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INTERMITTENT INCUBATION IN TWO NEOTROPICAL SWIFTS: AN ADAPTATION TO LIFE IN THE AERIAL ENVIRONMENT?

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Resumen. – Incubación intermitente en dos vencejos Neotropicales: una adaptación a la vida en el medio aereo? – Se examino el patrón de incubación de dos especies de vencejos cypseloidines: el Vencejo de cuatro ojos (*Cypseloides cherriei*) una especie de 23 g, que tiene una nidada de un huevo y un periodo de incubación de 29 días y el Vencejo de collar rojizo (*Streptoprocne rutila*) una especie de 21g, que tiene una nidada de dos huevos y un periodo de incubación de 25 días. La primera especie estaba 50% y la segunda 32% de las 12 horas del día fuera del nido durante la incubación. No se encontró correlación entre la lluvia caída diariamente y el patrón de incubación, probablemente porque las aves estaban fuera del nido forrajeando principalmente en las mañanas y en el área de estudio la lluvia caía principalmente en las tardes. Además no se encontró correlación entre las temperaturas diarias y el patrón de incubación. La especie que estaba menos tiempo en el nido tenía un huevo más grande y pesado. La larga incubación y el lento desarrollo de la especie de una nidada de un huevo versus el de la nidada de dos huevos, puede ser explicada en termino de mayor tiempo fuera del nido forrajeando. La especie con la nidada más baja estaba más tiempo fuera del nido y consecuentemente dejaba los huevos solos por tiempos más largos. Esto puede ser análogo a las especies de Procellariiformes. Ambos las especies de vencejos cypseloidines y las especies de Procellariiformes tienen que enfrentar condiciones de forrajeo muy impredecibles. La diferencia en estos dos grupos de aves es en la escala de tiempo para los vencejos es una escala de horas y para los Procellariiformes es en días.

Abstract. – The incubation pattern of two species of cypseloidine swifts was examined. The Spot-fronted Swift (*Cypseloides cherriei*), a 23-g bird, laid a one-egg clutch and had an incubation period of 29 days. The Chestnut-collared Swift (*Streptoprocne rutila*), a 21-g bird, laid a two-egg clutch and had an incubation period of 25 days. The former species spent 50% and the latter species 32% of 12 h daylight away from the nest during incubation. There was no correlation between daily rainfall and nest attendance, probably because the birds were out foraging primarily in the morning, whereas most rain at the study site was usually in the afternoon. Furthermore, there was no correlation between daily temperatures and nest attendance. The species that spent less time incubating each day has a heavier egg. The longer incubation period and slower growth rate of the one-egg clutch versus the two-egg clutch might be explained in terms of greater time spent away from the nest foraging. The species with the smaller clutch size spent more time away from the nest, and thus neglected the eggs more. This observation might be analogous to procellariiform seabirds. Both cypseloidine swifts and procellariiform seabirds face unpredictable foraging conditions and to a different degree seem to neglect their eggs. The difference is that the time scale for swifts is in hours, whereas for procellariiform seabirds it is in days. *Accepted 3 May 2008*.

Key words: Incubation patterns, Spot-fronted Swift, *Cypseloides cherriei*, Chestnut-collared Swift, *Streptoprocne rutila*, Costa Rica.

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INTRODUCTION

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" (or time away from the nest during the incubation period), 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).

Intermittent incubation or temporary egg neglect and a high degree of cooling tolerance by the embryo are widespread in procellariiform seabirds (Skutch 1976, Boersma & 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 positively correlated (Warham 1990). These authors interpreted this constellation of traits 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 similar foraging constraints to those of seabirds: they feed on unpredictable, patchy, and often ephemeral food supply (Marín & Stiles 1992). Among the Apodidae, the cypseloidine 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 & Stiles 1992). Brooks & 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 intermittent incubation or egg "neglect" is an adaptation to foraging conditions. To test this idea I present here mainly data from the two smallest species of cypseloidine swifts, the 23 g Spot-fronted Swift (*Cypseloides cherriei*) and the 21g Chestnut-collared Swift (*Streptoprocne rutila*). The former is the rarest Neotropical swift and is known from very few localities (Marín & Stiles 1993). The latter is probably the second most common and widespread cypseloidine swift. Nests of both species are rare and difficult to access, nesting in restricted areas behind or close to waterfalls (Marin & Stiles 1992). Although these two swifts are close in body mass, they differ in clutch size, the former having a single-egg and the latter a two-egg clutch (Marín & Stiles 1992). I also examined published and unpublished data on egg neglect or intermittent incubation for several other swift species.

