ORNITOLOGIA NEOTROPICAL 10: 179–192, 1999

GROWTH RATES IN THE BLACK SWIFT: TEMPERATE VERSUS TROPICAL COMPARISONS

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Abstract. The northern (45 g) and southern (35 g) subspecies of the Black Swift (*Cypseloides niger*) were compared with respect of postnatal growth. The data from the northern subspecies was gathered in southern California and the data for the southern form was from central Costa Rica. It was found that the southern subspecies have a longer incubation period, but both forms had an about equal nestling period. In terms of body mass per unit time, the temperate subspecies grew faster than the tropical subspecies, which is consistent with comparative observations on growth rates. The species contradict the general concept that small forms should grow faster than larger forms. Weather might play an important role for the species nestling development. *Accepted 15 March 1999.*

Resumen. La subspecie del norte (45 g) y la del sur (35 g) del Vencejo Negro (*Cypseloides niger*) fueron comparadas con respecto a su desarrollo postnatal. La información sobre la subspecie norteña fue obtenida en el sur de California y para la subspecie sureña en Costa Rica central. Se encontró que la subspecie del sur tenia un periodo de incubación mas largo que la del norte, pero ambas subspecies tenían un periodo de desarrollo similar. En términos de masa corporal por unidad de tiempo, la subspecie del área templada creció mas rápido que la subspecie del área tropical, lo cual es concistente con observaciones comparativas en tasas de crecimiento. La especie contradice el concepto general que las especies pequeñas deberían crecer mas rápido que las grandes. Clima en si puede jugar un papel muy importante en el desarrollo post natal de la especie.

Key words: Black Swift, Cypseloides niger*, Bergmann's rule, postnatal development, tropical versus temperate, comparisons.*

INTRODUCTION

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) con-

TABLE 1. Adult Black Swift (*Cypseloides niger*)parameters along the latitudinal gradient.

Degree of latitude North	Wing length (mm) ± SD	Mean adult mass (g) ± SD [range]	Incubation period (days)
c. 56° (Alaska)	168.8 ± 4.1 (n = 8)	46.0 ± 3.4 [41.3–53.4] (n = 16)	?
c. 35° (S. California)	168.8 ± 3.2 (n = 16)	44.1 ± 2.5 [37.2–51.3] (n = 16)	24
c. 17° (W. Mexico)	163.1 ± 4.3 (n = 18)	38.7 ± 2.4 [32,8–42.0] (n = 13)	?
c. 10° (Costa Rica)	159.7 ± 3.1 (n = 28)	35.4 ± 1.9 [32.0–40.0] (n = 19)	29

cluded 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. 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 & Sanchez 1998). Body size, expressed by mass and wing length varies with latitude (see below and Table1).

METHODS

Data for this study were gathered in southern California, in the San Jacinto area, Riverside Co., at 33°4'N the area was described in more detail by Marín (1997, 1999, and references therein), and in Costa Rica, in the Río Tiribí area, prov. San José, at 9°57'N, the site was described in detail by Marín & Stiles (1992). From May through August 1997, 30 visits were made to nests of the "tropical subspecies" during incubation and nestling periods at 1 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 & Stiles (1992). Nestlings were measured only in the morning between 08:00 and 11:00 h.

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). Swift chicks attain masses well above adult levels, 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

TABLE 2. Morphological measurements of adult Black Swifts (*Cypseloides niger*) from Costa Rica.

Parameters[a]	Mean	SD	n
Mass (g)	35.4	1.9	19
Tarsus length (mm)	13.1	0.5	26
Foot span (mm)	20.9	1.9	3
Gape width (mm)	13.9	0.4	4
Exposed culmen length (mm)	6.3	0.3	26
Head width (mm)	19.8	1.8	5
Wing length (mm)	159.7	3.1	28
Extended wing (mm)	184.5	3.0	4
Outermost primary (mm)	120.5	3.0	4
Tail length (mm)	53.6	3.5	25

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

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 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 Marín & Stiles (1992) and were complemented with measurements from adult birds I banded or collected from 1995 to 1997. Nest, and egg shape were described by Marín & Sanchez (1998). Adult body masses and measurements for southern Alaska and central Mexico were taken from museum specimens (see Acknowledgments).

