SOME ASPECTS OF THE BREEDING BIOLOGY OF THE BLACK SWIFT

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ABSTRACT.—Nests of the Black Swift (*Cypseloides niger*) usually are associated with water. Clutch size is invariably one. Incubation is by both adults and lasts ca 24 days, and the nestling period lasts ca 48 days. Nestlings reach and surpass adult mass before fledging and adult size in linear measurements after fledging. The species is single-brooded, probably because of the long incubation and nestling periods that must be accomplished in a brief period of time. *Received 13 Aug. 1996, accepted 11 Dec. 1996.*

RESUMEN.—El Vencejo Negro construye sus nidos en lugares húmedos cerca de agua. Invariablemente la postura es de un huevo, que es incubado por ambos sexos por un período de ca 24 días. El período de crecimiento dura ca 48 días. Las medidas de crecimiento se refieren por un lado a las que adquieren el tamaño de adulto antes de salir del nido y por otro lado las medidas lineares que adquieren el tamaño de adulto fuera del nido. El hecho de que esta especie tenga una sola nidada es debido a la larga incubación y al largo período de crecimiento, que debe ser completado en un tiempo restringido. Durante el crecimiento el polluelo acumula grasa por tres posibles razones: seguridad contra lo impredicible de la disponibilidad de alimento, ayuda para la termoregulación en el frío ambiente de los nidos y energía para su vuelo migratorio que posiblemente comience al salir del nido.

As the most aerial of birds, swifts are difficult to observe and identify in the field. Because access to nesting sites is often difficult, large gaps exist in our knowledge about the biology of many swifts. The Black Swift (*Cypseloides niger*) is found locally in northwestern North America south throughout Middle America and the West Indies (AOU 1983). Some observations of its nesting biology have been published (Vrooman 1901, 1905; Michael 1927; Dixon 1935; Knorr 1950, 1961, 1962; Knorr and Knorr 1989), but the most complete works on its breeding biology emphasize only its breeding distribution (Foerster 1987, Foerster and Collins 1990), leaving many aspects unknown. The goal of this study was to elucidate previously unstudied or little-known aspects of the breeding biology of the Black Swift.

STUDY AREA AND METHODS

From 1990 to 1992, I studied Black Swifts in the San Jacinto Mountains, Riverside Co., southern California. The habitat surrounding the study site was montane forest. Predominant tree species were ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and Coulter pine (*Pinus coulteri*). Other species present included incense cedar (*Calocedrus decurrens*) and white alder (*Alnus rhombifolia*). In the lower parts

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TABLE 1

DIMENSIONS AND MASS OF BLACK SWIFT EGGS (N = 50)

Feature	Mean	SD	SE	Range
Length (mm)	28.7	1.06	0.15	26.3–31.8
Width (mm)	18.8	0.52	0.07	17.4–19.7
Mass[a] (g)	5.5	—	—	5.1–6.4[b]

[a] Calculated from mean egg measurements; see methods.
[b] Mass from the smallest and largest egg from the sample.

of the canyon below the study site, montane chaparral was present, with predominant species on south-facing slopes being scrub interior live oak (*Quercus wislizenii*), black oak (*Q. kelloggii*), live oak (*Q. chrysolepis*), manzanita (*Arctostaphylos* spp.), and chamise (*Adenostoma fasciculatum*). More detailed information on the vegetation of the area can be found in Barbour and Major (1977).

The study site was a natural cave about 15 m deep and ca 7–8 m in height formed by the merging of large boulders in the North Fork of the San Jacinto River at 1500 m (ca 33°45′N, 116°43′W) near the town of Idyllwild. The stream flows year-round, forming a waterfall over the boulders, but flow varied substantially among years and seasons. The inside of the cavern had a substantial flow of water through a side wall, forming a small waterfall and several minor drips from the roof. This internal flow of water also varied among years.

Field data were collected during three visits in 1990, once each in June, August and September. In 1991 data were collected from late May to mid-September, in 21 visits. During incubation and nestling periods, nests were inspected at 1–6 day intervals. During 1992, the site was visited once in May and 15 times from early July to late September, usually every 1–3 days. The third year was used to supplement data from previous years and to carry out a preliminary twinning experiment. This experiment was conducted at two different stages (see below). Because I had to leave the area before the end of the experiment, J. Schmitt and W. Wehtje measured mass, wing, outermost primary, and tail from age 38 until fledging.

