging by the broad, soft, rufous fringes on the dorsal feathers, especially on the hindneck and rump. These fringes gradually wear away, however, and, in any case, young birds apparently undergo a complete postjuvenal molt at the same time as, or somewhat later than, the annual molt of the adults (see below).

Rectrices.—Patterns and shapes of typical examples of the rectrices of the adults of both sexes of all forms are diagrammed in Fig. 1; variations in the shape of certain rectrices are diagrammed in Fig. 2. The two most similar forms are undoubtedly *flammula* and *torridus.* The amount of black or dusky in the outer webs of the rectrices of adults is slightly more extensive on average, in the former, but there is much overlap in this character between the two forms. The amount of black on rectrix 1 in adult males varies from essentially none (most *torridus*) to a small amount at the tip (some *torridus;* most *flammula*), to virtually all the outer web and much of the inner web being black (a few *flammula*). The latter condition approaches that in *simoni.* The rectrices of *scintilla* differ strikingly from those of *flammula* and *torridus* in pattern (particularly in the amount of rufous) and in shape (particularly in the amount of emargination of the first two rectrices). The most interesting point, however, is the distinct difference between the rectrices of *simoni* and *ardens;* those of *simoni* resemble the rectrices of *flammula* and *torridus* except for being more extensively blackish, while those of *ardens* bear a rather less close resemblance to the rectrices of *scintilla.* The amount of black on the rectrices of *simoni* is apparently quite variable; whether this reflects age or individual variation is impossible to determine from the small series of *simoni* females available to me, only one of which is clearly immature (and has rectrices intermediate in color, but tending more toward the dark-tailed extreme). A few adult male *flammula* have tails virtually identical to some *simoni,* although on the average those of *simoni* are much blacker, practically lacking green in rectrix 1. The outer rectrices of female *simoni* are much more buffy at the tip than are those of *flammula* and *torridus* (with those of *flammula* averaging buffier than those of *torridus*). The outer rectrices of *ardens,* however, are tipped with still deeper buff to pale rufous, approaching the condition in *scintilla.* Thus, on the basis of the overall pattern and shape of the rectrices, the affinities of *simoni* are clearly with *flammula* and *torridus,* not *ardens.* In turn, *ardens* seems more nearly related to *scintilla* but is a good deal more distinct; it resembles *simoni* only in the large amount of black in the rectrices of adult males.

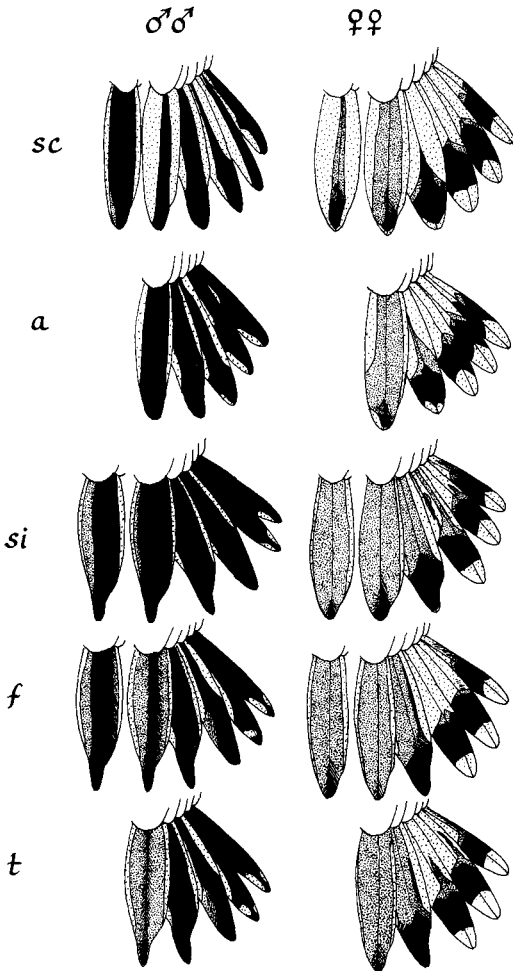Male *simoni* and *ardens* differ strikingly in

Fig. 1. Typical form and coloration of the rectrices of adults of five forms of southern *Selasphorus*, with variations in the pattern of rectrix 1. Abbreviations for forms: sc = *scintilla*, a = *ardens*; si = *simoni*; f = *flammula*; t = *torridus*.

Fig. 2. Variation in the degree of emargination in the tips of the first three retrices of adult males of southern *Selasphorus*. Abbreviations of forms as in Fig. 1.

rectrix shape (Fig. 2). The degree of emargination in rectrices 1–3 of *simoni* resembles or exceeds that found in rectrices of *flammula* and *torridus*, which resemble each other closely in this respect. The rectrices of *scintilla* are rather more acuminate but less emarginate, whereas those of *ardens* are the bluntest and least emarginate of all.

