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THE BREEDING BIOLOGY OF THE BISCUTATE SWIFT (*STREPTOPROCNE BISCUTATA*) IN SOUTHERN BRAZIL

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Resumo. – A biologia reprodutiva do Andorinhão-de-coleira-falha (*Streptoprocne biscutata*) no sul do Brasil. – A biologia reprodutiva do Andorinhão-de-coleira-falha (*Streptoprocne biscutata*) foi estudada em uma gruta situada no Estado do Paraná, sul do Brasil. O trabalho de campo consistiu no monitoramento dos ninhos, ovos, e filhotes a cada 2 dias durante o período reprodutivo e na marcação das aves adultas com anilhas e marcadores fosforescentes. A construção dos ninhos inicia em outubro, sendo a coleta do material nidular feita com o bico. Os sítios de nidificação são substratos rochosos horizontais ou ligeiramente inclinados em paredes verticais ou fendas. O material nidular é composto principalmente por líquenes, briófitas, pteridófitas, angiospermas e terra. Vistos de cima os ninhos podem ser circular, elipsóide, ou semicircular. A postura ocorre no começo de novembro, sendo o tamanho da postura de 1–4 ovos. O ritmo de ovoposição e o comportamento associado revelam a existência de um padrão de postura e de competição por ninhos. Os ovos são brancos com formas sub-elíptica alongada ou sub-elíptica. A incubação durou 24 dias em média e em pelo menos um ninho foi realizada pelo casal. A substituição do indivíduo que incuba foi realizada por um comportamento padrão. O período como ninhego é de 33 dias aproximadamente e após deixarem os ninhos eles ficam dentro da gruta por mais 10 dias. Ao nascer os filhotes são nus e cegos. A primeira plumagem consiste de penugens cinzas a qual alcança o completo desenvolvimento ao 13° dia. Com a idade de 34 dias o filhote tem a plumagem definitiva completa. O estudo do crescimento mostrou que as medidas lineares foram a asa e a cauda. Por fim, a reprodução do Andorinhão-de-coleira-falha mostrou-se semelhante ao padrão já descrito na literatura para outras espécies do gênero, mas aparentemente possui períodos mais curtos de incubação e de permanência no ninho.

Abstract. – The breeding biology of the Biscutate Swift (*Streptoprocne biscutata*) was studied in a cave located in the Paraná State, southern Brazil. Besides monitoring of the nests, eggs, and nestlings every 2 days, the field works involved banding of adult birds with metallic bands and phosphorescent markers. Nest building begins in October; the nest material is collected with the bill. Nest sites are horizontal or slightly inclined rocky substrata on otherwise vertical walls or crevices. Nest materials are mainly lichens, bryophytes, pteridophytes, angiosperms, and soil. Nests are circular, ellipsoid, or semicircular in shape. Laying takes place at the beginning of November, with a clutch sizes of 1–4 eggs. The laying rhythm and the behavior associated with it revealed the existence of a laying pattern and competition for nests. The white eggs are long subelliptical or subelliptical in shapes. Incubation lasted 24 days on the average and, in at least one nest, was shared by both parents. The exchange of the incubating bird was accompanied by a standardized behavior. The nestling period was about 33 days and, after leaving the nests, the fledglings stay in the cave for about 10 days. At hatching, the nestlings are naked and blind. The first feather coat consists of gray semiplumes and reaches its full development on the 13th day. At the age of 34 days, the nestlings have their full definitive teleoptile plumage. The study of chick growth showed that the linear measurements were the wing and tail. Finally, the reproduction pattern of Biscutate Swift is similar to that already described in the literature for other species of the genus, but apparently with shorter periods of incubation and permanence in the nest. *Accepted 1 May 2001.*

Key words: Biscutate Swift, *Streptoprocne biscutata,* Apodidae, Aves, breeding biology, Paraná State, Brazil.

INTRODUCTION

The Apodidae are widely distributed with species on almost all continents (Collins 1985). The family is mainly tropical and consists of about 92 species, of which about 23 occur in South America (Chantler & Driessens 1995).

Elements of the reproductive biology of the Apodidae, such as nest types, breeding places and clutch size have been used as characters for generic and subfamily levels (Lack 1956, Orr 1963, Brooke 1970, Marín & Stiles 1992, Collins 2000). Extensive studies of their breeding biology have been conducted for Asian, European and North American species (Koskimies 1950, Lack & Lack 1951, Fischer 1958). In South America, in spite of the large number of species including some endemic ones, there are only few published studies (Sick 1947, 1948a, 1948b, 1948c, 1950, 1958, 1959; Haverschmidt 1958, Collins 1968a, 1968b), all dealing with small species.

The Biscutate Swift (*Streptoprocne biscutata*) occurs in eastern Brazil from the state of Piauí south to Rio Grande do Sul, extending to northeastern Argentina in the province of Missiones (Meyer de Schauensee 1982, Nores & Yzurieta 1985, Chantler & Driessens 1995, Sick 1997). Published data on the biology of the species are limited to sparse comments on the few known colonies. There is a colony of about 80,000 birds in the region of Seridó in the state of Rio Grande do Norte (Sick 1997). This species inhabits also the Serra do Ibitipoca in the southern part of Minas Gerais State (Andrade *et al.* 1985, Andrade & Freitas 1987) where notes on the breeding biology of the species were taken for the first time (Andrade *et al.* 1985).

In southern Brazil, the studies are very scarce and limited. In northeastern of Rio Grande do Sul, in the region of the Aparados da Serra National Park, the observation of mixed flocks of Biscutate Swift and White-collared Swift (*Streptoprocne zonaris*) was noted (Belton 1994). In Santa Catarina, the species was recorded in the Mun. of Urubici and nearby regions (Sick & Bege 1984, Rosário 1996). For Paraná State, there was only one record of the species in the Mun. of Castro, dated 1907 (Pinto 1938). However, since 1992, the species has been recorded in several places (Pichorim & M. R. Bornschein unpubl. data), and the colony that is described in this study was discovered. Based on the recent discovery of the Biscutate Swift in Paraná, this study was carried out with the objective of describing for the first time the breeding biology of the species.

STUDY AREA AND METHODS

The study was carried out between 1994 and 1996 at Anhangava Hill, in the Serra da Baitaca. It is situated in the Mun. of Quatro Barras, State of Paraná, Brazil (25°22'S, 48°58'W). This region is part of the Serra do Mar, which consists of a large series of hills along the Brazilian coast. At the top of Anhangava, at 1420 m a.s.l., occur ecological refuges and dense ombrophilous high-altitude forest (following the classification of Fundação Instituto Brasileiro de Geografia e Estatística–IBGE 1992). At the base of the hill, the dense ombrophilous montane forest occurs between ombrophilous forest with *Araucaria angustifolia*. Above 1000 m, the area includes exposed granite rocks, which prevail in the local landscape at altitudes above 1200 m.

The overnight roosting and breeding site studied here was a cave of granite formed by a crevice of 120 m in length in the northern mountain face, at 1250 m a.s.l. Its width and height are highly variable (0.5–4.5 m and 4–15 m respectively), and so is the luminosity, the innermost portion being completely dark. The floor consists of chaotically piled rocky blocks with a deep guano accumulation that decreases in amount toward the innermost portion of the cave. Popularly, this cave is called the "caverna das andorinhas" (swallows' cave).

Biscutate Swifts inhabit this site during the whole year. However, the population size is not constant, having a maximum of about 260 individuals in spring (September–December) and a minimum of 150 in winter (June–August).

The regional weather type is cfb of the Köppen classification system, characterized by a warm and rainy summer and a cold winter with casual dry periods (Maack 1981). The region has a high rainfall index (about 2000 mm per month), a high relative humidity (the annual average is 90%), and is very cloudy (Roderjan 1994).

In order to identify individual birds during the reproductive period, an attempt was made to band the largest possible number of individuals in the colony during fourteen 3-day visits from March 1994 to December 1995. The birds were captured with a circular net similar to a butterfly net, but with a supporting ring of 2 m in diameter. The ring was made of flexible fiber glass rods (as used in tents for camping) and supported by a 4 m long tubular aluminum handle.

The basic procedure to capture adult birds consisted of awaiting their departure from the cave in the morning, near the frequently used exit. When the birds started to leave the cave, the net was quickly raised into the flock, capturing between 5 and 15 individuals each time. This procedure was repeated only three times in one day in order not to stress the birds excessively.

Metallic numbered bands of size " J " (inner diameter of 4.5 mm) were used. The bands were supplied by CEMAVE/IBAMA (Centro de Pesquisas para Conservação das Aves Silvestres/Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis).