I weighed body mass (to 0.1 g with a Pesola spring balance), and measured wing length (flattened), extended wing, 10th primary length, and tail length to 0.5 mm using a stopped wing ruler. Other measurements, such as tarsus length, exposed culmen, head width, foot span, and gape width, were measured to the nearest 0.1 mm with dial calipers (following Baldwin et al. 1931, Marín and Stiles 1992). Nestlings were measured mostly in the morning between 09:00 and 11:00 h. Any measurement taken later than 12:00 h. was given a half-day increment. Colors are those from Smithe (1975, 1981), with number and name (e.g., 83 Dark Neutral Gray). Egg shapes follow Preston (in Palmer 1962). Eggs measurements (Table 1) are mainly from museum specimens, measured to the nearest 0.01 mm with digital calipers. Average egg mass was calculated from museum specimens, using the formula (M = K·L·B^2), were L = length, B = breadth, and k was calculated by regression using fresh egg mass (Hoyt 1979). Temperature within the cave was measured with a portable thermometer placed upon arrival near the center of the cave and read just before leaving.

Adults had been banded by K. Foerster and C. Collins (see Foerster 1987), allowing recognition of individuals. On eight evenings, mist nets were set at dusk at the cave entrance in order to capture adults and to obtain an indication of the population size, body masses, and morphological measurements. Measurements of adults from the study site were taken

TABLE 2
MORPHOLOGICAL MEASUREMENTS OF BLACK SWIFTS[a]

Feature	Mean	SD	N
Mass (g)	44.1	± 2.49	(16)
Tarsus length (mm)	14.5	± 0.56	(9)
Foot span (mm)	21.6	± 1.14	(9)
Gape (mm)	16	± 0.92	(14)
Exposed culmen (mm)	6.6	± 0.44	(14)
Head width (mm)	21.6	± 0.41	(14)
Wing (mm)	168.8	± 3.16	(16)
Extended wing (mm)	187.5	± 7.47	(15)
Outermost primary (mm)	127.3	± 2.56	(11)
Tail length (mm)	55.4	± 3.18	(15)

[a] Table follows the same sequence as in Fig. 1 A–J.

as described above (Table 2). To complement the field data, other data were gathered from museum specimens and egg data cards (see acknowledgments).

RESULTS AND DISCUSSION

Nests.—As with other cypseloidine species (Snow 1962; Collins 1968; Whitacre 1989; Marín and Stiles 1992, 1993), Black Swifts breed in close proximity to water. The nests studied near Idyllwild were in the dim interior of a single large cave and placed in small niches formed by ledges or knobs. Nests of the Black Swift are almost invariably located in dim, moist areas away from sunlight (Knorr 1950, 1961, 1962; Legg 1956; Foerster 1987), although four of five active nests found by Hunter and Baldwin (1962) in Montana received direct sunlight late in the afternoon.

The angle or position of the nest depended on the angle of the substrate, which varied from a flat surface to a 45° angle. Height above ground varied from 0.4 to 6 m. The nest shape varied from a half-cup or inverted cone to a cup-shape depending on the substrate. The former was observed when the nest was attached to a knob, the latter shape when it was placed on a ledge. External measurements were highly variable, depending on substrate and manner of attachment, but the internal diameter was relatively uniform, averaging 9.0 cm (N = 12). Hunter and Baldwin (1962) reported 9.1 cm for Montana and Holroyd and Holroyd (1987) 8.5 × 7 cm for British Columbia, Canada. The nests near Idyllwild (N = 12) were composed entirely of mosses, with some mud in the base and a few pine needles in the lining. One species of moss (*Scleropodium touretii*) was identified on the nests, although others may occur. However, Foerster (1987) found the same species of moss in five of six nests. This species

of moss was found growing commonly in compact to spreading mats in soil on the cave walls.

Although mosses are the main nesting material in most Black Swift nests, it is not the only material reported. In California, coastal nests differ greatly from inland nests. Indeed, the first two nests described by Vrooman (1901, 1905) differed from many; he found in both cases that the egg was laid in a slight depression in the mud on sea-cliffs. Furthermore, Vrooman (1905) stated that "there was no nesting material whatever." Another coastal nest found in a sea cave was constructed of 90% green seaweed (Legg 1956). Egg data cards for the coastal nests show great variation in nest material and construction. Those from the California coast in Santa Cruz County (N = 51) indicated that 26% of the nests were built from seaweed, 4% were a mix of mosses and seaweed, 35% were composed of mosses, and 35% had no nest material at all. The inland nests (N = 43) all involved nesting material, especially mosses, although fern tips were mentioned for some. Pine needles as lining material were commonly mentioned in the egg-data cards for the inland nests; these were found in all nests in the San Jacinto Mountains.