In *flammula* and *torridus*, immatures can often (but perhaps not invariably) be distinguished from adults by the duller, less patterned rectrices (Fig. 3). In adult females, the black and
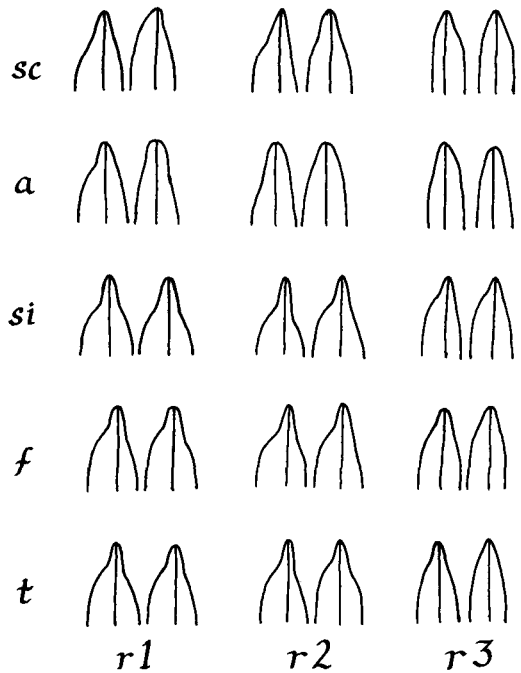
green areas of rectrices 2, 3, and 4 are usually quite distinct; the black is a deep purplish-black, the green bright and often slightly bluish. In young birds the black is duller, the green less distinct: sometimes there is only a dull green gloss on an otherwise dusky-black feather, or the entire feather (except for the rufous areas) may be a dull dusky green. The difference is most evident on the second rectrix. Young males usually have a good deal less white or buffy on the tip of the third rectrix than females have; young females have the least emargination on the first two rectrices. The same general differences seem to hold for *simoni*, although more data are required from definite immatures to confirm this. In *scintilla*, sex and age determination is easier. Young males differ from females of all ages in lacking rufous at the tip of the second rectrix and in having far less green in the tail in general (with the green more towards the edges or tips of the feathers, never extending to the bases). Young females have more green in the first two rectrices than adults have and the pattern is much less clean-cut. The one known young male of

ardens differs from the adult female most strikingly in the pattern of the second rectrix, which has much more green and only a very narrow pale tip; the immature female of *ardens* is unknown.

Other plumage features.—The form of the remiges is often modified in adult male hummingbirds (but only rarely in females) in relation to sound production during flight (Henshaw, in Bent 1940; Ortiz-Crespo, unpubl. data). In particular, the outermost primary is often modified at the tip. Such modifications occur in all three northern species of *Selasphorus,* with the modifications being most similar in the two most closely related species, *sasin* and *rufus* (Ridgway 1911). The southern *Selasphorus* break into two distinct groups on the basis of modifications of the tenth primary in adult males: in *ardens* and *scintilla* this feather is greatly attenuated at the tip, whereas in *simoni, flammula,* and *torridus* there is no evident modification whatsoever (Fig. 4). The wings of flying adult male *scintilla* produce a thin, rather insect-like trilling; unfortunately, nothing is known about the flight of *ardens.* No such trill is produced by males of the other three forms, although all are capable of producing a sharp deep buzz in certain situations. This buzz seems much like that produced by displaying Little Hermits (*Phaethornis longuemareus*) and other small hummingbirds with apparently unmodified primaries.

Gorget shape is another character sometimes used in classification of adult male hummingbirds, but I can find no clear-cut pattern among the forms treated here (Fig. 4). The various forms differ in the extent to which the gorget extends laterally into "wings." The most "winged" gorgets are those of *scintilla* and *torridus,* with that of *flammula* slightly to moderately less so. The gorget of *ardens* is not "winged" but square-cut, while that of *simoni* is typically slightly but distinctly "winged" (Fig. 4).

MEASUREMENTS

Measurements of bill, wing, and tail (Table 1) tend to emphasize the uniformity of the southern *Selasphorus* as a group, rather than showing any striking deviation from the overall pattern. In virtually all cases, adult males have significantly shorter bills and wings and longer tails than do adult females (the sole ex-
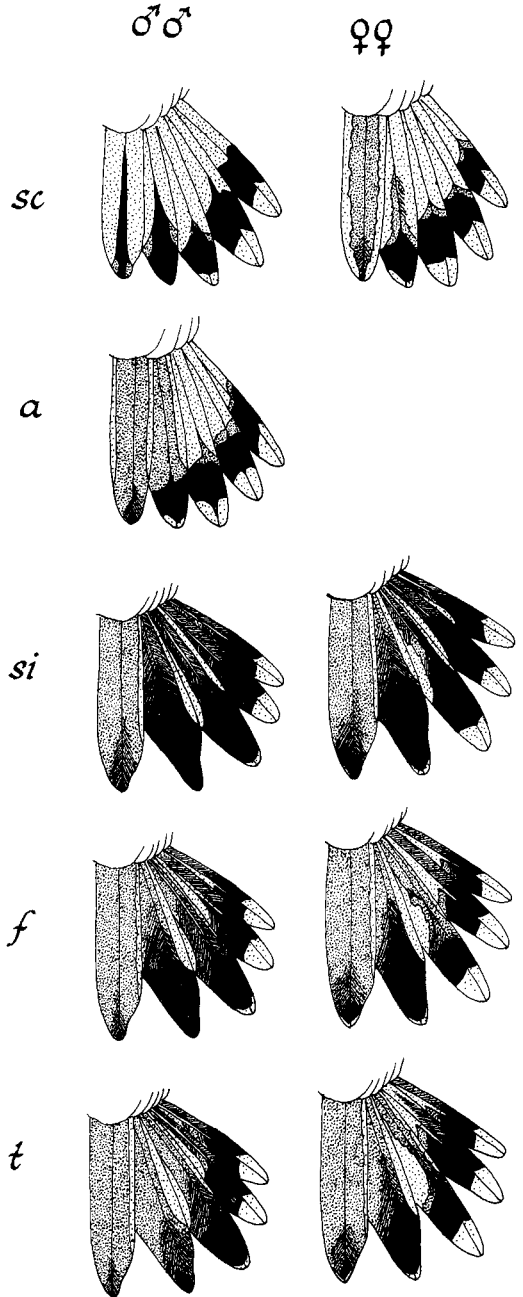

Fig. 3.   Representative patterns of rectrices of immatures of four forms of southern *Selasphorus.* Abbreviations for forms as in Fig. 1. Although the amount of black in the rectrices increases on the average from *torridus* to *flammula* to *simoni,* the degree of variation is such that many immatures cannot be assigned safely to form on this basis.

