Airbirds: Adaptative Strategies to the Aerial Lifestyle From a Life History Perspective.

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AIRBIRDS: ADAPTATIVE STRATEGIES TO THE AERIAL LIFE STYLE
FROM A LIFE-HISTORY PERSPECTIVE

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in
The Department of Zoology and Physiology

by
Manuel Marin-Aspillaga
B.S., California State University at Long Beach, 1991
December 1998
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ABSTRACT

"Airbirds" are defined as those birds that are adapted to almost constant life on the wing and do not perch, except for breeding and roosting. They use the air as the only medium in which to find and gather food. One taxon meets that definition: the swifts (Apodidae). Foraging zones of airbirds can be segregated in terms of clutch size, commuting foraging distance, nestling period, and nestling feeding rate.

This study looked at foraging behavior and nestling diet, incubation patterns and mode of development in cypseloidine swifts, that as a group has extreme life history patterns.

In a temperate one-egg clutch cypseloidine species, winged ants comprised 91% of nestling diet. Parents made foraging trips (3-7 h) at early hours and in the afternoon (6-8 h). Morning trips were observed only during the first half of the nestling period. During the second half, adults made one foraging trip per day for about 12 hrs. The morning trips presumably are for feeding the young, whereas the long afternoon bouts are also for self-maintenance. As nestling age increased, so did food bolus mass.

Based on a 12 h daylight, a one-egg species neglected the egg 50 % of the time and incubated for 29 days. A two-egg species neglected the eggs 32 % of the time and incubated for 25 days. Longer incubation and slower growth of the one-egg versus the two-egg clutch might be explained in terms of greater time away from the nest in foraging time.
Foraging and incubation patterns in cypseloidine swifts are analogous to procellariiform seabirds. The time scale for cypseloidine swifts is in hours, whereas for procellariiform seabirds, it is in days. Because they face similar constraints with respect to food and nest sites, convergence in their life-history patterns follows.

Postnatal growth pattern of Californian and Costarican subspecies of *Cypseloides niger* were compared. The Costarican subspecies has a longer incubation period, but both had roughly equal nestling periods. Nestlings of the Californian subspecies grew faster, as predicted by the general theory in growth rates. However, it contradicts the rule that smaller-bodied taxa grow faster than larger-bodied ones.
CHAPTER 1

INTRODUCTION

This dissertation focuses on the similarities in life-history patterns between two groups of birds: cypseloidine swifts (Apodidae) and procellariiform seabirds (Procellariformes). Procellariiform seabirds share a suite of unique and extreme life-history traits, and these features have been linked to their marine environment and their food sources (Ricklefs 1979, Warham 1990). Cypseloidine swifts also have many extreme life-history parameters comparable to those of procellariiform seabirds (Marín and Stiles 1992).

Swifts are the most aerial of all birds (Chantler and Driessens 1995). I refer to swifts as "airbirds" owing to their aerial life style. I define "airbirds" as those birds that are adapted to almost constant life on the wing. An important departure of "airbirds" from other birds is that they do not perch, except for breeding and roosting activities. Some even "roost" in the air (Lack 1958). These birds use the air as the only medium in which to find and gather food. One taxon of birds satisfy "airbirds" definition: the swifts, family Apodidae, represented by about 90-100 species (Chantler and Driessens 1995). Many groups of birds, such as kites (Accipitridae), crested swifts (Hemiprocnidae), nighthawks (Chordeilinae), and swallows and martins (Hirundinidae), are intermediate between perching birds and airbirds. These intermediate groups use the air extensively for feeding purposes, but they often perch.
Swifts have an almost worldwide distribution, except for the extreme latitudes. The feathers of swifts are compact. The plumage is predominantly in shades of black, grey, or brown. Some have striking black and white patterns, whereas others have subtle white markings, and only two species have reddish or chestnut coloration in their plumage. Swifts range in size from the small Pygmy Palm-Swift, *Tachornis furcata*, (ca. 8 g, 210-220 mm wing span) to the large White-naped Swift, *Streptoprocne semicollaris* (ca.160-210 g, 550-600 mm wing span). All swift species have a similar body shape: they are compact with a short neck, a short culmen with a wide gape, and small but strong feet. Most have long and pointed wings, although some species (relative to other swifts) have rather short and rounded wings (e.g., African Spine-tails *Neafrapus* spp.). Tails vary from very short and square to long and deeply forked (Chantler and Driessens 1995).

Most ecological studies, including those on birds, have focused on terrestrial and aquatic organisms. From an ornithological point of view, little attention has been paid to swifts. Because, swifts are difficult to observe and identify in the field. There are many cryptic species and because access to nesting sites is often difficult, large gaps exist in our knowledge about the basic biology of many swift species. Members of the subfamily Cypseloidinae are particularly difficult to study because they typically fly rapidly, often erratically, and usually high above the ground. Furthermore, they nest in deep gorges, caves, and next to or behind waterfalls (Marín and Stiles 1992).
Habitats are classified in time and space (Begon et al. 1986). The habitat of airbirds is three-dimensionally continuous, but seasonal and unpredictable. With the obvious influence of habitat structure on foraging behavior, the unique habitat of swifts should strongly influence their foraging behavior and, therefore, their life-history patterns.

To study the influence of foraging behavior on life-history patterns within airbirds, I propose a division of foraging zones for airbirds based on distance from a central place, the nest. Distance to food sources has a major influence on the general ecology and mode of nestling development in birds (Case 1978). Airbird foraging zones should be delimited by a combination of foraging distance from the nest and height above the ground, i.e., the "total commuting distance" to the nest. Because the lower troposphere has no strict layer boundaries (Byers 1959), strict categorization of airbirds with respect to feeding zone is difficult. Because adults are constrained with respect to food delivery to the nestlings, the zones are best categorized with respect to nestling feeding rate. The following categories of food delivery may afford the best typology for feeding zones (see Table 1.1): a) **HIGH FREQUENCY**: Species with a large clutch size of >3 eggs; short nestling period (30-40 days); birds usually forage close to the ground or tree tops, and within a few km from the nest. For example, for the Vaux’s Swift (*Chaetura vauxi*) with a clutch size of 5-6 eggs, Bull and Beckwick (1993) found that birds spent 60% of the time within 1 km from the nest and had a
TABLE 1.1. Relationship between clutch size and feeding rates in some swift species from the temperate zone.

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foraging radius of up to 5.4 km. These birds have a feeding rate more than 2.5 trips per hour; b) INTERMEDIATE FREQUENCY: Species with a clutch size of 2-3 eggs; nestling period of 40-47 days; birds forage 10-80 m above ground and several km away from the nest. These birds have a feeding rate of 2.5 trips or less per hour. For example, for the White-collared Swift (*Streptoprocne zonaris*), with a clutch size of 2 eggs, Whitacre (1991) found that the birds foraged over 25 km, but suspected a range of about 80 km; and c) LOW FREQUENCY: Species with single-egg clutches; long nestling period of 50-88 days; birds usually forage more than 50 m above the ground and gather food far from the nest. These birds have a feeding rate of fewer than 1 trip per hour. Unfortunately, I do not have any data on foraging radius for any species in this category. The relationship between food-delivery rate and clutch size occurs not only at the interspecific level but also to a lesser degree intraspecifically (Figure 1.1).

This dissertation focuses in cypseloidine swifts (Aves: Apodiformes: Apodidae: Cypseloidinae). The cypseloidine swifts are a distinctive group of 12-13 species from the Neotropics, and they share a particular suite of life-history patterns and ecological correlates: low clutch size, long incubation and nestling periods, relatively large size at hatching, slow growth pattern (with large fat storage by the nestlings, which exceed the adults in body mass), egg neglect, long life span, elongation of esophagus for long-distance food transport, nesting and roosting

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FIGURE 1.1. Relationship between arrivals per hour and number of nestlings at the nest, for the Common Swift, an intermediate frequency species. ($r^2 = 0.98$, $P = 0.0006$, $n = 6$; data from Pellantova (1981), representing 2000 observations from two consecutive years.

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Arrivals per hour vs. Number of nestlings
associated primarily with waterfalls, no saliva used in nest construction, "living" nests (nests composed of living plant material, and a diet high in lipids (Marín and Stiles 1992, Collins 1998). In this dissertation, I investigated three parameters of their life-history: foraging behavior, incubation patterns, and mode of development.

The unusual life-history patterns of cypseloidine swifts are comparable to those of procellariiform seabirds. I hypothesize that this similarity is due to convergent evolution between airbirds and seabirds, which are animals that differ in morphology (except for some resemblance in wing shape and ancestry. Although seabirds and airbirds live in different habitats, their habitats are similar in the dispersion pattern of resources: in that their food is patchily distributed and ephemeral. Lack (1948) was the first to notice some similarity in the growth rate patterns between the Common Swift (*Apus apus*) and the Manx Shearwater (*Puffinus puffinus*).

The independent evolution of structural, behavioral, or functional similarity in distantly related taxa, has been defined as convergent evolution (for recent definitions, see Lincoln et al. 1993, Ricklefs and Miles 1994). Most cases of convergent evolution had been studied in organisms from different lineages that have either behavioral or morphological similarities, usually as a result of living in similar habitats (for reviews, see Cody 1974, Cody and Diamond 1975, Pianka 1988, Wiens 1989). The convergence of similar traits in different lineages is one of the most powerful tests for adaptation (Brooks and McLennan 1991). In this study, I
approached a case of convergent evolution between airbirds and seabirds through the study of life-history patterns.

The procellariform seabirds share a distinctive suite of extreme life-history parameters: low clutch size, long incubation and nestling periods, relatively large size at birth, slow growth pattern, with large lipid storage by the nestlings, that exceed the adults body mass), and long life span (Ricklefs 1979, Warham 1990). The cypseloidine swifts have life-history parameters similar to those of procellariiform seabirds (Marín and Stiles 1992). Cypseloidine swifts are at the extreme end of the nest to food source continuum, having small clutch sizes and infrequent returns to the nest.

Some Old World swifts (Apodinae) are the best-studied swifts, and they can be placed in "intermediate frequency" category; however, some swiftlets (Collocalia sp.) and possibly other swifts whose nests are unknown should fit in the "low frequency" category. Airbird and seabird life-history patterns can be directly traced to their response to their food source. Each of the three main chapters documented one or more adaptation of cypseloidine swifts to the aerial environment and compared its resemblance with procellariiform seabirds.