I observed nest construction in detail only once, on 8 June 1991. One bird was observed gathering moss from the cave wall. This individual had lost its nest during the previous winter. The bird clung to the wall, wings extended, and gathered moss with its bill, similar to the manner of other cypseloidines (cf Marín and Stiles 1992). The bird did not use much nesting material, and the nest was built on a flat surface. I am not certain how many days it took to build its nest, but when first observed, construction had already begun, and by June 16 the nest had a fresh egg. During this study, each pair reused its old nest every year, adding small amounts of new material. There is only one other account of nest construction, on an egg data card (MVZ # 4309); according to the collector, C. P. Streator, "the nest was built in four days."

Based on Foerster's (1987) work, the San Jacinto Mountain nests had been used for ten years or more. During the three years that I worked there, the exact same sites were used every year and by the same birds; however, some birds rotated position or changed mates. A nest that Foerster studied in 1985–1986 was present in 1990. During 1991, early in the season there was a heavy rain and water destroyed the nest. The same bird constructed a new nest higher in the cave on a ledge that possibly was an older, unoccupied site. The only mate change recorded in the cave occurred in 1992, when a first-time breeder, present the previous year as a possible floater, mated with an older bird that already had a nesting site from previous years.

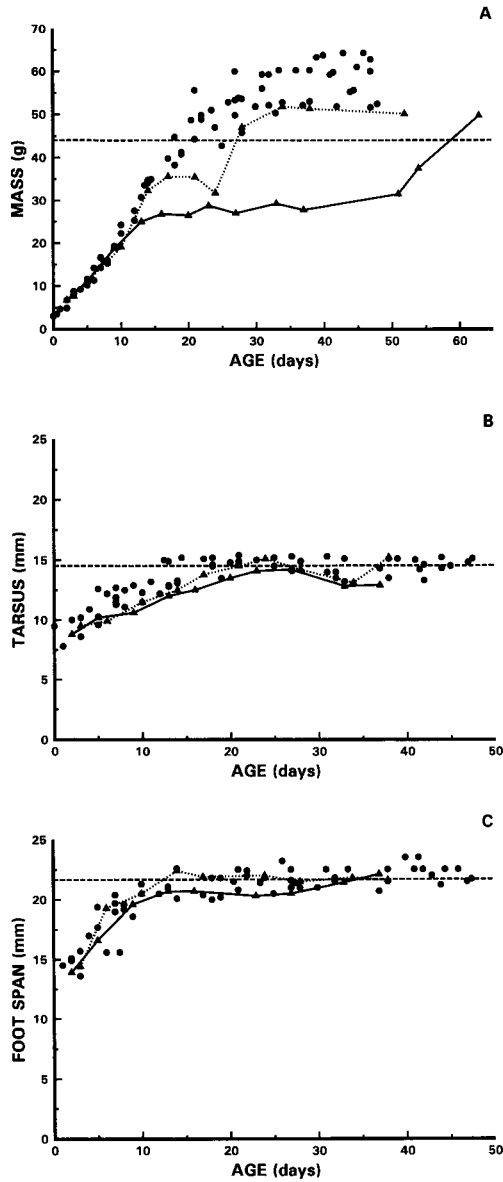*Eggs and incubation.* After nests were completed, roughly 10–14 days

