

CONDITIONAL USE OF NEST STRUCTURES BY WHITE-NAPED AND WHITE-COLLARED SWIFTS¹

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Abstract. Since the nesting of the White-naped Swift (*Streptoprocne semicollaris*) was first described (Rowley and Orr 1962), this species has been thought to differ from other cypseloidine swifts in failing to build a nest structure. I studied nesting of White-naped Swifts and White-collared Swifts (*Streptoprocne zonaris*) at colonies where earlier nest descriptions were made. Based on a larger sample than that available to previous authors, I found the two swifts to differ little in nesting habits. Both species built or used existing nest structures on slanted substrates where eggs and young would otherwise have been at risk of rolling or falling, and both often laid eggs and reared young without a nest structure where the substrate was level or naturally enclosed. Frequency of use of risky vs. safe sites differed between colonies, reflecting apparent differences in the availability of safe sites. White-naped Swifts used nest structures on the same ledges where they laid eggs without nest structures 22 and 24 years earlier. Probably due to periodic flooding, these ledges apparently were less sandy in 1983 and 1985 than in 1961, and the swifts had responded to substrate changes by building nest structures in the absence of sandy oviposition sites. The supposedly unique nesting habits of *S. semicollaris* have been used as partial justification for a monotypic subgenus, *Semicollum* (Brooke 1970). Evidence presented here brings this rationale into question. Nests of both species, when built, were typical of the Cypseloidinae, except that *semicollaris* used more mud than is typical. Stereotyped behaviors used in nest building, when it does occur, are probably safer indicators of phylogeny than is mere frequency of nest building, which can differ between sites and change rapidly at a given site.

Key words: White-collared Swift; *Streptoprocne zonaris*; White-naped Swift; *Streptoprocne semicollaris*; nesting habits; conditional nest construction; behavior; phylogeny.

INTRODUCTION

The White-naped Swift (*Streptoprocne semicollaris*) and White-collared Swift (*S. zonaris*) are large neotropical swifts which nest colonially in caves and behind waterfalls. Though similar in many respects, they differ in size and geographic distribution; *semicollaris*, at 170 to 200 g, is one of the world's largest swifts, while *zonaris* averages 100 to 124 g (Whitacre, unpubl.). The breeding range of *semicollaris* is restricted to the mountains of western Mexico, whereas the smaller *zonaris*, essentially parapatric in Mexico, is resident throughout much of the humid tropics and subtropics of the Americas.

The White-naped Swift has been thought, since Rowley and Orr (1962) first described its nesting, to differ from all cypseloidine swifts whose nests are known, in failing to build or use a nest structure. These authors found 16 clutches of White-naped Swift eggs which were all "situated in shallow depressions made by the birds in the dry, powdered sandstone on the ledges" of a cave.

"The only sign of outside material having been used was the presence of three fresh leaves . . ." at one nest site (Rowley and Orr 1962, p. 364).

The same authors (Rowley and Orr 1965) gave the first detailed account of nesting of the White-collared Swift. Nests they observed were shallow, cupped disks of mud, moss, and insect chitin, and resembled other described nests of the Cypseloidinae (Table 1).

Swifts use a variety of nest sites, materials, and construction, but this variety is mainly between, not within, genera. Members of each genus (and in the case of Cypseloidinae, of an entire subfamily, Table 1) share similar nest sites and construction (Lack 1956), and some phylogenetic significance has come to be attached to nesting habits in swifts (Lack 1956, Orr 1963, Collins and Brooke 1976). In particular, the oft-cited (Eisenmann and Lehmann 1962, Orr 1963, Brooke 1970, Collins and Brooke 1976) failure of the White-naped Swift to build a nest structure, along with morphological evidence, led Orr (1963) to predict that ultimately *S. semicollaris* would require a new genus separating it from *Streptoprocne*. Based on Orr's (1963) arguments, Brooke (1970) proposed a new subgenus, *Sem-*

¹ Received 3 January 1989. Final acceptance 6 July 1989.

TABLE 1. Characteristics of nests and nest sites described to date for cypseloidine swifts.¹

Species	Nest ² shape	Nest material	Substrate ³ angle	Nest environs	Source
<i>Cypseloides fumigatus</i>	nearly flat to truncated cone	mosses, ⁴ mud and pebbles	nearly vertical, "vertical"	vertical canyon wall	2, 26
<i>C. cherriei</i>	half-cup to cup-shaped, nearly conical mass	mosses, ferns, liverworts, mud base	30–70°, nearly vertical	shadowed overhanging rock surface, 2.5–5 m above stream; small ledges beneath overhang, behind or near waterfall	28
<i>C. phelpsi</i>	truncated cone	live moss	vertical, no ledge	1.5 m above floor of small cave among boulders along small stream	24
<i>C. rutilus</i>	truncated cone or disk, depending on angle	mosses, liverworts, ferns	45° or less to vertical	small outcrops, sometimes overhanging, along stream; cliff in river gorge; sea cave; cave with dripping water	1, 3, 4, 5, 6, 7, 8, 28
<i>C. cryptus</i>	bowl-shaped, half-cup shaped	mosses, liverworts, plant fibers, mud	23–65°, on knobs, ledges, in holes, niches	below ledges, behind or near waterfall; wet	28
<i>Nephoecetes niger</i>	disk	mosses, ferns, mud, seaweed	niche or ledge, angle not stated but probably horizontal to 45° or less	beside or behind waterfall; in sea cave; limestone cave with stream; sea cliff; on dry rock wall above small stream	9–18
<i>Aerornis senex</i>	cone, disk ⁵	moss, ⁶ pebbles, fastened with mud	horizontal ledge on vertical cliff	beside or behind waterfall	19, 20, 25
<i>Sireptoprocne zonaris</i>	disk or none	moss, mud, pebbles, ferns, other vegetation, chitin fragments	horizontal to 15° ledges, on knobs, in niches, potholes	large horizontal or vertical cave, often with stream or falling water; ledge, niche or knob on face of or usually beneath overhangs of waterfall, ledges over stream	22, 23, 28
<i>S. semicollaris</i>	disk or none	mud and vegetation, mostly rotten leaves	horizontal to 30°	same as <i>S. zonaris</i>	21, 23
<i>S. biscutata</i>	disk, shallow bowl	mosses, lichens, dry leaves	more or less horizontal?	ledges in large caves	27

