

Patterns of distribution of swifts in the Andes of Ecuador

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Abstract Trans-Andean elevational (above sea level) and vertical (above ground) patterns of distribution of the resident swifts species in Ecuador were examined. The four types of limits for species distribution along an elevational gradient proposed by Terborgh (1971) and Terborgh and Weske (1975) were assessed as to their effects in swift distribution. 1) "Natural terminus of the environmental gradient" might affect only two species. 2) "Factors in the physical or biological surroundings that change parallel with the gradient" were possibilities for six of 10 species. 3) "Competitive exclusion" was not found in the elevational gradient, but, is likely to operate in partitioning the vertical component. 4) "Vegetational ecotones" did not seem to affect the aerial guild.

Introduction

Little has been written on the distributional patterns of Neotropical birds along elevational gradients. The scant literature (e.g., Terborgh 1971, Terborgh and Weske 1975, Remsen and Cardiff 1990, Remsen and Graves in press) has considered the role of competition in shaping distributional patterns. None of these studies have described the patterns of elevational distribution in the aerial foraging guild, which in the Neotropics includes two families, Apodidae (swifts) and Hirundinidae (swallows and martins), as well as some subgroups such as the nighthawks (*Chordeilinae* spp. etc.) and some birds of prey (e.g., *Ictinia*, *Elanoides*). In this paper only the swifts, the core of the guild, will be treated.

Determining the distributional patterns of swifts is complex. Not only are they highly mobile, but they are also morphologically similar and difficult to distinguish in the field. Also, they usually fly fast and erratically, often high above the ground. Therefore, the core of the guild is a group difficult to observe, collect, and identify in the field. Furthermore, the elevational distribution of swifts has two distinct components: a) elevation above sea level, which I will refer to as "elevational", and b) altitude above the ground, which I will call "vertical." Only two studies, Hespdenheide (1975) and Waugh and Hails (1983) have described the vertical component of the aerial guild in the tropics. Both studies described foraging interactions and difference among swallows and

swifts. In this paper I will primarily present information on the elevational component of swift distribution, but I will also present some preliminary data on the vertical component.

Methods

Data on swift distribution in Ecuador were gathered from 1987-1992, while participating on expeditions to survey bird distribution sponsored by the Western Foundation of Vertebrate Zoology (WVZ). In total, over 15 months of field work were conducted during the five-year period. Selected stations (presented in Table 1) correspond to some WVZ camps or often-visited localities, where a large part of the data were obtained in the form of observations and specimens. To supplement these observational data on distributional patterns, a combination of extensive observations at random localities throughout the country, localities from museum specimens, and some published records were added. When the elevation or full locality were lacking for any museum specimen, they were supplemented by information obtained from Paynter and Traylor (1977). In addition, several road surveys on both sides of the Andes were conducted, mostly during the months of May through September, but with some data collected from November through January.

The main objective in this project was to delineate the upper and lower limits of distribution of each species.

Table 1. Selected working stations in Ecuador and relative abundance of swift species.

