

Breeding biology and natural history notes for White-collared Swift *Streptoprocne zonaris* in Costa Rica

by Manuel Marín

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SUMMARY.—The breeding biology of White-collared Swift *Streptoprocne zonaris* was studied in Costa Rica. Eggs were laid between mid April and mid May, and fledging occurred between late June and mid July. There are three clear nesting patterns for this wide-ranging species, which can be termed ‘northern’, ‘central’ and ‘southern’, all associated with the onset of the rainy season. My study was consistent with the breeding pattern elsewhere in the Northern Hemisphere. All nests were placed in sites with high humidity and were from 10 cm to 30 m or more above ground or water level. Nests were reused in subsequent seasons, and one nest was in use for at least 13 years. All observed clutches had two eggs and mean egg mass was 9.9 g. Egg ($n = 23$) were dull white and sub-elliptical (39%), long sub-elliptical (35%), short sub-elliptical (17%) or short oval (8%) in shape. Incubation period was 26 (25–27) days. Mean hatching mass was 8.8 g, and max. mass was reached at age 33 days (127% of adult size), thereafter it declined slightly. Fledging occurred at 47 (43–51) days. The growth constant $k = 0.225$ and $T_{(10-90)}$ period was 19.5 days. Most mortality occurred at the egg stage or in the early days of a nestling’s life. The major cause of nest failure was weather-related: flooding and starvation, but egg infertility and predation also occurred. Adult primary feather moult started in tandem with egg laying and lasted 6–7 months.

White-collared Swift *Streptoprocne zonaris* is the most widespread New World swift, ranging from Mexico (Guerrero in the west and Tamaulipas in the east), south through Middle America, and east to the Greater Antilles, as well as over much of South America, while the species is also a vagrant to the southern USA (AOU 1998).

Despite this broad distribution, almost nothing is known about the species’ breeding biology, mainly because access to nest sites is often difficult, and it has a prolonged breeding cycle. Consequently, most of what is known about the species concerns its distribution and breeding sites; for a summary, see Marín & Stiles (1992). Passeggi (2011) recently published information concerning breeding phenology and incubation from a site in north-west Argentina and Biancalana (2014) reported breeding data from south-east Brazil, both near the southern end of its breeding distribution at 23–24°S. Here I present new information on breeding phenology, nest sites, nests, eggs, incubation, growth, development, moult, mortality, etc.

Study area and Methods

The data reported here were gathered in Costa Rica, mostly in the gorge of the Tiribí River, San José province, at 09°57’N, 83°55’S, between 1,880 m and 2,100 m (see Marín & Stiles 1992 for details). In June–August 1995 and May–August 1996 and 1997, visits were made at 1–5-day intervals to nest sites, while some data from visits in 1984–86 are also included and, when relevant, data from other sites and other countries are also integrated.

I assessed nestling body mass to 0.1 g using an AVINET spring balance of 10, 30, 50, 100 and 300-g graduations depending on nestling age. I measured wing length (flattened)

and tail length to 0.5 mm using a metal wing rule with a perpendicular stop at zero. Tarsus length and exposed culmen were measured to the nearest 0.1 mm using dial callipers, following Baldwin *et al.* (1931) and Marín & Stiles (1992). Nestlings were measured only in the morning, between 08.00 and 11.00 h. Egg dimensions and mass were measured in the field to the nearest 0.1 mm using dial callipers. Egg-shape assessments are based on Preston (*in* Palmer 1962). The duration of 10–90% of body mass growth or $T_{(10-90)}$ period (Case 1978) and the growth rate constant K (Ricklefs 1976) were determined. Body masses and measurements of adult birds banded in the area were supplemented with data from museum specimens from the same geographic area (see Acknowledgements). Swifts possess ten primaries and their moult is bilaterally symmetrical, with the sequence from the innermost to the outermost primary feather. To assess moulting season, I assigned a numerical value or moult score of 0–1 for each feather, a fresh feather would have a score of 1, while a half-grown one would score 0.5, and a bird with all ten primaries replaced will score 10, these values based on % grown, following Stiles & Wolf (1974) and Marín & Stiles (1992). I used data from mist-netted birds at the study site as well as museum specimens (see above) from the general area to obtain moult scores. During incubation, nest attendance was measured using a temperature data-logger that operated between -5°C to $+37^{\circ}\text{C}$ (Stow Away XTI-8K, ONSET Computer Corporation, Pocasset, MA). An external sensor was attached to three nests, next to or below the eggs to record temperature at five-minute intervals. The number of days of useful data from each nest varied at 7–12 days, because adult activity occasionally dislodged sensors from the nests.