TABLE 1. Measurements of southern *Selasphorus* hummingbirds. Measurements given are mean, standard deviation, sample size, and range.

	scintilla	*ardens*	*simoni*	*flammula*	*torridus*
Adult males					
Exposed culmen	10.75 ± 0.41 (44) 9.7–11.4	11.54 ± 0.43 (8) 10.9–12.3	10.49 ± 0.53 (21) 9.5–11.4	11.75 ± 0.35 (34) 10.9–12.5	11.90 ± 0.41 (27) 11.3–12.7
Wing chord	32.71 ± 0.66 (46) 31.4–33.9	39.55 ± 0.48 (8) 38.8–40.1	39.20 ± 0.73 (21) 37.9–40.5	40.04 ± 0.74 (34) 38.3–41.3	40.09 ± 0.54 (26) 39.5–41.4
Tail length	23.56 ± 0.61 (46) 21.9–24.9	27.75 ± 0.68 (8) 27.2–28.9	26.81 ± 0.64 (22) 25–27.8	26.87 ± 0.73 (33) 25.6–28.4	27.26 ± 0.78 (25) 25.9–28.7
Weight	2.12 ± 0.12 (8) 1.9–2.3		2.60 ± 0.36 (4) 2.4–2.9		2.46 ± 0.30 (13) 2.05–2.75
Immature males					
Exposed culmen	10.74 ± 0.39 (20) 9.9–11.4	12.3 (1)	10.30 ± 0.75 (3) 9.5–11.0	11.61 ± 0.47 (10) 11.0–12.2	11.08 ± 0.58 (6) 10.5–12.2
Wing chord	34.57 ± 1.08 (21) 31.2–36.3	39.2 (1)	40.00 ± 0.40 (3) 39.6–40.4	40.48 ± 0.79 (10) 38.8–41.8	40.40 ± 0.72 (6) 39.8–41.8
Tail length	27.73 ± 0.71 (21) 21.2–23.9	23.3 (1)	26.70 (2) 26.5–26.9	25.91 ± 0.53 (10) 24.7–26.6	26.36 ± 0.82 (5) 25.1–27.3
Weight	2.15 ± 0.16 (5) 1.9–2.4		2.55 (2) 2.5–2.6		2.47 (2) 2.45–2.50
Adult females					
Exposed culmen	11.95 ± 0.56 (38) 11.1–13.3	13.33 ± 0.83 (3) 12.4–14.0	11.73 ± 0.39 (11) 10.9–12.3	12.90 ± 0.50 (21) 11.5–13.8	13.30 ± 0.50 (20) 12.3–14.2
Wing chord	35.81 ± 0.73 (39) 34.1–37.2	39.97 ± 0.67 (3) 39.4–40.7	40.93 ± 0.68 (11) 40.0–42.3	41.95 ± 0.69 (22) 40.0–43.0	42.06 ± 0.72 (20) 41.0–43.8
Tail length	22.84 ± 0.65 (39) 21.4–24.0	23.83 ± 0.32 (3) 23.6–24.2	25.95 ± 0.86 (11) 24.6–27.1	26.05 ± 0.76 (22) 24.9–27.6	25.77 ± 0.74 (15) 24.7–26.8
Weight	2.33 ± 0.10 (7) 2.2–2.5		2.83 (3) 2.6–3.1		2.75 ± 0.18 (17) 2.50–3.05
Immature females					
Exposed culmen	11.84 ± 0.44 (16) 11.3–12.8		11.4 (1)	12.79 ± 0.56 (10) 11.7–13.5	12.78 ± 0.76 (4) 12.1–13.7
Wing chord	36.08 ± 0.91 (18) 34.8–37.6		40.9 (1)	41.89 ± 0.65 (10) 40.9–43.1	41.73 ± 1.63 (4) 40.2–43.5
Tail length	22.55 ± 0.67 (17) 21.5–23.4		25.9 (1)	26.02 ± 0.40 (10) 25.4–26.7	25.43 ± 0.59 (4) 24.7–26.0
Weight	2.30 ± 0.11 (4) 2.2–2.4		2.6 (1)		2.77 (2) 2.75–2.80

TABLE 2. Results of statistical comparisons (Student's *t*) between measurements of different sexes, ages, and forms of southern *Selasphorus* hummingbirds.[a,b]

| | A. Intraspecific comparisons between different sex and age groups | | | | | | | | | |
| | Adult ♂♂ vs. adult ♀♀ | | | Adult ♂♂ vs. immature ♂♂ | | Immature ♂♂ vs. immature ♀♀ | | | Adult ♀♀ vs. immature ♀♀ | |
Form	EC	WC	TL	WC	TL	EC	WC	TL	WC	TL
scintilla	11.66***	20.20***	5.26***	8.87***	4.95***	7.22***	4.70***	0.85°	1.18°	1.48°
flammula	9.95***	9.86***	4.04***	1.71°	4.00***	5.24***	4.44***	0.55°	0.04°	0.18°
torridus	10.44***	10.43***	5.98***	1.13°	2.33*	3.99**	1.85°	1.91°	0.68°	0.85°
simoni	6.86***	6.49***	3.25**	1.83°	—	—	—	—	—	—
ardens	5.42***	1.24°	9.45***	—	—	—	—	—	—	—

| | B. Comparisons of *simoni* with other forms (adults) | | | | | |
| | Males | | | Females | | |
Form	EC	WC	TL	EC	WC	TL
flammula	10.71***	4.07***	0.28°	6.72***	4.06***	0.65°
torridus	10.40***	4.79***	2.12*	8.97***	4.26***	0.60°
ardens	4.48***	0.99°	3.63**	5.01***	2.17*	4.10**

[a] Measurements are: EC = exposed culmen; WC = wing chord; TL = tail length.
[b] Levels of significance are: ° = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

ception is *ardens*, where a very small sample of females averages barely larger than males in wing length). These sexual differences are generally less pronounced in juveniles than in adults. In particular, young males have slightly (*simoni, flammula, torridus*) to moderately (*scintilla*) longer wings than do adults; the greater difference in *scintilla* (the only such comparison to be statistically significant) doubtless reflects the modified tenth primary of adult males (Table 2). Bills of juveniles often average shorter than do those of adults of the same sex, due to the presence in samples of juveniles of very young birds with incompletely grown bills (Table 1).

