

# Population size, survival, longevity, and movements of the biscutate swift in southern Brazil

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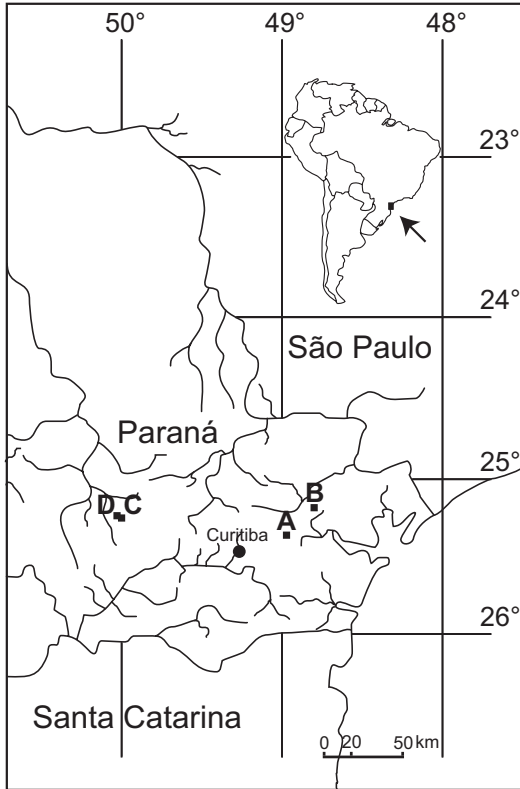
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We provide information on population parameters in colonies of the biscutate swift from southern Brazil using the capture–recapture technique. We captured 1020 adults, 233 nestlings and 25 subadults, totaling 1278 marked birds. Models with capture probabilities varying with time and individual animal (CAPTURE program), and with constant survival and time-dependent recapture (MARK program) best fit the data. The results of both methods were relatively similar because the models selected suggested that mortality, recruitment or movement events were unimportant. Population sizes were estimated to be between 187 and 1902 individuals in the four colonies studied. The estimated mean annual survival for the species was 0.88, a value corresponding to an average longevity of 18 years. Little individual movement occurred among the colonies; the largest displacement observed was 120 km. One of the colonies did not display the same capture pattern as that of the others, probably due to space conflicts or shelter occupation time. Our data show that in southern Brazil biscutate swifts do not migrate, possibly because food availability is more constant throughout the year than in other regions (southeast and northeast) where migration occurs.

## Introduction

Swifts are among the most aerial birds (Collins 1985). During the day, they generally fly uninterrupted, traveling hundreds of kilometers to find food (Chantler & Driessens 1995). They can also bathe and copulate in the air, and are capable of flying all night to avoid adverse weather conditions, returning to their roosting site when the weather improves (Sick 1997). The Cypseloidinae (*Cypseloides* spp. and *Streptoprocne* spp.) fly at great heights during the day and at night

use inaccessible places such as cliffs, caves and waterfalls for shelter. They gather overnight at these sites in the hundreds and even in the thousands to procreate. After reproduction some migrate while others do not. The migration routes of these populations are largely unknown. Knowledge of the seasonal movements of species of the genus *Streptoprocne* is scarce. The white-naped swift (*Streptoprocne semicollaris*) is endemic to Mexico and there is no evidence that it migrates (Chantler & Driessens 1995, Chantler 1999). The white-collared swift (*Strep-*



**Fig. 1.** Biscutate swift colonies studied in southern Brazil. **A:** Anhangava, municipality of Quatro Barras; **B:** Capivari, municipality of Campina Grande do Sul; **C:** Arenitos; and **D:** Furna 1, both in the Vila Velha State Park, municipality of Ponta Grossa.

*toprocne zonaris*), found throughout South and Central America, undertakes seasonal movements in several parts of its range, including altitudinal migration in the Andes (Marín 1993, Sick 1997). The biscutate swift (*Streptoprocne biscutata*) is found in eastern Brazil from the state of Piauí south to Rio Grande do Sul, extending to northeastern Argentina in the province of Misiones (Meyer-de-Schauensee 1982, Sick 1997). It exhibits a well defined migratory behavior in parts of its range. The subspecies *S. b. seridoensis* migrates to the northeast of Brazil during the non-breeding season, but its breeding area remains largely unknown (Sick 1991, 1997).

Knowledge about the colony size or population estimates of *Streptoprocne* spp. is also scant. There are reports of white-collared swift flocks containing hundreds and thousands of individuals (Beebe 1949, Belton 1994, Marín & Stiles

1992, Chantler & Driessens 1995, Sick 1997), and a single mention of a 25 000 bird colony in Mexico (Whitacre & Ukrain 1982). There is a report of a white-naped swift colony with 200 individuals at the Chontalcoatlán river, Mexico (Rowley & Orr 1962). There is one biscutate swift colony with approximately 100 000 birds in the Brazilian northeast, and two other colonies with 1000 and 1200 individuals in the southeast (Andrade & Freitas 1987, Sick *et al.* 1988, Sick 1991, Sick 1997, Vasconcelos & Ferreira 2001). Owing to scant knowledge of the genus and the absence of population studies of the biscutate swift, we investigated the movement, population size, survival and life span of four colonies from southern Brazil.