The dispersion pattern of food for cypseloidine swifts (Whitacre 1991, Marín and Stiles 1992) and for procellariiform seabirds (Ashmole 1971, Ricklefs 1979, Warham 1996) is usually patchy and unpredictable, resulting in considerable search time and travel distance to and from the nest. Distance to the food source has a major
influence on the general ecology and mode of nestling development in seabirds
(Ricklefs 1979). Among the many adaptations to distant food supplies,
procellariiform seabirds have increased efficiency of transporting food to their young

The proposed division of foraging zones for airbirds is analogous to that for
seabirds: This analogy is best measured with respect to clutch size, foraging distance
to the nest, and nestling feeding rate (Figure 1.2). Wynne-Edwards (1935) divided
seabird habitat and primary foraging zone into three categories based on distance
from shore and water depth: 1) INSHORE ZONE extending from coastline to ca. 8 km
offshore; 2) OFFSHORE ZONE extending from ca. 8 km to the continental shelf; and 3)
PELAGIC ZONE starting at the continental shelf and extending to the deep ocean.

Because the inshore and offshore zones are within the neritic oceanic province, they
are often combined into a single "offshore" category (e.g., Ricklefs 1990). Other
authors, such as Lack (1967, 1968) and Cody (1973), have divided seabirds into
inshore (inshore and offshore of Wynne-Edwards 1935) and offshore (pelagic of
Wynne-Edwards 1935) feeders. Regardless of terminology, all these classifications
of foraging zones were applied to the breeding season in birds whose movements
were constrained by their young at the nest. Consequently, non-breeders might
forage in any zone without having to return to the nest or central place. Because of
post-breeding movements, dispersal, and migration, membership in a category
FIGURE 1.2. Foraging zones during the breeding season for airbirds, and seabirds departing from the nest. As number of nestlings increases, the demand for food at the nest is higher and, consequently, the adults return at a faster rate to feed the young. The foraging zones of airbirds are a combination of foraging distance from the nest and height above ground (dotted lines), which equals "the total commuting distance" to the nest. Although the foraging zones of seabirds are primarily distance from the nests, water depth with respect to foraging dives probably adds a second dimension to the zonation.
AIRBIRDS

SEABIRDS

INSHORE | OFFSHORE | PELAGIC

COMMUTING DISTANCE TO NEST

Low   High

FEEDING FREQUENCY

1   2/3   >3

CLUTCH SIZE

>3   2/3   1
might shift at other times of the year. Although the physical boundaries between categories are not strict, seabirds nevertheless seem to segregate fairly clearly into the categories with respect to feeding.

Field data on swifts are usually difficult to gather, because of their aerial life style, the extreme similarity in plumage of many species, and their nearly inaccessible nests. Therefore, most studies on swifts are based on small sample sizes and are restricted to basic biological aspects. Thus, many areas remain open for research and exploration in respect to this group of birds.

This dissertation is organized in journal style, so that each chapter can stand on its own. In Chapter 2, I use the temperate subspecies of the Black Swift (*Cypseloides niger borealis*) to examine the foraging patterns and nestling diet of a species with a single-egg clutch. In Chapter 3, I ask how foraging affects incubation patterns. I compare incubation periods and patterns in the Spot-fronted Swift (*Cypseloides cherriei*), which lays a single-egg clutch, to those of the Chestnut-collared Swift (*Streptoprocne rutila*), which lays a two-egg clutch. In Chapter 4, I compare Black Swift populations from tropical (Costa Rica) to those of temperate (California) latitudes. I analyzed whether the pattern of growth rate (high lipid accumulation by the nestling) and clutch size of a species is constant throughout its geographic range. In Chapter 5, I summarize my conclusions regarding the life-history patterns of airbirds (cypseloidine swifts) and compares those patterns to seabirds (procellariiform seabirds).
REFERENCES


Swifts catch airborne insects and ballooning spiders (e.g., Lack and Owen 1955, Whitacre 1991). During the breeding season, breeding cypseloidine swifts accumulate insects and arachnids in the pharynx continuing into the esophagus and bind them with saliva to produce a conglomerate of insects (Collins 1998). This food bolus is produced exclusively to feed the nestling(s). Food boluses have never been reported outside the breeding season. The insects in the food boluses remain intact, and therefore, food boluses are ideal for identifying and quantifying diets. Hespenheide (1975) pointed out that one difficulty in analyzing avian diets is knowing whether the number or the size of food items is more important. Some studies of the diet of New World swifts have addressed both parameters (e.g., Whitacre 1991); however, most have emphasized only one of the variables or were based on small sample sizes (e.g., Collins and Landy 1968, Hespenheide 1975, Foerster 1987, Bull and Beckwith 1993, Marín and Stiles 1993). Other authors have considered only the number of prey items (e.g., Beebe 1949, Rathbun 1925, Rowley and Orr, 1962, 1965, Marín and Stiles 1992). One problem in quantifying swift diets, in particular, is the source of prey samples, i.e., stomach contents versus food boluses. Stomach contents of adults are prey that the adult has eaten, whereas food boluses are fed to nestlings. Thus, examination of stomach contents or food boluses...
might produce different results. Because my focus was on the diet of Black Swift
nestlings, I used only food boluses.

The Black Swift (*Cypseloides niger*) is a member of the subfamily
Cypseloidinae (Apodiformes: Apodidae) which consists of 12-13 species that are
mostly tropical or subtropical in their breeding distribution. The Black Swift is
found locally in the West Indies, Middle America, and much of western North
America as far north as southeastern Alaska (Bent 1940, AOU 1957, 1983). For a
species with such a wide latitudinal distribution, quantitative data on diet and timing
of breeding are rare. Most of what is known about the Black Swift is limited to
breeding and distributional records (e.g., Vrooman 1901, 1905, Michael 1927, Dixon
This lack of information reflects the difficulty of studying this species because of its
aerial life style and its usually inaccessible nests. Here I present new information on
the diet and the timing of breeding of this species.

The Black Swift is a summer breeding visitor to western North America and,
like many migratory species in this region, has a restricted breeding season.
Furthermore, it has a large egg relative to its body mass, a single-egg clutch, is
single-brooded, and has a long incubation and nestling period (Marín 1997). These
factors are expected to constrain variation in the timing of breeding of the Black
Swift.
STUDY SITE AND METHODS

Most data were gathered during a study of the breeding biology of the Black Swift in the San Jacinto Mountains, Riverside Co., 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 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*).

The study site was a natural cave about 15 m deep and ca. 7-8 m high formed by the merging of large boulders in the North Fork of the San Jacinto River at 1500 m elevation 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.

The study site was visited 40 times, from May to September, 1990 to 1992. Observations of the birds in the cave were made in blocks of 4 to 7 hours, from 05:00 to 12:00, 12:00 to 19:00, or 19:00 to 23:00 h, throughout the breeding season.

Data on nestling diets were obtained from regurgitated food boluses from adult swifts captured upon arrival at the nest. The boluses were weighed...
immediately (to nearest 0.1 g; Pesola scale) and placed in a vial containing alcohol. Insects in the boluses were counted and measured to the nearest 0.1 millimeter with an optical micrometer under a microscope.

Ten boluses (n = 1179 prey items) were collected from different adults at different dates and years throughout the study to minimize nest disturbance. Seven boluses were collected in 1991 and three during 1992. Mass and time of collection were recorded for nine boluses. I measured the length of 15 randomly selected individual items per species in each bolus, and then used the average length as the mean of that species in the specific food bolus. Insects were sorted to "morphospecies" and identified to family level by using Borror and Delong (1970), Borror and White (1970), and Powell and Hogue (1979).

To assess timing of breeding, I combined data from my field observations (n = 20) with archived nest and eggs data cards (n = 67), along with data from museum study skins and the literature. To determine the length of the breeding season, I recorded the timing of egg laying and hatching, and the length of the fledgling periods. I restricted analyses of egg data cards to two areas in California: mountains (San Jacinto area) and coastal (Santa Cruz Co.). I compared the estimated hatching date from the egg data cards (Marín 1997) to my own field data on hatching dates gathered at San Jacinto, to look for potential discrepancies between actual dates and estimated dates from data cards. The incubation stage given in the egg data cards...
(e.g., fresh, commenced, advanced, etc.) was extrapolated by using the known days of the incubation stage from San Jacinto (24 days; Marín 1997). I candled 16 eggs at San Jacinto and determined that no egg of this species could be blown without significantly damaging or destroying the shell by day 16-18. Thus, any museum egg specimen of this species was unlikely to have been collected beyond 16-18 days of incubation. I estimated the duration of each stage visible through candling as: "fresh" (0 - 4/5 days) "veins and small embryo" (5 - 10 days), "embryo" (11 - 14 days), and "large embryo" (>15 days). These data were then used to infer incubation stage (from the data cards) and to estimate egg-laying dates. I used the known incubation and fledgling period (24 and 48 days, respectively; Marín 1997); the estimated laying, hatching, and fledging dates were compared and then combined with field data. The dates were separated by month, and each month was subdivided into early, middle, and late stages.

Rainfall data were gathered for each month for the years of study (1990-1992) and also for 1963-1973, from the Idyllwild Fire Department weather station, ca. 1.5 km from study area (National Oceanic and Atmospheric Administration 1991, 1992) (Figure 2.1).

I was able to individually identify adults because they were already banded by C. Collins and K. Foerster (see Foerster 1987).
FIGURE 2.1. Rainfall at Idyllwild weather station. The long-term average monthly rainfall is from 1963-1973, and the mean monthly rainfall is for the years of study. The horizontal bar represents the breeding season, which is in the middle of the dry season, in contrast to tropical cypseloidines.
RESULTS

Nestling diet and foraging

All boluses were composed of one predominant prey species, suggesting that the birds had fed on swarming species, or highly localized prey. Winged ants were the majority of prey items (91%; Table 2.1). In 10 boluses the average proportion of female winged ants was 79.5 % (range 20 - 100%; n = 1179 prey items). Sexual dimorphism in ants accounted for prey size differences among boluses. Male ants were smaller, and their size ranged from 2 to 6 mm, whereas females ranged from 6 to 14 mm. Sometimes, a bolus contained a small number of female ants, but those ants were the largest prey. Thus, female winged ants formed the highest volume/prey ratio in all boluses. The average measurable prey size was 7.4 mm (range 1.8 - 14.5 mm; n = 1154). Three main size classes were found in the boluses: 6 mm (33%), 8 mm (39%), and 13 mm (12.2%; Figure 2.2). However, two length categories (6 and 8 mm) made up the bulk of the samples. Because only a few prey taxa were represented in the diet, size frequencies for all prey species follow a similar pattern.