¹ Cypseloidine species whose nests have not been discovered are *Cypseloides major* and *Nephoecetes lemosi*.² Photos on p. 270, 271 of Collins (1968) illustrate that nest shape depends largely on substrate angle. Disk-shaped nests (shallowly cupped and broadly based) occur on level to gently sloped substrates, whereas nests of the same swift species when on vertical or near-vertical substrate are cone-shaped or truncated cone-shaped. (Bowl-shaped and cup-shaped are essentially synonymous with cone-shaped.) Differences in nest shape between species may result more from differences in substrate angle than from intrinsic differences in nest shapes built by these species.³ Angles given are those reported to date and likely do not indicate extremes which may occur. Where the angle is given as vertical, it is not always clear whether this applies to the general environs or whether it indicates that there truly was no knob, niche, or small ledge upon which the nest was situated.⁴ As discussed by Collins (1968), Holt's (1928) attribution of a twig nest to this species is undoubtedly in error.⁵ Source says "solid cone" but presents sketch of a disk-shaped nest.⁶ Source states that saliva and mud are used, but presents no evidence of saliva use, which has not been shown for any cypseloidine swift.

Sources

- Collins (1980)
- Dabbeno (1918)
- Orton (1871)
- Belcher and Smooker (1936)
- Snow (1962)
- Collins (1968)
- Rowley (1966)
- Rowley (1984)
- Vrooman (1901)
- Dawson (1915)
- Michael (1927)
- Smith (1928)
- Dixon (1935)
- Legg (1956)
- Knorr (1961)
- Knorr (1962)
- Hunter and Baldwin (1962)
- Davis (1964)
- Allen (1893)
- Sick (1984)
- Rowley and Orr (1962)
- Rowley and Orr (1965)
- Whitacre, present study
- Rex Cocroft, John O'Neill, David Willard, pers. comm.
- De La Pena (1982)
- Manuel Marin R., pers. comm.
- De Andrade et al. (1985)
- Marrin and Stiles, unpubl.

icollum to separate *S. semicollaris* from its congeners *S. zonaris* and *S. biscutatus*.

During 1976–1978 and 1983–1985, I studied White-collared Swift biology at 12 colonies in the states of San Luis Potosí, Veracruz, and Chiapas, Mexico, and in 1983–1985 I studied White-naped Swifts at five colonies in Guerrero, Mexico. As part of this research I collected data on the nests and nest sites of both species at the same colonies studied by Rowley and Orr, and at one additional colony, allowing a reevaluation of nesting habits.

STUDY SITES

WHITE-COLLARED SWIFT COLONIES

Aguacero colony. This White-collared Swift colony occupies a waterfall known as “el Aguacero,” which drops into the Rio La Venta 15 km west of Ocozocuatlá, Chiapas, 3 km northwest of the highway to Cintalapa, Chiapas. This is the same colony along the Rio las Flores (=Rio la Venta) where Rowley and Orr (1965) described the nesting of this species. The Rio La Venta experienced a large flood, probably in 1979, which eroded the base of the falls. As a result, portions of the falls where we studied swift nesting in 1978 (Whitacre and Sharp, unpubl.) were either gone or inaccessible in 1983.

The Aguacero waterfall cascades over a series of rounded ledges formed by calcium carbonate deposition (Fig. 1a). Mosses grow profusely over spray-drenched surfaces, and ferns and other herbs occur in some areas. Calcite encrusts the vegetation and flotsam, resulting in growth of tufa aprons which are usually concave below, forming shaded overhangs and caves. Some swift nests were in niches in the exposed face of the falls, but most were in deep shadow beneath overhangs. Many nests were in niches and on small ledges in the ceilings of large overhangs, such that they were above a vertical drop of 6 m or more to the rock or water below (Fig. 1b). Other nests were on the floor, ledges, and ceiling niches of narrow caves that delved beneath the falls into regions of near-total darkness.

Chorreadero colony. This White-collared Swift colony occupies a cave known as “el Chorreadero.” It is 12 km from Chiapa de Corzo, Chiapas, along the highway to San Cristobal de las Casas, and is indicated by a sign for the “Balneario el Chorreadero,” a swimming hole formed by the stream that cascades from the cave mouth. This

is the same colony “along the Rio El Chorreadero, Chiapa de Corzo” where Rowley and Orr (1965) found nesting in progress, but were unable to reach any nests because of their location above a slippery, vertical wall.

At a point 100 m into this cave, the cave stream cascades over a 9-m vertical cliff, enroute to the cave mouth. Several of the swift nests I studied here in 1985 were on a broad ledge midway up this cliff, while others were in small niches on the cliff face. The majority of nests were above this cliff, on broad ledges which formed the passage floor, and in potholes in the cave walls on both sides of the cave stream (Fig. 1c–e).

WHITE-NAPED SWIFT COLONY

Dos Bocas colony. In 1983 and 1985, I studied the White-naped Swift nesting at a cave which again proved to be the very cave where Rowley and Orr (1962) first described the nesting of this swift (Fig. 2a). This colony is within the Parque Nacional las Grutas de Cacahuamilpa, 1 km from Cacahuamilpa, Guerrero. Near here, two rivers, the Rio San Jeronimo and Rio Chontalcoatlan, enter two large caves, converge while traveling several kilometers underground, and emerge from adjacent cave mouths, the “Dos Bocas.” White-naped Swifts occupy both cave mouths, but their nests were accessible to me only in Boca San Jeronimo were grottos in the ceiling, 30 m above the river. I refer to this colony as the Dos Bocas colony.

There can be no doubt that these three colony sites are the same ones visited by Rowley and Orr, as all are recognizable from descriptions, place names, and photos of the cave entrances given in Rowley and Orr (1962, 1965).

METHODS

TERMINOLOGY

The word nest denotes locations where eggs and/or nestlings were present prior to nestling wandering, and does not indicate a structure built by swifts unless so stated. Nest site refers to the physical characteristics of a site where a nest (eggs or nestlings) was present.