Reproduction took place from October to the middle of January in each of the three study years. At the beginning of this period, during each one of the study years, one visit per week was made to the cave with the purpose of finding the first signs of breeding activities. During these visits, a systematic and meticulous search for nests was made, covering about 70% of the whole internal area of the cave. When the first signs of nest building were detected, the frequency of visits was increased to two days per week.

The study of parental care were made on one pair of birds by a special marking developed for observation under aphotic condition. Plasticized disks of fine cardboard, 15 mm in diameter, were painted on both sides with phosphorescent ink. A black letter ("A" and "B") was printed on each of them. Two of these disks were used, with the same letter, for each one of the mates that made up the pair. The disks were glued on the coverts of both wings with instantaneous glue ("super bonder") while care was taken to not let it get in contact with the skin. These birds could be identified from a distance when they arrived at the nest, since the phosphorescent ink continued to irradiate the light that had been absorbed outside the cave for about 10 min, thus making the letter code visible. Through this method, it was possible to quantify the times of incubation for each adult bird.

A tent made of black cloth was used to hide the observer's presence inside the cave. The incubation activities of the marked pair were observed during six days. The observations in each day have started between 06:00 and 10:00 h and finished between 15:00 and 19:00 h (Eastern Standard Time). These began in the second day after marking the "B" individual.

The measurements taken for each nest were: the largest and smallest external width, the width of the nest cup, the external height and the depth of the nest cup in relation to

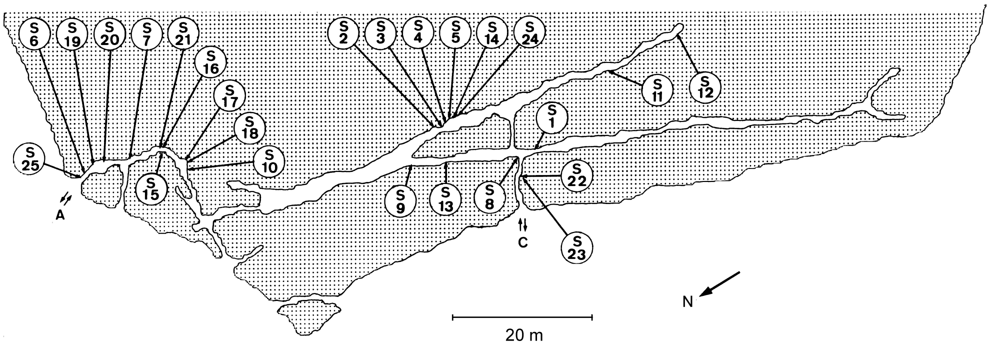

FIG. 1. Schematic drawing of the studied cave with the nest sites. The letters A, B and C indicate the three entrances used by the birds. Adapted from drawing made by Darci P. Zakrzewski.

the highest border. To calculate the average for the measurement for all nests, only the highest value obtained in each reproductive season was used, because variations occurred in the nest dimensions during the breeding season. The eggs were marked by a pencil, weighed and measured (width and length) during the visit in which each one was found for the first time (0 to 2 days after having been laid). The nestlings received plastic bands that were replaced by metallic ones when the birds were at a minimum age of 14–16 days. The following measurements were taken on each visit to the nest after hatching: mass, wing (flattened), tail, tarsus and exposed culmen. In addition, the development of the plumage and behavior were also described. The eggs shape description follows Baicich & Harrison (1997).

The measurements of the nestlings and eggs and the dimensions of the nests were taken with calipers to 0.05 mm and a metallic rule to 0.5 mm. The masses, including those of the adult birds, were obtained with pesola spring balances (50 g, 100 g and 300 g). Speleology equipment like carabiners, harness, tapes and electric head lanterns were used for the activities conducted inside the cave. To reach the nests, 25 steel pitons 15 cm in length and 12 mm in diameter were placed close to them. Nylon ropes (12 mm thick) were fixed to them. The ropes were not suspended in the air but lay flat against the rock walls, so that they did not interfere with bird flights inside the cave. These ropes facilitated a fast and safe access to the nests and did not appear to interfere in the reproductive activities of the birds.

RESULTS AND DISCUSSION

Nests. From August to October 1994, 21 nests were found, all having been built in areas that possessed an accumulation of nest material of the former breeding season. This implies that these places had already been used previously. In the next year, 21 nests were found, of which 19 were built in the same places used in the previous year. In 1996, 16 nest were found and their construction was again in the same areas used in the previous years. Thus, during these three years, 25 preferential places for nest construction were observed, which yielded 58 completed nests. These preferred areas are herein considered as "nest site" (Fig. 1).

The nest sites were characterized by a horizontal or slightly tilted rocky substratum located inside the cave at a height of 3–8 m. These places were quite inaccessible and con-

TABLE 1. Characteristics of the nest sites of Biscutate Swifts at the Anhangava Hill, southern Brazil.

Sites	Type[1]	Measurements[2]	Nest distance from the exit (m)	Usage[3] 1994	1995	1996
S1	A	58 cm/1000 cm^2	8.5	+	+	+
S2	A	40 cm/1200 cm^2	24	+	+	-
S3	A	20 cm/390 cm^2	24	+	+	+
S4	A	27 cm/1500 cm^2	23	+	+	-
S5	C	25 cm/1.3 m	23.4	+	-	-
S6	A	40 cm/1400 cm^2	1.7	+	+	+
S7	A	15 cm/720 cm^2	8.5	+	+	+
S8	B	650 cm^2	7.4	+	+	+
S9	B	*	19.4	-	+	-
S10	B	650 cm^2	15.4	+	+	+
S11	C	17 cm/4 m	25	+	-	-
S12	C	50 cm/7 m	39.4	+	+	-
S13	C	20 cm/4 m	17.7	+	+	+
S14	C	27 cm/90 cm	22	+	+	+
S15	C	20 cm/20 cm	13	+	-	-
S16	C	9 cm/70 cm	13	+	+	-
S17	C	28 cm/1.4 m	15	+	+	+
S18	C	*	15.4	+	+	+
S19	C	*	2.9	+	+	+
S20	C	*	4.5	-	+	+
S22	C	*	4.5	?	+	+
S23	C	*	4.5	?	+	+
S24	B	450 cm^2	21.7	+	+	-
S25	D	12 cm/18 cm	1.4	+	+	+

[1] The nest sites were classified in four types: A = stone arrested in vertical crevice, B = plateau in vertical wall, C = interior of vertical crevice, and D: interior of horizontal crevice.

[2] The measures were obtained at the spot used for the nest construction. Asterisks indicate nest sites where measuring was impossible. A sequence of presentation of the values was adopted for each site type, as follows: type A - width of the crevice in the used place and approximate area of the upper side of the stone where the nest was situated, type B - approximate area of the plateau, and types C and D - width of the crevice in the used place and depth until the nest.

[3] The sites were considered in use when any sign of nest construction was detected, even if laying had not yet begun.

sisted mainly of plateaus in vertical walls or crevices. A brief description of each nest site is given in Table 1. There were no perennial watercourses near any of the nest sites. This differs of what has earlier been reported for White-collared Swift, a species that seems to prefer humid areas (Marín & Stiles 1992, Sick 1997). However, some nests were located very close to temporary water streams that appeared only during intense rains, and which flooded all nest material and sprinkled the eggs and nestlings. After the breeding season, at such places, the remaining nest materials were totally removed by the action of the water along the year. In spite of this, in the next breeding season, the nests were rebuilt

TABLE 2. Dimensions (cm) of Biscutate Swift nests at three nest sites in the same reproductive season, at the Anhangava Hill, southern Brazil.

Sites	Date	Smallest external diameter	Largest external diameter	Smallest internal diameter	Largest internal diameter	Smallest external height	Largest external height	Depth
S 1	29 October 1994	14	16.5	7.5	8	1	5.5	3
S 1	16 November 1994	15	17	8	9.5	1.5	7	3.5
S 1	18 January 1995	-[1]	-	-	-	-	-	-
S 10	29 October 1994	17	22	10	10	2	3	3.5
S 10	16 November 1994	17	21	10	11	3	4.5	3
S 10	18 January 1995	17	20	10	10	3	4	2.5
S 17	29 October 1994	11.5	19.5	7.5	8.5	1	10.5	3
S 17	16 November 1994	12.5	19.5	7.5	9.5	1	9	3
S 17	18 January 1995	11.5	13.5	7	8.8	1	7	2

[1] The dash means total loss of the nest configuration, the measure being impossible to be obtained.

at the same specific site.