Nestling age and bolus mass were positively correlated ($r^2 = 0.93, P = 0.00006, n = 10$; Figure 2.3). No significant correlation was found between mean prey size per bolus and chick age ($r^2 = 0.08, P = 0.82$) or mass per bolus ($r^2 = 0.04, P = 0.89, n = 10$). No individual prey item was weighed, but female winged ants were likely to be the heaviest prey items because they were the largest. During the second half of the nestling period, I never saw adults feed young in the morning. As
nestlings became older, it seemed that they were fed mainly late in the evening (Figure 2.4). Other nestlings of unknown exact age, but definitely older than 30 days, were observed being feed late in the evening between 18:30 - 20:00 h. However, because it was not possible to determine their exact age, I excluded them from the analysis. Nevertheless, the pattern seems to be, a positive relationship between nestling age and bolus mass, and a negative relationship between nestling age and feeding rate (Figures 2.3 and 2.4).

Data gathered from adults that were feeding young at the nest showed two clusters of feeding times: between 8:30 and 12:30 and after 18:30 h (Figure 2.4). The birds usually left the cave between 05:30 and 06:30. This observation implies that they spent 3 - 7 hours searching for food for the first feeding bout. For the second bout, the birds were away from the nest for a longer time: 6 - 8 hrs (Figure 2.4). I never observed nestlings being feed between 12:30 and 18:30, nor feeding of older nestlings in the morning.

I did not gather data late in the evening or at night during the early nestling stage, so that late arrivals and feeding at that stage are possible. If the intervals between feeding bouts were consistent through the season, then nestlings older than 30 days often must have waited for more than 12 hrs between meals.
<table>
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</tr>
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</table>
FIGURE 2.2. Frequency distribution of prey sizes taken by the Black Swift (*Cypseloides niger*) in southern California. Data are from 10 food boluses (n = 1154 prey items); prey size categories are: 0.5-1.5 mm=1; 1.6-2.5 mm=2; 2.6-3.5 mm=3; etc.
FIGURE 2.3. Relationship between bolus mass and nestling age
($r^2 = 0.93; P = 0.00006$)
FIGURE 2.4. Time of feeding the young and nestling age. None of the birds were observed feeding young between the two feeding clusters or during early morning at a later age. Other not accessible nestlings, not quantified, but older than 30 days, were observed being fed late in the evening between 18:30 and 20:00 h.
Breeding season

Hatching dates were the main variables used to compare the timing of breeding between a mountain site (San Jacinto area) and a coastal site (Santa Cruz area). No significant differences were found between the coastal and mountain sites in the timing of hatching (Fisher's exact Test (2-tailed); $P = 0.36$). Therefore, I concluded that it was safe to combine both field and museum data for coastal and interior southern California. The results showed a distribution of dates with little spread in each category (Figure 2.5). Most eggs were laid during mid-June (40%), although 30% were laid during late June (Figure 2.5). The earliest laying date was estimated to be 18 May, from an egg set collected in 1960 near Santa Cruz, California. The latest date for egg laying on the data cards was estimated to be 12 July 1921 and from the same site as the earliest date. Some of the observed variation might be due to inter-year differences, which is difficult to evaluate with the present data are. Nevertheless, most eggs (81%) had an estimated laying date in June. The earliest estimated date for hatching was about 11 June (same nest as above), and the latest estimated date was about 5 August, also from the same site as the previous nests. In total, 89% of the hatching dates were in July; 24% of the estimated hatching dates were during the first 10 days of July and 53% during the middle third of July. Sixty percent of the young were estimated to fledge during mid to late August and 29% during the first 10 days of September. The highest proportion of
fledging (78%) was estimated to occur between late August and early September (Figure 2.5).

**DISCUSSION**

Contrary to most, if not all tropical cypseloidines, the southern California populations of the Black Swift breed during the dry season (Figure 2.1). For the small, tropical cypseloidine swifts, rainfall itself can be as important a stimulus as food in initiating breeding. For the tropical cypseloidines, moisture is needed to keep the appropriate conditions for nest "growth" and maintenance (Marín and Stiles 1992). Many Black Swifts did not build a nest at all and instead laid eggs directly on ledges, especially at the coastal sites (Marín 1997). This behavior might be related to the lack of the proper nesting materials, such as mosses and liverworths.

The breeding season of the Black Swift in southern California is spread over a 4½ - 5 months (Foerster 1987, Marín 1997). Lack (1954, 1968) observed that breeding in most species of birds is timed to occur when food is most abundant, especially in temperate regions.

In the western United States, Chapman (1954) noted that ants swarmed from May through September and that the peak of ant swarming was July. The observed peak of egg hatching in Black Swifts was also July coinciding with the peak of ant swarming (Figure 2.6). These data support Holroyd and Jalkotzy's [in Campbell et al. 1990] suggestion that the breeding of the Black Swift in southwestern Canada was timed to the swarming of flying ants (Hymenoptera). Chapman (1954) found that
FIGURE 2.5. Distribution of estimated dates of egg laying (unshaded bars), hatching (black bars), and fledging (shaded on bars) of Black Swifts in southern California. Data are primarily from egg data cards; months are subdivided into roughly 10-day periods, (E) early, (M) middle, and (L) Late.
ants in the western U.S. congregated in large numbers on mountain and ridge tops and that swarming lasted several days. The peak time of ant swarming observed by Chapman was from 7:00 to 14:00 h and coincides with the first period of shorter feeding bouts in the Black Swifts (Figure 2.4).

Collins and Landy (1968) and Foerster (1987) reported the only available prey sizes for this species, and the former study was based on a single bolus (n = 278 prey items). Foerster (1987) reported average prey sizes from two boluses (n = 289 prey items) as 9.9 and 10.2 mm, slightly larger than my averages; he did not report sizes smaller than 7 mm or larger than 13 mm. Foerster (1987) speculated on prey size selection by the swifts; however, I observed 46.5% percent of prey items below 7 mm and above 13 mm (n = 1179 prey items, 10 boluses). The wide size variation in the data from this and other studies (Collins and Landy 1968, Foerster 1987) suggests that prey items given to the nestlings are selected not by size but by insect taxon. However, this is probably a consequence of feeding on insect swarms. The large preponderance of winged ants in the nestling diet is similar that of other cypseloidine swifts (Whitacre 1991).

The main diet of Black Swift nestlings at San Jacinto was winged ants by both volume and proportion. These ants have a high fat content; the percent fat per dry mass in alate ants ranges from 23.8 to 59.5% in females and from 3.3 to 9.6% in males (Taylor 1975, Redford and Dorea 1984). A nestling of any bird species, which is fed a diet rich in energy, is expected to accumulate large amounts of subcutaneous...
fat. Before fledging, the young Black Swift accumulates much visible subcutaneous fat and reaches up to 148% of adult body mass; furthermore it reaches adult mass at 37-40% of the nestling period (Marín 1997). The limited inter-year sampling by Foerster (1987) and this study suggests that the swifts at San Jacinto, may specialize in exploiting local concentrations of two to three ant species (Camponotus spp.) during the breeding season. Winged ants are a temporarily superabundant, patchily distributed, and ephemeral, but lipid-rich, food source. Other important prey items included Hemiptera and Homoptera (Table 2.1).

Rathbun (1925) reported a large diversity of arthropods at the family and species level in the diet of the Black Swift. His samples were collected at different times of the day and dates from May through September, and they were based on stomach contents, not food boluses. Thus, his samples represent a direct sample of adult diet, whereas boluses reflect nestling diet.

From scattered observations (e.g., Michael 1927, Smith 1928, Bent 1940, Collins 1998, Collins and Peterson 1998), there is a general agreement that Black Swift nestlings are fed at long intervals, primarily early in the morning and late in the afternoon or at night. My data corroborate those observations (Figure 2.4).

Furthermore, the alternation of long and short foraging trips resembles a recently described strategy of energy expenditure on foraging and food delivery in pelagic seabirds. Chaurand and Weimerskirch (1994) and Weimerskirch et al. (1994) showed that certain seabirds went on long trips primarily for food acquisition for
FIGURE 2.6. Frequency of Black Swift hatching and ant swarming in southern California. Data for ant swarming are from Chapman (1954).
themselves as well as food gathering for nestlings, whereas short trips were used primarily to gather food for the nestlings. Although the duration of trips for seabirds are measured in days, instead of in hours for swifts, the reasons for the differences between long and short trips are presumably the same.

As in seabirds, it is possible that the Black Swifts gain weight on the long trips and lose it overnight. Black Swifts have a high metabolic rate and lose on average 7.9% of body mass overnight (Marín unpubl. data). Thus, the need for the long foraging bout is in accordance with the energy storage hypothesis (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1994). Black Swifts migrate immediately after the nestlings fledge. Other species of swifts, e.g., Chaetura spp., stay a few months after breeding, presumably to store some energy for migration (Marín 1997). Accordingly, the long single foraging bout might also serve to store energy for migration, particularly during the second half of the nestling season.

As the Black Swift nestlings get older, it seems that the adults feed them only late at night (see above). Quantitative data on feeding rates or number of trips per day with respect to nestling age are scarce; however, declines in the number of trips per day with nestling age have been reported also in other swift species (Malacarne et al. 1992, Oniki et al. 1992).

Lack (1954, 1968) suggested that seabirds with long nestling periods and single-egg clutches were energy-limited. This energy limitation concerned food-finding, food-delivery, or both. Some swifts, particularly cypseloidines, have life-
history parameters similar to those of procellariiform seabirds (Lack and Lack 1951, Lack 1956, 1968, Marín and Stiles 1992, Marín 1993). For example, the Black Swift rears a single, slowly growing nestling, which suggests a constraint, in either finding or delivering food. Because Black Swift nestlings require a highly specialized diet to grow fast and acquire a size larger than the adult quickly, I predict that the major constraint is food finding.

REFERENCES


Whitacre, D. F. 1991. Studies of the ecology of the White-collared Swift (Streptoprocne zonaris) and White-naped Swift (S. semicollaris), and of patterns of adaptation among the swifts (Aves: Apodidae). Ph. D. Diss., Univ. of California, Davis.
CHAPTER 3

EGG NEGLECT IN THE APODIFORMES: AN ADAPTATION TO LIFE IN THE AERIAL ENVIRONMENT

The developmental period of an avian embryo from egg laying to hatching is termed the incubation period. Birds use a diversity of incubation strategies. For most birds, incubation requires almost uninterrupted parental attention to keep the eggs warm and for the embryo to develop and hatch (Drent 1973, Skutch 1976). For many species in which only a single parent incubates, egg neglect during short foraging bouts is commonplace (Skutch 1962, 1976). However, for most species, leaving the nest for a long period can be lethal to the embryo (Drent 1973).