Observations in 1977 and 1978 at the Aguacero colony and in 1983 and 1985 at the Dos Bocas colony indicated that both species often reused previously built nests. In fact, the number of nests present changed very little between the years mentioned, with only a few newly built nests

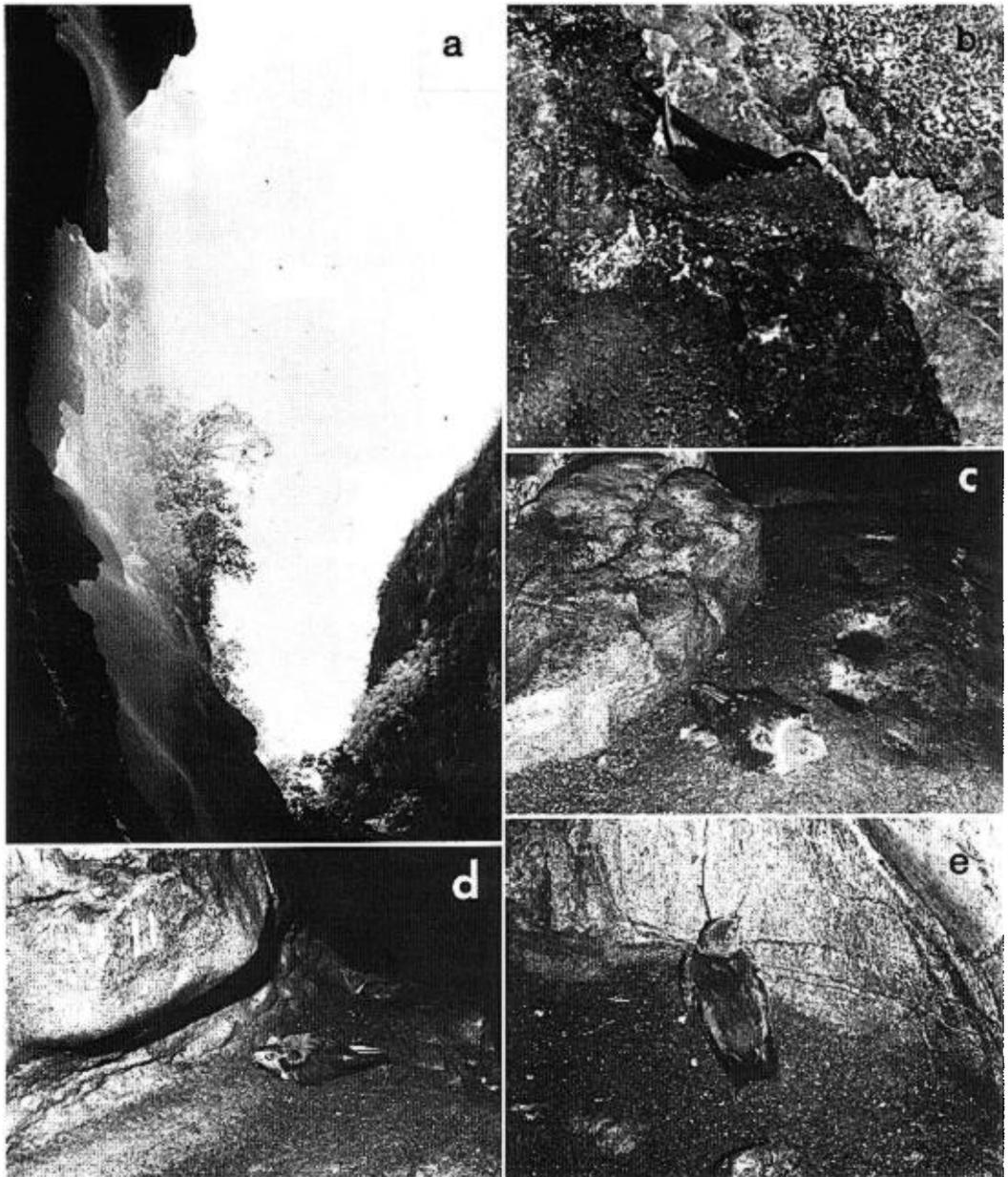


FIGURE 1. Colony site and nests of White-collared Swifts. (a) Aguacero waterfall, showing overhangs beneath which swifts nested; (b) Adult on a constructed Aguacero nest in a site typical of the high falling-risk category; (c) (d) and (e) Nestlings in Chorreadero nests lacking structure, in sites typical of low falling-risk category.

appearing in any year. When reusing old nests, swifts at least sometimes added fresh material to them. Since most nests in use at any time were old nests, I refer throughout to *using* nests rather than *building* nests, except where building was observed. Ultimately, however, all nests were built by the swifts of each colony, and so rela-

tionships described between nest-site features and nest *use* apply also to nest *construction*.

DATA COLLECTION

All nests discussed here were active, containing eggs and/or nestlings during the breeding season