Results and Discussion

Breeding phenology.—Egg laying in the Greater Antilles (Cuba and Dominican Republic) occurs in April and May (Bond 1980, 1984, Stockton de Dod 1981, Montes Espin & Garcia Rivera 2010). In southern Mexico egg laying is also from mid April to May (Rowley & Orr 1965, Whitacre 1989; West. Found. Vert. Zool. egg data cards). In Ecuador egg laying starts in December–January (Marín & Carrion 1994; MM unpubl.), i.e. 5–6 months earlier than more northerly populations. My limited Ecuadorian data on breeding, including inferences from moult patterns (see below), suggest that populations east and west of the Andes possess a similar breeding phenology. At the southern end of the species' breeding range, in north-west Argentina (Tucumán and Córdoba) and in south-east Brazil, the onset of the breeding season is mid October to late November, 2–3 months earlier than populations near the equator (de la Peña 2005, Passeggi 2011, Biancalana 2014; MM unpubl.). At the main study site in Costa Rica the onset of egg laying occurred between mid April and mid May, with 69% of eggs ($n = 36$) being laid by late April, following the northern breeding pattern. The nesting pattern in the Northern Hemisphere is similar among all of the areas for which I have data—southern Mexico, Greater Antilles and Central America (see above). There are three clearly different timings of breeding throughout the species' range: northern, central and southern. The fledgling period in Costa Rica occurred between late June and mid July, and once the nestlings left the nest they did not return to the area, even to roost. Banded nestlings were never recaptured. In contrast, in the slightly larger Biscutate Swift *Streptoprocne biscutata*, Pichorim (2002) reported that fledglings stayed around the cave for a few days before fully departing. This difference might reflect the nature of the study site itself, Pichorim's was a large cave that might act as a roosting site as well, while in the present study the nests were scattered in small cavities (see below) and if the birds roosted in a nearby area they went unnoticed.

Nest.—All nests found were closely associated with water and in sites with high humidity (never <95%) on caves or ledges behind or beside waterfalls. The caves may be

mere niches or holes no more than 50 cm deep, although some were in narrow caves 2–3 m deep, but no more than 1 m wide. These caves were formed naturally by large boulders along the river. Isolated nests were found, but also up to three nests within a single cavity. Along the river in one linear area of c.10 m up to nine nests were found. Most aggregations and colonies at the study site and elsewhere in the species' range are small in contrast to some of the large colonies of several thousand birds described in Mexico (Whitacre 1989, 1991). In Costa Rica, many of the caves and waterfalls that host large numbers of birds are mainly roosting sites, although some of them might also harbour nests. As far as is known, all of the large colonies in Mexico are occupied year-round as both roost and nest sites (D. F. Whitacre *in litt.* 2016).

Nests were located 10 cm to 30 m above ground or water level. Most were placed on level horizontal surfaces and were in total darkness. Three exceptions were: (1) four nests sited in a deep ravine on a small ledge c.3 m above the water level and 4 m from a waterfall; (2) two nests in a small cavity behind a large waterfall; and (3) one nest on a narrow shelf c.1 m above water level. However, the first four nests were in a semi-dark area of the ravine that was completely covered by tall vegetation forming a 'tunnel', and the nests received a constant fine spray from the waterfall. Only the second exception, behind the large waterfall, might have received some direct light during several hours of each day. All nests found were a saucer-shaped platform, constructed of mud, roots with some mosses, and were constantly moist. Depending on substrate, the amount of material placed on the base of the nest varied. One nest (of 13) in 1984–86 and one nest (of 36) in 1995–97 had no material, with the eggs being placed directly in small, sandy, narrow depressions, c.1–2 m above water level. In southern Mexico, Whitacre (1989) also found nests without materials, but in larger numbers. Absence of nest material has not yet been reported anywhere in South America for any *Streptoprocne* spp., e.g., Andrade *et al.* (1985), Pichorim (2002), Passeggi (2011) and Biancalana (2014).

I was unable to measure the duration of nest construction. However, during the early part of the nestling period, the adults sometimes added additional material, usually dry mosses and sometimes leaves, to the centre of the nest, when nestlings were hatching, presumably to keep the recently hatched young drier.