FIG. 1.   Growth curves of ten parameters in the Black Swift. Dashed horizontal lines represent average adult size and correspond to numbers from Table 2. Dotted and solid lines in the growth curve represent the twins experiment (see text).
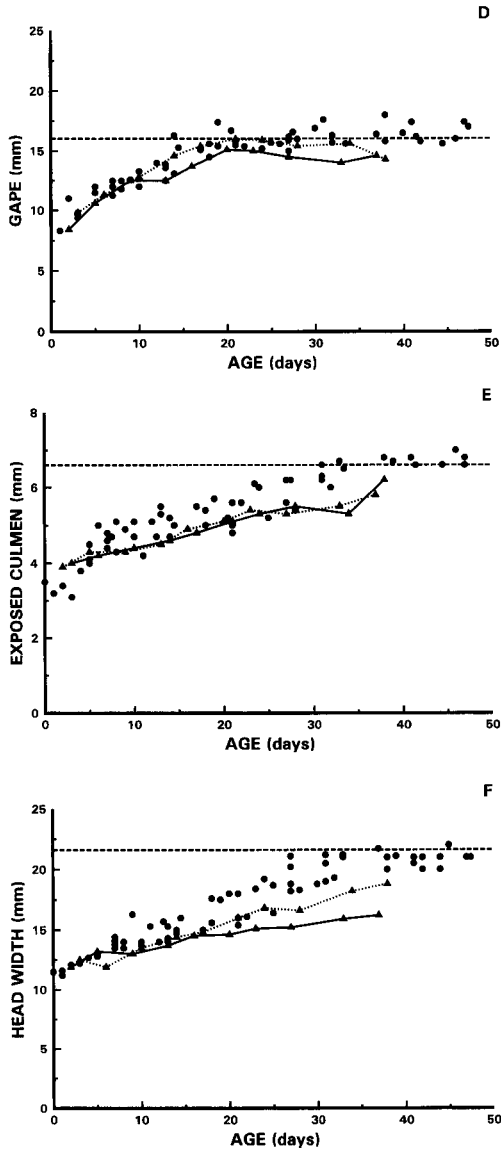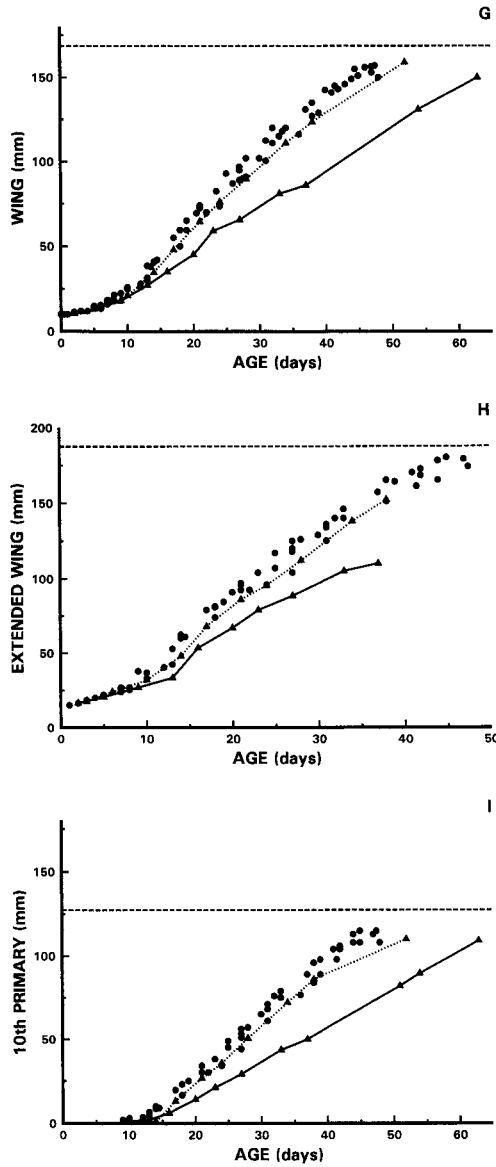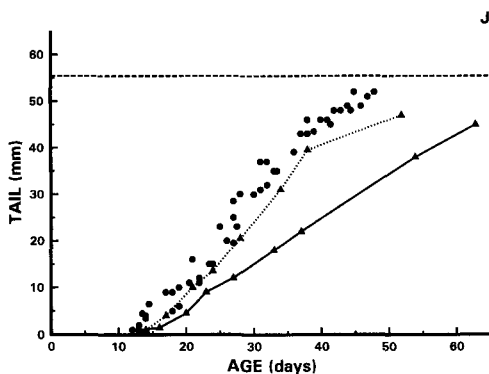
FIG. 1.   Continued.

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elapsed before eggs were laid. During this period, I observed on six oc-
casions one of the birds, presumably the female, spent more time on the
nest, although it is uncertain how many hours were involved. This pair
member behaved in each case as if it were incubating, but no egg was
found.

All clutches observed at this site were of single eggs (N = 16), as
elsewhere in the species (e.g., Bent 1940, Foerster 1987). The eggs (N =
50) were dull white, and their shapes were subelliptical (56%), long sub-
elliptical (20%), oval (16%), or long oval (8%). For egg measurements
and mass see Table 1.