TABLE 3. Percent of the nestling period necessary to acquire adult dimension in Black Swifts (*Cypseloides niger*).

Parameters	California	Costa Rica
Body mass	37.7	42.8
Tarsus length	24.3	31.6
Foot span	22.3	10.6
Gape width	29.2	41.2
Exposed culmen length	63.5	44.8
Head width	68.4	71.6
Wing length[a]	91.5	91.0
Extended wing length[a]	93.7	90.5
10th primary length[a]	86.7	87.5
Tail length[a]	88.8	87.8

[a] Maximum length in proportion of adult size at fledging time.

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, the average fresh egg mass was 5.5 g, and the mean incubation period was 24 (23–26) days (Marín 1997). The mean egg size for the tropical subspecies was 27.9 x 18.5 mm, the mean fresh egg mass was 5.26 (± 0.63) g (n = 3), and the mean incubation period was 29 (28–30) days (n = 2).

Nestling development. I studied the complete development of two nestlings for the Costa Rican subspecies from hatching through fledging (Fig. 1A–J). As with the temperate subspecies, the young were naked at hatching, with eyes closed, . and weighed 3.7 and 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.

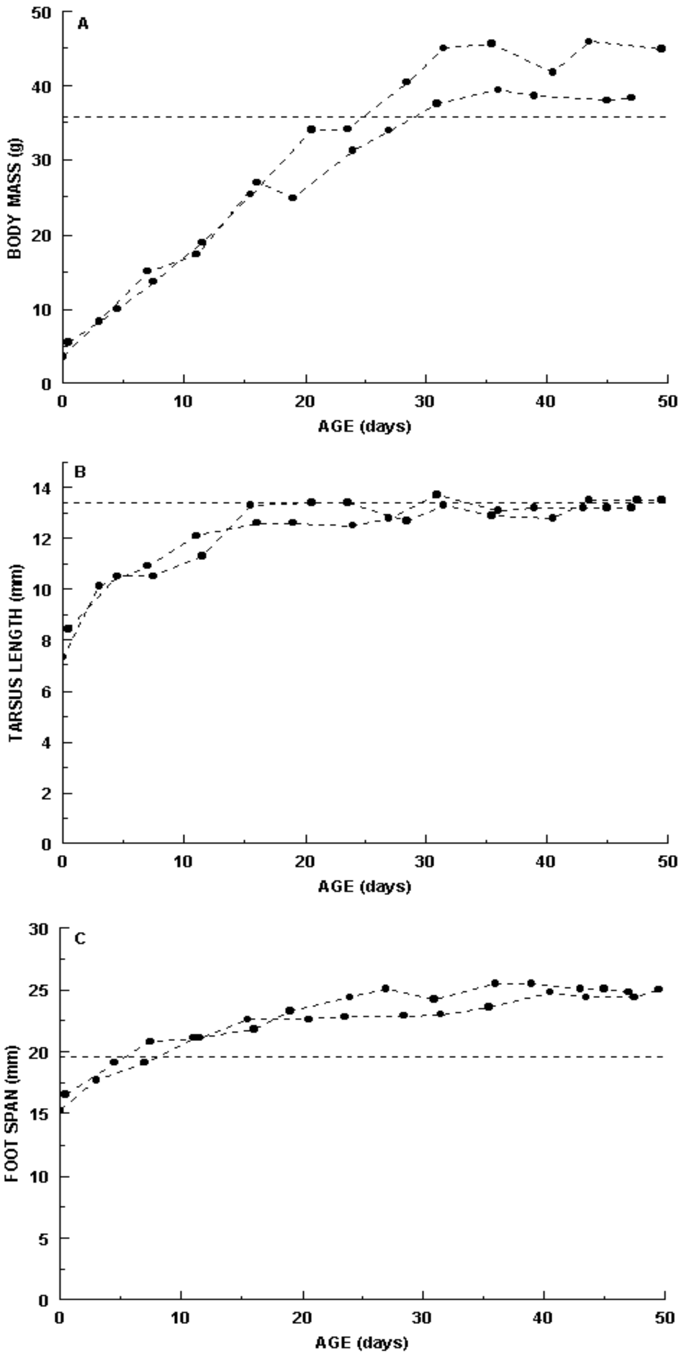
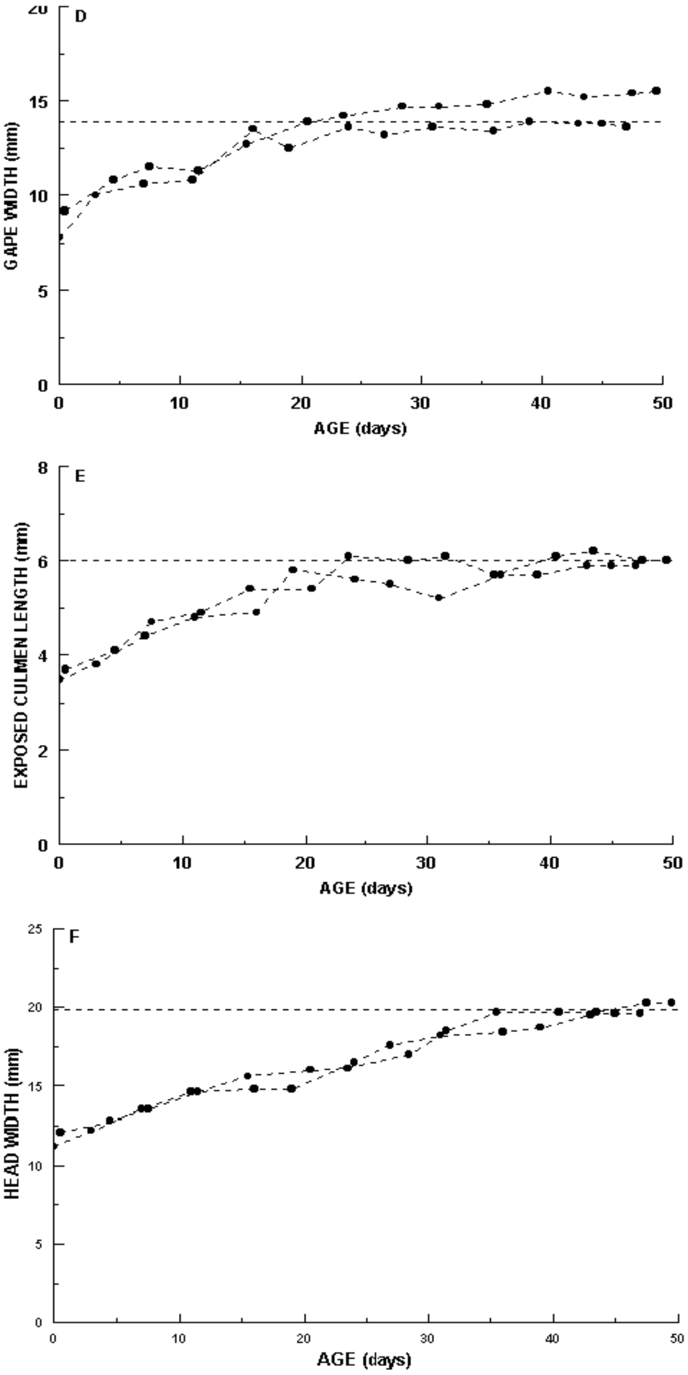


FIG. 1. Growth curves of ten parameters (A–J) in the two nestlings of the Black Swift in Costa Rica. Dashed horizontal line represents the mean adult size and corresponds to numbers from Table 2.