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 30-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,

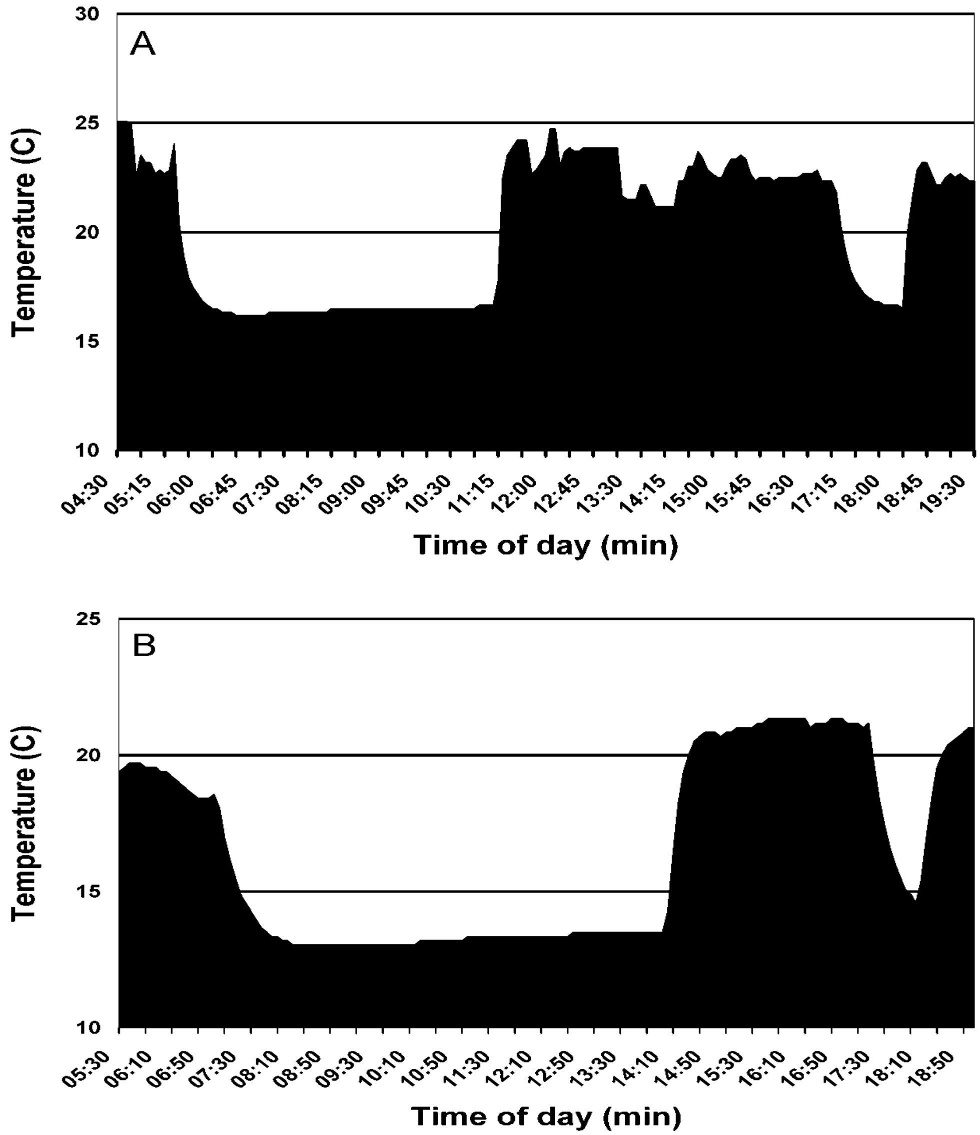

FIG. 1. Temperature at the nest, showing the daily incubation patterns indicating the long and the short period of egg neglect of A) the Spot-fronted Swift and B) Chestnut-collared Swift.

topography and geology, and vegetation of the site can be found in Marín & Stiles (1992).