As expected from plumage coloration, the two most similar forms in all measurements are *flammula* and *torridus*. *Simoni* averages significantly shorter than these in bill and wing length but not in tail length; indeed, its bill is the shortest of any of the forms considered here. The smallest form in wing and tail length (and only slightly larger than *simoni* in bill length) is *scintilla*. The most deviant form, in terms of measurements, is *ardens*; it shows extreme sexual dimorphism in bill and tail length, almost none in wing length. Compared with *simoni*, the bill is significantly longer, sex for sex, in *ardens*; males have significantly longer, females significantly shorter, tails than do males and females of *simoni* (Table 2).

For only two forms, *torridus* and *scintilla*, is there a reasonable sample of weights (Table 1). As would be expected from measurements, males are lighter than females, and *scintilla* is much lighter than *torridus*. Indeed, by weight *scintilla* is the smallest hummingbird in Costa Rica and, at most, is only slightly heavier than *Mellisuga helenae*, reputedly the world's smallest bird. The small sample of weights of *simoni* suggest that this form is about as heavy as (if anything, slightly heavier than) *torridus*.

ANNUAL CYCLES

Plumage data for all forms, gathered from museum specimens and mist-netted birds, are summarized in Fig. 5. In all forms the main molting season of adults is the late dry season to early wet season, roughly March to July; *torridus* appears to molt slightly earlier, and *scintilla* slightly later, than other forms. Given that the usual pattern in birds in general (Payne 1973) and hummingbirds in particular (e.g. Stiles 1980) is for breeding to precede molt with little overlap, one would expect the breeding seasons of all forms to be ending about March. The beginning of the breeding season is more difficult to gauge, because plumage condition per se gives little information on this point. In the best-studied form in the field, *torridus*, males may occupy breeding territories and be-
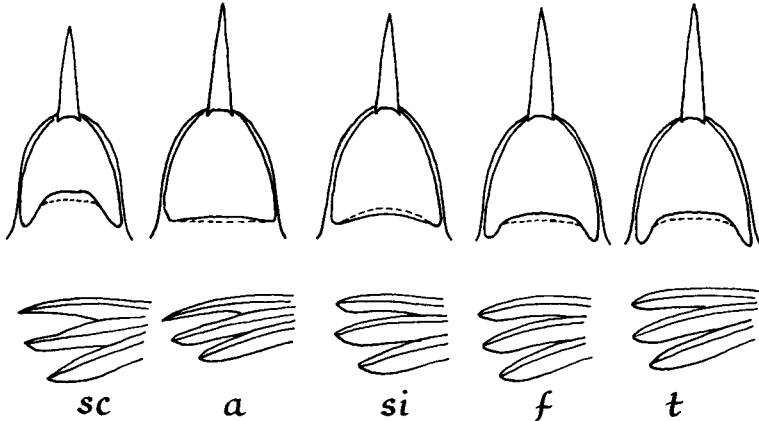
Fig. 4. Gorget shape (typical form with variants shown in dotted lines) and form of the tips of the three outermost primary feathers (primary 10 uppermost) in adult males of southern *Selasphorus*. Abbreviations as in Fig. 1.

gin dive displays as early as late July or August; the earliest nest I have found, however, was under construction in early September, and the earliest fledglings I have seen were in early November (cf. Wolf et al. 1976). The same seems to be true of *flammula*: I found males displaying and a just-completed nest on Volcán Irazú in late August 1968. The available data on other forms suggests a similar picture: an October nest was reported for *scintilla* by Wetmore (1968), and females of several forms with fairly fresh remiges and very worn belly plumage have been collected in November–December. Fresh-plumaged juveniles of *flammula, torridus,* and *scintilla* have been taken as early as November. The peak of the nesting season for *torridus* and *flammula* seems to be December–January (pers. obs.; R. G. Campos pers. comm.).

This pattern is somewhat complicated by the presence of occasional molting birds in August–October, rarely even as late as December. Wherever both the incoming and outgoing plumages can be clearly identified, however, these birds are seen to be undergoing the first prebasic (postjuvenal) molt. In species with protracted breeding seasons it is not unusual for some juveniles, presumably those fledged late in the season, to molt much later than do adults (cf. Williamson 1956 and Stiles 1973 for *Calypte anna*).

One other aspect of the annual cycle deserves mention: the possibility of local or altitudinal migrations. On the Cerro de la Muerte, *torridus* largely or entirely disappears from mid- to late March through June or July (Wolf et al. 1976). Although we once thought that this constituted mostly a shift to forest habitats, I am now convinced that a considerable altitudinal component is involved as well. I have seen definite adult male *torridus* as low as 1,350 m (Paraíso) and 1,600 m (Estrella de Cartago) in May and June but not at other times of year; this form has never been recorded breeding below 2,000 m (and rarely below 2,500 m, in my experience). Data for other forms are scarce, but J. E. Sánchez reported seeing a male *flammula* just east of Cartago (el. 1,350 m) in June 1973. By late August and early September, I have seen male *flammula* on territory and giving dive displays at elevations from 1,800 m to over 3,200 m on both Volcán Irazú and Volcán Turrialba. Unfortunately, practically none of the long series of *flammula* taken on these volcanos by Underwood and others has the elevation marked on the specimen label! Available data for *scintilla* suggest that it breeds mainly below 2,000 m in Costa Rica (see below). In August 1966, however, I collected a young male of this form in an overgrown pasture at about 2,450 m on Volcán Poás, suggesting that postbreeding wandering may sometimes be uphill in *scintilla.*