The use of the same sites for reproduction in successive years entailed only in a relining of the old nests, and not in a total reconstruction of them, except in cases where all old material had been washed away. The new nest material was added first in the worn borders of the old nest cup. This was clearly visible as the old material always was dry and compacted, contrasting with the greenish and damp fresh material. In the nests on inclined surfaces, the birds initially compensated by adding more new nest material to the lowest border, and built the remainder of the nest later. Starting at these points of repair, all old nest material was progressively covered by a layer of fresh material. The renovating of the first nests began at the beginning of October (2 October 1995 was the earliest verified date). However, some nests began to be renewed only at the end of that month (29 October 1994). The addition of material is not limited to the pre laying period; the adults continue to renew the nests at a seemingly lower intensity during incubation and in the initial phase of development of the nestlings. This behavior causes alterations in the nest dimensions during each single breeding season (Table 2).

Many species similarly utilize nests from the former reproductive season, or reconstruct them on the exact same site, e.g., White-collared Swift, White-naped Swift (*Streptoprocne semicollaris*), White-chinned Swift (*Cypseloides cryptus*), Chestnut-collared Swift (*Streptoprocne rutila*), Spot-fronted Swift (*Cypseloides cherriei*), Gray-rumped Swift (*Chaetura cinereiventris*), Chimney Swift (*Chaetura pelagica*) and Ashy-tailed Swift (*Chaetura andrei*) (Dexter 1952, Sick 1959, Snow 1962, Collins 1968b, Whitacre 1989, Marín & Stiles 1992). After studying the breeding of Biscutate Swift in the southern part of Minas Gerais State, Andrade *et al.* (1985) commented that the same individuals come back to the same caves in each reproductive period. However, it is not clear if the old nests were used again or not. The fidelity to nest sites seems to be related to the reproductive success that a certain place offers. In this study, it was observed that where eggs or nestlings were depredated the nest sites were not utilized again in the following year (see "*Eggs*").

The collection and transport of nest mate-

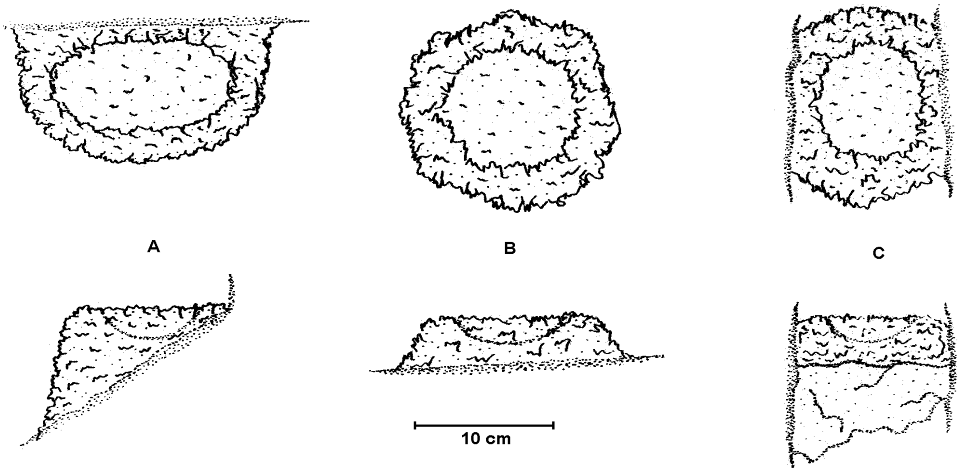

FIG. 2. Drawings of the three basic nest types of Biscutate Swift found between 1994 and 1996 at the Anhangava Hill, southern Brazil. A = semicircular, B = circular, and C = ellipsoid.

TABLE 3. Dimensions (cm) of Biscutate Swift nests found in 1994 and 1995 at the Anhangava Hill, southern Brazil[1].

	Smallest external diameter	Largest external diameter	Smallest internal diameter	Largest internal diameter	Smallest external height	Largest external height	Depth
Range	8.0-18.5	13-23	5-10	6-10	0.5-3.5	2.5-10	1-4.5
Mean	14.2	17.91	7.89	8.64	1.98	5.41	2.79
SD	2.88	2.39	1.29	1.16	0.93	2.52	0.71

[1] Only the largest measurement in each reproductive season was considered, as alterations did occur during the period as a whole. The sample consists of 23 nests.

rial was consistently observed to be gathered in the bill and taken from rocky walls or from the nearby soil, as already described for the White-collared Swift (Whitacre 1989, Marín & Stiles 1992). Medway (1962), proposed for swiftlets (*Collocalia*) that species that transport nest material with the bill have little capacity of echolocation, since species that really use this navigation mechanism transport nest material with the feet, leaving the bill free for the emission of sounds for orientation. If this hypothesis is correct for others swifts, the observed behavior of Biscutate Swifts with regard to the mode of nest material transport should indicate that this species has little or no capacity of echolocation. However, this subject requires more detailed investigation.

During the nest building period, fragments of mosses and lichens are abundant on the cave floor, particularly below the walls covered by such plants. Four swifts were observed collecting this material, and in one case a bird pulled pieces of incrusting bryophytes from a vertical wall and seemingly chewed them soon afterwards. Perhaps this represents a form of adding some saliva to

TABLE 4. Nest material found in 23 nests of the Biscutate Swift at the Anhangava Hill, southern Brazil, between 1994 and 1996.

Nest material	Number of nests where the item was found[1]
Lichens fragments	
Coccocarpia sp. (Coccocarpiaceae)	1
Ramalina camptospora (Ramalinaceae)	1
Usnea sp. (Usneaceae)	2
Cladia aggregata (Cladiaceae)	1
Cladonia sp. (Cladoniaceae)	1
Relicina abstrusa (Parmeliaceae)	1
Parmotrema wainii (Parmeliaceae)	2
Rimelia cetrata (Parmeliaceae)	3
Parmotrema delicatulum (Parmeliaceae)	1
Hypotrachyna peruviana (Parmeliaceae)	1
Parmelinopsis sp. (Parmeliaceae)	1
Unidentified Parmeliaceae	3
Bryophyta fragments	
Plagiochila sp. (Plagiochilaceae)	8
Plagiochila rutilans (Plagiochilaceae)	1
Frullania brasiliensis (Frullaniaceae)	14
Leucoloma sp. (Dicranaceae)	4
Campylopus sp. (Dicranaceae)	4
Campylopus aemulans (Dicranaceae)	5
Herberta sp. (Herbertaceae)	5
Polytrichum juniperinum (Polytrichaceae)	6
Leucobryum crispum (Leucobryaceae)	1
Phyllogonium viride (Phyllogoniaceae)	2
Syrrhopodon prolifer (Calymperaceae)	2
Syrrhopodon prolifer (Calymperaceae)	1
Lejeunea flava (Lejeuneaceae)	2
Omphalanthus filiforme (Lejeuneaceae)	1
Porotrichum longirostre (Neckeraceae)	2
Rhacocarpus sp. (Hedwigiaceae)	6
Schlotheimia tecta (Orthotrichaceae)	1
Macromitrium punctatum (Orthotrichaceae)	1
Schlotheimia rugifolia (Orthotrichaceae)	1
Sematophyllum caespitosum (Sematophyllaceae)	1
Squamidium leucotrichum (Meteoriaceae)	1
Zelometeorium recurvifolium (Meteoriaceae)	2
Pteridophyta fragments	
Rumobra adiantiformis (Dryopteridaceae) leaf fragment	5
Micrograma sp. (Polypodiaceae) fragment or entire leaf	5
Campyloneurum sp. (Polypodiaceae) entire plant	1
Hymnophyllum polyanthos (Hymenophyllaceae) root and entire leaf	3
Cochlidium punctatum (Grammitidaceae) entire plant	9

TABLE 4. Continued.