## Material and methods

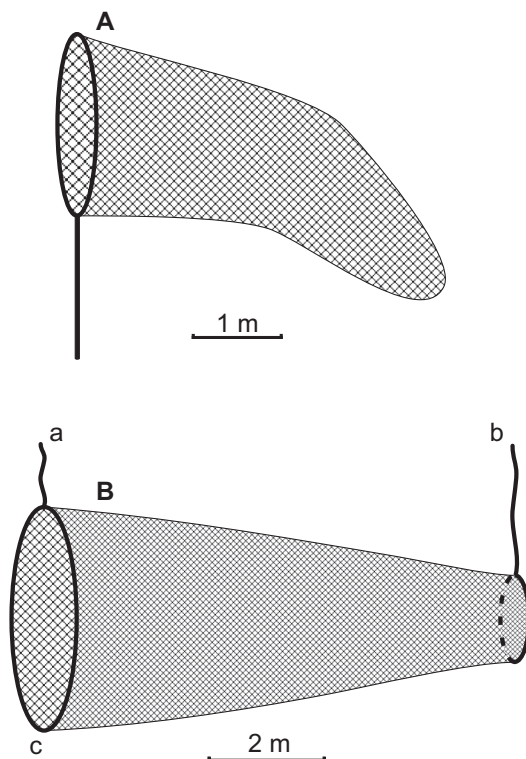
We studied four biscutate swift colonies located in the eastern part of the state of Paraná, southern Brazil. The Anhangava Hill colony, in the Serra da Baitaca (municipality of Quatro Barras, 25°22'S, 48°58'W, 1250 m a.s.l., **A** in Fig. 1) is a granite cave located 40 km from the capital Curitiba. Annual rainfall is around 2000 mm, and a more detailed description of the area can be found in Pichorim (2002). The Serra do Capivari colony (municipality of Campina Grande do Sul, 25°11'S, 48°51'W, 1050 m a.s.l., **B** in Fig. 1) is a granite crevice about 20 m high, 30 m deep and between 0.3 and 1 m wide. The inner walls are wet during and just after the rainy season. Atlantic Rainforest covers this study area, which is 70 km from Curitiba. The Arenitos and Furna 1 colonies are limestone rock sites located 4 km apart in Vila Velha State Park (hereafter VVSP), 80 km from Curitiba in the municipality of Ponta Grossa (25°15'S, 50°00'W, ± 1000 m a.s.l., **C** and **D** in Fig. 1). Natural grasslands, savanna and patches of Atlantic Forest with the Parana pine (*Araucaria angustifolia*) cover this region. Furna 1 is a natural soil depression resembling a large well with vertical and sub-vertical walls, measuring 57.8 m deep and 80 m in diameter (Soares 1989). At the bottom is a permanent groundwater pond. The walls are damp and contain several areas with water infiltration that drain into permanent streams, whose volume

depends on the amount of rainfall. A large population of white-collared swifts (about 1000 individuals) occurs at this site. The Arenitos site is a complex of crevices and small caves in a 5 ha limestone area. The crevices are used as shelter and nest sites, and are 10–30 m high, 10–60 m long and 0.5–8 m wide. The walls are vertical and water flows down them during or just after the rainy season.

Each colony was studied using the capture–recapture technique. We carried out field trips between 1999 and 2001, but in the Anhangava Hill colony we included earlier data, obtained between 1994 and 1995. For the captures we used 7–10 mist nets (mesh 60 mm, 4 shelves, 12 × 3 m). At some sites, up to five nets were overlapped horizontally to cover a larger area. We also used two other types of nets specifically made for capturing swifts. One was similar to a butterfly net, but with a 2 m diameter hoop, and a 4 m long net (10 mm mesh). The frame was made of flexible fiber glass rods (used in camping tents) connected to a 4 m long tubular aluminum handle (Fig. 2). The basic procedure to capture adult birds consisted of waiting for them to leave the cave in the morning via frequently used exits. When the birds started to leave the cave, the net was quickly raised into the flock. This procedure was repeated only three times per day in order not to stress the birds excessively.

The other net used was truncated cone-shaped in a laid down position (9 m long, 4 m and 1.5 m extremities, 10 mm mesh, *see* Fig. 2). The net was suspended, horizontally, with ropes so that the opening faced the exit of the overnight shelter used by the birds. This net was erected around 20 min before sunrise. When the birds left the site at high speed, they entered the net and concentrated at the closed end of the cone. After capture we took the net down and removed the birds. We used metallic numbered bands (4.5 mm inner diameter) to mark the captured birds. The bands were supplied by CEMAVE/ICMBio.