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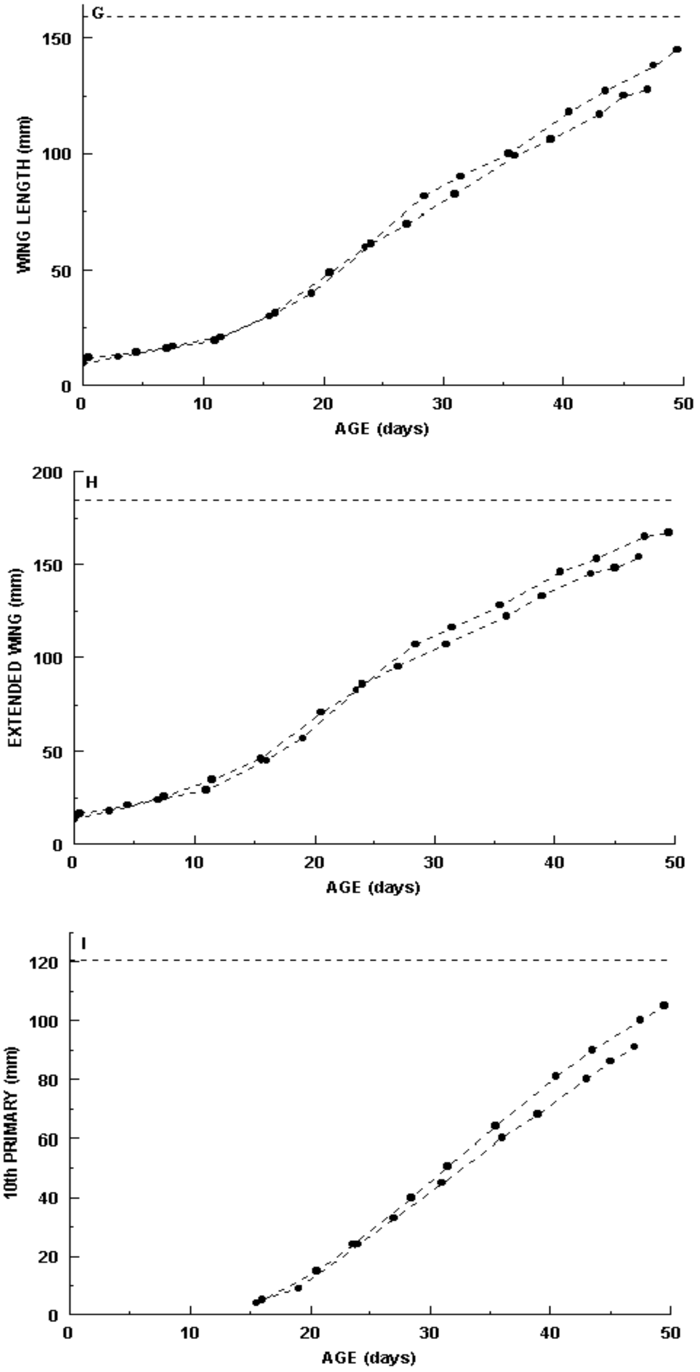

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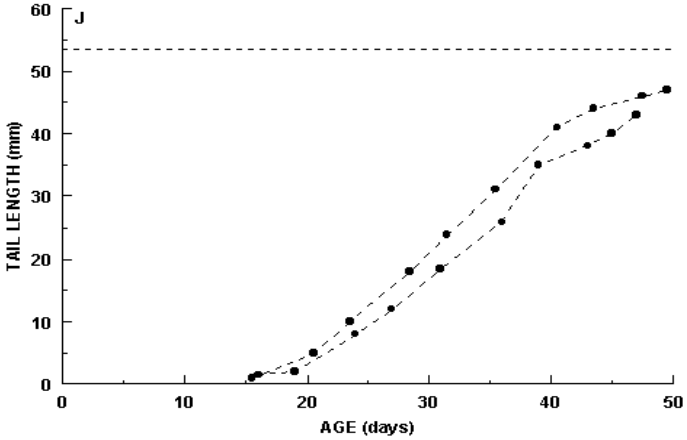

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The foot span was well developed at hatching (c. 75% adult size). The culmen was black with a prominent white egg-tooth, and the base of the culmen to the forehead was bright pink. Body mass increased rapidly from hatching until reaching well above adult size (Fig. 1A). Adult mass was reached between 20 and 23 days of age. The maximum body mass reached by either 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 (Fig. 1B–D). Exposed culmen and head width reached adult size on the mid to late part of the nestling period (Fig. 1E–F). Wing length, extended wing, 10th primary length and tail length reached adult size after fledging (Fig. 1G–J, Table 3).