During the three years of study, all eggs (N = 16) were laid in June,
most by mid-June. Twice, once in 1990 and once in 1991, eggs were lost,
and although both eggs were fresh, they were not replaced. I was unable
to fully document incubation pattern, but incubation spells were long,
often more than 4 h. Incubation periods at six nests averaged 24 days
(range = 23–26 d). The only two previous reports on the incubation
period of the Black Swift (Murphy 1951, Legg 1956) estimated the in-
cubation period at 24 and 27 days, from one nest each, in Colorado and
California, respectively.

The eggs were never left uncovered, and the birds sat closely when
nests were approached. Mates shared incubation and brooding. Data from
four nests indicated that one member of a pair, presumably the female,
spent somewhat more time incubating: in the first nest, one of the mates
was hand caught six of nine times or 66% of the time, in the second nest
three of five times or 66.6% of the time, on third nest one of the birds
was captured seven of 11 times or 63.3% of the time, and in the fourth
nest four of eight or 50% of the time.

I studied the full development of nine nestlings, not including those

used in twinning experiments (see below). Two nestlings were followed from hatching day zero, two from day one, and three from within 2–5 days of hatching through fledging (Fig. 1A–J). The nestlings at hatching were naked and helpless, with eyes closed, and they weighed 3.1–3.5 g. The hatched eggshells were not removed by the parents, but either rolled out or stayed near the nest until degradation. At hatching, the nestlings' skin was flesh colored ventrally and tinged gray dorsally with subcutaneous black dots. The feet were soft flesh-pink in color, with gray, white-tipped claws, and were well developed (64.6% of adult size). The bill was blackish with a conspicuous white egg-tooth. Disappearance of the egg-tooth varied from age 18 to 33 days (mean = 24 days, N = 6). Body mass increased almost linearly from hatching until reaching about 113% of adult size (Fig. 1A). Adult mass was attained at age 18 to 22 days (mean = 20, N = 7). Maximum body mass was reached, on average, by day 39 (range = 33–45 days, N = 7). No swifts fledged at less than 50 g or 113% of adult size. The maximum mass reached by any nestling was 64.3 g or 148% of adult mass. Tarsus, foot span, and gape all reached adult size at an early age (Fig. 1B–D).

The eyes were barely open by day 7–8 and fully open by day 14–16. Semiplumes were sprouting over the head, back, and upper chest by 6–7 days. By 13–14 days, the nestlings were nearly fully covered with dark-gray, downlike semiplumes, but these were still growing on the sides of the forehead which were noticeably naked. These downlike semiplumes (near 83 Dark Neutral Gray) were darker than those of *Streptoprocne* spp. but lighter than those of other *Cypseloides* spp. (cf Marín and Stiles 1992). The forehead feathers began to emerge between 18–21 days. The secondaries emerged by 8–10 days, broke their sheaths by day 13, and were fully grown by 32–33 days. The outer primaries began to emerge by day 13 and grew steadily until fledging (Fig. 1G). Nestlings usually fledged by day 48, or when the 8th primary was fully grown and the 10th was 90% of adult size (Fig. 1I). The rectrices began to sprout by age 12–14 days, and sheaths were broken by 20–22 days. The rectrices reached about 90% of adult size by fledging time (Fig. 1J). The fledgling plumage was uniformly blackish (between 82 Blackish Neutral Gray and 119 Sepia), with most feathers having a white edging that produced a scalloped effect. The only feathers or areas without white edging were the two outermost primaries, the outermost underwing primary coverts, and those of the nape, hindneck, throat, upper breast, and the side of the neck. Most white edging wore away rapidly, but in some areas, primarily the abdomen, vent and crissum, the white tipping was broader, and based on museum specimens, I suspect that this would persist for at least three years and possibly more.