Temporary egg neglect and cooling endurance by the embryo is widespread in procellariiform seabirds (Skutch 1976, Boersma and Wheelwright 1979, Warham 1990). Procellariiform seabirds are characterized by having a low clutch size, and long incubation and nestling periods (Lack 1967, 1968, Drent 1975, Warham 1990). Within the procellariiforms, length of incubation and length of nestling period are strongly correlated ($r^2 = 0.79; P < 0.001$) (Warham 1990). These authors interpreted this relationship as an adaptation to long foraging trips and to patchy and ephemeral food sources.

The Apodidae, with 90-100 species worldwide, is an avian group that shares the same foraging constraints as those of seabirds: they feed on unpredictable, patchy, and often ephemeral food supply (Marin and Stiles 1992). Among the
Apodidae, the cypseloidinae swifts, a group of 12-13 species from the Neotropics, resemble procellariiform seabirds in having small clutch sizes (1-2 eggs) and relatively long incubation and nestling periods (Skutch 1976, Marín and Stiles 1992). Brooks and McLennan (1991) pointed out that one of the most powerful tests for adaptation is convergence of similar traits in different lineages. Thus, cypseloidine swifts provide an independent test of the hypothesis that egg "neglect" is an adaptation to foraging conditions. To test this idea I used data from two species of cypseloidine swifts, the Spot-fronted Swift (*Cypseloides cherriei*) and the Chestnut-collared Swift (*Streptoprocne rutila*). The former is one of the rarest Neotropical swifts and is known from few localities (Marín and Stiles 1993). The latter is probably the second-most common and widespread cypseloidine swift. They have a similar body mass, 23g and 21g, respectively; however, they differ in clutch size, the former having a single-egg and the latter a two-egg clutch (Marín and Stiles 1992).

**STUDY AREA AND METHODS**

Data on swift incubation patterns were gathered in central Costa Rica from May through August of 1996 and 1997. The study site was about 13 km ENE of the city of San José, between 1800 and 2200 m elevation, along the Río Tiribí. The river forms the boundaries between San José and Cartago provinces. The study area was divided naturally in two areas along the river, an upper and a lower site. The upper study site was delimited upstream by a bridge on the Rancho Redondo - LLano
Grande Road and downstream by a 50-m high waterfall. The lower site was delimited downstream by a hydroelectric plant and upstream by a 30-m high waterfall. Meteorological data came from the "El Avance" and "Rancho Redondo" weather stations, less than 1 km west and 1 km east of the main study area, respectively. Detailed information on climate, topography and geology, and vegetation of the site can be found in Marin and Stiles (1992).

Measurements of egg mass and size are from samples from the study site and were complemented by additional samples from museum specimens. From the mean egg size, I calculated the mean egg mass, by using a mean of the constant \( k \), calculated by regression from the fresh egg mass. I used the formula \( M = k LB^2 \) to calculate the mean egg mass (see Hoyt 1979).

Nest attendance during incubation was measured by using a temperature data-logger that operated at a temperature range of -05° C to +37° C (Stow Away XTI-8K, made by ONSET Computer Corporation, Pocasset, Massachusetts). For each nest, an external sensor of the data logger was placed at the center of the nest, in a position where the sensor would be directly below or next to the egg. All data loggers were set up to record the temperature at 5-min. intervals. I determined the presence or absence of the bird on the nest by the drastic temperature changes registered on the data-logger. As soon as the bird left the nest, the temperature dropped quickly to ambient temperature, and as soon as it returned, the temperature increased quickly, usually by over 10 degrees. The number of days of useful data on
an individual nest varied from 12 to 33. This variability came about because nests were found at different stages of the incubation period, or because eggs were lost to predation or excessive rainfall.

For the Spot-fronted Swift, I recorded data for a total of 59 days from three nests (one complete set plus partial data sets from two other nests). For the Chestnut-collared Swift, I recorded data for 44 days from two nests (one complete and one nearly complete incubation period). When comparing species, all data for a particular species were pooled as one set. Percent of attendance at three nests of the Spot-fronted Swift nests did not differ significantly (ANOVA, $F_{(2,56)} = 1.47, P = 0.24$), nor did it differ between the two nests of the Chestnut-collared Swift (Students's Paired $t = 1.03, P = 0.31$, d.f. = 41). Because the presence of the adult was continuous at night, the percent of nest attendance was measured on a 12-hr basis, starting at first departure time, usually at sunrise. This was normally within the 12-13 hrs of day light.

RESULTS

**Egg size and incubation**

Eggs of both species are white. The eggs of the Spot-fronted Swift were matte in texture, whereas those of the Chestnut-collared Swift were glossy. Egg shapes of the two species (breadth / length ratio) differed significantly (Students's $t = 2.75, P = 0.008$, d.f. = 47) (see Table 3.1). Both egg length and breadth were significantly larger in the former species (Student's $t = 3.31, P = 0.002$, d.f. = 47; and
TABLE 3.1. Egg measurements and mass, mean and standard deviation (SD) of the Spot-fronted (C. cherriei) and the Chestnut-collared (S. rutila) swifts. All differences in measurements are statistically significant at $P < 0.01$.

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<th>S. rutila (n=24)</th>
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<td>Length (mm)</td>
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<td>23.4 (0.96)</td>
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<tr>
<td></td>
<td>Width (mm)</td>
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<td>15.3 (0.42)</td>
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<td></td>
<td>Mass (g)</td>
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<tr>
<td></td>
<td>Incubation period (days)</td>
<td>29 (2.50)</td>
<td>25 (1.0)</td>
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</table>
Mann-Whitney U-test; \( U = 310, P < 0.001 \), respectively). The egg of the Spot-fronted Swift was significantly heavier than that of the Chestnut-collared Swift (Mann-Whitney U-test; \( U = 300, P < 0.001 \)). The egg of the Spot-fronted Swift was 16.4% of the adult body mass, whereas the egg of the Chestnut-collared Swift was only 13.7% of the adult mass (see also Table 3.1).

The average incubation period for the Spot-fronted Swift was 29 days (range 26-34; \( n = 10 \)), whereas for the Chestnut-collared Swift it was 25 days (range 24-26; \( n = 5 \)). Incubation periods differed significantly (Students’ t = 3.72, \( P = 0.003 \), d.f. = 13). The latter species had on average a 13.7% shorter incubation period with less variability (coefficient of variation; \( CV = 8.5\% \) versus \( 4.0\% \) of variation, respectively). The complete incubation period, from egg laying to hatching, for the Spot-fronted Swift was based on the 47,520 min (33 days) of recorded time from laying to hatching; the egg was neglected for 12,500 min (26.3%). This egg had a total of 24.3 days of effective incubation time. For the complete data set of incubation periods of the Chestnut-collared Swift, with 34,560 min (24 days) recorded, indicated 5,020 min (14.5%) of neglect. This egg had a total of 20.5 days of effective incubation time. The two species had similar values in grams of egg per incubation time, 0.135 versus 0.141 g/day, respectively.

**Nestling period and nest attendance**

The nestling period of the Spot-fronted Swift was highly variable, and ranged from 54 to 88 days (\( x = 65; n = 5 \)). The mean nestling period for the
Chestnut-collared Swift was much shorter and less variable: 41 days (range 40-44; n = 7). In both species, the nestling became heavier than the adult: 115 % adult mass (n = 10) for the Spot-fronted and 120 % of the adult mass (n = 11) for the Chestnut-collared Swift (Marín unpublished).

For the Spot-fronted Swifts, the relationship between nest attendance and length of the incubation period was negatively correlated, but not significant in the first nest (Pearson correlation coefficient; $r^2 = 0.43, P = 0.163, n = 12$); in the second nest there was no correlation ($r^2 = 0.33, P = 0.055, n = 33$); and for the third nest the correlation was statistically significant ($r^2 = 0.69, P = 0.006, n = 14$; Figure 3.1a). For the Chestnut-collared Swifts, percent nest attendance and incubation period were significantly correlated in both nests ($r^2 = 0.60, P = 0.001, n = 24$; and $r^2 = 0.49, P = 0.03, n = 19$; Figure 3.1b). Based on counts of 12 hrs/day, the Spot-fronted Swift averaged less time on the nest (49.8 %, SD = 21.8, n = 59) than did the Chestnut-collared Swift, which spent 68.0 %, (SD = 21.1, n = 44) of the time on the nest; the species differed significantly (Students's $t = 4.1, P = 0.00009$, d.f. = 97).

The mean daily time out of the nest for Spot-fronted Swifts was 361.8 min./12 hr (SD = 161.5, range 60-765; n = 59 days), and the mean daily time spent out of the nest by Chestnut-collared Swifts was 230.3 min./12 hr (SD = 151.7, range 0-635; n = 44 days).

Most egg neglect in the Spot-fronted Swift occurred in a single bout beginning in the early hours in the morning. Departures (n = 59; 42%) were typically
FIGURE 3.1. Daily attendance, based on 12 hr count: a) data from a complete nest of the Spot-fronted Swift; b) data from two nests of the Chestnut-collared swift. Zero marks the laying of the egg.
between 06:00 and 07:00 hrs, with 34% occurring between 05:00 and 06:00 hrs, 22% between 07:05 and 08:00 hrs, and 5% later than 8:05 hrs. The earliest departure was at 05:10, and the latest departure was at 08:25 hrs. The data logger recorded that the birds took a second trip out of the nest on 15 of 59 Days (25 %)(Figure 3.2). This second trip was usually short and just before sunset. The birds usually departed from the nest at about 17:15 hrs and stayed away about 50 minutes on average. The second bouts lasted from 15 to 65 minutes.

Most egg-neglect in the Chestnut-collared Swifts occurred in the early morning hours. The departure times were later than for the Spot-fronted Swifts: 17 % of departures were between 05:00 and 06:00 hrs, 12 % between 06:05 and 07:00 hrs, 27 % between 07:05 and 08:00 hrs, and 43 % later than 08:05 hrs. The difference between the two species was significant (G = 30.18, d.f. = 5). As with the previous species, a second trip was recorded in the evening, but more often (56% of the time; Figure 3.3). Departures times for this second trip were very erratic, but most departures were recorded around 17:30 hrs. The earliest evening departure was at 13:50, and the latest was at 18:10 hrs. On average, the second bouts lasted 83 minutes (range 15 to 265 min ).