Unfortunately, little can be concluded regarding the annual cycle of *ardens*. The type series in the British Museum contains the only molting specimen I have seen, but unfortunately only the year of collection appears on
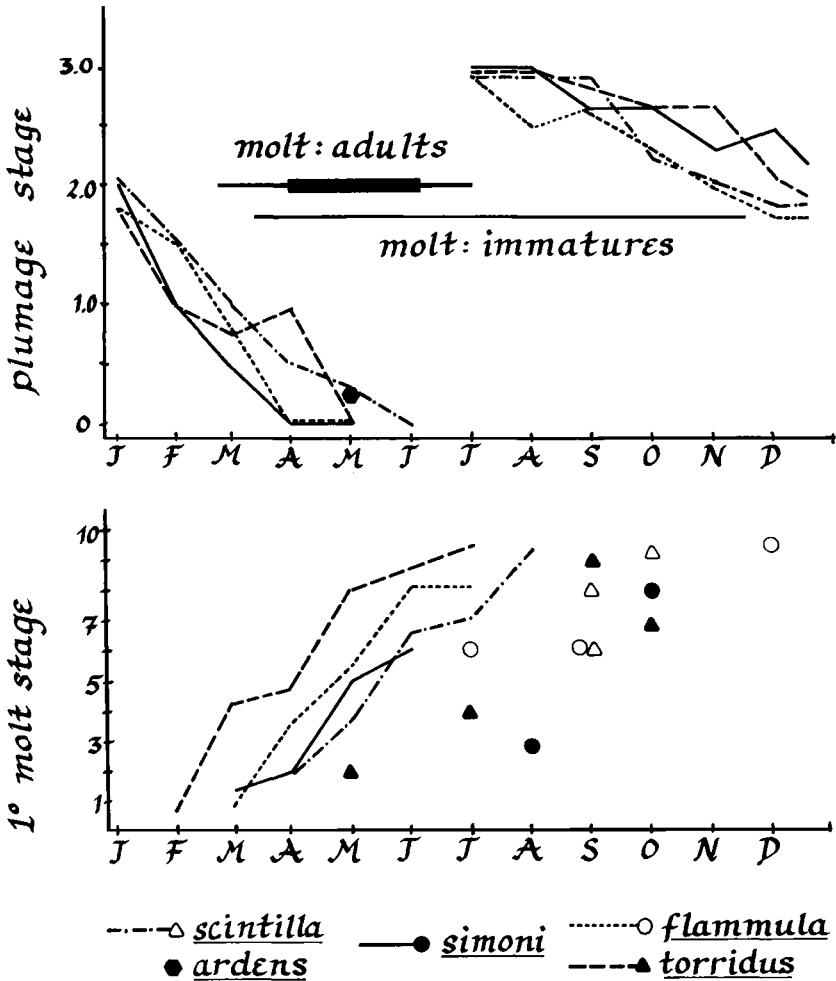
Fig. 5. Annual cycle of plumage and molt in five forms of southern *Selasphorus*. Upper graph: variation in mean plumage stage (on a semiquantitative scale of from 0 = very worn to 3 = fresh) for nonmolting adults. Molting periods indicated by horizontal bars; narrow bars = 50% or fewer of individuals in sample undergoing primary molt; thick bar: over 50% of individuals molting. Note the longer molting period and lower synchrony in molt of immatures (first prebasic molt). Lower graph: progress of primary molt in adults (lines connecting monthly means) and immatures (unconnected points). Primary molt stage = number of full-grown new primaries. Sample sizes for molt and plumage stages not indicated, but usually small, five or fewer individuals per species per month.

the label! All dated specimens I have examined are moderately worn birds taken in the month of March. These birds are about as worn as specimens of *scintilla* taken in March in Chiriquí (Fig. 5), suggesting that the annual cycles of *ardens* and *scintilla* may be similar.

DISTRIBUTION

The breeding distributions of all forms of southern *Selasphorus*, based upon specimens and sightings, are presented schematically in Fig. 6. The following overall pattern seems to emerge: *simoni*, *flammula*, and *torridus* are high-elevation forms, found mostly near the tops of the higher mountains of the Cordillera Central and the Cordillera de Talamanca; *scintilla* is a middle-elevation form, found mostly lower down on all of these mountains (and extending north to the Cordillera de Tilarán); and *ardens* is restricted to the Serranía de Tabasará, a much lower range east of the Talamancas in western
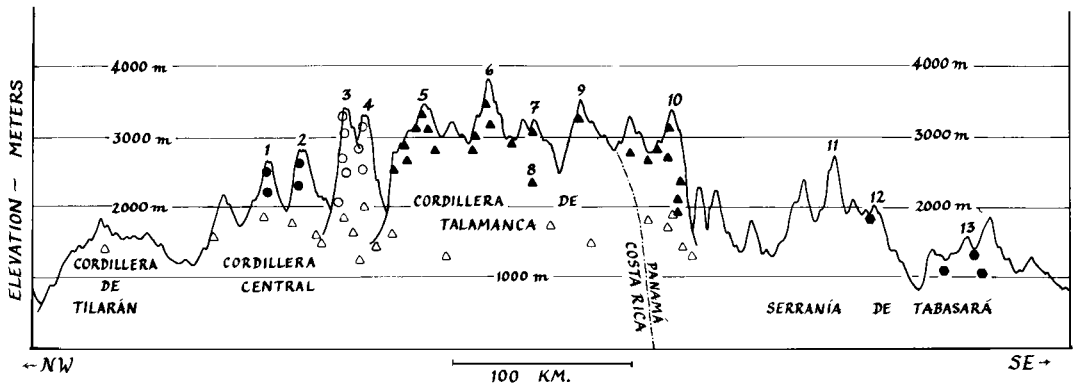
Fig. 6. Schematic diagram of major mountain areas of southern Central America, with known breeding distributions of *Selasphorus* hummingbirds (as indicated by sightings or specimens in the breeding season, as well as actual nesting reports). All localities known for *ardens* are plotted, although most records are for the month of March, which may be after the breeding season for this form (see text). Numbered localities are: 1 = Volcán Poás; 2 = Volcán Barba; 3 = Volcán Irazú; 4 = Volcán Turrialba; 5 = Cerro de la Muerte; 6 = Cerro Chirripó; 7 = Cerro Dúrika; 8 = Sabanas de Dúrika; 9 = Cerro Kamuk; 10 = Volcán de Chiriquí; 11 = Cerro Santiago; 12 = Cerro Flores; 13 = Cerro Tute. Symbols for forms as in Fig. 5.