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 (Fig. 1G). Both nestlings fledged by age of 49–50 days, or when the 10th primary was about 90% adult size (Fig. 1I). 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 (Fig. 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. Breeding birds had this white edging in different degrees and this decreased with age (Marín & Stiles 1992).

TABLE 4. Comparison of the developmental parameters of the tropical and temperate subspecies of the Black Swift (*Cypseloides niger*).

Direct measurements	California	Costa Rica
Adult mass (g)	44.1	35.4
Clutch size	1	1
Incubation (days)	24	29
Fledging period (days)	48–50	49–50
Maximum nestling mass (g)	64.3	45.9
$T_{(10-90)}$ (days)	16.6	20.7
Grams per day at $T_{(10-90)}$ period	2.72	1.43
Time to acquire asumptotic size (days)	42	43
Time to acquire adult size (days)	17.6	20.9
Growth constant (K_G)	0.179	0.144
Measurements in proportion to adult size		
Percent of nestling period to attain adult size	18.1	21.2
Peak mass as percent of adult mass	145.8	129.5
Percent of the nestling period to attain peak mass	85.7	87.7
Percent of adult mass at hatching	7.9	10.7
Mean egg mass per adult mass	12.47	14.83
$T_{(10-90)}$ as proportion of adult size (days)	24.5	24.3

Both nestlings fledged at age 49–50 days and in the morning before 09:00 h and were not seen again.

Latitudinal trends. Adult 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 1). The difference in mean wing length of the four sites 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 (t-test = 10.33, $P < 0.00001$, df = 33, and t-test = 9.80, $P < 0.00001$, df = 42, respectively). Differences between Mexico and California populations in body mass and wing length were statistically significant (t-test = 5.35, $P < 0.001$, df = 45, and t = 4.19, $P < 0.001$, df = 35, respectively). Mass differed slightly between the California and southern Alaska populations, but not significantly (t-test = 1.73, $P = 0.093$, df = 30), and wing length did not differ (Table 1). The differences 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 ($r^2 = 0.91$; $P < 0.05$ and $r^2 = 0.94$; $P = 0.05$, respectively).

Egg mass was proportionally larger in the tropical subspecies (Table 4). The tropical

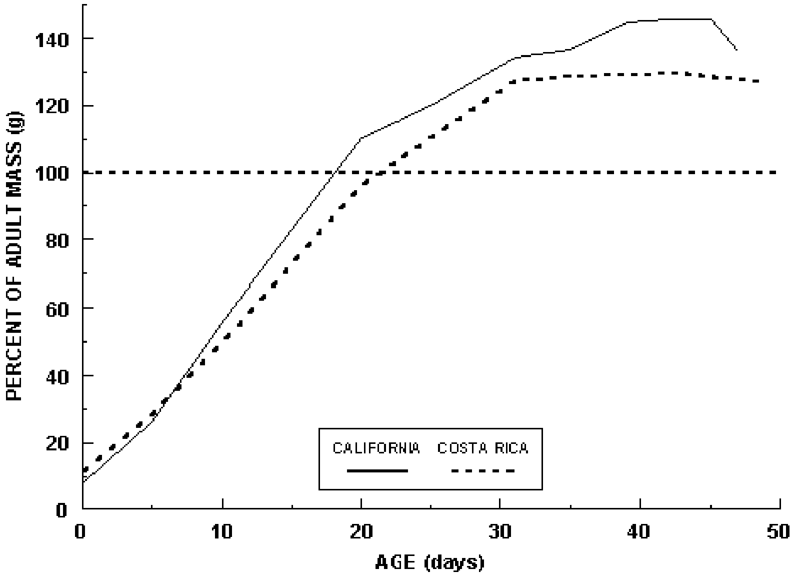

FIG. 2. Comparative growth curve of the Black Swift in California and Costa Rica as a proportion of adult mass, showing the similar patterns in magnitude and shape of the growth curve.