Most nests studied in 1995–97 were c.500–1,000 m higher along the river than the main study area of 1984–86. Nevertheless, four nests that were used 1984–86 were still active during the seasons of 1995–97. Although it is unknown if they were used by the same birds, this might have been the case. F. G. Stiles and I, during our previous work in the area in 1984–86, banded a pair of adults on 29 April 1986 at a cave in which later the same year they nested. On 12 July 1995, at the same site, I recaptured one of the birds banded there in 1986 (G-93, re-banded B-21). The band was worn on one side but readable. The same bird was recaptured in 1996 and 1997 at the same site, and in May 1996 the G-93 band was gone, but B-21 was in good shape, indicating that plastic bands last c.10 years. Thus the same birds can use the same nest for at least 13 years, providing an indication of their longevity. All members of this subfamily are suspected to be very long-lived species. For example, for Black Swift *Cypseloides niger* Lowther & Collins (2002) reported max. age as 16 years and one month, and for the same species Marín (1997) reported re-use of the same nest for >21 years, although it was not certain if the same birds were involved.

Eggs and incubation.—All clutches observed were of two eggs, as in other colonies of White-collared and the larger White-naped Swift *Streptoprocne semicollaris*, with the exception that Biancalana (2014) found a nest with three nestlings of *S. zonaris* in south-east Brazil. In the intermediate-sized Biscutate Swift, nests with 3–4 eggs have been recorded (Andrade *et al.* 1985, Pichorim 2002), but all of those cases of nests with more than two