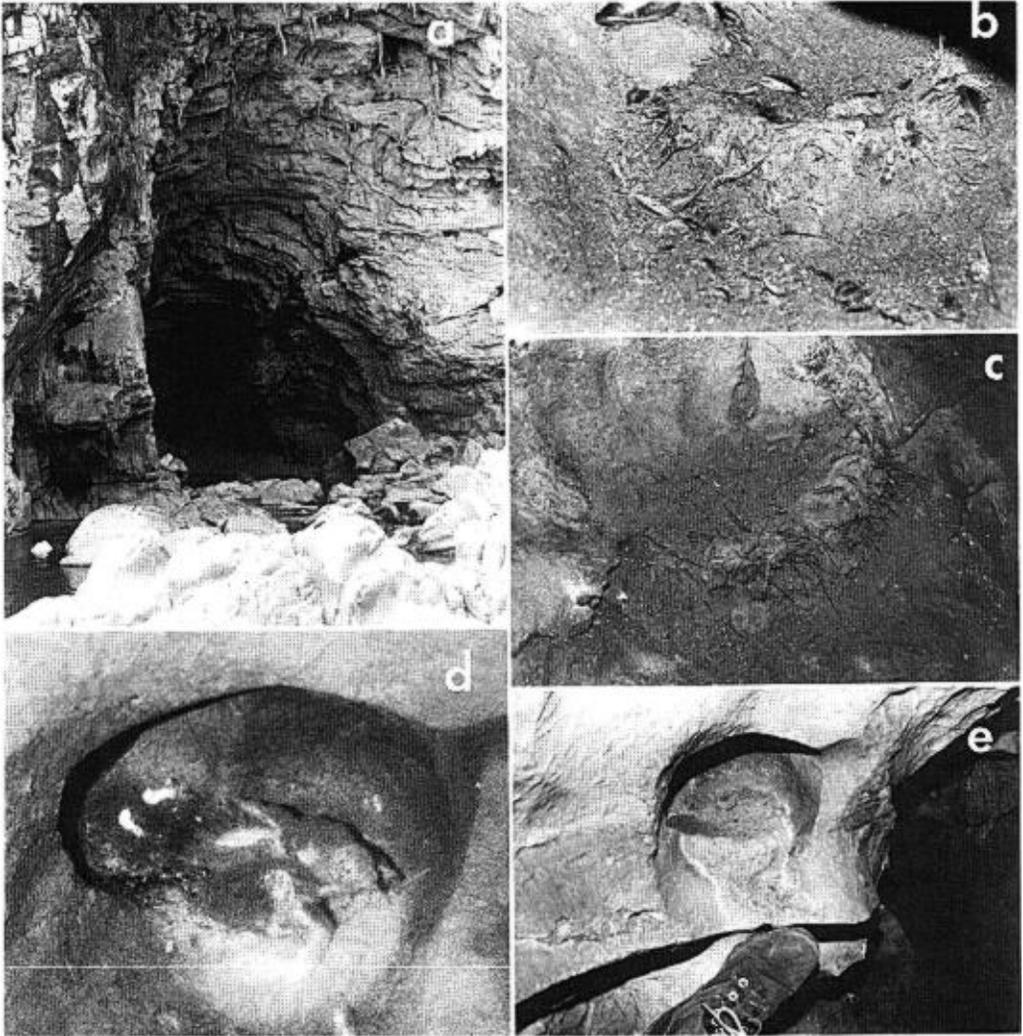


FIGURE 2. Site and nests of Dos Bocas White-naped Swift colony. (a) Boca Chontalcoatlan (which housed colony) in Parque Nacional las Grutas de Cacahuamilpa, Guerrero; (b) (c) Two Dos Bocas nests constructed of mud and rotten leaves on slanted substrates, typical of structured, high falling-risk categories; (d) White-naped Swift nestlings in nest (photo courtesy of Fran Miller); (e) Same nest as in Figure 2(d) showing structure of mud and vegetation, and situation of high falling risk.

when descriptive data were recorded. For each nest described in detail, a data sheet was used to record each of several attributes. I did not take data on all nests which I found at all colonies, but rather, on all nests within large, heterogeneous subregions of each colony. Under Results, numbers of nests discussed with respect to various characteristics do not always sum to the same total because not all data were recorded for all nests.

METHODS OF ANALYSIS

To test whether the use of a nest constructed by the birds vs. oviposition without a constructed nest was correlated with physical attributes of nest sites (and hence falling risk to eggs and young), I classified all nests with respect to nest structure and nest-site physiognomy. All nests with a structure built by the swifts were placed in one class, and those without a built structure

were placed in another. Nests on surfaces that sloped toward drop-offs or passage floors, without naturally rimmed or dished substrate to contain eggs and young, and without substantial level areas around the nest, were placed in the "slanted" category. Common sense dictates that such nest sites had a higher inherent risk of eggs and young rolling or falling. In such sites, an egg laid without a nest structure would simply have rolled away. Hence, this category is also referred to as the "high falling risk" category. Nests within a natural bowl or rim and/or having substantial level area surrounding the nest were placed in the "level or enclosed" category, also referred to as the "low falling risk" category. The only risks considered were those of rolling or falling of eggs or young. Risk of nest predation, though likely also nest-site related, has not been considered here. Statistical procedures were taken from Sokal and Rohlf (1981).

FIELD METHODS

We reached Aguacero nests by free-climbing on the brittle tufa deposits formed by the spray of the falls. I used rock-climbing methods to reach all Chorreadero nests and most Dos Bocas nests. A 9-m lead climb was required in the Chorreadero, and a 14-m lead climb in the Dos Bocas site. Protection was via webbing loops threaded through bedrock eyes, expansion bolts, and one piton (to rappel off the Chorreadero cliff). I belayed myself by means of a harness and prusik knot (Thrun 1973) on the climbing rope which I anchored at the foot of the climb. This allowed me to be safe while working alone, as I did much of the time.

To enter the Chontalcoatlan boca (Dos Bocas colony), I had to cross the Rio San Jeronimo between the two cave mouths. In the dry season I did this by swimming, but during the rainy season I was forced to throw a rope across the river until it wedged on something, pull myself hand-over-hand across the current, and then rig a Tyrolean traverse (Peters 1982) for subsequent crossings.

The Chorreadero cave stream and the Rios Chontalcoatlan and San Jeronimo are subject to sudden and severe flooding due to upstream rains. Anyone visiting these caves during the rainy season (May to October) should exercise extreme caution.

RESULTS

WHITE-NAPED SWIFT NESTS AT THE DOS BOCAS COLONY

Number and location of nests. Rowley and Orr (1962) found White-naped Swift nests in the Dos Bocas cave in two areas, the first being a group of cavities some 8 m above the floor, reached by a sloping ledge, and the second being a grotto 5 m above the floor. They found 12 nests along the sloping ledge and four nests in the lower grotto. On 29 June 1983 I found seven active White-naped Swift nests in the lower grotto and one in another location. I did not ascend the sloping ledge at this time. Several of the nests consisted of structures of mud and plant material, clearly constructed by the swifts.