LOCALITY; PROVINCE	SPECIES ¹									
	<i>Str. zonalis</i>	<i>Str. rutila</i>	<i>Cyp. cherrei</i>	<i>Chae. cin.</i>	<i>Chae. brach.</i>	<i>Chae. spin.</i>	<i>Chae. egregia</i>	<i>Pan. caye.</i>	<i>Tac. squam.</i>	<i>Aeron. mont.</i>
Western Slope										
above Cotocollao (3300 m); Pichincha	C	-	-	-	-	-	-	-	-	-
Las Palmeras (1900); Pichincha	U	C	R	-	-	-	-	-	-	-
near Nanegalito (1500 m); Pichincha	C	C	-	-	-	U	-	R	-	-
Near Piñas (900 m); El Oro ³	C	R	-	C	U	-	-	R	-	-
Near Vicente Maldonado (600 m); Pichincha	C	R	-	-	-	C	-	U	-	-
La Mana (550 m); Cotopaxi	U	-	-	C	-	U	-	R	-	-
Chindul Mts. (450 m); Manabi	U	U	-	C	-	U	-	-	-	-
Maicito (300 m); Manabi	U	-	-	C	-	-	-	R	-	-
Inter-Anden Valleys										
Tanlahuila (2700 m); Pichincha	R	-	-	-	-	-	-	-	-	C
near Puellaro (2000 m); Pichincha	R	-	-	-	-	-	-	-	-	C
6 Km E Chota (1500 m); Carchi	-	U	-	-	-	-	-	-	-	C
Eastern Slope										
La Virgen (4000 m); Napo	C	-	-	-	-	-	-	-	-	-
NE Archidona (1400 m); Napo	C	U	-	-	-	-	-	-	-	-
Pachicutza (1000 m); Zamora-Chinchipec	C	U	-	C	-	-	U	-	C	-
Tayuntza (600 m); Morona-Santiago	C	U	-	C	-	-	U	R	-	-
near Coca (300 m); Napo	U	-	-	-	C	-	-	U	U	-

¹ *Cypseloides cryptus* was excluded, because of uncertainty in locality.

² Relative abundance indicated as: C = common, recorded daily or every other day in moderate to large numbers > 15; U = uncommon, recorded every few days in small numbers < 10; R = rare, few < 5 birds recorded for the area.

³ Data from Robbins and Ridgely (1990) and personal observation.

Table 2. Swifts species that occur in Ecuador, with clutch size, growth rates, body mass, and foraging stratum.

Species	Clutch size ¹	Growth ²	Body mass ³ (g)	Vertical foraging ¹
White-collared Swift <i>Streptoprocne zonalis</i>	2	Slow	103.7	High
Chestnut-collared Swift <i>Streptoprocne rutila</i>	2	Slow	21.3	High*
Spot-fronted Swift <i>Cypseloides cherriei</i>	1	Slow	23.2	High
White-chinned Swift <i>Cypseloides cryptus</i>	1	Slow	35.2	High
Chimney Swift <i>Chaetura pelagica</i>	4	Fast	23.6	Low*
Gray-rumped Swift <i>Chaetura cinereiventris</i>	4	Fast(?)	18.6	Low*
Short-tailed Swift <i>Chaetura brachyura</i>	3-4	Fast	18.3	Low*
Band-rumped Swift <i>Chaetura spinicauda</i>	?	Fast(?)	15.9	Low*
Pale-rumped Swift <i>Chaetura egregia</i>	?	Fast(?)	22.6	Low*
White-tipped Swift <i>Aeronautes montivagus</i>	?	?	19.6	Low
Lesser Swallow-tailed swift <i>Panyptila cayennensis</i>	2-3	?	18.1	High
Fork-tailed Palm-Swift <i>Tachornis squamata</i>	3	?	11.7	Low

¹ Summaries in Collins (1968b), Sick (1986) and Marín and Stiles (1992).

² Growth (days): Fast = < 40; Slow = > 40 (summary in Marín and Stiles 1992).

³ Body masses from above citations and Marín *et al.* (1992).

¹ Foraging strata in mixed-species flocks. For simplicity the vertical component was subdivided into high and low (ca. first 15 m above ground or vegetation for low.); (*) = species that might use either stratum, but only primary stratum is given.