Twinning experiment—To determine the capacity of the parent to feed a supranormal brood size and to test the growth constraints imposed on the chick, I conducted twinning experiments. In cypseloidine swifts, and probably in most swifts, brooding seems to be a critical factor in the first 13–14 days of life, or until acquisition of thermoregulatory ability. Foerster (1987) noted that the body temperature of a 4-day-old Black Swift dropped 15°C in 28 minutes. Collins (1968) found that the body temperature of the Chestnut-collared Swift (*Streptoprocne rutila*), also a cypseloidine, approached an asymptote, hence thermoregulatory ability, by age 12–13 days, coinciding with the full growth of the downlike semiplumes. In several species of swifts, mortality is higher in the first 10–13 days of life (Lack and Lack 1951, Tarburton 1986, Francis 1987, Malacarne and Cucco 1991). Following these parameters as a guideline, I conducted experiments in two parts: (1) at the point when I assumed that young had acquired thermoregulatory ability (or close to it) at age 13–14 days, when the semiplumes were well grown, and (2) before 13–14 days, when they were assumed not to be homeothermic. The first set of twins (the added nestling A, dotted line, and the original nestling B, solid line, on Fig. 1A–J) were within a half day of being the same age. All parameters were measured from hatching until age 38, but only four parameters were measured until fledging. During the first 10 days of the experiment, fluctuations of the growth curve implied that nestlings competed for food (Fig. 1A). From the 10th day of the experiment (at 25 days of age) to the 38th day, the larger nestling (A) became aggressively dominant. From 25 days of age onward, nestling B began to shiver as soon as it was separated from its sibling, an indication that most energy or food was allocated for growth rather than temperature regulation. Nestling A increased its body mass almost linearly, reaching asymptotic mass at age 34. Nestling B remained at about 25–28 g, for about 39 days, until nestling A fledged at age 52 (Fig. 1A). Nestling A was only four days behind the normal nestling period, fledging at 50.1 g (or 113% of adult size). Nestling B increased its body mass linearly (1.65 g/day) from day 52 to 63, reaching the same fledging mass as nestling A in 11 days. The minimum fledging mass for this species seems to be ca 50 g.

Surprisingly, both nestlings grew within the normal measurements for some parameters, e.g., tarsus and foot span, (Fig. 1B, C). Gape, exposed culmen, and especially head width, grew somewhat more slowly (Fig. 1D–F). From day 11 onward, nestling B lapsed progressively behind in wing and tail measurements (Fig. 1G–J), reaching fledging mass and size dimentions 15 days later than the average nestling.

The second twinning experiment was undertaken when the nestlings were eight days old. The added nestling disappeared within three days,

probably removed by a human. The small number of nests precluded additional experimentation.

Fledging.—Four Black Swift nestlings fledged in the morning before 8:00 h. Morning departure, often before 8:00 h, is typical in the Common Swift (*Apus apus*) and also in many other swift species (reviewed by Lack 1973). The cue for fledging might be attainment of a particular mass. In the twinning experiment, the parents did not abandon the second nestling until it reached the same mass as its artificial sib.

In central and southern California, the Black Swift seems to migrate primarily in small groups, and migration lasts for about a month from late August to mid September (Rathbun 1925, Marín, unpubl. data). At San Jacinto, most birds ceased to frequent the cave during the last week of August or first week of September, with the latest observation in all three years being 9 September. Foerster (1987) found a similar chronology for southern California. Once youngs fledged, no adult or young birds were observed in the cave. Because suitable roost sites are limited, it seems likely that if the birds had remained anywhere in the vicinity after fledging, they would have continued to use the cave as a roost. Therefore, it seems more likely that all birds, including young, left for migration as soon as the young fledged. To date there is no evidence that Black Swifts roost aerially as does the Common Swift (*Apus apus*) at times. In the latter species the young do not return to the nest after they fledge, presumably migrating immediately (Lack and Lack 1952). A juvenal Common Swift banded in Britain that fledged on 31 July was found four days later 1275 km away in Spain (Cramp 1985).

The location of the wintering grounds of the Black Swift is still a mystery; however, the recent records by Stiles and Negret (1994) in Colombia suggests that they winter much farther south than previously thought.

Knorr (1961) proposed five ecological requirements for nest sites of the Black Swift: water, high relief, inaccessibility, unobstructed flyways, and darkness. Marín and Stiles (1992) reexamined these "requirements" and concluded that cypseloidine swifts breed in close proximity to water for two major reasons: (1) to have a more constant environment to ameliorate daily temperature changes around the nest and (2) to have high humidity for nest attachment to the substrate. Three of Knorr's (1961) five requirements (high relief, inaccessibility to the nest by terrestrial predators, and unobstructed flyways) were believed to be secondary consequences of nesting behind or next to waterfalls.