subspecies also had a longer incubation period and produced proportionally larger nestlings (Table 4). However, the fledging period was about the same for both subspecies (Table 4). 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: in most cases, it also took one day faster to fledge than the tropical subspecies (Table 4). 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). 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.

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 (Fig. 2). Both temperate and tropical subspecies had similar magnitude in their growth curve (Fig. 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).

The Black Swift nestlings fledged when they acquired about 90–95% of the adult wing length. The $T_{(20–80)}$ period for wing

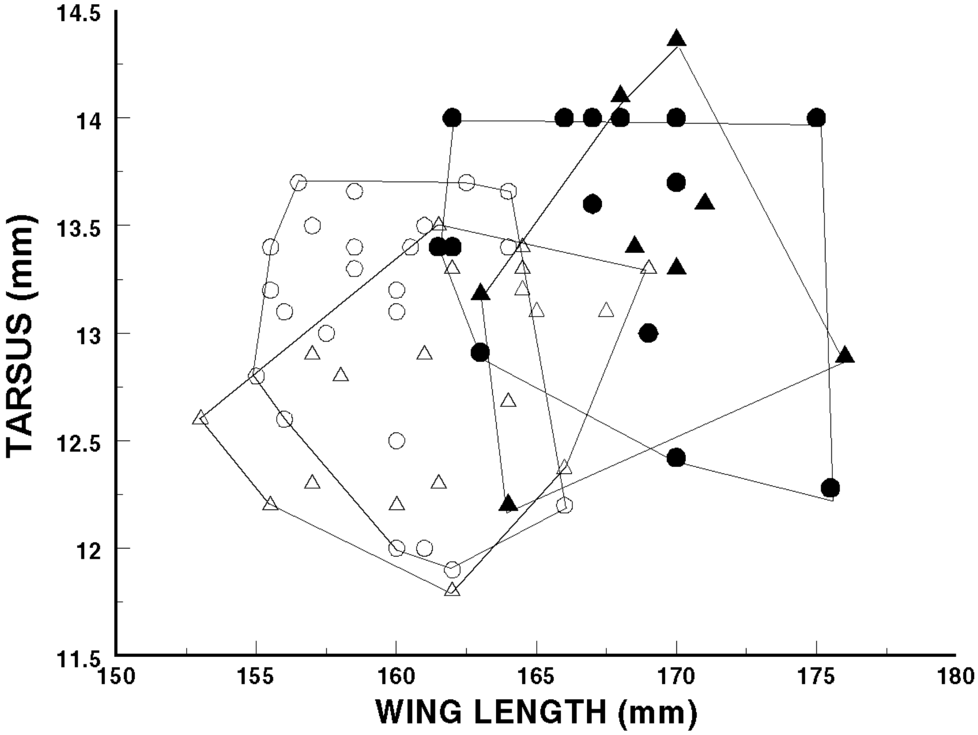

FIG. 3. Scatter plot of tarsus length versus wing length of the Black Swift showing specimens from Alaska (solid triangles), California (solid circles), Mexico (hollow triangles), and Costa Rica (hollow circles) (see also Table 1).

length 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 3). In all linear dimensions, both subspecies left the nest with dimensions proportionally equal to adult size (Table 3).

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. Relatively to the adult, larger eggs seem to be 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 either or both, advanced embryonic development and for the naked hatchling. Because of the long foraging trips made by the adults, the incubated egg and the recently hatched young endure 5 or more h of neglect daily (Marín 1998). In addition, particularly in the tropics, a recently hatched nestling depends on a variable food supply. In case of bad weather, a hatchling from a larger egg might 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 & Chorley 1982).