Weather and temperature

For the Spot-fronted Swift, I used rainfall data from "Avance de Tres Rios". I found no significant relationship between daily rain fall and percent nest attendance ($r^2 = -0.18, P = 0.56, n = 12; r^2 = 0.33, P = 0.24, n = 14; r^2 = 0.28, P = 0.11,$)
n = 33)(see also Figure 3. 4A). For the two nests of the Chestnut-collared Swift, I used data from the "Rancho Redondo" weather station, which was closer to the nests, and I found no significant relationship between daily rain fall and percent nest attendance \((r^2 = -0.005, P = 0.98, n = 24, \text{ and } r^2 = 0.11, P = 0.65, n = 19)\)(see Figure 3.4B). The lack of correlation between daily rain fall and nest attendance is probably because the birds are away from the nest primarily in the morning (see above) whereas the rains are usually early in the afternoon, as is the case elsewhere in the tropics (Foster 1974).

Ambient temperatures did not seem to affect the percent of nest attendance in both species. For the most complete nest data set of the Spot-fronted Swift, I found no significant relationship between minimum and maximum daily temperature for the area and percent nest attendance \((r = 0.11, P = 0.55, \text{ and } r^2 = -0.02, P = 0.87, n = 33, \text{ respectively})\) (Figures 3.5A, 3.5B). When combining all data for the Chestnut-collared Swifts, I found no relationship between percent daily attendance and mean daily temperature \((r^2 = -0.05, P = 0.73, n = 42)\).

The data loggers recorded the minimum and maximum temperature reached at any nest for the Spot-fronted Swift were 13.9° C and 35.1° C, and, for the Chestnut-collared Swift, 12.7° C and 26.8° C. For both nests the minimum temperature was the same as the minimum for the specific site.
FIGURE 3.2. Daily incubation patterns indicating the long and the short period of egg neglect of the Spot-fronted Swift.
FIGURE 3.3. Daily incubation patterns indicating the long and short period of egg neglect of the Chestnut-collared Swift.
DISCUSSION

The Spot-fronted and the Chestnut-collared swifts are closely related and are similar in size. However, they vary greatly in their growth rates and life history strategies. The fastest growing nestling of the Spot-fronted Swift was 18.5% slower than the slowest nestling of the Chestnut-collared Swift. The differences in egg mass and hatching mass were 22.8% and 19.0% respectively. They had, however, similar egg mass per incubation time (see above).

The proportionately larger ratio of egg mass to body mass, the longer incubation period, and the slower growth rate of the Spot-fronted Swift versus the Chestnut-collared Swift can be explained in terms of time spent foraging. Birds that need to spend a long period of time foraging away from the nest also need to adjust the incubation rhythm. One way to adjust to an irregular incubation regime would be through changes in the egg-shell: by increasing thickness, decreasing porosity, or both. Both will decrease water loss and provide some protection against drastic temperature changes (Rahn and Ar 1974, Ar et al. 1974, Drent 1975). For any egg mass, the length of the incubation period is inversely proportional to water loss of the egg, which depends on egg-shell thickness and porosity (Rahn and Arr 1974). Egg mass was the parameter that differed most between the two species (see above and Table 3.1). Egg shell thickness would be a way to further clarify differences in the incubation regime between these two species.
FIGURE 3.4. Relationship between percent of daily nest attendance and daily rain: a) Spot-fronted Swift, \( r^2 = 0.21, \ P = 0.094, \ n = 59 \) and b) Chestnut-collared Swift, \( r^2 = 0.019, \ P = 0.903, \ n = 42 \). (All data for each individual species were combined).
Spot-fronted and Chestnut-collared Swifts live in the same area and breed at about the same time. Thus, there is much overlap in hatching time (Marin and Stiles 1992). The large amount of yolk in eggs of swifts has been interpreted as an adaptation that enables the recently hatched nestling to survive in case of inclement weather (O'Connor 1979). Assuming that O'Connor's (1979) interpretation is correct, I believe that it is unlikely that two species facing the same weather would evolve a large difference in egg yolk proportions. Furthermore, the egg environment was about the same for both species (see above). Thus, the difference in egg mass between the two species might be explained in terms of egg-shell thickness and porosity. Whether the two species differ in egg-shell thickness or porosity, however, is not known. The rate of water loss might be a more important component to explain the different incubation regime between these two species.

Both species have a long incubation period, on average 29 days for the Spot-fronted Swift and 25 days for the Chestnut-collared Swift. The long incubation period contrasts with the typical period for birds similar in body mass, such as many passerines, which sometimes have larger body masses than these swifts and have incubation periods that range from 12-18 days (Skutch 1976). The long incubation periods of procellariiform seabirds are correlated with low water loss (Rahn and Ar 1974, Warham 1990), and the same might be true for cypseloidine swifts.

Egg neglect has been reported primarily for procellariiform seabirds, and the general consensus is that it is related to the foraging conditions of the individual.
FIGURE 3.5. Data for a Spot-fronted Swift nest showing relationship between a) minimum and b) maximum daily temperature and percent of nest attendance.
species (Boersma and Wheelwright 1979, Warham 1990). Boersma and Wheelwright (1979) found two major requirements for egg neglect to occur in seabirds and hypothesized that egg neglect should be more common in: a) species that have more protected nests that reduce the effect of extreme temperatures and predation, and b) the more distant forager. Below I examine these ideas with respect to cypseloidine swifts that as a group share the same foraging constraints as procellariiform seabirds.

**Nest protection**

All swifts nest in protected sites, although some species have more protected sites than others, and all swifts should show some degree of egg neglect. Cypseloidine swifts have the most stringent nest-site requirements behind waterfalls in the Apodidae, and they have also the more extreme life-history patterns of the swifts in terms of low clutch size, long incubation period, long nestling period, etc. They nest behind, next to, or adjacent to waterfalls or river gorges and suffer reduced nest predation, but the trade-off for safety from predators is nest vulnerability due to weather conditions, primarily flood-producing rainfall. Procellariiform seabirds nest on oceanic islands that have few or no predators, at least until the human introduction of predators to many islands, and they also face weather-related nest failure. For birds that do neglect their eggs for long periods of time, a safe nest site is an important requirement for leaving the eggs unattended. Both pelagic seabirds and swifts nest in safe sites that permit the adults to range widely for food. They differ in
time scales of their foraging bouts: several days for the Procellariiformes versus several hours for the Apodidae.

For swifts in general, data on leaving the eggs unattended for long periods of time are few, and most records are from the Old World. For the tropical Palm Swift (*Cypsiurus parvus*) with a clutch size of two eggs, Moreau (1941) found that the eggs were uncovered on average 30% of the day-light hours (based on observation periods of 9 hrs). During observations of seven nests for 9 hrs the White-rumped Swift (*Apus caffer*), with a two-egg clutch, exhibited intervals over 90 minutes of neglect in all nests and over 120 minutes in six nests (Moreau 1942b). Furthermore, Moreau (1942b) mentioned 13 cases of egg neglect over 120 minutes (on average 226 min.) and reported that the eggs were neglected 31% of 350 hours of observation. For species with larger clutch sizes of 2-4 eggs, such as the Common Swift (*Apus apus*), which breeds in temperate latitudes, Lack and Lack (1952) reported egg neglect for intervals varying from 1 to 390 minutes (6.5 hrs). Long periods of inattentiveness were rare, but Lack and Lack (1952) indicated that they occurred when the sitter had not been relieved for a long time. In the warmer Mediterranean climate, Malacarne et al. (1992) mentioned two cases of very infrequent incubation for the Pallid Swift (*A. pallidus*). Both the Common Swift and the Pallid Swift neglect their eggs, but to a lesser degree than cypseloidine swifts. In the lowlands of tropical latitudes, Moreau (1942a) reported an average of 26% of egg neglect, based on nine hour periods, for the Little Swift (*A. affinis*). For the same species in India, Razack (1968)
observed 24 nests and found a decrease in egg neglect as the incubation period advanced. His data show great individual variation in the degree of egg neglect, ranging from 20 to 100% of sessions with absences lasting 6.5 - 7 hrs. For a New World temperate species, the Chimney Swift (Chaetura pelagica), with a large clutch size of 5-6 eggs, Kendeigh (1952) reported egg neglect by using a thermocouple for 15 days in a nest. His data indicated that for 8 of 15 days, the eggs were neglected 12 times for periods of 19-84 minutes, averaging 46.3 minutes. All the above cases of egg neglect were associated with normal hatching success. Thus, it seems that as clutch size increases, egg neglect decreases (Spearman Rank Correlation $r^2 = -0.941$; $P = 0.016$; n=6; Table 3.2).

Foraging distance

All swifts seem to forage at some distance from the nest; however, in swifts the term "distance" is a combination of either or both height above the ground and horizontal foraging distance from the nest. Because the actual distance has never been measured, it would be best to describe the "distance" as time spent away from the nest. A species with a large clutch has shorter incubation period and a higher demand for food by the nestlings. Thus, if this "time-distance" parameter is associated with clutch size, then a large clutch species should have less egg neglect and forage closer to the nest, whereas a small clutch species should have more egg neglect and forage farther from the nest. For the Vaux's Swift (Chaetura vauxi), with a large clutch size of 5-6 eggs, Bull and Beckwith (1993) found that it spent 60% of
TABLE 3.2. Summary of egg neglect in swifts in relation to clutch size and latitude.

<table>
<thead>
<tr>
<th>Species</th>
<th>Clutch</th>
<th>Latitude</th>
<th>Mean percent or minutes per day</th>
<th>Recorded Intervals per day</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cypseloides cherrici</em></td>
<td>1</td>
<td>Tropical</td>
<td>50%</td>
<td>12 hrs</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Streptoprocne rutila</em></td>
<td>2</td>
<td>Tropical</td>
<td>32%</td>
<td>12 hrs</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Cypsiurus parvus</em></td>
<td>2</td>
<td>Tropical</td>
<td>30%</td>
<td>9 hrs</td>
<td>Moreau (1941)</td>
</tr>
<tr>
<td><em>Apus caffer</em></td>
<td>2</td>
<td>Tropical</td>
<td>31%</td>
<td>6 hrs</td>
<td>Moreau (1942b)</td>
</tr>
<tr>
<td><em>Apus apus</em></td>
<td>2-4</td>
<td>Temperate</td>
<td>Irregular 1-390 min.</td>
<td>10 hrs</td>
<td>Lack and Lack (1952), Lack (1973)</td>
</tr>
<tr>
<td><em>Apus pallidus</em></td>
<td>2-4</td>
<td>Temperate</td>
<td>Twice</td>
<td>8 hrs</td>
<td>Malacarne et al. (1992)</td>
</tr>
<tr>
<td><em>Apus affinis</em></td>
<td>2-3</td>
<td>Tropical</td>
<td>26%</td>
<td>9 hrs</td>
<td>Moreau (1942)</td>
</tr>
<tr>
<td><em>Apus affinis</em></td>
<td>2-3</td>
<td>Tropical</td>
<td>20-100%</td>
<td>6.5-7 hrs</td>
<td>Razack (1968)</td>
</tr>
<tr>
<td><em>Chaetura pelagica</em></td>
<td>5</td>
<td>Temperate</td>
<td>6.5%</td>
<td>12 hrs</td>
<td>Kendeigh (1952)</td>
</tr>
</tbody>
</table>
the time within 1 km from the nest and had a foraging radius up to 5.4 km. Fisher (1958) found that some color-marked Chimney Swifts (C. pelagica) fed at a distance of ca. 1-6 km from the nest. Quantitative data on altitude are scarce; however, for the Common Swift, Gustafson et al. (1977) found that the maximum flight altitude in clear weather was 3600 m (average 2300 m), whereas that for cloudy was much lower, 1720 m (average 700 m). Williams (1956) gave three altitudinal records, for the Chimney Swift ranging from 1980 to 2225 m, viewed from an airplane.