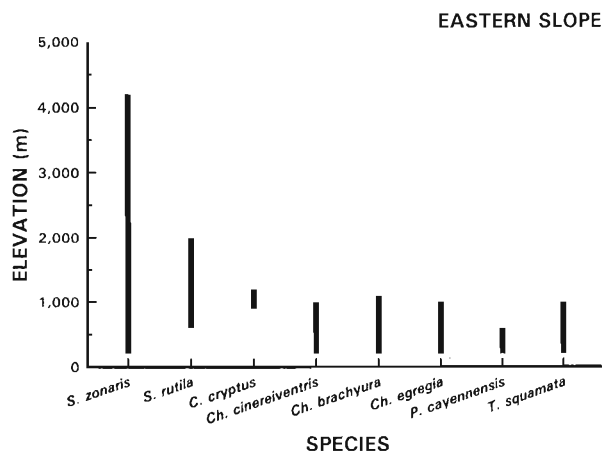
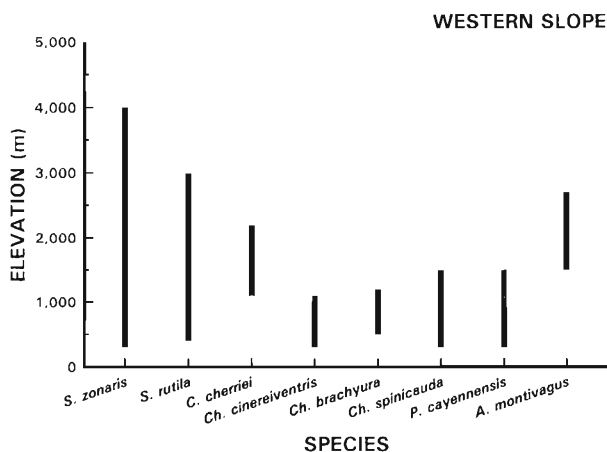


Figure 1. Elevational distribution of swifts in western Ecuador. Although *C. cherriei* is known from only one locality in Ecuador, the upper and lower limits from elsewhere in its range was used here (c.f. Marín and Stiles 1993).

Figure 2. Elevational distribution in eastern Ecuador. (Although the distribution of *C. cryptus* in Ecuador is of uncertain status; see text for basis for its inclusion in this figure).

Consequently, the abundance of each species throughout its elevational distribution was assessed only generally. For some species, especially those with a broad elevational range, some semi-quantitative measures of abundance will be introduced (“common”, “uncommon” and “rare”; Table 1).

I encountered many problems with attempting to quantify relative species abundance. Some swifts can easily use the complete altitudinal gradient on a daily basis and move across land barriers that would be difficult, if not impossible, to overcome for many terrestrial birds. Furthermore, some species move extensively along both gradients, elevational and vertical, making independent observations difficult. In a matter of hours they can cover perhaps the entire gradient more than once. Distribution of species in the genus *Streptoprocne* is particularly difficult to quantify because of this; not coincidentally, these species have the broadest distributional range of the species studied (see Figs. 1 and 2). Further complications arise in the vertical component, because most species forage in mixed-species flocks, and some species are difficult to distinguish. Nevertheless, some patterns did emerge, and these can be used for future lines of inquiry.

Ecuador presents an unique opportunity for a trans-Andean distributional survey. The Ecuadorian andes consist of a relatively uniform main chain, located between ca. 1° N and 4° 30' S. Both slopes of the Andes are rather steep, ascending quickly to tree line or above. As a result, access to the highlands on either slope of the Andes is limited. Inter-Andean valleys, usually arid and formed by rivers that flow either east or west, form the division between the eastern and

western slopes. The river generally descend gradually through the inter-Andean valleys, but form narrow canyons with steep slopes as they descend through mountain gaps. On both sides of the Andes the gradient ranges from tropical lowland forest to páramo and snow line. Altitudinal divisions used here are: Tropical 0-1200 m; Subtropical 1200-2300 m; Temperate 2300-3100 m; and Páramo 3100-5000 m; inter-Andean valleys occur at 1500-3200 m.

Results

Based on present taxonomy and knowledge of the Ecuadorian avifauna, the country contains 11 species of swifts in six genera (Table 2).

One of these species is a long-distance migrant, from North America, the Chimney Swift (*Chaetura pelagica*). Because of its transient status, this species was excluded from the figures.