Panama, and occupies about the same elevations as does *scintilla* to the north and west. Published information (e.g. Slud 1964) and museum specimens suggest considerable overlap between *flammula* and *torridus*, due mainly to the occurrence of the latter on Volcán Irazú and Volcán Turrialba. Inspection of the *torridus* records concerned, however, reveals that all of them fall between March and July and that most of the specimens are molting birds. This is precisely the time that *torridus* moves downhill from its known breeding haunts on the Cordillera de Talamanca; evidently this postbreeding movement may carry the birds not only downhill but up the other side, onto the Cordillera Central. Particularly interesting in this connection are two green-gorgeted *torridus* from Volcán Poás, in the range of *simoni*. Both are in heavy molt and were collected in May. A male *flammula* taken on Volcán Barba in April suggests that postbreeding movements to other ranges occur in that form also. Thus, the available data indicate that the breeding ranges of *torridus*, *flammula*, and *simoni* are entirely separate but that postbreeding movements result in some mixing, most notably from an influx of *torridus* onto the Cordillera Central. I emphasize that this picture is derived from the study of adult males; I cannot distinguish most adult females of *flammula* from those of *torridus*, and some females of *simoni* are virtually indistinguishable from the smaller examples of

either *flammula* or *torridus*. Thus, it remains an unproven assumption that movements of females (or immatures) parallel those of their respective adult males, although at this stage I certainly see no reason to suspect otherwise.

The breeding distribution of *scintilla* is centered lower than that of the aforementioned forms. Some overlap may occur locally at around 2,000 m (cf. Wetmore 1968). Both *scintilla* and *ardens* have been taken on Cerro Flores, in the western part of the Serranía de Tabasará in extreme eastern Chiriquí. These birds were collected in March, however; the *scintilla* in question were a worn male beginning body molt and a juvenile female, both of which could have arrived via postbreeding dispersal. There is thus no evidence that *scintilla* breeds east of Volcán Chiriquí. It therefore appears that the breeding ranges of *ardens* and *scintilla* are also separate, on present evidence (but see below).

DIVE DISPLAYS

I present descriptions of the dive displays of the four forms of *Selasphorus* resident in Costa Rica; I have never seen *ardens* in the field, and published information on its behavior does not exist. The following are excerpts from my field notes:

(a) *torridus* (8–11 February 1972, Cerro de la Muerte): "Displays are of the pendulum type. U-shaped—bird makes next dive from same

side as preceding one ends up; dives at a steep angle from a height of 50–75 feet, not quite vertical; high, thin whistles are heard on both dive and upswing—the former louder and scratchy, the latter softer and clearer, sometimes lacking? At the bottom, four rapid-fire dry clicks: fut-fut-fut-fut, reminiscent of bottom sound of *Selasphorus platycercus.*"

(b) *flammula* (13 January 1979, el. 2,900 m, Volcán Irazú): "a U- or J-shaped dive (U-shaped if more than one dive per bout); bird dives from height of 15–20 m, near vertical at start, describing arc of a circle at bottom. High, thin whistles given both coming and going [*sic*], that of the dive louder than that of the upswing; at bottom four dry "chuts" in a quick sputter."

(c) *simoni* (16 March 1972, Volcán Poás): "only single dives seen; birds evidently near end of breeding season, many immatures about; some adults starting to molt. Dive is J-shaped, nearly vertical from a height of 50–60 feet. A high thin whistled note as bird comes down, slightly higher and thinner than that of *flammula* (= *torridus*); at the bottom 3–4 sharp dry "fut's" in a sharp sputter. Overall very similar to dive of *flammula.*"

Clearly the dive displays of these three forms are virtually identical, far more similar than those of any two North American species of *Selasphorus,* even the very closely related *S. rufus* and *sasin* (Ortiz-Crespo and Stiles unpubl. data). The minor differences noted in the dive of *simoni* most likely reflect the late date (the end of the breeding season) and the fact that only single dives were seen; the lack of a pronounced upswing following the dive (i.e. for a second dive) probably accounted for the lack of a softer "upswing whistle" in the observed dives.

(d) *scintilla* (7 November 1982, Las Cóncavas, Prov. Cartago, el. 1,320 m): "a U-shaped dive, ca. 15 m in height, the dive less steep and the arc broader than in *flammula* et al. The wing-trill is heard during the dive itself, and at the bottom the bird makes a dry, rippling sputter of 7–8 dry clicks or snaps, less sharp and loud than the corresponding sounds of *flammula.* Halfway up the climb to begin the next dive, the male's trajectory becomes violently undulating or zigzag, as he weaves abruptly from side to side—the amplitude of the zigs ca. 50 cm. During this zigzagging flight the wing-trill sounds broken rather than continuous as during the rest of the dive."

The dive display of *scintilla* thus differs strikingly from those of the preceding three forms in three major respects: the longer sputter at the bottom (twice as many syllables) the arc sound provided by the wing-trill, and the presence of a zigzag flight during the climbing phase.