Nest material	Number of nests where the item was found[1]
Liliopsida	
Tillandsia sp. (Bromeliaceae) entirely or slightly fragmented plant	4
Orchidaceae, entire or fragmented leaf	2
Bambusoidae (Poaceae) entire or fragmented leaf	9
Poaceae, entire or fragmented leaf	11
Liliaceae, leaf	2
Magnoliophyta	
Tibouchina sp. (Melastomataceae), fragmented leaf	7
Croton sp. (Euphorbiaceae), entire or fragmented leaf	11
Peperomia sp. (Piperaceae), whole leaf	2
Rapanea sp. (Myrsinaceae), leaf	1
Mimosaceae, leaf rachis	9
Myrtaceae, leaf	1
Bignoniaceae, leaf	1
Leaf fragments, little twigs, barks and unidentified roots	17
Byproducts	
Biscutate Swift's remiges and rectrices	7
Biscutate Swift's guano (elytra and membranous insect wings)	17
Sand (quartz grains of 0.5-1.5 mm in diameter)	17
Soil (a mixture of earth, small sand particles and guano)	23
Synthetic material	
Synthetic blue thread of 10 cm length	1

[1] Only the presence and absence was considered and not the used amount.

the nest material, once some authors consider such activity occurs to some extent in all members of the family (Sick 1947, Lack 1956, Snow 1962). However, in Cypseloidinae, the size of salivary glands is greatly reduced and the production of saliva is lower (Johnston 1961). For Biscutate Swifts, nothing has so far been published on this matter, but in some nests I observed the presence of a viscous substance in the moss fragments recently added to nests. However, when the nest is dry it does not reveal the existence of any agglutinative substance. Perhaps the effectiveness of the saliva is not as important for this species as it is for many others, because its nest is just a simple construction on a horizontal substratum.

The nests when seen from above were circular, ellipsoid and semicircular in shape (Fig. 2). These variations seem to be related to differences in the available space at the chosen nest site. When the space alongside was narrow, the form was ellipsoid; when the available space was plentiful, the nest was circular, and in cases where the nests were compressed against a vertical wall, they became semicircular. In lateral view, the base was always wider than the upper part, making them shaped like a crater. At uneven places the lowest margin of a nest always included a larger accumulation of material than on the opposite side, resulting in different external heights at opposite sides of the nest. A compensation for similar unevenness was already

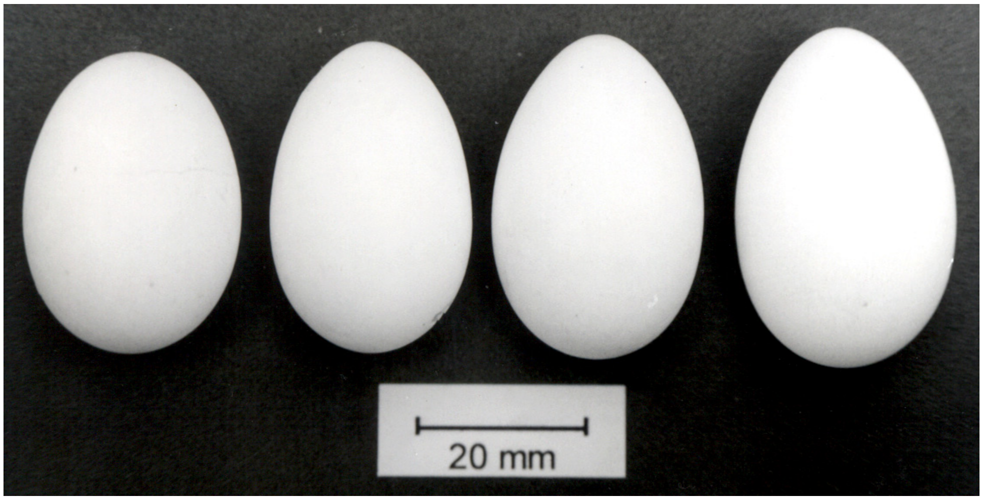

FIG. 3. Typical shapes of Biscutate Swift eggs observed at the Anhangava Hill, southern Brazil.

observed in the Waterfall Swift (*Hydrochous gigas*) (Becking 1971). Inside the nest, an incubating chamber always exists which consists of a circular or ellipsoid depression. In general, the aspect of the nest of Biscutate Swift was similar to that described for the White-collared Swift (Whitacre 1989, Marín & Stiles 1992). Table 3 indicates the variation in dimensions of 23 monitored nests.

The nests were principally composed of a compact mass of lichens, bryophytes and small roots (Table 4). Elytra and membranous wings of insects were also found mixed with the nest material and were probably derived from the birds' feces. The presence of fecal remnants in the nests does not mean that this material is an important component for nest construction. These insect remains, though frequently encountered, were not abundant. Thus, defecation in the nest during nest construction should not be considered indispensable for the achievement of its final structure.

Soil and sand were also found in the nests, but I never observed a deliberate deposition of these materials. They probably arrived stuck to the plant material. Besides, the nests located at specific sites that were totally washed by the infiltrating water always contained little soil and they were composed mainly of plant parts. Thus, only the nests that maintained their original structure throughout the year possessed plenty of soil, which was probably brought in attached to vegetative material during successive nest renovations.

The incubation chambers of the nests were covered with leaves and thin twigs of angiosperms and feathers of Biscutate Swift (Table 4). These feathers probably did not belong to the birds that built the nests, as they consisted of molted remiges and rectrices, and the molt period occurs after incubation (pers. observ.). They probably represent feathers of previous molt periods, and remiges and rectrices from previous molts could be found easily inside the nesting cave. Apart from the natural materials mentioned above, one nest contained a piece of synthetic blue thread 10 cm in length. This thread probably originated from climbers' rope material, as the area is in use for trekking and rock climbing activities.

TABE 5. Biscutate Swift clutch sizes encountered between 1994 and 1996 at the Anhangava Hill, southern Brazil.

Clutch size	Amount of clutches found
1	9
2	21
3	5*
4	1*
Mean = 1.94 egg/nest, SD = 0.71	

*Probably the result of layings by multiple females, see text.

Eggs. There was only one clutch laid per nest per reproductive season in each of the study years (1994, 1995 and 1996). The eggs of all birds of the colony were laid synchronously, in a very restricted time, between 1 and 9 November. After this period, no additional egg laying was observed. Thus, the last week of October and the first week of November was the most critical period for the reproductive success of the colony.

Fresh eggs had a smooth, opaque and unmarked white shell. Sometimes later during the incubation period eggs were found dirty from soil in the nests. The egg shape was long subelliptical or subelliptical (Fig. 3). They had a length of 33.9–39.7 mm (mean = 37.2 mm, SD = 1.5, n = 49), width of 22.3–25.8 mm (mean = 24.2 mm, SD = 0.7, n = 49) and a mass of 10–14.3 g (mean = 11.6 g, SD = 0.9, n = 48). The observed eggs were very similar to those of White-naped Swift and White-collared Swift in nearly all characteristics (Rowley & Orr 1962, De La Penha 1982, Marín & Stiles 1992), except for the ratio between their mass and the adult bird mass in the breeding season (mean = 119.4 g, SD = 9.0, n = 85), which was equal to 9.7%. This is a slightly lower value than the one obtained by Marín & Stiles (1992) for White-collared Swift (10.2%). This difference exists in spite of the average mass of the Biscutate Swift eggs being larger than that of White-collared Swift.

The clutch size varied from one to four eggs, the modal value being two (Table 5). In the nests that received up to two eggs, it appeared that one egg was laid per day. In some cases, nests that contained three or four eggs were observed to receive up to two eggs in a single day. This is probable consequence of intraspecific brood-parasitism, where a same nest is used by more than a single female. In other swifts (not belonging to the genus *Streptoprocne*), collective clutches have been described, including some cases where the birds also divided the incubation task (Lack & Lack 1951, Dexter 1952, Sick 1959, Snow 1962). In White-collared Swift and White-naped Swift only clutch sizes of one or two eggs have been reported (Rowley & Orr 1962, De La Penha 1982, Marín & Stiles 1992); in Biscutate Swift, previous records were of two or three eggs (Andrade *et al.* 1985), which was questioned by Marín & Stiles (1992).

The pattern of egg laying in Biscutate Swift demonstrated the existence of a confusing and complex behavior. In the beginning of November of each study year, many eggshells were found on the cave floor. With certainty they were not eggshells of recently hatched chicks, as in this period the adult birds had only started egg laying and incubation. These eggshells were initially considered as resulting from the predation of recently laid eggs. However, not only were small pieces of eggshells found, but also entire shells, both found at the same place. In some cases, the internal content of the eggs, yolk and albumen, could be seen. This fact indicated that these eggs had not been eaten. Nevertheless, the possibility remained that some predator had rolled the eggs out of the nest while trying to eat them, or that the eggs were accidentally ejected from the nest by the breeding adult birds. Doubts remained as the broken eggs were found below areas used only for roosting and which did not have appropriate sites to support nests.

In order to clarify this, in 1996 a tulle net was suspended about 1 m above the floor of the nest cave in an area above which no nests were located. This net would catch any falling eggs. Eggs falling from nearby nests would be broken on the rocks below with only pieces of shell possibly reaching the net. Thus, only eggs dropped or laid by birds perching on the rock surface exactly above the net would arrive intact in it.