The nests examined in this study varied from 0.5 to 8 m or more in height above the cave floor. During 1990, a very dry year, we found remains of one adult from a low nest, probably eaten by a terrestrial

predator, as the remains were well inside the cavity. Some nests were far from "a clear flyway," and the birds maneuver well in enclosed spaces. Lastly, there appears to be no reason why darkness *per se* is not also simply a byproduct of site selection.

The internal temperature of the cave throughout the field season fluctuated no more than 2°C. Readings taken at night and very early in the morning differed only 1–2°C from those taken during the day. Furthermore, cave temperatures throughout the season were just above the minimum external temperature. External temperatures fluctuated daily on the order of 10–20°C. Similarly, Foerster (1987) reported steady temperatures for the same site. He also reported an increase in temperature between months, with a significant difference between the upper and lower nests in the cave: throughout the season upper nests had a maximum temperature of 9.5°C and lower nests, 5.5°C. Foerster (1987) reported a range of humidity from 54 to 96% throughout the season. I took only a few humidity readings, mainly during the early part of the 1992 season; these were in the 80–90% range but decreased as the summer advanced. Most nests were in the lower, wetter part of the cave, where temperature variation was less. This effect certainly would assist nestlings in maintaining a steady body temperature when adults are away from the nest.

Dawson (1915), while collecting nests of Black Swifts along the coast in Santa Cruz County, California, noted that the area had the same cold and moisture found at higher elevations. Most egg collectors remarked on the egg data cards how damp and muddy the nest sites were. All the inland nests were made of mosses, and the common characteristics were "wet" and "green"; these same words were applied to the coastal nests made of seaweed. On the data cards for the coastal nests with no nest materials, words such as "damp" and "muddy" were mentioned frequently. In fact, all sites so far reported present the same microclimatic conditions.

Several California egg collectors, including as L. T. Stevens, W. E. Griffee, and A. G. Vrooman, visited particular Black Swift nesting sites for many years and reported that these sites were regularly used by the species. For example, L. T. Stevens wrote on an egg data card that the same nest was used for 21 years, and W. E. Griffee reported one used for 13 years or more. Collins and Foerster (1995) reported a bird using the same site for at least 10 years. Although there is no evidence that the same bird used the same nest, the specific site of the nest seems to be a critical factor. Nest microclimate influences daily energy requirements which can be crucial to the adult during incubation and to the young when adults are away foraging (Gill 1995).

Although the humid nest site is important for diel temperature amelio-

ration for the Black Swift, it is evidently not as important for attachment of the nest to the substrate as is the case for the Spot-fronted Swift (*Cypseloides cherriei*) and the Chestnut-collared Swift (*Streptoprocne rutila*) (see Marín and Stiles 1992), because nest placement and construction varies greatly in Black Swifts. Most nests, particularly the coastal ones, were built on flat surfaces; 35% (N = 49) of these nests had no structure built by the swifts. This may serve to eliminate time and energy involved in nest construction, because nests built at an angle would need more specific construction material and probably would take more time in the accretion of the mosses (Marín and Stiles 1992). The lack of nest construction and nest site variability may also result from lack of competition with other species of cypseloidines for nest sites or from strong intraspecific competition for quality nest sites. Lack of nest construction has been found also for the White-naped Swift (*S. semicollaris*) and the White-collared Swift (*S. zonaris*) in Mexico (Whitacre 1989) and for the White-collared Swift in Costa Rica (Marín and Stiles 1992); but for these species lack of nest construction might reflect intraspecific rather than interspecific competition for quality sites. However, because all cypseloidines nest in similar sites, nest substrate, angle and body mass can be an important means of partitioning nest sites (Whitacre 1989, Marín and Stiles 1992).

The Black Swift lays a single egg, and, if this egg is lost, there is no attempt to replace it. Single-broodedness is rare among birds and occurs in some seabirds and some raptors (Wynne-Edwards 1955). The two one-egg cypseloidines, the sedentary tropical species, White-chinned and Spot-fronted swifts studied in Costa Rica by Marín and Stiles (1992), replaced lost eggs within a month or so. Black Swift egg mass was lighter relative to body mass (12.5%) than in these other one-egg *Cypseloides* spp. (16.4 and 16.7%, respectively, Marín and Stiles 1992). Thus the lack of egg replacement in the Black Swift may be related not to egg size but to the fact that the long incubation and nestling periods must be accomplished in a more restricted time period than in the tropical one-egg species.