Although data on flight altitudes on swifts are scant, this can be an important parameter in combination with foraging distance. For the White-collared Swift (Streptoprocne zonaris), with a clutch size of 2 eggs, Whitacre (1991) found that the birds moved over 25 km from the colonies but suspected a much wider foraging range on the order of 80 km. With present data, it seems that the lower the clutch size, the larger the foraging "distance." Because the only data from small clutches are from the White-collared Swift (S. zonaris), the effect of body size cannot be ruled out (i.e., larger, faster-flying species travel farther).

Thus, some or near all, swifts seem to neglect their eggs, although to different degrees. Judging from the published information, there seems to be two potential trends: a) egg neglect seems to occur more often and for longer periods in tropical latitudes, and b) it seems to occur for longer periods of time in species with smaller clutch size (Spearman Rank Correlation $r^2 = -0.941; P = 0.016; n=6; Table 3.2$).

The higher occurrence of egg neglect in more tropical latitudes might be because weather changes are more frequent and complex (Barry and Chorley 1982).
In addition, tropical swifts breed during the rainy season. In tropical latitudes, the rainy season is the time of peak food abundance (Fogden 1972, Pearson 1977, Wolda 1978), but rains in turn could negatively affect foraging conditions at least in the afternoons, because there is more rainfall (Foster 1974), and this should place a restriction for the aerial feeding birds. Foraging conditions works in the same fashion for pelagic seabirds, but in reverse, because, the highest species diversity and dietary biomass for pelagic seabirds is in high latitudes not low latitudes, and, for pelagic seabirds, egg neglect seems to be more common at high latitudes (Warham 1990, 1996) and not low latitudes, as in swifts.

The second trend, egg neglect increases in species with smaller clutch size, might be explained as a response to longer time spent away from the nest. The time spent away from the nest in relation to clutch size would be analogous to pelagic seabirds. Both cypseloidine swifts and pelagic seabirds face the same foraging conditions and neglect their eggs. Although in seabirds the egg neglect is one of days, versus one of hours in swifts, they might well be because analogous reasons. That would be the distribution of prey items, which is patchy and ephemeral, at least during the breeding season.

REFERENCES


CHAPTER 4

GROWTH RATES IN THE BLACK SWIFT: TEMPERATE VERSUS TROPICAL COMPARISONS

Lack (1967, 1968), Ricklefs (1968, 1973, 1979, 1983), Case (1978), and O’Connor (1984) noted that variation in nestling growth rates, and hence the length of the nestling period, among birds is related to: a) the manner of nestling development, within the altricial-precocial spectrum, with altricial birds developing faster than precocial ones; b) ecological factors, including sibling competition, nestling mortality, and food availability; c) geography, with tropical species developing more slowly than counterparts at higher latitudes; d) environment, which includes season and climate; and e) body size, with smaller species developing faster.

Ricklefs (1976, 1983) found that tropical species grow more slowly than temperate ones. This finding, however, was based on comparisons of similar-sized congeneric species rather than intraspecific comparisons. Nevertheless, Ricklefs (1983) recognized that there might be a phylogenetic component to his comparisons. Based on intrapopulation studies on growth rates, Ricklefs (1983) concluded that intraspecific variation can be caused by one or several factors related to the life history, geography, or diet of the individual.

The goal of this study is to give some insight into how body size and latitudinal differences affect intraspecific postnatal growth rates.
<table>
<thead>
<tr>
<th>Degrees of Latitude North</th>
<th>Wing length (mm) (SD)</th>
<th>Mean adult mass (g) (SD)</th>
<th>Mass range (g)</th>
<th>Incubation period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ca. 56° (Alaska)</td>
<td>168.8 (± 4.1)</td>
<td>46.0 (± 3.4)</td>
<td>41.3 -- 53.4</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td>(n=8)</td>
<td>(n=16)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ca. 35° (S. California)</td>
<td>168.8 (± 3.2)</td>
<td>44.1 (± 2.5)</td>
<td>37.2 -- 51.3</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>(n=16)</td>
<td>(n=16)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ca. 17° (W. Mexico)</td>
<td>163.1 (± 4.3)</td>
<td>38.7 (± 2.4)</td>
<td>32.8 -- 42.0</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td>(n=18)</td>
<td>(n=13)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ca. 10° (Costa Rica)</td>
<td>159.7 (± 3.1)</td>
<td>35.4 (± 1.9)</td>
<td>32.0 -- 40.0</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>(n=28)</td>
<td>(n=19)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
To address this question, I compared nestling growth rates in two subspecies of the Black swift (*Cypseloides niger*) (Apodidae; Cypseloidinae), which is found locally from northwestern North America to Middle America and the West Indies. The two subspecies were *C. n. borealis* from California [hereafter referred as the "temperate subspecies"] and *C. n. costaricensis* from Costa Rica [hereafter the “tropical subspecies”]. Both subspecies have a single-egg clutch (Marín 1997, Marín and Sanchez 1998). Body size, mass, and wing length vary with latitude (see below and Table 4.1).

**METHODS**

Data for this study were gathered in southern California, in the San Jacinto area, Riverside County, at 33° 45' N (see Chapter 2, Marín 1997, and references therein), and in Costa Rica, in the Río Tiribí area, province San José, at 9° 57' N (see Chapter 3 and Marín and Stiles 1992). From May through August 1997, 30 visits were made to nests of the "tropical subspecies” during incubation and nestling periods at 3 to 5 day intervals. Body mass was weighed with an AVINET spring balance to 0.1 g. I measured wing length (flattened), extended wing, tail, and outermost primary to 0.5 mm using a stopped wing ruler. Other measurements (tarsus length, exposed culmen, gape, head width, and foot span) were measured to the nearest 0.1 mm by using a dial caliper, following techniques described by Baldwin et al. (1931) and Marín and Stiles (1992). Nestlings were measured only in the morning between 08:00 and 11:00 hrs.
Differences in growth rate between the tropical and the temperate subspecies of the Black Swift were assessed by comparing the mass and wing length increase per unit time. The increase in mass of birds can be described by three parameters: rate, magnitude, and form (Ricklefs 1968). The increase in mass of Black Swift nestlings seems to be best fitted to the Gompertz equation, and so the growth constant $K_G$ was used for comparisons. The constant $K_G$ (days$^{-1}$) is an overall expression of growth rate that is independent of body size (Ricklefs 1967, 1968, 1973). The magnitude of swifts growth curves are characterized by being well above adult mass, and the point of maximum mass is one index of variation in the form of the growth curve.

I compared the body mass growth during the phase of fastest growth, measured in grams per day, during the $T_{(10-90)}$ period (Case 1978). Similarly, I compared growth of wing length during the fastest growth measured in millimeters per day during the $T_{(20-80)}$ period. Furthermore, to avoid the effect of body mass or wing size differences, I compared those results relative to adult mass and adult wing length, respectively. For wing length, I chose values from a different period than for mass, because the initial wing growth was very slow, and the nestlings fledged when they had acquired about 90-95% of adult wing size.

Adult body masses and measurements for the Costa Rican population (Table 4.2) were taken from adult birds in the field and were supplemented with museum specimens from nearby geographic areas and for the Californian population were taken from Marín (1997). For Costa Rican birds, measurements were taken from
TABLE 4.2. Morphological measurements of adult Black Swifts from Costa Rica*.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass (g)</td>
<td>35.4</td>
<td>± 1.9</td>
<td>19</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>13.1</td>
<td>± 0.5</td>
<td>26</td>
</tr>
<tr>
<td>Foot span (mm)</td>
<td>20.9</td>
<td>± 1.9</td>
<td>3</td>
</tr>
<tr>
<td>Gape width (mm)</td>
<td>13.9</td>
<td>± 0.4</td>
<td>4</td>
</tr>
<tr>
<td>Exposed culmen length (mm)</td>
<td>6.3</td>
<td>± 0.3</td>
<td>26</td>
</tr>
<tr>
<td>Head width (mm)</td>
<td>19.8</td>
<td>± 1.8</td>
<td>5</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>159.7</td>
<td>± 3.1</td>
<td>28</td>
</tr>
<tr>
<td>Extended wing (mm)</td>
<td>184.5</td>
<td>± 3.0</td>
<td>4</td>
</tr>
<tr>
<td>Outermost primary (mm)</td>
<td>120.5</td>
<td>± 3.0</td>
<td>4</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>53.6</td>
<td>± 3.5</td>
<td>25</td>
</tr>
</tbody>
</table>

* Table follows the same sequence as in Figure 4.1 A-J.
Marín and Stiles (1992) and were complemented with measurements from adult birds I banded or collected from 1995 to 1997. Nest, egg mass, and egg shape were described by Marín and Sanchez (1998).

RESULTS

Eggs and incubation

For both subspecies, every nest observed had a clutch of one egg. The average egg size for the temperate subspecies was 28.7 x 18.8 mm, and the average egg mass was 5.5 g (Marín 1997). The mean egg size for the tropical subspecies was 27.9 x 18.5 mm, and the mean fresh egg mass was 5.26 (± 0.63) g (n=3). The mean incubation period was 24 days for the temperate and 29 days (n=2) for the tropical subspecies (Marín 1997, Marín and Sanchez 1998).