Both subspecies have a single nestling; therefore, hypotheses concerning, sibling competition, and hatching position do not apply to this species. The lack of sibling competition, is probably one of the factors that contribute to the slow nestling growth in this species. As other species with higher clutch size grow faster (see review in Marín & Stiles 1992)

Geography and weather. In the Black Swift the latitudinal trend in body mass and wing length follows Bergmann's Rule (Fig. 3 and Table 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, AOU 1998). 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 Fig. 3).

As postulated by Case (1978) and Ricklefs (1979, 1983), 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 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 & Sanchez 1998, and references therein). Nevertheless, the temperate subspecies breeds during the dry season, whereas the tropical subspecies breeds during the rainy season (Marín 1998, 1999, Marín & 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 & 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 & Malacarne 1996a, 1996b). 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 & 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 (Marín & 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, Marín 1999, 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 & 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 (Fig. 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 (Marín & 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 Figs 1 and 2 and Table 4). 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.

ACKNOWLEDGMENTS

I thank R. Corado, L. Lyon, D. MacLean, J. Schmitt, C. Sumida, and W. Wehtje for their companionship and field help in California. I thank R. Corado, A. Jackson, and J. Sanchez for field help in Costa Rica. This paper benefitted greatly by comments by K. Brown, M. Cucco, M. Fitzsimons, D. Homberger, J.V. Remsen, R. Ricklefs, A. Styring, and K. Naoki. I thank the following museums: P. Sweet, M. LeCroy, and F. Vuilleumier, American Museum of Natural History, New York; G. Stiles, Museo Universidad de Costa Rica, San Jose; J. Sanchez, F. Duran, and G. Alvarado, Museo Nacional de Costa Rica, San Jose; N. Johnson and C. Cicero, Museum of Vertebrate Zoology University of California, Berkeley; R. Prys-Jones and M. Walters, Natural History Museum, Tring (ex British Museum of Natural History); P. Collins, Santa Barbara Museum of Natural History, Santa Barbara; L. Kiff, C. Sumida, R. Corado, and W. Wehtje, Western Foundation of Vertebrate Zoology, Camarillo. Permits to work in Costa Rica were provided by Ministerio de recursos Naturales Energia y Minas, and I am very grateful to Licenciado Javier Guevara, whom facilitated the permits. Field work was supported by Chapman Fund of The American Museum of Natural History, New York, National Geographic Society (Grant NGS # 5870-97), and The Western Foundation of Vertebrate Zoology, California.

REFERENCES

American Ornithologists' Union. 1957. Check-list of North American birds. 5th ed. American Ornithologists' Union, Port City Press, Baltimore.

American Ornithologists' Union. 1998. Check-list of North American birds.7th ed. American Ornithologists' Union, Washington, D.C.

Baldwin, S. P., H. C. Oberholser, & L. G. Worley. 1931. Measurements of birds. Sci. Publ. Clevel. Mus. Nat. Hist. 2: 1–165.

Barry, R. G., & R. J. Chorley. 1982. Atmosphere, weather and climate. Methuen, London.

Case, T. J. 1978. On the evolution and adaptative significance of postnatal growth rates in terrestrial vertebrates. Quart. Rev. Biol. 55: 243–282.

Cory, C. B. 1918. Catalogue of the birds of the Americas and the adjacent islands. Publ. Field Mus. Nat. Hist. 197, Vol. 13, Part 2, No1.

Cucco, M., & G. Malacarne. 1996a. Effect of food availability on nestling growth and fledging success in manipulated Pallid Swift broods. J. Zool. (Lond.) 240: 141–151.

Cucco, M., & G. Malacarne. 1996b. Reproduction of the Pallid Swift (*Apus pallidus*) in relation to weather and aerial insect abundance. Ital. J. Zool. 63: 247–253.

Foster, M. S. 1974. Rain, feeding behavior, and clutch size in tropical birds. Auk 91: 722–726.

Gory, G. 1987. Influence du climat méditerrané en sur la reproduction du Martinet noir (*Apus apus* L.). Oiseau 57: 69–84.