Measurements of egg mass and linear dimensions are from the study site, complemented by data from museum specimens from the study area. 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 of a newly laid egg. To estimate egg mass of some eggs, I

TABLE 1. Egg measurements and mass, mean and standard deviation (SD) of the Spot-fronted (*Cypseloides cherriei*) and the Chestnut-collared (*Streptoprocne rutila*) swifts. All differences in measurements are statistically significant at $P < 0.01$.

Features	Species	
	Spot-fronted (n = 25)	Chestnut-collared (n = 24)
Mass (g)	3.7 (0.32)	2.9 (0.16)
Length (mm)	24.4 (1.04)	23.4 (0.96)
Width (mm)	16.5 (0.59)	15.3 (0.42)
Breadth/length index from the means	0.67	0.65

used the formula $M = k\ LB^2$, where M = mass of the whole fresh egg (g), k = is a constant, L = length of egg (mm), and B = breath of egg (mm) (see Hoyt 1979). I used Ratcliffe's (1967) index for egg-shell thickness (IEST) whose formula is: IEST = M/LB, where M is mass of the empty shell (mg), L = length of egg (mm), and B = breath of egg (mm).

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, Pocasett, 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 when it returned, the temperature increased quickly, usually by over 10 degrees (see Fig. 1A,B). 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 or data loggers fell by excessive water flow on the waterfalls or rivers.

For the Spot-fronted Swift, I recorded data for a total of 59 days from three nests (one complete incubation period 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 attendance did not differ significantly at three nests of the Spot-fronted Swift (ANOVA, $F_{2, 56} = 1.47$, $P = 0.24$), nor did it differ between the two nests of the Chestnut-collared Swift (t = 1.03, $P = 0.31$, df = 41). Because the presence of the adult was continuous at night, the percent of nest attendance was measured on a 12-h basis, starting at first departure time, usually at sunrise.

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 slightly glossy. Egg shapes of the two species (breadth/length ratio) differed significantly (t = 2.75, $P = 0.008$, df = 47) (see Table 1). Both egg length and breadth were significantly larger in the former species (t = 3.31, $P = 0.002$, df = 47; and 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 1). The mean index of egg-shell thickness of the Spot-fronted Swift was 0.474, (SD = 0.046, n = 6) and that of the Chestnut-collared Swift was (mean= 0.396, SD = 0.022, n = 13) and were significantly different (t = 5.03, $P < 0.001$, df = 17). These findings indicated, that Spot-fronted Swift egg's shells were thicker than those of the Chestnut-collared swift.

In both species both genders seem to incubate in about equal proportion. 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 (t = 3.72, $P = 0.003$, df = 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%, respectively). For the complete incubation period (egg laying to hatching), the egg was unattended for 12,500 min (26.3%) for the Spot-fronted Swift (n= 47,520 min (33 days). This clutch had a total of 24.3 days of actual incubation time. For the complete data set of incubation periods of the Chestnut-collared Swift, with 34,560 min (24 days) recorded, indicated 5020 min (14.5%) without attendance. This clutch had a total of 20.5 days of actual incubation time. The two species had similar values of per-egg mass/ actual incubation time: 0.152 versus 0.141 g/ incubation time, respectively.

Nestling period and nest attendance. The nestling period of the Spot-fronted Swift was highly variable, and ranged from 54 to 88 days (mean = 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 unpubl.).

Based on counts of 12 hrs period per day, the Spot-fronted Swift averaged 49.8% (SD = 21.8, n = 59 days, 3 nests) of the time on the nest, which is less than the Chestnut-collared Swift, at 68.0%, (SD = 21.1, n = 44 days, 2 nests). Comparing on a daily basis the amount of time left the eggs without attendance the species differed significantly (t = 4.1, $P = 0.00009$, df =101). 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, 3 nests), 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, 2 nest).

The Spot-fronted Swift left unattended the egg primarily in the mornings and occurred as a single foraging bout in the early hours in the morning and sometimes a short foraging bout in the afternoon. Of 59 departures, 42% were typically between 06:00 and 07:00 h, with 34% occurring between 05:00 and 06:00 h, 22% between 07:05 and 08:00 h, and 5% later than 8:05 h. The earliest departure was at 05:10, and the latest departure was at 08:25 h. The data logger recorded that the birds took a second trip out of the nest on 15 of 59 days (25%) (Fig. 1A). This second trip was usually short and just before sunset. The birds usually departed from the nest at about 17:15 h and stayed away about 50-min on average. The second bouts lasted from 15 to 65-min.