On 25 and 26 May 1985 I searched the lower grotto again and ascended the sloping ledge. I found nine nests in the lower grotto and 23 along and above the sloping ledge. There is no doubt that these two nesting areas are the same two visited by Rowley, because there is only one other climbable portion of cave wall in the portion of cave used by the swifts, and it bears no resemblance to the areas described by the earlier authors. Although I found 23 nests along and beyond the sloping ledge where Rowley and Orr (1962) found only 12, there were not necessarily more nests here in 1985 than in 1961. Unlike Rowley, I was belayed, and probably felt more secure than he to search for nests at leisure. Also, I explored a nesting tunnel at the top of the ledge which he may not have explored.

Nest structure and composition. Of the 32 nests I examined here in 1985, 26 included structures which showed obvious signs of having been constructed by the swifts, while the remaining six nests showed no such structure. All of the nest structures I found were comprised mainly of mud. Four nests included fresh (wet) mud as well as older mud, while one appeared by its dark color to have been entirely built recently. Of 12 nests for which I recorded details of composition, 11 included substantial plant material, mostly very rotten leaves with only veins remaining. Also present were less decayed leaves, twigs, and unidentified plant fibers in one case each, and evident grass in two cases, while one nest was composed of mud with only traces of vegetation. Where present, vegetation was incorporated with the mud into the nest structure. Only three of

these 12 nests were complete, circular nests in the form of mud disks up to 6 cm tall and shallowly dished. Eight of the nine remaining nests were partial mud disks representing 40 to 75% of a full circle, being truncated on the uphill side by the sloping substrate upon which the nests were built (Fig. 2b–e). The remaining nest consisted of no more than a mud dike built across a gap in a naturally bowled area in the substrate, within which the eggs had been laid. I did not witness nest building during my visits to the cave, which were late enough in the season that nest building had probably ceased.

Nest lining. Data on nest lining were recorded for 27 nests, 18 of which were lined and nine unlined. Eleven nests were lined with fresh green vegetation and seven nests had vegetal lining which was less fresh. Five nests were lined with moss, four with ferns, one with grass, one with a seed pod, one with twigs up to 6 mm in diameter, and 16 with leaves or sprigs of broad-leaved plants, including a sprouting cotyledon and a small purple flower.

Composition of nest substrate. Ten of 15 nests were on firm substrates; six of these were on bedrock and four were on solid clay. Two nests were partly on firm and partly on loose substrates; one of these was on rock and guano, and the other was on bedrock, loose clay, and guano. Only three of 15 nests were completely on loose substrates; one of these was on guano, one was on sand and guano, and the remainder was on soft loose clay and guano.

Angle and physiognomy of nest substrates and environs. Two of 15 nests had a natural rock rim that would tend to prevent eggs or nestlings from rolling or falling from the nest. The slope of the substrate upon which they were built was recorded for 15 nests: four were on level substrate and the remaining 11 had substrates slanting outward toward the cave floor or drop-off. Approximate substrate slopes for these 11 nests were 7% (one nest), 10% (three nests), 15% (two nests), 20% (four nests), and 30% (one nest).

WHITE-COLLARED SWIFT NESTS AT THE AGUACERO COLONY

Nest structure and composition. In 1978, we (Whitacre and Sharp, unpubl.) took data on nest site and structure of 41 Aguacero nests. All 41 nests had at least a partial structure built by the swifts, although in five cases, the nest structure

was so flimsy (probably old) as to be scarcely discernible. Nests were raised disks, usually 6 to 8 cm tall at the rim and 12 to 14 cm in diameter, with shallow cups of variable depth. Most nests were built partly or largely of moss. They may also have contained bits of tufa, soil, and other substances. Substantial quantities of mud or clay were not noted. A typical nest and nest environs are shown in Figure 1b.

Nest construction and renovation. Fresh moss had been recently added to several nest cups when we discovered them on 29 April 1978, judging from their appearance and the presence of loose piles of fresh moss on ledges below, where it had fallen during nest construction or renovation. One nest was in the initial stages of construction on 2 May and was finished or nearly so on 10 May when it held two eggs. Most nests here received eggs in the first few days of May 1978.

Nest lining. Some nests were lined with fresh dicotyledonous leaves or fern fronds before they received eggs, but the amount of such fresh vegetal lining was noticeably greater on 25 May when eggs were near hatching than on 10 May when most nests were ending their first week of incubation. Commonly used as nest lining were leaves and flowers of *Achimenes cottoana* H. E. Moore (Gesneriaceae) and fronds of the fern *Adiantum capillus-veneris* L.

WHITE-COLLARED SWIFT NESTS AT THE CHORREADERO COLONY

Nest structure and composition. Of 48 nests I described in detail at this colony in 1985, only six entailed structures built by the swifts (Fig. 1c–e). Two of the six were comprised largely or exclusively of chitinous insect parts, whereas three contained these and plant fibers. The remaining nest appeared to incorporate rotten vegetation.

Composition of nest substrate. Only six of 47 nests were completely on a firm substrate, bedrock. Nine were on both bedrock and guano, and one was on bedrock, sand, and guano. The remaining 31 nests were completely on loose substrates: 26 were on guano, one was on sand, and four were on sand and guano.

Nest location. Few nests were in the broad open expanse of a shelf or passage floor. Most were near or against rock walls, often in areas with low ceilings, resulting in a secluded nest site. Thirty-nine nests were situated on passage floors or broad ledges (a few to several meters wide),

whereas 18 were on small ledges or in potholes or niches in the cave walls.

Nest lining. Thirty of 44 nests had no lining and the remaining nests were scantily lined with one or more of the following materials: pine needles, fresh green leaves, dried grass and leaves, fibers of polypropylene rope, dried rootlets, and Northern Flicker (*Colaptes auratus*) remiges.

Angle and physiognomy of nest substrates and environs. Forty-two nests were in level or naturally bowled areas, and six were on substrates that sloped toward a drop-off or passage floor. Twenty-six of 48 nests had a natural rock rim that created at least a partial barrier around the nest.

NEST-BUILDING BEHAVIOR

On 2 May 1978 we observed nest-building behavior at one Aguacero nest. While settling and circling in the nest, a swift picked moss from the cave wall and placed this in the nest. It then crawled up the cave wall and plucked moss from the rock with its bill, settling on the nest once more, and evidently adding the fresh moss to the nest.