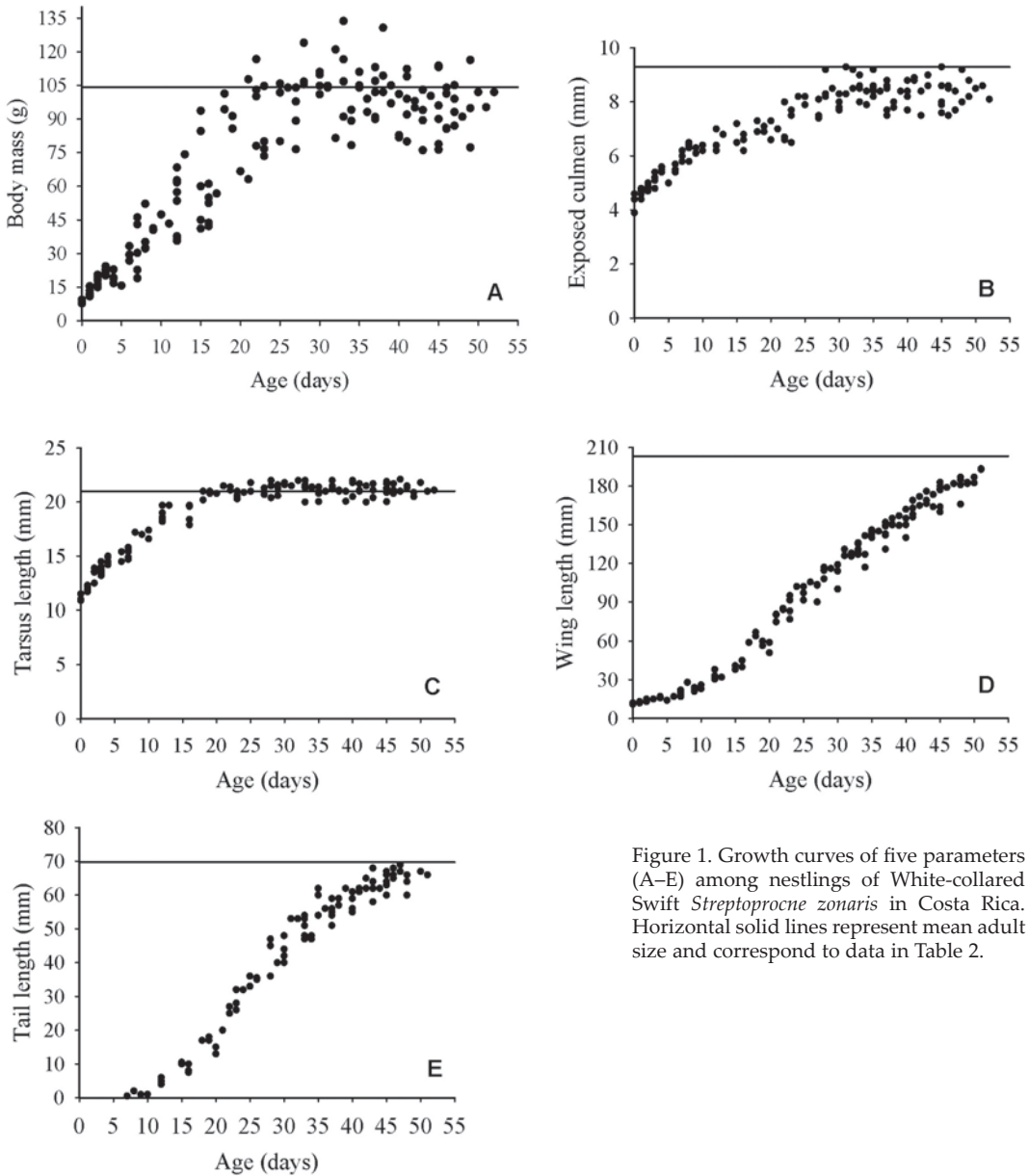


Figure 1. Growth curves of five parameters (A–E) among nestlings of White-collared Swift *Streptoprocne zonaris* in Costa Rica. Horizontal solid lines represent mean adult size and correspond to data in Table 2.

eggs might reflect intraspecific parasitism, as clutch size appears to be naturally two eggs and because the birds in those cases were nesting in a more congested space. The issue warrants genetic study of nests containing more than two nestlings, to prove or disprove this hypothesis.

Eggs were dull white but become dirty (due to mud) as incubation proceeds. Mean fresh egg mass was 9.85 g (9.4% of adult mass) and egg shapes were sub-elliptical (39%), long sub-elliptical (35%), short sub-elliptical (17%) and short oval (8%) ($n = 23$). For egg measurements and mass, see Table 1. I was only able to determine the precise incubation period at three nests, and the mean was 26 days (25–27 days). Previously, Marín & Stiles (1992), in a comparative study of several Cypseloidine species, estimated the incubation

period at c.30–35 days, in the absence of actual data. This was based on body and egg size relative to the smaller species (i.e., larger species, larger egg, thus longer incubation period). However, Marín & Stiles (1992) were incorrect in this assumption. In this respect, among the Cypseloidine swifts there appears to be some emerging trends. More tropical species have a longer incubation period than more temperate representatives. For example, in the tropical population of *S. zonaris* (present work) the incubation period was 26 days, vs. 22 days for a subtropical population in Argentina (Passeggi 2011). In a one-egg species, Black Swift has both tropical and temperate populations with the same trend, 29 vs. 24 days (Marín 1999). Secondly, two-egg species (*Streptoprocne*) have a relatively shorter incubation period than one-egg species (*Cypseloides*). For example, two similar-sized species lay two- and one-egg clutches respectively, Chestnut-collared Swift *Streptoprocne rutila* (25 days) and Spot-fronted Swift *Cypseloides cherriei* (29 days; Marín 2008).

For the subtropical population of Biscutate Swift, a two-egg species that is only marginally larger than White-collared, Pichorim (2002) found that the mean incubation period was 24 (22–28) days, i.e. well within the range for two-egg species. Biscutate Swift also has more tropical populations and it would be most interesting to discover their incubation period and to see if it follows the same trend.

The incubation pattern observed for White-collared Swift using the data from the temperature data-loggers indicated an irregular schedule. Data from three nests and 26 days of useful data indicated that the adults incubated a mean 65% of daylight hours. The birds left the eggs uncovered for long periods of time, with a gap sometimes of several hours (1–8 hours) in the morning and a short gap of 45–60 minutes during late afternoon. However, on some occasions they incubated nearly the entire day. This pattern was also observed in the smaller Chestnut-collared Swift in the same study area (Marín 2008).

Nestling development.—I followed the development of 33 nestlings, but I was only able to obtain full data from hatching (day zero) to fledging for five nestlings. Partial data (2–9 data points) were gathered for 28 nestlings of known age (Fig. 1A–E). The species had a high mortality rate during the early stages (see below), making it difficult to gather complete datasets.

Soon after hatching, eggshell remains were not removed by the adults but remained in the nests or beside them, until they were dissolved by the high humidity at the site. On hatching nestlings were naked, with eyes closed, skin was pink-flesh, with the skin between the culmen and forehead bright pink, while the distal part of the culmen was blackish with a well-defined egg tooth. Feather papillae were barely visible as subcutaneous dashes. The feet were pinkish and claws greyish tipped black; at hatching they were 45.4 % of adult size.