Elevational patterns (from sea level): Eight species of swifts were detected on each side of the Andes (Figs. 1 and 2). At no elevation on either side did all eight species overlap. The maximum number of swift species found at a single site at the same time was five, but regularly two-three species per locality were encountered (also cf. Table 1). *Streptoprocne* spp. were abundant throughout the gradient. The White-collared Swift *Streptoprocne zonaris* was found to have the broadest elevational, distribution, from 300-4000 m on the western slope and from 300-4200 m on the eastern slope. This species was almost equally abundant at all elevations, surprisingly, even at 4000 m (e.g., at La Virgen, above Papallacta, prov.

Pichincha). The highest breeding record for the species is from a locality above Quito at 3200 m (Lönnerberg and Rendahl 1922). Only one other species, the Chestnut-collared Swift (*S. rutila*) (For the inclusion of this species in *Streptoprocne*, see Marin and Stiles 1992), had as broad an elevational range with its highest breeding record at 2300 m (Kiff et al. 1989); however, it was rather uncommon at high elevations. *Streptoprocne rutila* was more abundant in the mid-elevations of its range, ca. 800-1500 m (Figures 1 and 2).

In contrast, there were very few records for the *Cypseloides* spp. For example, the White-chinned Swift (*C. cryptus*) might occur on both slopes of the Andes in Ecuador, because there are some specimens from southern and northern Colombia, along the central and western Andes (Eisenmann and Lehmann 1962). However, the only Ecuadorian specimen of *C. cryptus* lacks specific locality data (British Museum Natural History # 8873066, ex-Gould coll.). *Cypseloides cryptus* was placed on the eastern side of the Andes (Fig. 2), based on speculation that the specimen originally identified as the Sooty swift *C. fumigatus* (Hartert 1892), but later shown to be *C. cryptus* (Collins 1968a), came from the Napo region. I suspect that this specimen was included in a collection from the Napo that J. Gould received in about 1854 and sent to P. L. Sclater at BMNH for identification (Chapman 1926). There are many records for the species north of Ecuador and the type locality for the species is in southeastern Peru (Zimmer 1945), making the presence of *C. cryptus* in eastern Ecuador likely. A second bird reported as *C. fumigatus* by Salvadori and Festa (1900) from eastern Ecuador, Gualaquiza, prov. Morona-Santiago, might also be *C. cryptus*, because many old specimens reported as *C. fumigatus* were actually *C. cryptus* (Zimmer 1945). In other parts of its range *C. cryptus* has been found from sea level to 2000 m (Rogers 1939; Marin and Stiles 1992). Likewise, the Spot-fronted Swift *C. cherriei* is known only from one locality in Ecuador, Las Palmeras (1900m), prov. Pichincha. Elsewhere in its range, it is found in the subtropical belt from 1100 to 2200 m (Marin and Stiles 1993).

The Lesser Swallow-tailed Swift (*Panyptila cayennensis*) was present on both slopes. It was never abundant and was found mainly in small groups of 3-5, or as solitary individuals. On the western slopes I found it in the upper tropical-subtropical range from 300 to 1500 m (Fig. 1), whereas on the eastern slopes it had a narrow range in the tropical zone from 200 to 600 m (Fig. 2). It is likely that the species occurs at

higher elevations on the eastern slope, although less abundantly. On both slopes, I found it most common in the 300-500 m range.

The White-tipped Swift (*Aeronautes montivagus*) was found only in the inter-Andean zone, from 1500 to 2700 m (Fig. 1), in valleys dropping to the west, where it was abundant but patchy in distribution. It should also be present in valleys dropping to the eastern slopes; however, I did not encounter it there, and I did not adequately survey most of those valleys. The Fork-tailed Palm-Swift (*Tachornis squamata*), another species with a patchy distribution, was present only on the eastern slope of the Andes in the tropical zone from 200 to 1000 m and was always found associated with palms.