THE CASE OF *SELASPHORUS* "*UNDERWOODII*"

The long-standing treatment of *S.* "*underwoodii*" as a synonym of *scintilla* originated with Carriker (1910) and was emphatically endorsed in a footnote by W. J. Holland, who edited Carriker's manuscript. Carriker based his proposal on the individual variation in his series of *scintilla* as compared with Salvin's description of *underwoodii.* Carriker stated clearly that he did not actually examine Salvin's type specimen, and evidently subsequent authors who followed his suggestion did not do so either. I recently was able to examine the type of *underwoodii* in the British Museum and find that not only is it definitely not *scintilla,* but it differs from all other forms of *Selasphorus* in several respects! The specimen is an adult male collected by C. F. Underwood on 20 February 1896 at an unspecified elevation on Volcán Irazú; it is in fairly worn plumage. The gorget is a curious pale purplish-red with a strong golden-orange sheen. The underparts have much less rufous than those of *scintilla,* more closely approximating those of *flammula* in the amount of green flecking and buffy feather-edgings. The rectrices differ from those of *scintilla* not only in the greater amount of black (cited in Salvin's description), but in having considerable green on the first rectrix and in the tips of the first two rectrices being more emarginate (approaching the condition in *flammula*); the fifth rectrix is identical in pattern to that illustrated (Fig. 1) for *simoni.* The outermost primary is less attenuated at the tip than that of *scintilla.* The measurements (exposed culmen 11.2 mm, wing 35.4, tail 24.9) equal or exceed the maximum values for *scintilla* (cf. Table 1). In short, I conclude that *S.* "*underwoodii*" cannot be anything else but a hybrid between *scintilla* and some other form, almost certainly *flammula* in view of the locality, date, and gorget color. This is the first hybrid reported for the southern group of *Selasphorus* (and, indeed, the first intrageneric hybrid for the genus; cf. Banks and Johnson 1961).

DISCUSSION

The major taxonomic conclusions of this study are the following:

(a) The five forms considered here break into two distinct groups: *flammula, torridus,* and *simoni;* and *scintilla* and *ardens. Simoni* and *ardens* are not closely related; the fact that males have similarly-colored gorgets and similar wing lengths is best ascribed to convergence (or coincidence).

(b) Similarity of plumage and displays indicates that *simoni, flammula,* and *torridus* are best considered subspecies of a single species, *S. flammula* Salvin. The allopatric breeding distributions of these forms eliminate previous doubts about considering them as subspecies (especially *flammula* and *torridus*); the similarity in displays suggests that the three are probably not reproductively isolated (see below).

(c) While closely related, *scintilla* and *ardens* differ from each other considerably more than do any two members of the *flammula* complex. Especially considering the lack of information on displays of *ardens,* I think it wisest to continue to recognize them as distinct species. Together, *scintilla* and *ardens* might comprise a superspecies.

(d) *S. "underwoodii"* is a hybrid between *S. f. flammula* and *S. scintilla.*

The most radical change from previous classifications is the association of *simoni* with the *flammula* group and *ardens* with *scintilla.* That this arrangement has not been suggested heretofore is probably due to the preoccupation of previous authors with the color of the males' gorgets to the exclusion of other characters: thus, from its original description to the present time, *simoni* had always been compared to the similarly red-gorgeted *ardens,* never to *flammula* and *torridus.* Color of the rectrices has been cited cursorily, and details of their shape and pattern largely ignored. From previous experience with the northern members of *Selasphorus* (Stiles 1972), however, I regard the form and patterns of the rectrices as an extremely useful guide to affinities in this group.

The taxonomic arrangement proposed here makes good sense ecologically and zoogeographically as well. The three members of the *flammula* complex are all high-elevation hummingbirds of páramo or páramo-like habitats: clearings, forest edge, scrub, etc. Such habitats occur at very high altitudes above timberline

but can also be produced naturally by landslides or volcanic activity or artificially by human activity in forested areas. All three subspecies of *S. flammula* are associated with flowers like *Fuchsia microphylla, Tropaeolum* spp., and *Salvia* spp. during breeding and also visit a variety of largely insect-pollinated flowers in families like Ericaceae, Rosaceae, and Melastomataceae (cf. Wolf et al., 1976). If one views *simoni, flammula,* and *torridus* as members of a single complex, certain trends in the complex become evident over its entire range. There is a trend toward smaller size from south to north, paralleled by trends toward increasing buffiness in the ventral plumage and the tips of the rectrices in females and toward increasingly brighter, redder, and less "winged"gorgets in the males. In all of these features the difference between *simoni* and *flammula* is greater than that between *flammula* and *torridus.* I think that this pattern may have a simple historical explanation, related to the amount of breeding habitat available to each of the forms and their consequent population sizes.

At the present time, and probably for much of the recent past, the amount of good breeding habitat available to *simoni* has been far smaller than that available to *flammula;* in turn, *flammula* has had far less available habitat than *torridus.* The two peaks that comprise most or all of the breeding range of *simoni,* Volcán Poás and Volcán Barba, are much lower (2,704 and 2,906 m, respectively) than the two peaks of the Irazú-Turrialba massif (3,452 and 3,328 m, respectively) that form the breeding range of *flammula.* The area above timberline on the latter massif is quite extensive, and eruptions of Volcán Irazú have also helped to produce large areas of stunted scrub that are slow to return to forest in the cold temperatures at 3,000 m and above. By contrast, neither Poás nor Barba extends appreciably above timberline, although both have wind-stunted elfin forest near their respective peaks, and eruptions of Volcán Poás have also produced areas of stunted scrub. The Cordillera de Talamanca, on the other hand, has extensive areas of páramo on at least a dozen peaks that rise well above 3,300 m; much of the spine of this range is above 3,000 m and is covered with páramo or subpáramo vegetation in which *torridus* is common. Thus, based on available habitat, I believe that the total population of *simoni* is, and probably has always

been, much smaller than that of *flammula*, whose population is in turn much smaller than that of *torridus*. This is reflected in the far smaller number of specimens of *simoni* that have been collected as compared to *flammula*, especially considering that all of the volcanos concerned are close to major cities on the Meseta Central. The relatively small number of *torridus* in most museums reflects the relative inaccessibility (until recently) of most peaks of the Cordillera de Talamanca and is not due to any scarcity of the birds themselves. While it is probable that deforestation of the Pacific slopes of the major volcanoes of the Cordillera Central in the last two centuries or so has augmented the amount of good *Selasphorus* habitat, and doubtless *Selasphorus* populations as well, this effect has probably been most pronounced on Volcán Irazú and has therefore not greatly affected the relative sizes of the populations of the three forms.