Nest material was not always gathered at the nest site, however. On 7 May 1978, when most Aguacero nests held fresh clutches, we saw a swift fly into the cave with a golfball-sized wad of nesting material in its bill. On other occasions both at this colony and at a White-collared Swift colony at Salto de Eyipantla in Veracruz, swifts were observed flying in the immediate vicinity of the colony site with nesting material in their bills. Although nest material is not always collected at the immediate nest site, it is sometimes and perhaps usually collected in the colony environs. White-collared Swifts were observed plucking moss on the face of two waterfalls supporting nesting colonies (the Aguacero colony and the Cascadas de Agua Azul colony near Palenque, Chiapas) (Whitacre and Sharp, unpubl.).

NEST STRUCTURE IN RELATION TO SLOPE AND PHYSIOGNAMY OF NEST SITE

In 1978 we studied rates and sources of nesting mortality at the Aguacero colony (Whitacre and Sharp, unpubl.). We found that rolling and falling of eggs and young from the nest site were major sources of nesting mortality. Additional observations at the Chorreadero colony in 1985 and the Dos Bocas White-naped Swift colony in 1983 and 1985 suggest that falling of eggs and young

are often important mortality sources for both swift species. This fact suggested the common sense proposition that whether eggs were laid with or without a nest structure at a given nest site might be related to the risk of rolling or falling inherent in that site's physical attributes.

When pooled Aguacero and Chorreadero White-collared Swift data (Table 2, $n = 86$ nests) were subjected to χ^2 analysis, this prediction was vindicated. The null hypothesis of independence between nest structure and nest-site angle and physiognomy was rejected at $P < 0.001$ ($\chi^2 = 18.89$, $df = 1$). Eggs were laid without any nest structure only in sites that were level or enclosed and presented little risk of rolling or falling. White-naped Swift data subjected to the G -test with Williams' correction lead to identical conclusions for that species ($P < 0.025$, G adj. = 5.65); all (nine) nests on slanted substrates had structures built by the swifts while half (three) of those in safe sites had no structure.

Because no two caves or waterfalls are identical, it is likely that swift colony sites differ in the availability of level or enclosed (low falling risk) nest sites. Though no quantitative measure of the abundance of safe and risky *potential* nest sites was undertaken, it appeared obvious that the Chorreadero site possessed a higher ratio of safe to risky sites than did the Aguacero. At the Chorreadero, many swifts nested in natural depressions on broad, flat ledges, whereas Aguacero nests were often situated in tiny niches above long drops. To test whether swifts used high falling-risk and low falling-risk nest sites with similar frequency at these two colonies, I subjected the data in Table 2 to a χ^2 test. Aguacero swifts used slanted sites more often than did Chorreadero swifts ($P < 0.001$, $\chi^2 = 11.60$, $df = 1$), which supports the apparent difference in availability of safe sites in the two colonies.

Since these colonies apparently differed in the availability of low falling-risk nest sites, one might ask whether birds at the two colonies showed differences in their overall propensities to build or use nest structures. To address this question, I again compared structure and site characteristics of nests at the Aguacero and Chorreadero colonies, this time using only those nests in the level or enclosed (low falling risk) category (Table 2). The null hypothesis of homogeneity was rejected at $P < 0.001$ ($\chi^2 = 56.61$, $df = 1$). Proportionally more Aguacero swifts than Chorreadero swifts had laid their eggs in a constructed

TABLE 2. Incidence of structured vs. structureless nests among 86 active nests at sites with high and low falling risk in two White-collared Swift colonies. Assignment of nests to risk categories is explained in Methods.

	Aguacero Colony (waterfall; sites with low risk of falling appear rare)		Chorreadero Colony (cave; sites with low risk of falling are common)		
	Nests with structure	Nests without structure	Nests with structure	Nests without structure	
Low falling-risk sites	26	0	Low falling-risk sites	3	39
High falling-risk sites	15	0	High falling-risk sites	3	0

nest, even in sites presenting little risk of eggs or young falling. In fact, none of the Aguacero nests lacked a structure, whereas 93% of Chorreadero nests in low falling-risk sites lacked a structure.

Because all Aguacero nests had some structure, I did one further analysis to examine more closely the relationship between nest structure and risk factor of nest sites. Eleven of 41 Aguacero nests had much less substantial structure than did the remainder. Nine of these were in low risk sites and two were in high risk sites. Chi-square analysis of Aguacero nests categorized this way did not permit rejection of the null hypothesis of independence ($P < 0.10$). The degree of robustness of nest structures here was independent of the falling-risk factor of nest sites.

DISCUSSION

The locations within colony sites which were chosen for nesting by these two species did not differ noticeably. Nest structures of the two species were also similar, except that White-naped Swift nest structures were made primarily of mud and dead leaves, whereas most White-collared Swift nest structures were made of moss and chitinous fragments. In fact, the White-naped Swift nests which I examined made greater use of mud than has apparently been reported to date for any cypseloidine swift (Table 1). However, all of these nests were in a single cave, and so conclusions about nest materials should be extrapolated with caution. As indicated earlier, White-collared Swifts at least sometimes collect nesting material in the immediate vicinity of the colony. If White-naped Swifts do likewise, the composition of nests may vary depending on local availability of materials. Hence, overlap of materials used by the two species (and other cypseloidines) is likely.

As indicated in Table 1, differences in nest shape within a swift species appear to result largely from differing substrate angles, and this may account also for much of the difference in nest shape between swift species. The kinds of nest environs

used by cypseloidine swifts are broadly similar, but the detailed choice of nest environs, including substrate angle, may well represent one of the main axes of resource partitioning within this subfamily. One might expect the larger swifts to be restricted to low-angle substrates where firm support is provided for a substantial mass of nest, nestlings, and adults. Smaller swifts are probably more free to exploit vertical and near-vertical substrates with minimal rugosity, ledges, or niches for nest support.