Nestling development

I studied the complete development of two nestlings for the Costa Rican subspecies from hatching through fledging (Figure 4.1 A-J). As with the temperate subspecies, the young were naked at hatching, with eyes closed, and weighed 3.7 - 4.8 g. At hatching, the nestlings' skin was a pinkish color ventrally and grayish dorsally, and the claws were grayish and white-tipped. Feather papillae were visible as subcutaneous dots. The feet were well developed at hatching (ca. 75% adult size). The culmen was black with a prominent white egg-tooth, and the base of the culmen to the forehead was bright pink. Body mass increased at a fast rate from hatching until reaching well above adult size (Figure 4.1 A). Adult mass was reached between
FIGURE 4.1. Growth curves of ten parameters (A-J) in the two nestlings of the Black Swift in Costa Rica. Dashed horizontal line represent the mean adult size and correspond to numbers from Table 4.2.
E

EXPOSED CULMEN LENGTH (mm)

AGE (Days)

F

HEAD WIDTH (mm)

AGE (days)
20 and 23 days of age. The maximum body mass reached by any of the nestlings was 45.9 g, or 127% of adult size, by 43 days of age. Tarsus, foot span, and gape reached adult size at an early age (Figure 4.1 B-D). Exposed culmen and head width reached adult size on the mid to late part of the nestling period (Figure 4.1 E-F). Wing length, extended wing, 10th primary length and tail length reached adult size after fledging (Figure 4.1 G-J, Table 4.2).

The semiplumes were ready to emerge on the back and lower sides by the 3rd or 4th day. By age 6-7 days, semiplumes emerged, and white-tipped feathers were beginning to emerge. On 2 July the youngest of the nestlings (age 11) had 5 botfly larvae on the nape, upper back, chest, underwing, and anal area. By day 13-15 both nestlings were fully covered with semiplumes, except on the forehead. The eyes were fully open by days 15-17, and the forehead feathers began to emerge at 22-23 days. Subcutaneous fat was visible on the lower chest and belly up to days 28-30 or until belly was covered with feathers. The egg tooth disappeared by 27-32 days. Wing coverts emerged by day 15-16, and primaries, secondaries, and rectrices emerged by day 17-18, and all were white-tipped. The secondaries were pin feathers by days 9-11 and broke their sheath by days 19-20. The primaries were pin feathers by days 11-12 and broke their sheaths by days 20-21. The outer primaries grew continuously until fledging (Figure 4.1G). Both nestlings fledged by age of 49-50 days, or when the 10th primary was about 90% adult size (Figure 4.1 I). The rectrices began to emerge by days 11-12, and their sheaths were broken by days 21-
22. They reached about 90% adult size around fledging time (Figure 4.1J). By fledging, most feathers had a white edging that produced a scalloped effect; this was pronounced in lower chest, belly, undertail coverts, mid-primaries, and secondaries. The white edging probably persists for several years, on the lower chest, belly, and undertail coverts (Marín and Stiles, 1992). Breeding birds had this white edging in different degrees and this decreased with age (Marín and Stiles, 1992).

Both nestlings fledged at age 49-50 days and in the morning before 9:00 hrs and were not seen again.

**Latitudinal trends**

Wing length and mass increased with latitude from 10 to 56 degrees north, showing a positive relationship ($r^2 = 0.94, P = 0.05$) (Table 4.1). The difference in mean wing length of the four samples is statistically significant (ANOVA, $F_{3,69} = 22.03, P < 0.001$). All pairwise multiple comparisons (Tukey Test) for wing length revealed no statistical differences ($P > 0.05$) between the means of the Alaska and California, and the Mexico and Costa Rica populations. Populations from Costa Rica and California, differed significantly in body mass and wing length (Student’s $t = 10.33, P << < 0.00001$, d.f. = 33, and $t = 9.80, P << < 0.00001$, d.f. = 42, respectively). Differences between Mexico and California populations in body mass and wing length were statistically significant (Student’s $t = 5.35, P = < 0.001$, d.f. = 45, and $t = 4.19, P = < 0.001$, d.f. = 35, respectively). Mass differed slightly between the California and southern Alaska populations, but not significantly (Student’s $t = 1.73,$
\( P = 0.093, \text{ d.f.}=30 \), and wing length did not differ (Table 4.1). The difference in both wing length and body mass was more pronounced, however, between Mexico and California. Although overlap was extensive, both body mass and wing length showed a positive relationship with latitude \( (r^2 = 0.91; P < 0.05 \text{ and } r^2 = 0.94; P = 0.05, \text{ respectively}) \).

Egg mass was proportionally larger in the tropical subspecies (Table 4.3). The tropical subspecies also had a longer incubation period and produced proportionally larger nestlings (Table 4.3). However, the fledging period was about the same for both subspecies (Table 4.3). During the time from 10\% to 90\% of the maximum mass or asymptote or \( T_{(10-90)} \) period, the larger or temperate subspecies gained more grams per day and took one more day to fledge than the tropical subspecies (Table 4.3). The temperate subspecies reached adult size at 18\% of the nestling period, over 3 days before the tropical subspecies. The growth constant \( K_g \) was 19.5\% higher for the temperate subspecies (Table 4.3). Taking into account body size, the temperate subspecies grew 47\% faster than the tropical subspecies during the fastest growth period or \( T_{(10-90)} \) (2.7 versus 1.4 g/day). However, factoring out the body size effect, by measuring grams per day as proportion of adult size during the \( T_{(10-90)} \), the temperate subspecies still grew faster 6.1\% versus 4.0\%.

Furthermore, both in the period from hatching to adult size and from hatching to maximum nestling mass (as a proportion of adult mass), the temperate subspecies grew faster, 15.8\% faster in the first period and 13.0\% faster in the latter.
FIGURE 4.2. Comparative growth curve of the Black Swift in California and Costa Rica as a proportion of adult mass, showing the similar pattern in magnitude and shape of the growth curve.
TABLE 4.3. Comparison of the developmental parameters of the tropical and temperate subspecies of the Black Swift.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>CALIFORNIA</th>
<th>COSTA RICA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Direct measurements</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult mass</td>
<td>44.1</td>
<td>35.4</td>
</tr>
<tr>
<td>Clutch size</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Incubation</td>
<td>24</td>
<td>29</td>
</tr>
<tr>
<td>Fledging period</td>
<td>48-50</td>
<td>49-50</td>
</tr>
<tr>
<td>Max nestling mass (g)</td>
<td>64.3</td>
<td>45.9</td>
</tr>
<tr>
<td>$T_{10-90}$ (days)</td>
<td>16.6</td>
<td>20.7</td>
</tr>
<tr>
<td>Grams per day at $T_{(10-90)}$ period</td>
<td>2.72</td>
<td>1.43</td>
</tr>
<tr>
<td>Time to acquire asymptotic size (days)</td>
<td>42</td>
<td>43</td>
</tr>
<tr>
<td>Time to acquire adult size (days)</td>
<td>17.6</td>
<td>20.9</td>
</tr>
<tr>
<td>Growth constant ($K_g$)</td>
<td>0.179</td>
<td>0.144</td>
</tr>
<tr>
<td><strong>Measurements in proportion to adult size</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent nestling period to attain adult size</td>
<td>18.1</td>
<td>21.2</td>
</tr>
<tr>
<td>Peak mass as percent adult mass</td>
<td>145.8</td>
<td>129.5</td>
</tr>
<tr>
<td>Percent of the nestling period to attain peak mass</td>
<td>85.7</td>
<td>87.7</td>
</tr>
<tr>
<td>Percent adult mass at hatching</td>
<td>7.9</td>
<td>10.7</td>
</tr>
<tr>
<td>Mean egg mass per adult mass</td>
<td>12.47</td>
<td>14.83</td>
</tr>
<tr>
<td>$T_{(10-90)}$ as proportion of adult size (days)</td>
<td>24.5</td>
<td>24.3</td>
</tr>
</tbody>
</table>

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Most swift nestlings have a similar magnitude in their growth curves, that is they reach a peak well above adult mass. Subcutaneous fat deposits are typical for many swifts and are particularly conspicuous in the Black Swift, as reflected in the magnitude of the growth curve (Figure 4.2). The maximum nestling mass or asymptotic size was 64.3 g (145.8 % of adult mass) for the temperate and 45.9 g (129.5 % adult mass) for the tropical subspecies. Maximum mass was attained basically at the same time, at age 42 days in California and 43 in Costa Rica (Table 4.3).

The Black Swift nestlings fledged when they acquired about 90-95% of the adult wing length. The wing length during the $T_{(20-80)}$ period was one day longer in the tropical subspecies (23 days) than the temperate subspecies. Wing growth during the $T_{(20-80)}$ was 3.4 mm/day in the tropical versus 3.8 mm/day in the temperate subspecies. Factoring out adult wing length, nestlings of both subspecies were growing at a similar rate, 2.1 % per day of the adult wing size in the tropical versus 2.2 % per day in the temperate subspecies.

In most directly compared parameters and those compared as a proportion of adult size, the temperate subspecies grew faster. Exceptions were foot span and exposed culmen (Table 4.4). In all linear dimensions, both subspecies left the nest with dimensions proportionally equal to adult size (Table 4.4).
### TABLE 4.4. Percent of the nestling period to acquire adult dimension.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>CALIFORNIA</th>
<th>COSTA RICA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>37.7</td>
<td>42.8</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>24.3</td>
<td>31.6</td>
</tr>
<tr>
<td>Foot span</td>
<td>22.3</td>
<td>10.6</td>
</tr>
<tr>
<td>Gape width</td>
<td>29.2</td>
<td>41.2</td>
</tr>
<tr>
<td>Exposed culmen length</td>
<td>63.5</td>
<td>44.8</td>
</tr>
<tr>
<td>Head width</td>
<td>68.4</td>
<td>71.6</td>
</tr>
<tr>
<td>Wing length*</td>
<td>91.5</td>
<td>91.0</td>
</tr>
<tr>
<td>Extended wing length*</td>
<td>93.7</td>
<td>90.5</td>
</tr>
<tr>
<td>10th Primary length*</td>
<td>86.7</td>
<td>87.5</td>
</tr>
<tr>
<td>Tail length*</td>
<td>88.8</td>
<td>87.8</td>
</tr>
</tbody>
</table>

*Maximum length in proportion of adult size at fledging time.
DISCUSSION

Ricklefs (1983) found that intraspecific variation in postnatal growth can be caused by one or many factors related to three broad categories: a) life histories (egg size and composition, body size, brood size, and hatching position); b) geography and weather (locality, habitat, season, rain, and temperature), and; c) diet (availability, quality, and quantity of food). Below I examine these factors with respect to the temperate and tropical populations of the Black Swift.

Life histories

Both subspecies produce one-egg clutches and have a large egg relative to adult mass, although the tropical subspecies had a proportionally a larger egg mass than the temperate subspecies. Larger eggs are more advantageous for hatching at a greater mass or for greater reserves for the nestling (Lack 1968, O’Connor 1979, 1984). The Black Swift nests in cool, wet environments, and therefore, greater reserves might be important for both advanced embryonic development and for the naked hatchling. The incubated egg and the recently hatched young endure 5 or more hours of neglect daily. In addition, a recently hatched nestling depends on a variable food supply. In case of bad weather, a hatchling from a larger egg can potentially survive for a longer period without food or warmth than a hatching from a smaller egg. The faster incubation period found in the temperate subspecies might be related to the shorter breeding season, longer days, fewer
weather fluctuations (in tropical latitudes weather changes are more frequent and complex, Barry and Chorley, 1982).