During the cooler temperatures of the Pleisitocene, it is probable that páramo-like vegetation extended as low as 1,500–2,000 m in southern Central America (cf. Wolf 1976 and included references). It in thus quite likely that the ancestral proto-*flammula* population was distributed continuously from northern Costa Rica south at least to Volcán Chiriquí. With the warming trend of the last several thousand years, the páramo habitat and its associated hummingbirds, specifically *Selasphorus*, have been restricted to progressively higher elevations. The concomitant fragmentation of the breeding habitat in turn caused fragmentation of the ancestral proto-*flammula* population; the fate of the different segments of this population became linked to the ecological characteristics of their respective highland refugia. The smallest and most distinct such refugium was that on Volcán Poás and Volcán Barba, and the proto-*flammula* population there was probably the smallest and subjected to the most intense selection. It has long been a basic tenet of population biology that evolutionary responses to selection and divergence proceed most rapidly in small populations (e.g. Mayr 1963). Thus, the greater divergence of *simoni* relative to *flammula* and *torridus* would be expected on the basis of the probable evolutionary history of this population.

Is gene flow occurring between these populations at present? This question is difficult to answer with the available data. The probable direction of gene flow, based upon population sizes, would be *torridus* to *flammula* to *simoni*; certainly this agrees with available data on postbreeding migrations. The variability in tail pattern of female *simoni*, and the close approach of some males of *simoni* and *flammula* in this character, might indicate gene flow. Also, I have seen several *flammula* males with a few duller, *torridus*-like feathers at the edge of an otherwise typical *flammula* gorget. By contrast, I have seen no approach to *flammula* color in the gorgets of *torridus* males on the Cerro de la Muerte, the northernmost major massif of the Cordillera de Talamanca; the degree of variability, from dull green to greyish-purple, seems similar along the length of this range (I certainly have seen nothing to substantiate Berlioz' claim of *flammula*-like gorgets among the *torridus* of Volcán Chiriquí). It would be interesting to know whether or not and how the relative proportions of greenish- and purplish-throated males vary along the Talamancas. The very existence of this variability is interesting regardless of its cause; it suggests that gorget color *per se* may not be terribly crucial in mate choice by females of this group. This in turn would argue for the possibility that gene flow could still occur between *simoni, flammula,* and *torridus*—especially in view of the similarity of their dive displays. I should note at this stage that dive displays may not be the most critical isolating mechanisms in these hummingbirds (Stiles 1982). The close-range displays that immediately precede mating, however, have not yet been described for southern *Selasphorus*, and in North American hummingbirds as a group, divergence in these displays roughly parallels the divergence in dive displays (Stiles and Ortiz-Crespo unpubl. data).

The divergence between *scintilla* and *ardens* is less easy to explain, especially as the distribution and ecology of the latter are so poorly known: ornithologically, the Serranía de Tabasará is among the least known areas in Panama (E. Eisenmann pers. comm.). It is conceivable that *scintilla* breeds on the western part of this range; contact between the two forms during the breeding season should not be ruled out. For middle-elevation birds, the gap between Volcán Chiriquí and the Serranía de Tabasará hardly seems commensurate with the degree of divergence between *scintilla* and *ardens*. This barrier may have been more pronounced in the past, however, or may have

persisted for a long time, to judge from the striking degree of divergence in other groups (e.g. *Chlorospingus, Pselliophorus*) between the same two ranges. Historical factors, rather than present ecological conditions, must have played a dominant role in producing this situation.

As far as I am aware, the specimen of *S. "underwoodii"* is unique: no other hybrids between *scintilla* and any member of the *flammula* complex have ever been observed or collected. The rather frequent hybrids between northern *Selasphorus* and members of related genera (*Archilochus, Stellula, Calypte*) tend to occur mostly where one species is rare and/or invading the range of another (Banks and Johnson 1961, Lynch and Ames 1970, Wells and Baptista 1979). It is likely that a century ago deforestation was still advancing up the slopes of Volcán Irazú, breaching the band of forest that probably once separated the breeding areas of *scintilla* and *flammula*. The fact that no hybrids have been reported since may mean that a possible burst of hybridization and perhaps competition as contact was being established may have selected for refinements in microhabitat and perhaps flower choice that reduced the frequency of interspecific encounters. I know of no locality where the two species breed sympatrically at present, although they may approach each other closely: in November 1971 I found apparently territorial males of *scintilla* and *flammula* at different sites, separated by less than 2 km and 100 m elevation, near Tierra Blanca (ca. 2,100 m) on Volcán Irazú above Cartago.

At this time, it seems rather premature to attempt a detailed assessment of the relationships between the northern and southern groups of *Selasphorus*. The modifications of the outer primary and rectrices of *scintilla* and *ardens* seem fairly similar to those of the northern *S. platycercus*; the bottom sound of the dive display of the latter is strikingly similar to those of members of the *flammula* complex (Bent 1940, Ortiz-Crespo 1980). Thus, it is not improbable that, of the northern group, *platycercus* is the most closely related to the southern *Selasphorus*, as would be expected on geographical grounds. Details of these relationships, however, will only be elucidated by more comprehensive data, including sonagrams, on the display repertoires of all of the southern species (especially *ardens*) and the completion of a detailed analysis, currently in progress, of the

displays of the northern *Selasphorus* and their close relatives in the genera *Archilochus, Stellula,* and *Calypte* (Stiles and Ortiz-Crespo in prep.).

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