TABLE 1
Dimensions and mass of White-collared Swift *Streptoprocne zonaris* eggs ($n = 23$) at the study site in Costa Rica.

Feature	Mean	SD	SE	Range
Length (mm)	34.9	1.59	0.33	32.4–38.6
Width (mm)	23.3	0.49	0.10	22.2–24.3
Mass ^a (g)	9.9	0.95	0.30	8.6–11.5

^a Mass from fresh eggs; sample size $n = 10$.

TABLE 2
Measurements of adult White-collared Swifts *Streptoprocne zonaris* at the study site in Costa Rica.

Feature	Mean	SD	SE	Range	n
Mass (g)	104.8	7.6	0.7	87–129	109
Exposed culmen (mm)	9.3	0.4	0.03	8.5–10.4	99
Tarsus length (mm)	21.1	0.9	0.1	19.0–23.2	96
Wing length (mm)	203.4	6.3	0.6	186–218	104
Tail length (mm)	69.9	6.1	0.6	48–85	100
Wingspan (mm)	515.2	11.1	1.4	487–541	58
Tail fork (mm)	12.6	5.8	0.7	0–29	62

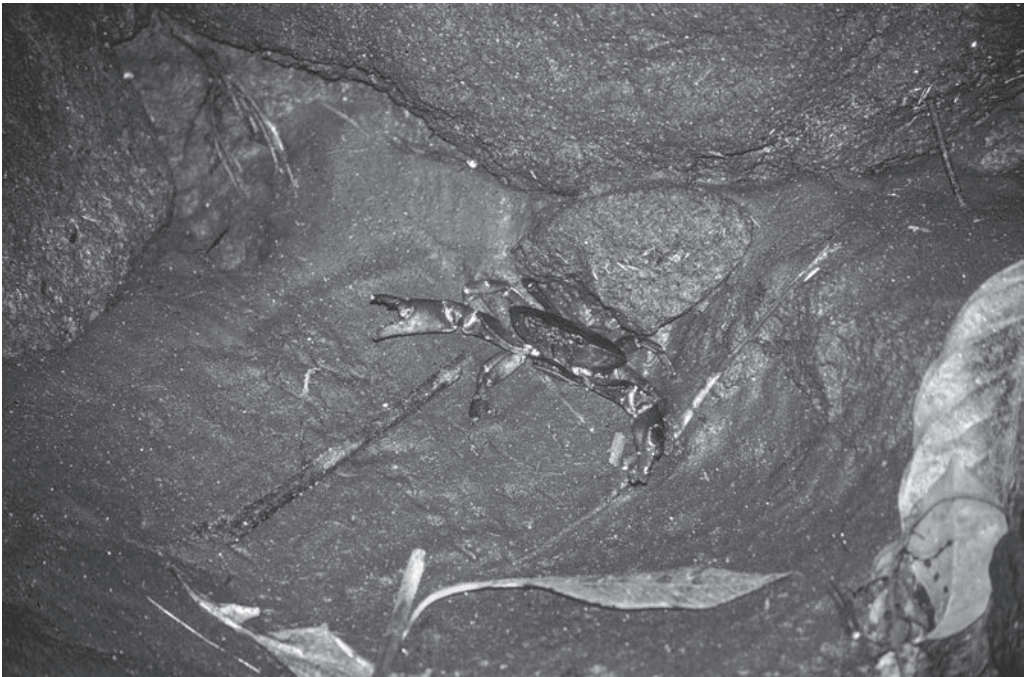


Figure 2. A potential additional predator of young swifts, a crab in the family Pseudothelphusidae, which was observed on 4 June 1996 carrying a moribund nestling from a nest placed near water level (Manuel Marín)

On hatching (day zero) nestlings had a mean mass of 8.75 g ($n = 6$; range 7.7–9.4 g, or 8.3% of adult size; for adult size see Table 2). Body mass increased fast, healthy nestlings reached adult mass by days 21–22 (Fig. 1A). On average, max. body mass reached by nestlings was 110.9 g (105.9% adult size) by 33 days. The max. body mass reached by any nestling was 133.7 g, or 127.6% of adult mass, at age 33 days. The growth constant was $k = 0.225$ and $T_{(10-90)}$ period was 19.5 days. During the $T_{(10-90)}$ period the fastest-growing birds increased mass at a rate of 4.1 g per day, or 3.19% of adult mass per day. Within the Cypseloidine, the growth trend is that the largest species are fastest and the smallest are slowest, in direct contrast to most avian groups (Gill 1990, Marín & Stiles 1992, Marín 1997, 1999).