Both subspecies have a single nestling; therefore, hypotheses concerning, sibling competition, and hatching position do not apply to this species.

**Geography and weather**

In the Black Swift the latitudinal trend in body mass and wing length follows Bergmann's Rule (Table 4.1). Two subspecies are recognized in the continental range: *Cypseloides niger borealis* from southeast Alaska south to the highlands of Guatemala and Honduras, and *C. n. costaricensis* in the highlands of Costa Rica (Cory 1918, AOU 1957). The former is 19.7% heavier and has a 5.4% longer wing than the latter. By mass and wing length, however, two clusters are formed: larger birds from California north to Alaska and smaller birds from central Mexico south to Costa Rica (see above and Figure 4.3).

As postulated by Ricklefs (1979, 1983) and Case (1978), differences in body mass reflect differences in growth. In the Black Swift, however, body mass contradicts the postulate that larger birds develop more slowly than the smaller ones (Ricklefs 1973, Case 1978, Stearns 1992). The temperate subspecies grew 47% faster than the tropical one, during the fastest growth period or $T_{(10-90)}$, and 32% faster in the period from hatching to maximum nestling mass. Furthermore, the temperate subspecies acquired adult size 16% faster than the tropical subspecies. Nevertheless, factoring out body mass, the temperate or heavier subspecies grew
FIGURE 4.3. Scatter plot of tarsus length versus wing length of the Black Swift showing specimens from Alaska (solid triangles), California (solid circles), Mexico (hollow triangles), and Costa Rica (hollow circles) (see also Table 4.1).
faster 19% (by the growth constant, $K_g$), and 34% (in the grams per day during the $T_{(10-90)}$ period as a proportion of adult mass), and 16% faster to acquire adult mass. All of these parameters are independent measures of body mass, and they support Ricklefs's (1968, 1983) findings that tropical bird species or subspecies increase their body mass more slowly than temperate ones. In terms of wing length as a proportion of adult length, however, both the temperate and the tropical subspecies grew at the same rate. Thus, differences in latitude override differences in adult mass in determining growth rates of nestlings Black Swifts.

The two subspecies nest in similar habitats: dark to semi-dark areas; deep gorges, canyons, sea caves; all near water, waterfalls, or rivers; and all in areas with high humidity (Knorr 1960, Marín 1997, Marín and Sanchez 1998). Nevertheless, the temperate subspecies breeds during the dry season, whereas the tropical subspecies breeds during the rainy season (Chapter 2, Marín and Sanchez 1998). For temperate populations breeding in a colder climate, such as some populations of the Common Swift ($Apus apus$), weather variability influences growth rate of the nestlings and is the primary cause of nestling mortality (Lack 1973). In temperate breeding populations of the Little Swift ($A. affinis$), changes in temperature affect dates of egg laying (Hotta 1996). Depending on the locality and time of the day, the combination of either or both rain and cold temperature strongly affect insect movements (Taylor 1963, Johnson 1969). Weather changes will produce insect shortages that influence nestling growth or egg laying (e.g., Koskimies 1950, Lack

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and Lack 1951, Lack 1956, Hotta 1996). For populations of the Common Swift and the Pallid Swift (*Apus pallidus*) that breed in the warmer Mediterranean climate, the primary limiting factor seems to be temperature, not rains (Gory 1987, 1993, Thibault et al. 1987, Cucco and Malacarne 1996a, b). The southern California population of the Black Swift breeds in a Mediterranean climate during the dry season, and thus temperature could be an important factor.

There are no drastic changes in temperature in the tropics; however, Naik and Naik (1966), working in a tropical population of Little Swift (*Apus affinis*) in India, found that relative humidity affected the food supply, as probably would be the case in the southern Black Swift. Foster (1974) pointed out that the rainy season has a two-sided effect on food availability. Although food abundance peaks during the rainy season, rain can hinder the birds in finding and capturing the insects. Furthermore, excess rain can cause high mortality rate of nestlings in cypseloidine swifts by flooding nests or by reducing rates of provisioning (Marin and Stiles 1992). Thus, weather seems to be a major factor influencing swift postnatal mass growth. Because the tropical subspecies breeds in the middle of the rainy season, food availability and food gathering should be a major constraints. I have no data regarding food gathering, but, if differences occur, they probably are related to daily limitations in the tropics, e.g., day length, and weather effects of insect abundance.
Diet

Cypseloidine swifts feed primarily on aerial insects with patchy and ephemeral distributions, such as swarming species of ants, which are rich in energy (e.g., Whitacre 1991, Chapter 2 and references therein). Winged ants have a high fat content, and the percent fat per dry weight in alate ants ranges from 24 to 60% in females and from 3 to 10% in males (Taylor 1975, Redford and Dorea 1984). A nestling of any bird species fed a lipid-rich diet is likely to accumulate subcutaneous fat. Nestlings of both subspecies of the Black Swift accumulate much subcutaneous fat, and their growing mass reaches values well above of adult body mass: 146% in the temperate and 130% in the tropical zones (Figure 4.2). Because both subspecies accumulate much subcutaneous fat, I predict that both should have relatively similar diets, a large preponderance of winged ants.

The tropical subspecies breeds during the rainy season and probably has to adjust to more stochastic foraging conditions (Marin and Stiles 1992). The Black Swift in other parts of its range, e.g., British Columbia, might face similar conditions, (e.g., Udvardy 1954). Most nestlings of aerial feeders accumulate subcutaneous fat deposits to use in case of food shortage, and this is particularly noticeable in the Black Swift (see Table 4.3, Figure 4.1). This strategy was labeled by O'Connor (1978) as the "Resource Storage Strategy" for short-term food interruptions, for birds whose food supply is patchy and ephemeral. Subcutaneous fat is particularly noticeable in procellariiform seabirds and swifts, particularly cypseloidine swifts. In
swifts, interruptions in food availability can be long-term, on the order of several
days, at least in the tropics. Aerial feeders, particularly swifts, seem to have a special
physiological mechanisms to slow down the process of growth in response to a food
shortage (Koskimies 1950). Because the proportionally equal growth in wing length
and the less mass acquired by the tropical nestlings, the differences in the latter
parameter between the temperate and the tropical subspecies, independent of adult
size, might be because of the more temporal pattern in food availability in the tropics
leading to a more unfavorable foraging condition for the tropical subspecies.

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CHAPTER 5

SUMMARY AND CONCLUSIONS

In this dissertation I hypothesized convergent evolution between airbirds and seabirds. During the breeding season, both groups of birds have an analogous division of foraging zones, and this is with respect to foraging distance from the nest. The segregation of foraging habitats is reflected in their life-history patterns. Within the airbirds, I examined some of the life-history patterns presented in cypseloidine swifts and compared them to those of procellariiform seabirds. Both of these groups have extreme life-history patterns.

In Chapter 2, I studied the influence of foraging behavior on the life-history of a species with a single egg-clutch. The convergence between cypseloidine swifts and procellariiform seabirds was supported by the foraging strategy adopted by the Black Swift (a cypseloidine swift). During the breeding season, parent birds alternated short and long foraging trips. This resembles and probably serve analogous purposes to the strategy of energy expenditure on foraging and food delivery described for procellariiform seabirds. Furthermore, similar to procellariiform seabirds, the Black Swift nestlings were fed in diet rich in lipids.

In Chapter 3, I studied the incubation pattern in two species of cypseloidine swifts, the Spot-fronted Swift which lays a single-egg clutch, and the Chestnut-collared Swift which lays a two-egg clutch. Both species showed long periods of egg-neglect. The single-egg clutch species neglected the egg for a longer period of
time, and had a longer nestling period than the species with two-egg clutch. I can infer that the single-egg species forages farther away from the nest than the two-egg species. Egg-neglect is known to occur in procellariiform seabirds that have long incubation periods, small clutch size, forage far away from the nest, and have patchy, and unpredictable food sources.

In Chapter 4, I found that the growth rate of the Black Swift, which is characterized by a high subcutaneous lipid accumulation, does not change with latitude. Fat accumulation by the nestlings has been attributed as a strategy to respond to short-term food interruptions. The nestlings of both cypseloidine swifts and procellariiform seabirds accumulate large amounts of subcutaneous fat, because the food source of both groups is patchy and unpredictable.

I predict, that between cypseloidine swifts and procellariiform seabirds, not only the mentioned patterns converge, but probably most life-history patterns. The main difference in some of these patterns between these two groups is the time scale: hours in cypseloidine swifts versus days in procellariiform seabirds. Lack (1948) concluded that the similarities in developmental patterns between the Common Swift and the Manx Shearwater were an adaptation to a scarce food supply. I agree with Lack (1948), but also believe that the multiple similarities in the life-history patterns, between the cypseloidine swifts and the procellariiform seabirds, are primarily due to similarities in the distance of their food source from the nest and food unpredictability.
There are several ways to further test this convergence between the different categories of airbirds and seabirds. One valuable contribution would be to measure daily foraging ranges of species with different clutch sizes by using radio-telemetry. Another would be to study feeding rates, and nestling diet, particularly in single-egg clutch species. One could also determine any correlation between feeding range, egg-shell thickness, and egg neglect.

REFERENCES

VITA

Manuel Marín Aspillaga, was born on 31 January 1960, in Santiago de Chile, Chile. He attended high school in Santiago de Chile and graduated in December 1977. From 1978 to 1982 he worked as a freelancer naturalist and photographer in southern South America. From 1976 to the present he became associated with the Instituto de Estudios y Publicaciones Ignacio Molina in Chile, and worked in close association with Professor and naturalist Luis Peña Guzman. Marín moved to California in 1982 and became associated with the Western Foundation of Vertebrate Zoology and traveled extensively for them between 1982 and 1992, in Central America, South America and southeast of Asia. While in California he pursued his bachelor of science degree in Zoology at California State University at Long Beach. He is completing his degree Doctor of Philosophy at Louisiana State University in the Fall of 1998. Following graduation, he will work for the Western Foundation of Vertebrate Zoology in California.
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Candidate: Manuel Marin-Aspillaga

Major Field: Zoology

Title of Dissertation: Airbirds: Adaptative Strategies to the Aerial Life Style from a Life-history Perspective

Approved:

[Signatures]

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Ken Brown

Dr. Wen-kay

Dr. Michael Fitzgerald

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Date of Examination:

November 4, 1998