Gory, G. 1993. Effets du climat sur la reproduction du Martinet noir (*Apus apus* L.). Synthèse de observations réalisées dans le Sud de la France. Avocetta 17 (Spec. Issue): 177–188.

Hotta, M. 1996. Timing of laying in multiple-brooded Little Swifts *Apus affinis*. Jpn. J. Ornithol. 45:23–30.

Johnson, C. G. 1969. Migration and dispersal of insects by flight. Methuen, London.

Knorr, O. 1961. The geographical and ecological distribution of the Black Swift in Colorado. Wilson Bull. 73: 155–170.

Koskimies, J. 1950. The life of the Swift, *Micropus* *apus* (L.), in relation to the weather. Ann. Acad. Sci. Fenn. Ser. A IV Biol. 15: 1–151.

Lack, D. 1956. Further notes on the breeding biology of the Swift *Apus apus*. Ibis 98: 606–619.

Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Proc. Int. Ornithol. Congr. 14: 3–42.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lack, D. 1973. Swifts in a tower. Chapman and Hall, London.

Lack, D., & E. Lack. 1951. The breeding biology of the Swift *Apus apus*. Ibis 93: 501–546.

Marín, M. 1997. Some aspects of the breeding biology of the Black Swift. Wilson Bull. 109: 290–306.

Marín, M. 1998. Airbirds: adaptative strategies to the aerial life style from a life history perspective. Ph.D. diss., Louisiana State Univ., Baton Rouge, Louisiana.

Marín, M. 1999. Food, foraging, and timing of breeding of the Black Swift in California. Wilson Bull. 111: 30–37.

Marín, M., & J. Sánchez. 1998. Breeding of the Black Swift (*Cypseloides niger*) in Costa Rica. Ornitol. Neotrop. 9: 219–221.

Marín, M., & F. G. Stiles. 1992. On the biology of five species of swifts (Apodidae, Cypseloidinae) in Costa Rica. Proc. West. Found. Vertebr. Zool. 4: 287–351.

Naik, S., & R. M. Naik. 1966. Studies on the House Swift, *Apus affinis* (G. E. Gray). 6. Body weight. Pavo 4: 84–91.

O' Connor, R. J. 1978. Growth strategies in nestling passerines. Living Bird 16: 209–238.

O' Connor, R. J. 1979. Egg weights and brood reduction in the European Swift (*Apus apus*). Condor 81: 133–145.

O'Connor, R. J. 1984. The growth and development of birds. John Wiley, Chichester, UK.

Redford, K. H., & J. G. Dorea. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. J. Zool. (Lond.) 203: 385–395.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978–983.

Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110: 419–451.

Ricklefs, R. E. 1973. Patterns of growth in birds. II: Growth rate and development. Ibis 115: 177–201.

Ricklefs, R. E. 1976. Growth rates of birds in the humid New World tropics. Ibis 118: 179–207.

Ricklefs, R. E. 1979. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. 54: 269–290.

Ricklefs, R. E. 1983. Avian postnatal development. Pp. 1–83 *in* Farner, D. S., J. R. King, & K. C. Parkes (eds.). Avian Biology, Vol. 7. Academic Press, New York.

Taylor, L. R. 1963. Analysis of the effect of temperature on insects in flight. J. Anim. Ecol. 32: 99–117.

Taylor, R. L. 1975. Butterflies in my stomach. Or: insects in human nutrition. Woodbridge Press, Santa Barbara, California.

Thibault, J.-C., D. Brunstein, E. Pasquet, & I. Guyot. 1987. La reproduction du Martinet Pâle (*Apus pallidus*, Shelley) sur des îlot satellites de la Corse: ses relations avec les facteurs climatiques. Rev. Ecol. (Terre Vie) 42: 277–296.

Stearns, S. C. 1992. The evolution of life histories. Oxford Univ. Press, New York.

Udvardy, M. D. F. 1954. Summer movements of Black Swifts in relation to weather conditions. Condor 56: 261–267.

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