As with other cypseloidines, Black Swift nestlings developed slowly, slower than the species of *Streptoprocne* but faster than other two *Cypseloides* species so far studied (see above). It is uncertain whether this is an effect of latitude or body size. The larger species in this group tend to grow faster, which is contrary to the Class Aves as a whole (Marín and Stiles 1992). In the Black Swift, different aspects of nestling growth fell into three basic patterns: non-linear measurements that acquired adult size within the first 10–15 days of life (Fig. 1A–D); non-linear measurements that reached adult size late in the breeding cycle (Fig. 1E, F); and linear measurements that reached adult size after fledging (Fig. 1G–J).

The first four measurements (Fig. 1A–D) were probably the most critical in acquiring adult size early in the nesting period. The initial fast growth of mass is probably linked to acquisition of homeothermy, whereas rapid growth of tarsus and foot span is associated with avoiding rolling out of the nest and that of gape size with intake of large food boluses.

Mass, wing, and tail length measured by Foerster (1987) presented a trend similar to that of the present work.

Manipulations to test the adaptive nature of clutch size and growth constraints have shown that many species of birds can raise an extra nestling (see below). However, experiments on species with small clutches have been conducted primarily on seabirds (reviewed by Ydenberg and Bertram 1989, Stearns 1992). The single experiment carried out on one-egg swifts showed that 29% of the manipulated nestlings survived, versus 76% in the control group (Lee and Kang 1994). Nevertheless, several experiments involving the addition of an extra nestling in swift species with a higher clutch size (2–3) (e.g., Perrins 1964; Bryant and Hails 1983; Tarburton 1987, 1990; Lee and Kang 1994) resulted in a range of nestling survival between 25–50% vs 58–96.5% in the control group. However the broad range of the results might be a sampling artifact, because sample size varied from two to 16 sets (ca 6–66 nestlings). The range of variation of nestling survival in two to three egg clutches (manipulated versus normal brood) is not as large as in one egg clutch species. Experiments on reducing the clutch size from two to one egg showed no major difference in survival or growth, in spite of the parents presumably having the capacity to provide extra food to the remaining nestling (Marín and Stiles 1992, Lee and Kang 1994).

Nestlings of many swift species store fat, and the fat storage capacity of the nestling might influence the upper mass limit during growth. If no major difference in growth occurs when brood size is reduced from two to one, the upper mass limit is probably imposed by food assimilation. The two one-egg clutch cypseloidines for which I have data, *C. cryptus* and *C. cherriei,* are tropical, non-migratory species, and they do not accumulate as much fat as *C. niger.* The maximum mass attained by nestlings of *C. cryptus* was 118.4% and *C. cherrie* was 111.7% of adult mass (Marín and Stiles 1992 and Marín, unpubl. data). While the maximum mass attained by *C. niger* nestlings was 148% of adult mass. The large quantities of fat accumulated by Common Swift (*Apus apus*) nestlings in England has been interpreted as an insurance against variable feeding and weather conditions (Lack and Lack 1951). However, for the Black Swift, this interpretation *per se* seems unsatisfactory, because weather conditions during the summer differ between England and the western United States, with far more rain in the former. Regardless, Lack's "insurance" hypoth-

esis against unpredictable food supplies should apply to all aerial feeders, although in different degrees. An additional factor that should be considered to explain energy storage is that nestlings of both species become independent from the parents for food as soon as they fledge. Furthermore, in both *A. apus* and *C. niger*, nestlings fledged early in the morning and none came back to roost at the nesting site, presumably they had migrated (Lack and Lack 1952, this study). At least in the Black Swift there seems to be a lower mass limit to fledging, which is still ca 113% of adult mass (see above); thus the extra stored energy would be needed for the first few days of independence or possibly as a "starter" supply of energy for the presumed migration. If migration occurs immediately, the storage of energy for migration while in the nest would be more efficient than waiting a further period of time to store energy. In other migratory swift species, at least in the New World, e.g., Chimney Swift (*Chaetura pelagica*), the nestlings return to roost to their nesting site for a few days, and they do not accumulate as much fat (Fischer 1958). Furthermore, they stay in communal roosts for at least two months before departure to the south (Marín, unpubl. data). In the Black Swift, the nestlings grew fast for the first days, and size of the nestlings was 75% of adult size when they became thermally independent. This fast growth and high energy storage also probably allows the nestling to survive low ambient temperatures and become thermally independent as early as possible. This permits the parents to conduct longer food-gathering trips. Thus, fat storage in Black Swift nestlings probably serves several functions.

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