In those White-collared Swift nests composed solely or mainly of chitinous fragments, it remains a mystery what agent, if any, binds these particles together to form the rigid nest cups which these nests possessed. Rowley and Orr (1965) also described nests of this swift which incorporated large amounts of insect chitin in the nest structure, and they suggested that use of saliva may have contributed to the texture of nests. No cypseloidine swift has yet been proven to use saliva in nest building, but balls of arthropod prey regurgitated by adult White-collared Swifts were sometimes coated with saliva or mucus. Some swifts are known to regurgitate pellets of chitinous fragments (Duke 1977). If such pellets are egested into the nest by *S. zonaris*, along with a mucus or saliva coating, this could explain the rigidity of some nests which appeared to be composed solely of chitinous fragments.

Since rolling and falling of eggs and young are major sources of nesting mortality in these swifts (Whitacre and Sharp, unpubl.), it could be argued that selection would scarcely be expected to lead to the apparently facultative manner in which these swifts approach nest building. Such an argument might assert that even a marginal increase in fledging success due to nest construction should be favored, leading to unanimous building of nest structures. However, the less than total commitment to nest building which I observed may result from a trade-off between its costs and benefits. Benefits of nest building no

doubt include enhanced survival of eggs and young due to prevention of falling. By permitting the use of substrates which would otherwise be too steep for nesting, nest building probably enhances nestling and adult survival because such steep areas are relatively secure from terrestrial predators. By the same token, nest building probably facilitates escape from nest-site limitation.

Nest building can entail a significant energetic cost. Weeks (1978) found that Eastern Phoebes (*Sayornis phoebe*) using preexisting nests laid larger clutches than did individuals building nests earlier during the same nesting cycle, presumably because the former had larger fat stores. Other costs of nest building might include decreased time and energy available for feeding, mating, and other activities, and increased exposure of adult swifts to predation. Observations cited above of swifts gathering nesting material in exposed colony environs suggest that this activity may increase a nest-building swift's exposure to predation. Some colonies of both swift species attract avian predators, principally Peregrine Falcons (*Falco peregrinus*), which wait at colony sites to catch swifts as they leave or enter (Whitacre and Sharp, unpubl.). This is a common occurrence at the Dos Bocas (White-naped Swift) colony, though less common at the particular White-collared Swift colonies discussed here. Hence, swifts often pass through a window of predation risk when they enter or leave the colony site, which may constitute selection pressure to minimize the number of trips to and from the nest. The balance of such countervailing selection pressures could lead to the conditional nest-building behavior demonstrated here.

Nest predation has not been considered in this paper since it should not bear on the relationship between nest structure and nest-site characteristics. It may, however, play an important role in nest-site selection, for it is sometimes an important source of nesting mortality. In 1978 we saw a young Virginia opossum (*Didelphis marsupialis*) eating eggs at White-collared Swift nests at the Aguacero colony, and the same or some other small mammal ate many nestlings throughout the nesting season (Whitacre and Sharp, unpubl.). Some nests, however, were clearly inaccessible to any tetrapod. Since these were generally nests with high falling risk (e.g., in niches in cave ceilings), it seems likely that there is often a trade-off between the twin perils of falling and nest predation. Such a risk trade-off does not always

exist, since broad ledges with essentially no falling risk may be predator-free if situated above unclimbable cliffs. This appears to be the case at the Chorreadero, where a mouse (*Peromyscus* sp.) was the only mammal seen above the waterfall cliff, and no evidence of nest predation was seen. If nest predation varies between colonies, it may interact with falling risk in such a way that swifts may not value predator-immune nest sites and low falling-risk nest sites equally within or between colonies.

Two explanations are possible for why more Aguacero (waterfall) White-collared Swift nests were in high falling-risk sites than was the case for Chorreadero (cave) nests of this species (Table 2). First, this may simply reflect the apparent paucity of low falling-risk sites at the Aguacero (waterfall) colony. That is, low falling-risk and high falling-risk sites at both colonies may have been used in proportion to their relative abundance. Second, swifts at the Aguacero (waterfall) colony may have used high falling-risk sites preferentially because these sites are probably safer from nest predation by tetrapods than are sites with low falling risk. As mentioned above, nest predation at the Aguacero (waterfall) colony was much more frequent than at the Chorreadero (cave) colony, and was due to tetrapod(s).

When analysis is restricted to sites with low falling risk, there is a dramatic difference between colonies. At the Chorreadero (cave, predominantly broad ledge-nest) colony, none of the low falling-risk nests employed structures, while at the Aguacero (waterfall, predominantly overhanging niche nest) colony, 90% of nests in low falling-risk sites employed structures (Table 2). This suggests that swifts in the two colonies applied different "standards" in the decision of which nest sites were usable with and without nest structures. Several explanations are possible for this apparent difference. First, the difference may be a historical artifact. Under this scenario, the degree of saturation of sites by nest structures could be lower at the Chorreadero (cave) colony for one of the following reasons. Nests here could be removed by floods more frequently; this could be the case, though due to the shape and volume of the passage, I doubt that floods often reach the main nesting ledges. This colony could have a shorter history of swift occupancy, leading to a smaller accumulation of nests, though both sites have been occupied at least since 1965 and possibly for centuries. Differing age structure of the

two populations could have an effect if age classes differ in their tendency to build nests; there is no particular reason to suspect such a difference in age structure between the colonies.

Another family of explanations assumes that the same "standard" of nest-site and structure usability is employed by birds of the two colonies, but that physical characteristics of the two colony sites lead to a difference in the average level of nest-structure use. First, the cost/benefit ratio of nest building may differ between the two colonies. Since falling risk of sites is held constant in this analysis, the benefit of nest building should not vary between sites, but the cost may well differ. The Aguacero waterfall is profusely covered with moss, the swifts' main building material. The Chorreadero cave has much less moss, restricted to the small cascade in the cave mouth. Nesting material in the colony vicinity thus appears quite limited at the Chorreadero relative to the Aguacero, and the time and energy costs of building may differ accordingly. Similarly, different degrees of nest-site competition, or in fact, anything which leads to differences in the energy budgets of swifts of the two colonies, could likewise alter the cost of nest building relative to that of other essential activities. Proximity to foraging areas could be relevant here; the Aguacero colony seems atypical in the degree to which swifts remain close to the colony at times during the day, perhaps due to uniquely suitable foraging and soaring opportunities (Whitacre and Sharp, unpubl.). Hence lower costs of foraging could contribute to more favorable energy budgets at this colony.