The Chestnut-collared Swifts unattended the eggs in the early morning hours and in the late afternoon. The departure times were later than for the Spot-fronted Swifts:(n = 44; 17% of departures were between 05:00 and 06:00 h, 12% between 06:05 and 07:00 h, 27% between 07:05 and 08:00 h, and 43% later than 08:05 h. The difference between the two species was significant ($G = 30.18$, $P < 0.05$, df =5). As with the previous species, a second

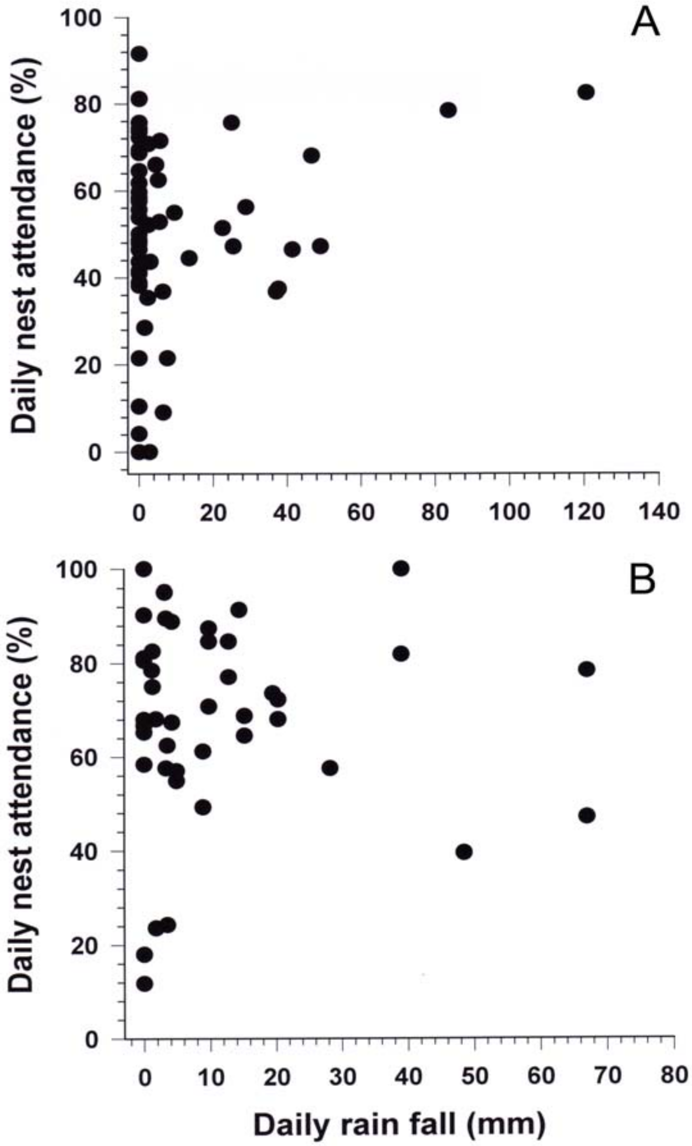

FIG. 2. Relationship between percent of daily nest attendance and daily rain: A) Spot-fronted Swift, r = 0.21, *P* = 0.094, n = 59, and B) Chestnut-collared Swift, r = 0.019, *P* = 0.903, n = 42. All data for each individual species were combined.

foraging trip was recorded in the evening, but for 56% of the time (Fig. 1B). Departure times for the second foraging trip were very erratic. However, most departures were recorded around 17:30 h. The earliest evening departure was at 13:50, and the latest was at 18:10 h. On average, the second bouts lasted 83-min (range 15 to 265-min).