On hatching the exposed culmen was 4.3 mm (41.1% of adult size) and reached adult size at age 31–32 days (Fig. 1B). Tarsus length at hatching was 11.22 mm (51.25% adult size), being the most advanced feature on hatching, and acquired adult size by 20–21 days (Fig. 1C). On hatching wing length was 11.5 mm (5.6% adult size) and reached adult size post-fledging. The max. wing length of any nestling was 193.5 mm at age 51 days (95.1% adult size; Fig. 1D). The tail feathers started to emerge by days 7–8 and in some nestlings reached near-adult size at the time of fledging (Fig. 1E). Semi-plumes began to appear by age 7–8 days and by 11–12 days the greyish semi-plumes covered the entire body, except the face, chin, belly and distal part of the wing. At age 23–27 days body feathers began to replace the semi-plumes. From 27–28 days the collar was well defined, and feathers on the forehead, breast and lower belly (not undertail-coverts) were very finely white-edged, with some variation, as several birds ready to fledge had broad white-edged feathers on the lower belly, but most had finely white-fringed feathers. Primaries, secondaries and rectrices become broadly white-tipped and very finely white-edged. Eyes were fully open by days 12–13. For other growth parameters see Table 3. Nestlings departed the nest on average by age 47 (43–51) days, in broad agreement with other findings, i.e. 40–48 days in north-central

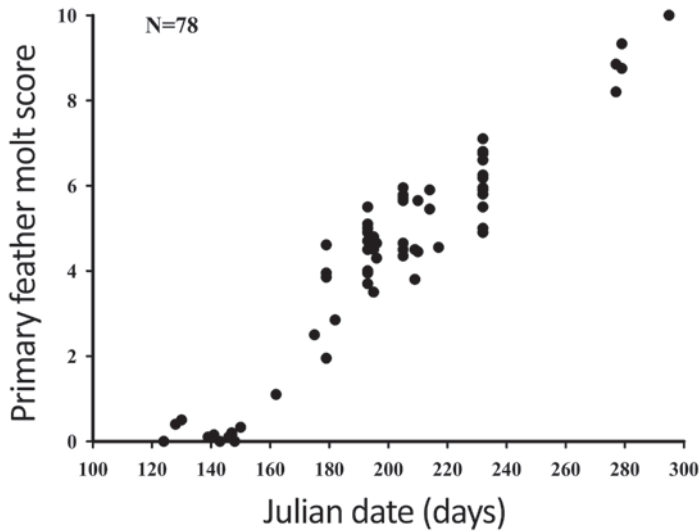


Figure 3. Primary moult score by Julian date in the central Costa Rican population of White-collared Swift *Streptoprocne zonaris*. Julian day 100 = 9 April; day 150 = 29 May; day 200 = 18 July; day 250 = 6 September; day 300 = 26 October. For determination of moult scores see Methods.

Argentina (Passeggi 2011) and 41–51 days in southern Brazil (Biancalana 2014). In terms of nestling development, there appears to be little difference between White-collared and Biscutate Swifts (Pichorim 2002).

Mortality.—Most mortality occurred at the egg or early nestling stage. During 1995–97 I followed the fate of 32 nests: of 64 eggs, only 49 nestlings (76.5%) hatched. Egg rolling or eggs falling from the nest was the major cause, with a total of ten eggs lost in such circumstances, two were added, two were flooded due to an increase in river water levels, and one loss was due to unknown causes. Egg rolling occurred more frequently when 2–3 nests were close together and was observed more often during the early or mid-incubation stages. It possibly is indicative of disputes for nest sites or mates. If birds lost their eggs there was never any re-nesting attempt. Of 49 nestlings that hatched, only 21 fledged (57%) and among the 28 fatalities 50% died before age five days. Overall nesting success was 32.8%. The study period (1995–97) was thus characterised by very low nesting success compared to that found in the same area during 1984–86, cf. Marín & Stiles (1992). However, most mortality was during the early stages of life and was weather-related. The 1996 season was extremely wet, with some 655 mm of rain in the area during May, whereas the 45-year mean for the same month and area is 288 mm (Instituto Meteorológico Nacional, Costa Rica, Rancho Redondo weather station). Similarly, during 1997, heavy rainfall occurred in June, >40% above average for the area. These unusually wet years produced substantial flooding, destroying many nests and probably

TABLE 3
Major developmental events in White-collared Swift *Streptoprocne zonaris* nestlings in Costa Rica.