After five days in position, the net contained two intact eggs. They were not damaged, in spite of haven fallen about 6 m. It is likely that the majority of eggs found broken on the floor of the cave in the beginning of the oviposition period each year had not proceeded from predation or from accidentals ejections. This seems more likely the consequence of a peculiar behavior of this species that can be explained by two hypotheses, described below.

The first interpretation would be that brood parasitism or dispute for nests occurs in this species. Parasitizing females remove the eggs in a nest to lay their own eggs in it. If this is the case, the presence of the intact eggs observed in the tulle net can be explained by the fact that the intruding female had seized the eggs in the host nest, carried them to a roosting site and there dropped them. In this case, each egg would have been transported individually in the bill (it is impossible for a bird to carry more than a single egg inside the mouth). In another five nests, a kind of behavior was observed that can be interpreted also as either brood-parasitism or as competition for nesting space. In these cases, the eggs were not carried far away from the hosts' nests. At the beginning of the laying period, one egg was found in these nests; the egg was marked with a pencil. After two days, during the next inspection, these eggs were found intact but they were outside the nest cup, but near the nests on the nearby nest ledge. In the nest cup of each nest was a new egg, which also received a pencil mark. The expelled egg was put back in each nest but two days later it was out of the nest again, and a second new egg was in the nest. In two nests, there was a third egg. The first eggs were put back again and during the next inspections some had disappeared while others had not been expelled and were being normally incubated. These observations suggest that the firsts laid eggs were deliberately expelled from the nests, as it is hard to believe that the observed ejections could have happened accidentally and repeatedly. Koskimies (1950) observed the expulsion of eggs from nests of the Common Swift (*Apus apus*) and he attributed this behavior mainly to climatic changes, or due to a mechanism of the species to control the number of nestlings to be fed.

This first hypothesis (brood-parasitism or dispute for nest site) would explain the broken eggs found on the cave floor, as well as those two eggs captured by the tulle net. However, it would mean that on some occasions the eggs were transported a large distance from the parasitized nest and in other cases, they were just pushed outside the nest cup. This hypothesis does not explain the reasons of occurrence of two different behaviors, as both lead to the same function. Why in some occasions would the parasite birds carry the eggs away to a rocky wall roost site to release them and, in other occasions, simply expel the eggs outside the parasitized nests? In addition, if the transport of eggs to a long distance from the nests was really happening the total eggs that disappeared during the laying period should be high. Nevertheless, this was not the case. The number of eggs that disappeared was low, as each egg recently found in a nest received a pencil mark on the day of its discovery, and it was observed individually during the following inspection. Few disappearances of eggs happened after the laying period when several broken eggs had been detected on the cave floor. That is to say, a large number of broken eggs were found in the beginning of the laying period and the few disappearances of eggs occurred later, during incubation.

From the observations made in the five nests mentioned above, it must be concluded that brood-parasitism and/or competition for nests were occurring. This behavior could result in apparent clutch sizes of three to four eggs, but at these nests more than one female is laying. The only observed clutch size of four eggs occurred under a peculiar circumstance; three eggs were inside the nest cup and the last one was on the nest material of the nest's side. The frequency of laying in these nests with enlarged clutches indicates that the laying was probably done by more than one female, since in some situations these nests received up to two eggs in one day. A laying rate of one egg per day was typical of other observed nests.

The second hypothesis that could explain the recover of eggs in the tulle net and others found broken on the cave floor would be that some females could be laying directly on the vertical rock walls. As mentioned, broken eggs were found under areas used only as roosts, and from these places the females would drop their eggs directly on the ground. The situation that would lead to this behavioral pattern is unclear. An explanation could be the immaturity of females which would tend to waste their eggs owing to inexperience. Another possibility could be that some females were not inseminated, due to a low density or low fertility of males or due to a deficiency in the aerial copulation. In these cases, the eggs would be infertile and the birds would have the capacity to distinguish this and to reject them by dropping them. This behavior has not been documented for other species. However, aerial copulation has already been considered disadvantageous or unlikely for Cypseloidinae (Marín & Stiles 1992, Marín 1999).

Another factor that could be related to the appearance of broken eggs and with the expulsion of eggs from the nests would be a low density of appropriate nest sites. This would cause more than one pair to try to occupy the same nest site during the same reproductive period. Females would compete for the same nest in which to lay their eggs, explaining the observed cases of expelled eggs. Those females that were not successful in getting a nest site tend to let their eggs fall freely on the cave floor. A competition for nest sites has been described for Glossy Swiftlet (*Collocalia esculenta*) (Spenneman 1928 *fide* Medway 1962) and Common Swift (Lack 1956 *fide* Medway 1962). Nest site competition has not been recorded until now for the genus *Streptoprocne*.

Some authors have previously commented on the presence of broken eggs of swifts close to nests. This was usually interpreted as an accidental ejection, or caused by fighting birds (Lack & Lack 1951, Medway 1962, Snow 1962). In another colony of Biscutate Swifts, the presence of broken eggs below nest sites has been noted, but no explanation was proposed (Andrade *et al.*1985). Broken eggs of the White-naped Swift found upon the guano accumulation on the floor of the cave has been also noted (Rowley & Orr 1962). Whitacre (1989) said that eggs being rolled out of the nests are the principal cause of reproductive failure in White-collared and White-naped swifts in Mexico.

An experiment was conducted with the two eggs captured by the tulle net, in order to determine their fertility. One of them was placed in a nest that contained another egg and then observed to see if it would hatch. After eight days of incubation, the foreign egg disappeared, probably having been ejected. In this case, the ejection might have happened for two reasons: infertility or rejection due to a lack of recognition. The other egg was put in an electric incubator at 39°C, with relative humidity controlled by the presence of a wet sponge nearby; the position of the egg was changed every eight hours. After 30 days, this egg had still not hatched and no embryo was found in it. Apparently both eggs were infertile. In Common Swift, the expulsion of infertile eggs in the beginning of the period of oviposition had already been reported (Koskimies 1950). However, it is also possible that the eggs of the Biscutate Swift recovered by the tulle net did not develop due to internal damages resulting from the fall that they had suffered. Thus, in spite of the indications of infertility, these results should not be interpreted as conclusive.

If the dispute for space really exists, it would explain the loss of eggs of females that does not find places to lay. But when considering the whole internal area of the studied cave and taking in consideration only the dimensional characteristics of the nest sites, there appeared to be several unused places that were very similar to other commonly used as nest sites. Also, it was observed that some nests, though having been built, did not receive eggs. In 1994, nests were built at the sites S 21 and S 25, but there were no indications of laying or of predation or any other reason that would justify the disappearance of the eggs. The same occurred in 1995 in the sites S 1 and S 8. In spite of the nests space available, the broken eggs on the cave floor and the probable disputes for nests continued. Perhaps, apart from the dimensional aspects, there are also other factors important in the choice of the place to built nests. One possibility could be the degree of access of sites to predators.

In spite of predation mostly not being directly related to the observed broken eggs, it sometimes happened and it could be detected. In seven nests, eggs were found with a great opening at the side or at one pole; in some of these nests, totally broken eggs were found. In all these cases, no remains of the eggs' internal content was found. The breeding pair could hardly have accidentally damaged these eggs in this fashion and these cases are probably due to predation. Apart from this, predation of the eggs and one adult bird were recorded in five nests. At the places where this kind of predation happened, only pieces of eggshells were found and some feathers of the depredated birds, including remiges and rectrices that had the calamus visibly gnawed. In two cases, the metallic bands that had marked the birds were found in the nests. In a depredated nest (S 12), a carcass was found with its wing, back and tail still together. This was identified as being a male, as the gonads were intact. In the places where this kind of predation took place, no footprints were found or any other type of sign to identify the predator. The structure of the depredated nests was not damaged and remained intact.

I have never observed or heard bats in the cave and there are no carnivorous bats registers in the region, so I presumed the predator was a small terrestrial mammal. To capture the possible predators, 15 live traps were set in several parts of the cave, all of them baited with bacon. Over 12 days the traps captured one roof rat (*Rattus rattus frugivorus*) (Rodentia: Muridae), three grass mice (*Akodon* sp.) (Rodentia: Cricetidae) and five common gray four-eyed opossums (*Philander opossum*) (Marsupialia, Didelphidae). The rodents were captured in the traps placed in the entrance of the cave and the *P. opossum* were captured inside the cave, in less accessible and darker places. One of the opossums was captured within 1 m of a nest that had been recently depredated.