Weather and temperature. For the Spot-fronted Swift, I used rainfall data from "Avance de Tres Rios" weather station. For each individual nest, I found no significant relationship between daily rainfall and percent of nest attendance during incubation (all $P > 0.1$) (see also Fig. 2A). 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 again found no significant relationship between daily rainfall and percent nest attendance during incubation (all $P > 0.6$) (see Fig. 2B). The lack of correlation between daily rainfall and nest attendance may result from the birds being away from the nest primarily in the morning (see above) whereas the rains usually occur 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 during incubation 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, $P = 0.55$, and r = -0.02, $P = 0.87$, n = 33, respectively). When combining all data for the Chestnut-collared Swifts, I found no relationship between percent daily attendance and mean daily temperature (r = -0.05, $P = 0.73$, n = 42).

The minimum and maximum temperature at any nest for the Spot-fronted Swift they 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 temperature recorded for the general area near the specific nest. The mean minimum temperature for the general area from the weather stations was only 1-2°C below the minimum recorded for any nest. The slightly higher temperature at the nests compared with the general area may be due to the effect of water ameliorating the diel variations of temperature at the nest.

DISCUSSION

The Spot-fronted and the Chestnut-collared swifts are closely related and they are the smallest cypseloidines that are relatively similar in size. However, they differ greatly in their growth rates and life history strategies (Marin & Stiles 1992). The fastest growing nestling of the Spot-fronted Swift grew 18.5% more slowly than did the slowest growing nestling of the Chestnut-collared Swift (Marin unpubl.). The difference between single-egg mass and nestling hatching mass between the two species was 22.8% and 19.0%, respectively. The two species, however, had similar egg mass per incubation time 0.152 versus 0.141g/per effective incubation time, respectively.

One possible explanation of the proportionately smaller ratio of clutch mass to body mass or larger ratio of single-egg mass to body mass, the longer incubation period, and the slower growth rate of the Spot-fronted Swift versus the Chestnut-collared Swift life history tactics, would be in terms of time spent away from the nest foraging. Birds that need to spend a long period of time foraging away from the nest need to adjust the egg or eggs to water loss and long periods of cooling. One way to adjust to this 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 & 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 & Ar 1974). Egg mass was the parameter that differed most between the two species (see above and Table 1). The index of egg-shell thickness was statistically different, with the

Spot-fronted having a thicker egg-shell (see also above) and this might reflect the differences in the incubation regime between these two species. An egg with a thicker egg-shell will loose less water and should be more resistant to chilling.

Spot-fronted and Chestnut-collared Swifts live in the same area and breed during the rainy season at about the same time. Thus, there is much overlap in hatching time (Marín & Stiles 1992). The large amount of yolk in eggs found on some 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 conditions would evolve a large difference in egg yolk proportions. Furthermore, the egg's environment was about the same for both species (see above). The two species differ greatly in their egg-shell thickness index (see above) but, whether the two species differ in egg-shell porosity, is not known. The rate of water loss might be an 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 & Ar 1974, Warham 1990), and the same might be true for cypseloidine swifts.

Long term intermittent incubation or 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 species (Boersma & Wheelwright 1979, Warham 1990). Boersma & Wheelwright (1979) hypothesized that egg neglect in seabirds should be more common in: a) species that have more protected nests that reduce the effect of extreme temperatures and predation, and b) more distant foragers. Below I examine these ideas with respect to cypseloidine swifts that as a group share the similar foraging constraints to those of procellariiform seabirds.

Nest protection. All swifts nest in protected sites, although some species have more protected sites than others. Cypseloidine swifts probably have the most stringent nest-site requirements in the Apodidae, behind or next to waterfalls, and as a group perhaps 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 or adjacent to waterfalls, or in river gorges and have reduced nest predation, but the trade-off for safety from predators is nest vulnerability due to weather conditions, primarily flood-producing rainfall (Marín & Stiles 1992). 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 leave unattended their eggs for long periods of time, a safe nest site is an important requirement. Both pelagic seabirds and swifts nest in safe sites that permit the adults to range widely for food. If the hypothesis stated by Boersma & Wheelwright 1979, is correct, all swifts should show some degree of egg neglect.

For swifts in general, published 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

TABLE 2. Summary of egg neglect in swifts in relation to clutch size and latitude (see also text).