Secondly, if swifts adjust their nesting behavior based on experience, then a difference in the availability of safe vs. risky sites at the two colonies could lead to different patterns of nest-structure use. At the Aguacero colony, swifts should frequently experience sites with high falling risk. "Bad" experiences with high falling-risk sites could perhaps lead, in subsequent nesting attempts, to a high degree of nest-structure use, even at sites with little falling risk (Table 2).

A final possibility is that genetically based differences in the behavioral "standards" governing nest-structure use exist between colonies. This could occur if the fitness difference due to a genetically based trait exceeds the fraction of immigrants into one colony from the other (Slatkin 1987). I have no data on either of these parameters.

The question remains why I found White-naped Swifts utilizing nest structures on the same ledges where 22 and 24 years earlier, Rowley and Orr (1962) had observed this species breeding without the use of nest structures. The answer may lie in the behavior of the Rio Chontalcoatlán which flows through the nesting cave. This river drains hundreds of square kilometers of agricultural land, pine-oak forest, and other subhumid vegetation types before entering the large cave through which it passes several kilometers to exit at the mouth where I studied these swifts. Typical of rivers of subhumid vegetation zones, this river is prone to flash floods, and often floods during the summer rains. I witnessed substantial floods, and local people working as cave guides in the national park that includes this cave allege that the river sometimes floods nearly to the cave ceiling, carrying trees and livestock through the cave (Jose Luis Gomez-Reyes, pers. comm.). Rowley and Orr (1962) found the swifts here nesting on sandy ledges. As noted earlier, only one of 32 nests I examined here was on sand and guano. Ten were on bedrock or solid clay, while the others were on some combination of rock, clay, and guano. Since there is no question that these were the same ledges where Rowley and Orr described swift nests, it seems clear that there is now less sand on these ledges than in 1961. Periodic flooding could easily change conditions on these ledges by adding or removing sand, clay, or other materials. Bare rock and hard clay ledges no doubt present a greater risk of eggs rolling than do sand-covered ledges. Evidently the swifts have responded to substrate changes by building nest structures in the absence of sandy oviposition sites.

Orr (1963) cited the White-naped Swift's presumably unique nesting habits as partial evidence that this species may not belong in the genus *Streptoprocne* along with *S. zonaris* and *S. biscutatus*. Brooke (1970) went on to propose, again partly on the basis of nesting habits, a new subgenus, *Semicollum*, for this species. The similarity of nesting habits of the White-collared and White-naped swifts demonstrated here require that this subdivision be reevaluated. Though I have no opinion regarding the morphological traits listed by Orr (1963) and Brooke (1970) as grounds for concluding that these two species are not congeneric, alleged differences in nesting habits must be dropped from the list of justifications for such a split. The two swift species

considered here are in my opinion exceedingly similar in behavior and ecology. Whether this results from convergent or parallel adaptation to similar nesting and other conditions, or from phylogeny, awaits further study.

In a review of the Old World swift genus, *Hirundapus*, Collins and Brooke (1976) conclude that the only unquestionable descriptions of nesting for the genus are of *H. caudacutus* and *H. giganteus*, whose nests are mere lined or unlined depressions or scrapes in the detritus in the bottom of hollow trees. These authors conclude that persistent allusions in the literature to other types of nests and nest sites for this genus are mostly erroneous, and that nesting without any constructed nest in the detritus in hollow trees is typical of the genus.

This conclusion further erodes the supposed uniqueness of the White-naped Swift. It is now shown to be only one of four swift species in two genera which often lay eggs without a constructed nest. On the other hand, the facultative nest building in *Streptoprocne* for which I here present evidence suggests that we can expect further fieldwork to confirm that *Hirundapus* swifts do indeed build at least rudimentary nests at times, depending on nest-site characteristics; their large body mass, however, probably precludes reliance on the weight-bearing properties of the glued-twig saliva nest expected based on nearest relatives (Charles T. Collins, pers. comm.).

These results point out a risk inherent in the use of building vs. nonbuilding of nests as an indicator of phylogeny. Nesting habits and persistent nonbuilding of nests may indeed reflect phylogeny in swifts, but if nests are sometimes built by the taxon in question, it is safer to base phylogenetic inferences on the behaviors employed when nests *are* built, than on the mere frequency of nest building. The stereotyped behaviors employed in nest construction might reasonably be expected to show greater evolutionary conservatism than does the frequency of nest building (and presumably its adaptive value) which, as shown here, can differ between sites and can change at a given site over a brief span of years. This conclusion should apply equally well to other bird groups or other organisms and perhaps to other categories of behavior.

ACKNOWLEDGMENTS

I am grateful to Devora Ukrain Sharp for allowing me exclusive use of data we gathered together in 1978. I

thank several individuals who helped me in the fieldwork: Maurice A. Whitacre and Kathleen A. Whitacre helped for 1 to 2 months each, under frequently arduous conditions, while Gladys F. Whitacre, Martha Van der Voort, Fran Miller, Sandie McLaurin, and Agnes Winther all helped for lesser time periods. Dennis E. Breedlove and Alan R. Smith identified plants used as nest lining. Don Coons first told me of the Dos Bocas colony. W. Grainger Hunt, Robert L. Rudd, and George W. Salt provided advice and encouragement. For reading and making useful comments on various drafts of this manuscript, I thank Gary A. Falxa, Robert L. Rudd, George W. Salt, and T. W. Schoener. Profitable discussions were had with Mark Dybdahl and Peter Sherman. I thank Manuel Marin R. for providing unpublished data and hard-to-find reprints. I am grateful to reviewers, Charles T. Collins and Raymond O'Connor, for their helpful criticisms of the manuscript. Funds for 1978 research were provided by the Chihuahuan Desert Research Institute and the National Audubon Society. Financial support during manuscript preparation was provided by the University of California, Davis Institute for Population Biology, and the Greta Kramer and James Hilary Balderston Memorial Fund. I am grateful to the many Mexican people whose friendship helped make my fieldwork rewarding and who aided me in countless ways.

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