To test its ability to depredate swifts eggs, a female *P. opossum* was maintained in captivity

TABLE 6. Biscutate Swift incubation periods observed in the reproductive seasons of 1994 and 1995 at the Anhangava Hill, southern Brazil.

Years	Incubation periods (days)					
	18–22	20–24	22–25	23–27	24–28	n
1994	1	6	3	8	2	20
1995	0	0	2	0	2	4
Total	1	6	5	8	4	24
Mean[1] = 24, SD = 1.67						

[1] The mean is based upon the median values of each incubation period.

for five days. It was given eggs of Japanese Quail (*Coturnix japonica*), similar in mass and size to Biscutate Swift eggs, and those of Domestic Fowl (*Gallus gallus*). The opossum managed to open only the eggs of Japanese Quail, sipping the content without spilling. The shell of the offered eggs was broken at the sides or at the poles, just as in depredated eggs of Biscutate Swifts. Therefore, the predator of the studied swift is probably the *P. opossum*, a species that is common in the study area and possesses a great abilities as a predator. Research has already shown that this marsupial can locate prey (at least frogs) acoustically in aphotic places (Tuttle *et al.* 1981), and this might be happening in the case of predation on Biscutate Swifts.

In the three years of the study, adult bird predation occurred only during egg laying and incubation periods, perhaps due to the fact that a bird on the nest is more vulnerable to predation than when it is at a vertical overnight roosting perch. It is also probable that the birds avoid leaving their eggs when the predator appears, which eases their capture. Finally, the broken eggs found on the cave floor at the beginning of each reproductive season can be a stimulus to the predator to explore the entire cave, which in turn may result in the discovery of adult birds and eggs in the nests.

The five nest sites that lost one of the adult birds by predation were not reused in the following reproductive season. Amongst the seven observed nest sites at which only the eggs were apparently depredated, just three were reused in the following year. These observations suggest a relationship amongst the nest site and the history of predation of the chosen place. This could be one of the main factors that influences choice of an nest site. The non reuse of sites where an adult bird was depredated could also be related to a dissolution of the pair. This could be the case if the species is monogamous and the pairs always reuse the same place for breeding as already have been shown in part for Black Swift (*Cypseloides niger*) (Marín 1997). The individual that survives a predator's attack but looses its mate might abandon the site previously used due to the absence of the mate. Some evidence was obtained that this can happen. In the breeding season of 1995, a banded pair was captured while reconstructing the nest in site S 17. In the following months, the reproduction of this pair was monitored. In 1996, the same site was being renewed prior to laying, but one of the birds was depredated during the first days of incubation. When the remains of this bird were found, it was possible to recover its band, which turned out to belong to one of the individuals that had used the same site in 1995. This observation proves that at least one of the birds was faithful to the same nest site for two consecutive reproductive seasons. If that is the pattern for all pairs of the colony, this would not explain why new pairs does not occupy abandoned nest sites.

Incubation. Incubation began in the beginning of November, after the last egg of each nest had been laid, and it finished near the end of the same month or in the first week of December. The average duration of the incubation period was 24 days (SD = 1.7, n = 24;

see Table 6). These periods differ considerably from those estimated for the White-collared Swift (between 30 and 35 days, according to Marín & Stiles 1992).

During the breeding season of 1995, the incubation behavior in the nest located at site S 17 was closely observed. The two birds that built this nest were captured and marked with metallic bands and with phosphorescent disks (see Methods). It was observed that the incubation was done only by both of the two marked birds. The sex of these two monitored birds could not be identified, but it is presumed that they were a male and a female. It thus appears typical that no extra-parental cooperation occurs in Biscutate Swift, although this behavior has been shown for other swifts (Dexter 1951, 1952). However, the possibility of these birds being two females that used the same nest should not be excluded, since indications of oviposition of more than one female per nest exist, and this could also result in a cooperative incubation. During the breeding season of 1994, a male was observed participating in the incubation of the eggs of site S 12. This male was depredated while sitting on the eggs. These observations suggest that the both members of the pair participate in incubation, although this has not been proven completely.

The pair marked with phosphorescent disks was observed during 42 h and 22 min in six days. Of this time, the bird marked with disk "A" remained on the eggs for 19 h and 21 min (45.7%) and the "B" for 19 h and 37 min (46.3%), showing a considerable equivalence of effort. The whole period of unattendance lasted 3 h and 24 min (8%). The individual periods of incubation for each bird were also similar. Four individual periods of incubation were observed for bird "A" and five for the "B", the average of them being 4 h and 12 min and 3 h and 43 min, respectively (Table 7). At least in the studied case, the incubation was biparental as is the case in the Black Swift (Marín 1997), but it was quite similar in magnitude for both sexes.

The incubation intervals were long, perhaps related to the need of the pair to fly great distances for feeding, as was already noted for other Cypseloidinae swifts (Marín & Stiles 1992). The bird that incubates stays on the nest for a long interval and, in some cases, it abandons the nest before the mate has returned. Two entire periods of prolonged unattendance were observed, and averaged 98 min. They did not cause the embryo's death. Perhaps, these unattendance periods do delay the development of the embryo, culminating in an extended incubation periods. The great variation of incubation periods that were observed for the nests reinforces this idea (Table 6).

The replacement of the incubating bird was always made in a similar way. First of all, the bird that was outside the cave arrived and perched on the vertical rock wall about two meters below the nest. Next, it uttered some sharp swishes as that were sometimes answered by a similar sound emitted by the bird that was on the nest. After 1–3 min, the recently arrived bird climbed the wall in the direction of the nest. Using its feet, it crawled over the rock and flapped the wings freely. Then, it stopped nearer the nest and made the same sound again. After that, the bird that was sitting on the nest left and perched on a nearby wall leaving its place on nest free for the returning bird. Finally, the returning bird climbed the last part of the wall and settled on the eggs.

Probably, the behavior of the returning bird is a way to announce itself to the bird that is incubating, as a visual contact is largely impossible due to the darkness at the site. This behavior may also fill the gap of time necessary for visual conditioning to darkness. In the cases where the nest was already abandoned, the returning bird approached the nest like described above. It landed and remained

TABLE 7. Periods spent incubating eggs and periods of unattendance observed in a pair of Biscutate Swift in November of 1995 at Anhangava Hill, southern Brazil.

	Periods spent incubating the eggs, periods of unattendance, and the respective day an time of observation (h:min)					Mean (h:min)
Bird A	03:06[1]	03:15[1]	04:57[2]	05:30[2]	–	04:12
	14	10	17	20		SD = 01:12
	13:40–16:46	11:05–14:20	08:40–13:37	06:00–11:30		
Bird B	02:14[3]	02:22[1]	03:55[2]	04:14[1]	05:48[2]	03:43
	14	10	22	17	24	SD = 01:28
	16:46–19:00	14:20–16:42	10:30–14:25	14:35–18:49	09:07–14:55	
						01:38
Unattendance[4]	01:30	01:45	–	–	–	SD = 00:11
	22	10				
	14:25–15:55	09:20–11:05				

[1] Period recorded from the exact moment of the arrival until departure of the bird of the nest.
[2] Period recorded in the morning when the observation started with the bird on the nest.
[3] Period recorded in the afternoon when the observation finished with the bird on the nest.
[4] Only entire unattendance periods were considered.

quiet close to the nest for similar periods. This could indicate that the bird that arrives can not see if the other bird is on the nest, and really needs some time to accommodate to the darkness of the cave.

During the observed individual incubation periods, it was not possible to see any associated behavior, due to the darkness. However, some noises from the nest were heard constantly. On two occasions, the bird that was incubating was observed to leave the nest and fly to another place inside the cave where there was an accumulation of plant material, including leaves and mosses. There, it collected some leaves in the bill and returned to the nest, where I heard the same noises already registered. These probably were made by incubating birds during the arranging of the nest material, or perhaps when turning the eggs. In addition, the bird that was incubating occasionally uttered the ascending call that is characteristic of the collective flights outside the cave. This reaction was apparently related to the observer's presence in the cave, as it happened in response to some noises from inside the observation tent.

Nestlings. During the three years of study, nestlings hatched between the end of November and early December. In cases where the clutch size was two, the second nestling hatched usually one day after the first. In at least seven of 12 nests observed, hatching of the two chicks took place on different days. As previously noted, in the clutch sizes larger than two, always one or more of the eggs were expelled during incubation, which resulted in a maximum of two nestlings per nest.

The nestling period varied from about 28–39 days, the average being 32.7 days (SD = 3.4, n = 17) (Table 8). After leaving the nest, they stayed perched on the nearby rocky walls where they continued to be attended by both parents. They stayed inside the cave and were cared by adult birds for a period that could not be measured precisely. However, it

TABLE 8. Nestling and fledgling periods observed for the Biscutate Swift between 1994 and 1996, at the Anhangava Hill, southern Brazil.