Two *Chaetura* spp., the Gray-rumped Swift (*C. cinereiventris*) and the Short-tailed swift (*C. brachyura*), were present on both slopes. The former was common on both sides of the Andes, from ca. 200-1000 m (Fig. 1 and 2). However, on the eastern slope it gradually increased in abundance toward the upper part of its range, whereas on the western slope it was gradually more abundant in the lower part of its range. East of the Andes, *C. brachyura* seems to have a slightly broader elevational range than on the western slope. However, on the western slope *C. brachyura* seems to be present only in the south; there are no specimens north of prov. El Oro. Nevertheless, there are some specimens from western Colombia and from the southern end of El Valle del Cauca (specimen at Museo de Zoología, Universidad del Valle, Cali, Colombia, ex-INCIVA and Lehmann collection). *C. brachyura* ranges on the eastern slope from 200-1100 m (Fig. 2) and was the most abundant species of *Chaetura* in the lower part of its range (ca. 200-500 m). The Band-rumped Swift (*C. spinicauda*) had the broadest elevational range of any *Chaetura* spp., mainly in the lower subtropical zone from 300-1500 m (Fig. 1); however, it was more abundant in the 450-900 m range. The Pale-rumped Swift (*C. egregia*) replaced *C. spinicauda* on the eastern slope, ranging from 200-1000 m, where it was abundant in the higher portion of its range. *C. pelagica* has been recorded on both sides of the Andes in South America. In Ecuador I have records from 300-1000 m on the eastern slopes and in the inter Andean Valle de Quito at ca. 2500 m. This species is also expected to pass through the western slope, because it has been recorded in coastal or western Colombia, Peru, and Chile (Miller 1962, Koepcke 1964, Araya et al. 1972, Plenge 1974), but at present there are no definitive records for western Ecuador.

Vertical patterns (from ground): This is most the complex distributional component of the aerial guild, and a paucity of data prevents a quantitative analysis of vertical differences. However, Marín and Stiles (1992) suggested one way that non-congeneric swifts might divide their aerial resources. These authors suggested an analogy with seabirds, in which species with large clutch sizes, and thus fast growth rates, should forage closer to the nest (and thus also closer to the ground), whereas species with small clutch sizes, and slower growth rates, should forage farther away from the nest (and thus also higher above the ground). Indeed, *Chaetura* spp., which all have large clutch sizes, do forage nearer to the ground than other swift species (cf. Table 2). For example, in one assemblage of four species on the western slopes (such as at Chindul Mts.; Table 1), vertical stratification was observed when two or more species were present. However, when two or three smaller species (*S. rutila*, *C. cinereiventris* and *C. spinicauda*) were present, there was no clear division, especially between the two *Chaetura* spp. When all species foraged together at one site, the stratification was fairly distinct. In order decreasing foraging height, it was as follows: *S. zonaris*, *S. rutila*, *C. cinereiventris*, and *C. spinicauda*. An assemblage of five species on the eastern slopes at Pachicutza (Table 1) was organized similarly (decreasing height): *S. zonaris*, *S. rutila*, *C. egregia*, *C. cinereiventris* and *T. squamata*. On both sides of the Andes, the vertical stratification between the *Streptoprocne* and *Chaetura* spp. correlates with clutch-size and growth-rate. Although there are no data on clutch size or growth rate for all *Chaetura* spp., those species in this genus for which data are available all have a large clutch size and a fast growth rate (Table 2). It was difficult to distinguish any clear vertical segregation between *C. egregia* and *C. cinereiventris*, but *C. egregia* seemed to predominate in the upper strata. On the other hand, *T. squamata* has a clutch size smaller or equal to *Chaetura* spp., but is much smaller in body size (Table 2). In the presence of most species, *Panyptila cayennensis*, with an intermediate clutch size of three eggs, usually foraged in the upper stratum. However, when *P. cayennensis* was in the presence of *S. zonaris* and *Cypseloides* spp., it used a lower stratum. When *P. cayennensis* and *T. squamata* foraged together, *T. squamata* (also with a clutch size of three) used the lower stratum. Also, when *P. cayennensis* foraged with any species of *Chaetura* it used the upper stratum.