Species	Clutch size	Latitude	Mean percent of neglect per day	Recorded intervals per day	Number of nests sampled	Sources
Cypseloides cherriei	1	Tropical	50%	12 h	3	Present study
Cypseloides cryptus	1	Tropical	54%	12 h	3	Marin unpubl.
Streptoprocne rutila	2	Tropical	32%	12 h	2	Present study
Streptoprocne zonaris	2	Tropical	35%	12 h	3	Marin unpubl.
Cypsiurus parvus	2	Tropical	34.8%	6 h	7	Moreau (1941)
Apus caffer	2	Tropical	31%	6 h	7	Moreau (1942b)
Apus apus	2–4	Temperate	Irregular 1-390 min.	10 h	?	Lack & Lack (1952)
Apus pallidus	2–4	Temperate	Twice	8 h	?	Malacarne *et al.* (1992)
Apus affinis	2–3	Tropical	26%	9 h	5	Moreau (1942)
Aeronautes saxatalis	4	Temperate	17%	12 h	2	Marin unpubl.
Chaetura pelagica	5	Temperate	6.5%	12 h	1	Kendeigh (1952)

uncovered on average 34.8% of the day-light hours (based on observation periods of 6 h). During observations of seven nests for 6 h each per day the White-rumped Swift (*Apus caffer*), with a two-egg clutch, exhibited more than 90-min of egg neglect in all nests and > 120-min in six nests (Moreau 1942b). Furthermore, Moreau (1942b) mentioned 13 cases of egg neglect > 120-min (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 & Lack (1952) reported egg neglect for intervals varying from 1 to 390–min (6.5 h). Long periods of inattentiveness were rare, but Lack & 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 much 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) and Razack & Naik (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 h. 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 unattended 12 times for periods of 19–84-min, averaging 46.3-min. For the temperate White-throated Swift (*Aeronautes saxatalis*) with a clutch size ranging from 3–6 eggs, most often 4 eggs, data from two nests (32 days in total) (Marin unpubl.) egg neglect ranged from 10 to 570-min, with a mean of 17% of egg neglect. In the White-throated Swift, egg neglect decreased with increasing incubation time. For two other tropical species, the White-chinned swift (*Cypseloides cryp-*

tus) a one-egg clutch species neglected the eggs 54% of the time (based on a 12 h period, data from 3 nests) and for the large White-collared swift (*Streptoprocne zonaris*) a two-egg clutch species neglected the eggs for 35% of the time (based on a 12 h period, data from 3 nests) (Marin unpubl.). All the above cases of egg neglect were associated with normal hatching success. Thus, it seems that as clutch size increases, egg neglect decreases (r_s = - 0.953; $P = 0.000$; n = 9, see also Table 2).

Foraging "distance"or time away from the nest. All swifts seem to forage at some distance from the nest; however, in swifts this "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 trend is that in swifts a species with a large-clutch has shorter incubation period and presumably 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. Although data on flight altitudes on swifts are scant, this can be an important parameter in combination with foraging distance. For the Vaux's Swift (*Chaetura vauxi*), with a large clutch size of 5–6 eggs, Bull & Beckwith (1993) found that it spent 60% of 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 c. 1–6 km from the nest. Williams (1956) gave three altitudinal records, for the Chimney Swift ranging from 1980 to 2225 m, viewed from an airplane. 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 weather was much lower, 1720 m (average 700 m). For the White-collared Swift (*Streptoprocne zonaris*), with a clutch size of 2 eggs, Whitacre (1991) found that the birds moved at least 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" or more time spend away from the nest. 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 most likely probably all, swifts seem to neglect their eggs, although to different degrees. Judging from the published and unpublished information, there seem 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 or as clutch size increases, egg neglect decreases.

On the first trend, higher occurrence of egg neglect might occur in more tropical latitudes because weather changes are more frequent and complex (Barry & Chorley 1982). 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 might place a restriction on the aerial feeding birds. In addition, tropical swifts breed during the rainy season. Foraging conditions works in similar fashion for pelagic seabirds, but in reverse, because, the highest species diversity and dietary biomass for pelagic seabirds occurs at high latitudes and not low latitudes. Furthermore, 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 foraging 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 similar foraging conditions and neglect their eggs. They differ in time scales of their foraging bouts: several days for the Procellariiformes versus several hours for the Apodidae (Marín 1999). Although in seabirds intermittent incubation or egg neglect is one of days, versus one of hours in swifts, they might well occur for analogous reasons, in both groups, the patchy and ephemeral distribution of prey items, at least during the breeding season.

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