Nestling periods (days)	Sample size	Fledgling periods[1] (days)	Sample size
27-29	1	1-5	1
28-30	4	4-8	3
30-32	2	5-9	1
32-34	5	-	-
34-36	1	-	-
36-38	3	-	-
38-40	1	-	-
Mean[2] = 32.7	n = 17	Mean[2] = 5.6	n = 5
SD = 3.4		SD = 1.5	

[1] This is a partial fledgling period, in which the nestling had already left the nest but stayed near the nest on rock walls. The birds left the cave later and so the whole fledgling period could not be measured because it was impossible to distinguish the young.

[2] The mean is based upon the median values of each period.

is known that at the time of abandoning the nest, one nestling had a wing 150 mm in length approximately, and the wing growth rate of the nestlings was about 4 mm per day. Considering that the nestlings only start to leave the cave when their wings measure about 90% of the adult wing (mean = 207.4 mm, SD = 4.3, n = 66), it is possible to estimate as 10 days the minimum time fledglings remain inside the cave after leaving the nest. The earlier young bird captured outside the cave occurred on 20 January; its age was estimated to be between 48 and 52 days.

The recently hatched nestlings (0–2 days of life) have the eyes closed and are naked with the pterylae little visible; the posterior part of the pteryla spinalis is most visible. In the dorsal posterior border of each wing, there is a line of small filamentous tips feathers (not surpassing 1 mm in length). It is from this line that later the greater coverts will grow. Due to the absence of pigmentation and the skin's transparency, tarsi, nostrils and the tip of the bill are pinkish. The base of the maxilla and a small area at the base of the mandible are gray. The claws are pinkish white, but a small portion of their bases and the extreme tips of the toes are light gray. The chicks remain quiet before being touched and maintain the head prostrate on the border of the nest. After being touched, they do anxiously lift the trembling head and utter a low sharp peep. When being removed from the nest, they hold fast to the material of the nest cup with the feet, which are already anisodactylous. Nestlings of this age are generally brooded by both parents and, when being manipulated, they drop body temperature quickly. The extremities of the body are whitish.

At 2–4 days of life, the nestlings begin to acquire the first feather coat, which is constituted of covering of gray down-like semiplumes, as in other swifts (Collins 1963, Collins 1968b, Marín & Stiles 1992). These feathers are visible especially on the back. On the ventral surface of the body, the feathers of the pteryla ventralis are visible on the flanks; however, no pinfeathers are erupted through the skin. The nostrils have become grayish and the dark pigmentation of the bill, tip of the toes and base of the claws has increased. The rest of the body still possesses a pinkish coloration. These nestlings are quiet and, when being touched, they raise the head, lean on the belly and leave the tarsi forward. They peep and open the bill more frequently than in the previous stage. The eyes remain closed and, when the nestlings are removed, they hold on to the nest material. They cool down quickly. The extremities of their body are whitish and they tremble a lot when handled. It is common to observe an adult bird on the nest or close to it.

Between the sixth and the tenth days of life, the semiplume covering has grown over nearly the entire back, with the posterior portion covered by a layer about 5 mm thick. On the wings, the number of feathers is less and nude areas still exist. There is a line of small semiplumes in the pteryla of the greater secondary coverts. The pinfeathers of the remiges are already visible, but the tips of the feathers have not yet erupted. On the head, the semiplumes between the eyes start to appear. On the belly, the semiplumes cover the flanks leaving a great central nude apterium and, on the throat, the first emerging feathers are grayish white. The entire bill is grayish black, including the margins of the gape. Only the tip is paler (pearl gray) and the egg tooth is still visible as a small white point. The nostrils are entirely dark gray. The opened eyes have an opaque blue color with the pupil not distinguishable. The eyes open between the sixth and the tenth day of life. This variation seems to be related to the amount of light at the nest site; nestlings opened their eyes earlier at the illuminated nests than at the darker sites. The tarsi are distinctly gray, the callus of support being darker. The tip of the toes and the convex part of the claws are gray. The nestlings are quiet and let the head rest on the edge of the nest. When handled, they do not try to escape or to peck, but hold fast to the material of the nest cup. Upon first contact, they raise the head, lean with the tarsi forward, peep and open the bill. They still cool down during handling, but less than in the previous stage.

Between 12 and 16 days of life, the back of the nestlings is totally covered by gray semiplumes with a thickness of 10 mm in the posterior region. A small bare pinkish area on the neck can only be seen when the neck is stretched. On the head, the bare areas of the forehead and crown are gray and pinfeathers of the teleoptile feathers are visible but the tips are still sheathed. The bare skin of the wings is gray and the pinfeathers of the greater coverts begin to show unsheathed tips. The remiges measure approximately 15 mm and their unsheathed tips measure 2 mm. The rectrices are 10 mm long. Outer rectrices have only the tip of the rachis unsheathed and the central ones already show part of the vanes. The ventral bare area is pinkish and is restricted to a small portion of the neck and abdomen, where sheathed teleoptile feathers exist without erupted tips. The bill is black with only the extreme tip being paler and still showing a tiny portion of the egg tooth. The eyes have a dark brown iris and an opaque blue pupil. The tarsi are brownish gray with the callus being darker. The toes are dark gray and the claws gray, with the tips and the convex part of them paler than the rest. The nestlings at this age are quiet and rest the head on the edge of the nest when they are not disturbed. When being removed from the nest, they hold fast to the nest material but neither try to escape nor to peck. When handled, they peep and are agitated until they can fix their feet in some substratum. At this age, they emit a strong peep with quite variable notes. They do not cool down and are not closely brooded by an adult bird as in the previous phases.

Between 16 and 20 days of life, the uppertail coverts show unsheathed tips. In the bare areas of the crown, forehead and face the first contour feathers appear, mainly in the area below the eyes. The feathers of the white patch of the nape show tips 1–2 mm in length, which are not readily visible as they are hidden under the gray semiplumes. The white patch is less developed on the lower throat and upper breast. The ventral bare area still exists, but is only visible when the neck is stretched. The unsheathed tips of the greater wing coverts begin to expose and the unsheathed tips of the remiges have reached 5 mm in length. The rectrices all have the same size (± 10 mm, including the pin), but the internal ones have longer rachis tips than the external ones. The throat and the ventral portion of the neck have light gray semiplumes. On the belly, there are no erupted tips of the pinfeathers and the central nude area is quite reduced. The bill is all black with a whitish tip and the egg tooth has disappeared. The nostrils are black. The tarsi are dark gray as well as the toes and the claws, which have a whitish tip. The nestlings of this age are quiet and always stay still on the nest. When being removed from the nest, they hold fast to the nest material. When held they peep less than at the previous ages and get calm when they manage to hold on to some substratum.

The head of nestlings 22–26 days old has more contour feathers than semiplumes. The feathers of the forehead and throat are grayish white. The white patch of the nape is very distinct, however it is narrower than in an adult bird as the feathers have not fully developed. The ventral white patch is also visible, but it has the form of a small triangle and not of a belt. The upper breast still shows a narrow bare strip. The back is predominantly covered by semiplumes, but many contour feathers form a longitudinal band. The largest of these feathers have exposed tips 10 mm in length and occur in the lower part of the back. On the flanks and on the undertail covert area, the first contour feathers are mixed with the semiplumes. The tips of the greater coverts are about 5 mm out of the sheath, leaving the dorsal wing face almost entirely covered, and without semiplumes. On the ventral face of the wings, there are some unsheathed pinfeathers and few semiplumes. The remiges are well developed and all have about the same size. All rectrices have their distal portions with vanes erupted from the sheath. The bill is black with a small whitish tip. The nostrils are black and the pupils remain opaque blue. The tarsi are brownish black as well as the toes. The claws are dark gray with whitish concave part. When a person approaches, the chicks hide in nearby crevices, but do not fly and only rarely climb the nearby vertical rocks. When handled, they hold fast to the nest and do not peep, but sometimes emit a strident call.