When *Tachornis squamata* was together with any species of *Chaetura* or *Streptoprocne*, it primarily used the lower stratum. *Aeronautes montivagus* rarely was observed foraging with other swift species. However, most of the time *A. montivagus* foraged in the lower stratum, even in the presence of other species. Although these general patterns of vertical segregation were evident, it must be emphasized that any species foraging in a single-species flock or singly might forage in any or all strata.

Discussion

Terborgh (1971) and Terborgh and Weske (1975) proposed four types of limits for species distribution along an elevational gradient: 1) natural terminus of the environmental gradient, 2) factors in the physical or biological surroundings that change parallel with the gradient, 3) competitive exclusion between congeners, and 4) vegetational ecotones. The natural environmental or vegetational terminus as a distributional limit seems likely for two Ecuadorian swifts. *Tachornis squamata* is found associated primarily with, and thus limited by, palm distribution, mainly that of *Mauritia* spp., on which it depends for nesting sites. *Aeronautes montivagus* is virtually restricted to arid or semiarid habitats, primarily along the inter-Andean valleys. Other species are more flexible in their habitat; as noted earlier *S. zonaris* can be found from the tropical lowlands to the páramo. Many factors in the physical and biological surroundings change in parallel with the gradient, especially temperature, rainfall, and presumably insect density. Because all resident species of *Chaetura* were found only in the lowlands, it is possible that some physical or biological factor influences their elevational distribution. The two species of *Cypseloides* were found primarily in the subtropical zone; however, little can be inferred from the few records available for the country. *Panyptila cayennensis* and *T. squamata* were also restricted to the tropical lowlands. For species in the genus *Streptoprocne*, specially *S. zonaris*, specific physical or biological factors are more difficult to identify because of their broad elevational ranges, and probably wide daily foraging range. I found no example of abutting elevational ranges in Ecuadorian swifts that might suggest competitive exclusion. However, in the vertical dimension competitive exclusion seems more likely. When foraging in the same area the species pairs,

P. cayennensis - *T. squamata* or *S. zonaris* - *S. rutila*, the larger species foraged in the upper strata. Between or among *Chaetura* spp., the species with the larger body size usually occupied the higher stratum. For example, when *C. cinereiventris* foraged with *C. spinicauda*, the former predominated in the upper strata, but when *C. cinereiventris* foraged with *C. egregia*, the latter species seemed to predominate in the upper strata (for body masses see Table 2).

Previous studies on the vertical component in the aerial guild in the lowlands on Central America and Malaysia (e.g., Hespeneide 1975, Waugh 1978, Waugh and Hails 1983) have indicated that flight behaviour, mode of foraging, prey type, and prey size might be important mechanisms of ecological isolation. Further attention to these variables and the behavior of species foraging alone and together may help to clarify possible competitive interactions and resultant resource partitioning mechanisms.

The fourth factor mentioned by Terborgh and Weske (1975), ecotones, does not seem to apply to swifts, because they are so highly mobile that they easily move across such barriers; vegetational distribution patterns probably influence their elevational limits only very indirectly at best.

Many gaps in our knowledge of the distribution and possible resource partitioning still exist for the aerial guild. Although some potential patterns were identified, the few data available make little more than speculation possible at this point. Further field work on the aerial guild in the tropics, in Ecuador or elsewhere, should look more closely at the vertical component, especially among congeners.

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Resumen - Se examinaron los patrones de distribución elevacional (sobre el nivel del mar) y vertical (sobre el nivel del suelo) a lo ancho de los Andes de las diez especies de vencejos residentes en Ecuador. Tergorgh (1971) y Terborgh and Weske (1975) propusieron cuatro tipos de límites que pueden afectar la distribución de los vencejos: 1) "El término natural de un ambiente afectado por una pendiente pudo afectar a sólo dos especies", 2) "Los factores físicos o biológicos del lugar, que pueden cambiar paralelamente con la inclinación de la pendiente" pudieron afectar a seis de las diez especies; 3) "La exclusión competitiva" no se registró en la pendiente elevacional, pero sí parece ser importante en la distribución vertical; 4) No pareció que "los ecotonos" afectaran a la comunidad de aves aéreas.

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