Event	Age (days)
Semi-plumes emerge	3–4
Semi-plumes sprouting	7–8
Full coat of semi-plumes	11–12
Eyes start to open	7–9
Egg tooth disappears	13–21
White collar defined	21–23
Pin feathers on primaries emerge	12–16
Pin feathers on primaries break sheaths	15–16
Inner primaries fully grown	34–37
All secondaries fully grown	40
Pin feathers on rectrices emerge	8–9
Pin feathers on rectrices break sheaths	11–13
Active when handled	8–9
Fledge	43–51

limited food provisioning for the young at the most critical stage or the very early stages before reaching homeothermy. This was reflected in the large mortality and starving early-stage nestlings. Seventeen nestlings were found dead, principally due to starvation and mainly during 1996. Of the 17, eight were found dead outside their nests, six were drowned due to rising water levels, and five disappeared without trace, all of them from low (10–40 cm above ground level) nests. On 4 June 1996, I found a crab (*Pseudothelphusidae*; Fig. 2) carrying a moribund nestling from one of the nests near water level, which might explain the disappearance of some or many other nestlings. On 8 and 11 July 1996, along the river I found two moribund but recently fledged young just below a large waterfall. There was an inaccessible large cave behind this waterfall, with a large but unknown number of nesting birds. On 8–9 July 1996, there were heavy rains in the area (55–60 mm during the morning) and the river was overflowing, but there was no route by which water could have entered the cave, thus it is probable that on leaving their nests, the birds miscalculated and hit the water ‘curtain’ covering the cave entrance. Whitacre (1989) found that at some Mexican colonies rolling and falling of eggs and young was the major cause of mortality.

Primary moult.—Swifts are highly dependent on their flight feathers and, like most bird species, must moult their primary feathers, with this replacement occurring once per year and sequentially, progressing from the innermost to outermost feather. Both wings are moulted symmetrically. Adult White-collared Swifts began to moult the inner primaries between mid April and late May (Fig. 3), coinciding with egg laying. At the study site, there was only very slight inter-year variation in primary feather moult. For example, a bird banded on 12 July 1995 had a primary moult score of 2.95, while on 14 July 1996 the same bird had a score of 3.5, and another individual on the same dates had scores of 3.7 and 3.5, respectively. I have several such examples, making it reasonable to combine the annual data. However, the different breeding populations are well synchronised, even between years. Wing moult started with the inner primaries and coincided with late incubation or hatching of the nestlings. For example, several adults captured at their nests in mid–late May had the innermost primary new in sheath, with a moult score of 0.1–0.2, and the same birds when recaptured three months later, in late August, had moult scores of 5.9–6.6. Several individuals captured in early October had scores of 8.2–9.3. A single example from late October had a score of 10, or 100%. Thus, breeders completed primary moult by late October to mid November, after *c.*6 months. However, non-breeders started their primary feather moult 1.5–2.0 months earlier, and in some cases perhaps even before thus. For example, at a site in Bijagua, northern Costa Rica, where there is a large waterfall used only as a nocturnal roost and shelter during large storms, no nest was found in either 1984–86 or 1995–97. Birds captured there between mid and late July in different years had a mean moult score of 7.75 (SD = 1.1, *n* = 20). Thus, non-breeders had finished their wing moult earlier, around August–September (*cf.* Fig. 3). For swifts in general, moult is a long process occupying 5–6 months, being similar in duration across the family in many different species, e.g., House Swift *Apus affinis* (Zhitong 1982), Chestnut-collared Swift (Marín & Stiles 1992), White-throated Swift *Aeronautes saxatilis* (Marín 2003) and several *Chaetura* spp. in central and South America (MM unpubl.). However, for future moult studies it is important to be aware that non-breeders follow a slightly different moulting schedule to breeders, *c.*1.5–2.0 months earlier.

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- Address:* Museum of Natural Science and Dept. of Biological Sciences 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA, e-mail: mma95@hotmail.com. Current address: Casilla 15 Melipilla, Chile.