When the nestlings are between 28 and 32 days of life, they have the contour plumage of the body completely developed. On the dorsum, semiplumes are still visible only in a narrow strip from the nape to the uppertail coverts. On the ventral part, semiplumes are still present on the flanks and in the center of the belly; however, the contour feathers are more obvious than the semiplumes. The greater coverts cover the whole dorsal surface of the wings, and all semiplumes have been covered. The tips of the under coverts are about 8 mm long. The remiges and rectrices have reached half the size they will have when adult. The bill is all black, as well as the nostrils. The pupils remain opaque blue. The tarsi and toes are brownish black and the claws dark gray with the concave part much paler. The nestlings still stay on the nests, but eventually they can be seen perched on the nearby vertical rocky walls at distances of up to 50 cm. When threatened, they still do not fly, but try to flee by climbing the rock wall with a certain difficulty. When captured they hold fast to the wall and scream.

At the stage of 32–40 days of life, the nestlings stay clinging to the vertical walls within about 2 m of the nest; when approached, they try to flee by climbing the rock and flapping the wings (they still do not fly). It is possible that this type of behavior also serves as an exercise for the wings, making them stronger and prepared to the first flights. The dorsum is entirely covered by contour feathers, without any semiplumes showing. On the venter, semiplumes are seen only on the flanks and thighs, and the contour feathers have a narrow whitish edge. At this age, the wing (flat) and the tail have reached respectively 80% and 90% of the length of an adult bird. The pupils are less opaque and the

TABLE 9. Morphological and behavioral changes during the nestling development of Biscutate Swifts at the Anhangava Hill, southern Brazil.

Morphological and behavioral changes	Estimated age (days)
Semiplumes emerge	3
Eyes open	6
Rectrices emerge out of pinfeather sheaths	8
Remiges emerge out of pinfeather sheaths	13
Semiplume plumage totally developed	13
Contour feathers emerge out of pin-feather sheaths	15
First escape behaviors noticed	24
Climbing of the nearby vertical rocks with return to the nest	27
Climbing of the nearby vertical rocks with abandonment of the nest	32
Body contour plumage complete	34
First flights made inside the cave	40
First flights outside the cave	48

tarsi, nostrils and bill are black.

The nestlings 40–48 days old are totally feathered but appear more sooty than the adults. The forehead, chin and wing edges are whitish. Besides, the feathers of the ventral part have a narrow grayish white edge and the remiges, particularly the secondaries, have a narrow gray margin in the internal vexillum. The nestlings stay clinging to the vertical walls within about 5 m from the nests. They are captured with difficulty, as they climb the rock with much agility and flee amongst crevices of the nearby walls. They do not leave the cave and are thus still fed by the adults.

The whole post-embryonic development of the studied nestlings are summarized in Table 9.

Nestling measurements and development. The structures that had linear growth were the wing (flat) and tail (Figs 4A and 4B). However, the tail starts to develop only after the eighth day of life, and this can hinder the age evaluation of younger individuals. In these cases, the exposed culmen would be the viable option for aging because it had a linear growth in the first 10 days of life (Fig. 4C).

The mass increase was hardly linear (Fig. 4D). Just after hatching, the chicks weighed about 77% of eggs mass in average (mean = 9.0 g, SD = 0.6, n = 12). The mass rate gain was very high during the first 20 days of life and, at the end of this period, the mass of the nestlings was 13 times higher than when just hatched. After 20 days of life, the rate of mass gain decreases day by day and the mass peak stabilizes at an age of about 27 days. Nestlings of this age had an average mass of 136.2 g (SD = 5.6, n = 9), which surpasses by 12.3% that of the adults. In the breeding season of 1994, a 28 days old nestling weighed 147 g, which exemplifies the high growth rate of this species in the first month of life. The stabilization of the mass coincides with the period of larger growth of the remiges, rectrices and contour plumage. After the thirtieth day of life, the nestlings begin to show mass recession. This loss of mass is probably related to the abandonment of the nest and to the behavior of climbing the nearby rocks. Such events and activities certainly consume more energy and the success of a nestling in this phase should be related to the fat accumulation that was obtained during the previous period. Chicks 41 days old weighed in average 123 g (SD = 5.7, n = 2), which indicates a loss of 9.7% from the 27 days old nestlings mass prior to the birds having left the nest cave. The sub-adults captured in February and March had an average mass of 91.0 g (SD = 3.6, n = 3), which showed a loss of 33.2% of the peak mass of the chicks as they left the nest. Certainly, the cause of this is the intense physical activity and the reduced ability to obtain food. It is probable that only the nestlings that manage to accumulate great fat reservations in the first 30

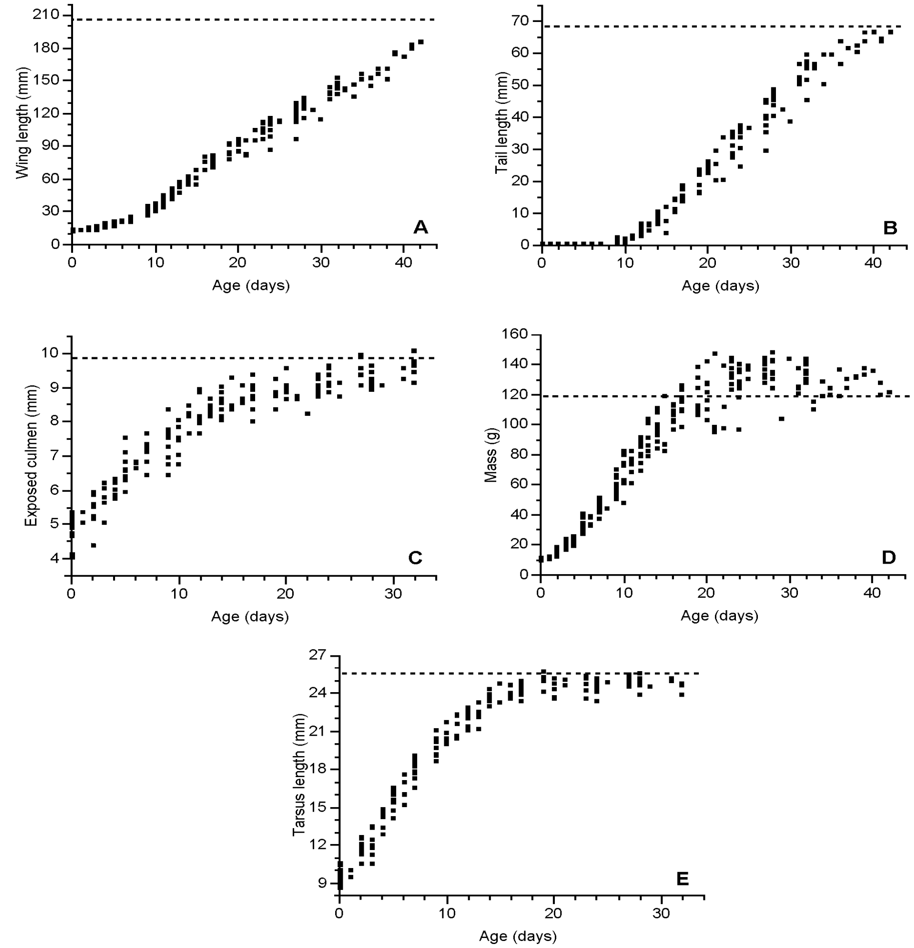

FIG. 4. Growth curves of wing, tail, exposed culmen, mass and tarsus in Biscutate Swift nestlings. Dashed line represents the mean adult size.

days of life can survive this intense physical drain. This fact perhaps indicates the existence of some control mechanism to maximize nestling size, perhaps limiting to two the maximum brood size to be raised by one pair.

The tarsi showed a rapid growth, reaching maximum development at the 19th day of life (Fig. 4E). This pattern can be related to the need for the nestlings to have the hind limb developed quickly for holding themselves in the nests, avoiding accidental falls or expulsions. Certainly, the capacity of holding itself in the nest is the major defense mechanism that a nestling has. Therefore, the ideal period to band the nestlings with metallic bands is after the 19th day of life.

In general, the development of the plumage and the growth pattern observed in Biscutate Swifts was similar to that observed by Marín & Stiles (1992) for White-collared Swift. For both species the length of the wing is the best age indicator and the mass reaches its highest value at about the 30th day of life, and then decreases about 10% to 15% after leaving the nest site. The most conspicuous differences in these two species concern the incubation and growth periods, the values for Biscutate Swifts were shorter than those estimated for White-collared Swifts by Marín & Stiles (1992). Biscutate Swifts observed at the Anhangava Hill had greater body masses than White-collared Swifts from Costa Rica and still grew more quickly and had a shorter incubation. Although these differences could be explained by the geographical position of each study area or by other ecological factors, I think they can also be explained by the fact that the White-collared Swift data were estimated, and maybe are unreliable. Thus, for the genus *Streptoprocne*, the data about incubation and nestling periods presented in this paper are the only ones based on exhaustive observations.

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