Based on the capture histories of each colony, we tested the null hypothesis of population closure using the “Test Closure” routine of the CAPTURE program (Otis *et al.* 1978). When the closure premise was accepted, we considered the population size of the colony constant during the study period, despite ongoing bird movement,



**Fig. 2.** Schematic drawings of the nets used to capture swifts. **A:** butterfly-type net. **B:** truncated cone-shaped net in a laid down position (a and b are suspension points, and c is the access to the net).

births and deaths. We also used the CAPTURE program to test which model best fit the data by “Model Selection” and obtained the estimated population size by using the “Estimate” routine. A detailed description of the models tested using this program can be found in Otis *et al.* (1978) and Seber (1986).

For survival estimates we used the MARK program ver. 2.1 (White 2001) with the option “Recaptures only” and followed the procedures suggested by Cooch and White (2001). The basic routine of this program initially enabled us to choose which model best fits the data, and from this model to estimate the population parameters. The four predefined models check the dependence of survival and capture probability as a function of time. The program initially considers the most general model, designated  $\phi(t)p(t)$  (standard Cormack–Jolly–Seber model, Cormack 1964, Jolly 1965, Seber 1965), where both survival and recapture are time-depend-

ent. It then considers the models with reduced parameters:  $\phi(\cdot)p(t)$  (constant survival and time dependent recapture probabilities) and  $\phi(t)p(\cdot)$  (time dependent survival and constant recapture probabilities). Finally, it analyzes the  $\phi(\cdot)p(\cdot)$  model with both constant survival and recapture probabilities. To choose which model best fits the data, Cooch and White (2001) suggested adopting the following criteria: lowest Akaike's Information Criterion (AICc),  $\Delta \text{AICc} > 2$  (difference in AIC between two models), superiority of the Akaike Weight, Variance Inflation Factor ( $\hat{c}$ )  $\approx 1$ , and the bootstrapped GOF ( $P_{\text{DGOF}}$ ) testing the probability of a deviance as large or greater than the observed value. After model selection, survival between sampling periods (Sbsp) can be estimated. Annual survival was obtained using the equation:  $\phi = \text{Sbsp}^{\text{Nsa}}$ ; where  $\phi$  = annual survival, Sbsp = survival between sampling, and Nsa = number of sampling periods in one year. The mean life span of an adult (Mls) was calculated according to Boano *et al.* (1993) as:  $\text{Mls} = 1/(-\log\phi)$ .

We considered individuals younger than one year of age as subadults. Subadult status can be determined for marked nestlings captured after leaving the nest, and for individuals captured without evidence of molting remiges and retrices between January and March, the months in which all adults molt (M. Pichorim pers. comm.).

## Results

In the four colonies studied, we marked a total of 1278 individuals: 1020 adult birds, 233 nestlings and 25 subadults (Table 1). For the Anhangava, Capivari and Arenitos colonies, the Mth model (capture probabilities vary with time and indi-

vidual animal) of the CAPTURE program best fitted the data, and in case of the MARK program the  $\phi(\cdot)p(t)$  model (constant survival and time dependent recapture probabilities) best fitted the data (Table 2). In the Furna 1 colony, the Mtbh model (capture probabilities vary with behavioral response to capture, time, and individual animal) of the CAPTURE program best fitted the data, and in case of the MARK program three models fitted the data equally well (both survival and recapture constant, survival constant and recapture time dependent, and survival and recapture are time dependent). Estimated population sizes varied from 159 (Anhangava) to 1902 (Arenitos) individuals (Table 2). If the two phases in the Anhangava colony are considered as separate sampling periods (1994–1995 banding trips and 1999–2001 recapture trips), survival between these sampling periods was 0.40, with annual survival being 0.83. Of 189 birds marked during the first sampling period, we recaptured 30 during the second period, after a mean interval of five years. The longest period observed between the capture and recapture of a bird was six years, seven months and 27 days (10 October 1994–4 June 2001).

The population closure hypothesis was supported for the four colonies, except in phase one of the Anhangava colony (*see* Table 2). In the Furna 1 colony, the best-fit models were more complex than in the other colonies. Mtbh (capture probabilities vary with behavioral response to capture, time, and individual animal) is a model where capture depends on behavioral response as a function of previous captures, in addition to the other factors acting on the Mth model (Otis *et al.* 1978). This model considers invalid the premise that the initial capture does not affect the capture probability on subsequent occasions. All three factors that may affect capture probabilities are assumed to be operating. Unfortunately, this precludes the model from having any practical use on the estimation of population size (Otis *et al.* 1978). As an alternative for estimating population parameters, we used the next-best model, the Mh (capture probabilities vary with individual animal). The basis of this model is the assertion that each member of the population has its own capture probability, independent of all other members

**Table 1.** Number of ringed birds in four biscutate swift colonies from southern Brazil.

Colony	Adults	Subadults	Nestlings	Total
Anhangava	220	4	76	300
Capivari	116	3	17	136
Arenitos	506	–	140	646
Furna 1	178	18	–	196
Total	1020	25	233	1278

**Table 2.** Population parameters and outputs from the CAPTURE and MARK programs for five biscutate swift colonies in southern Brazil.

Colony, (capture trips), period	Capture			Mark									
	Population closure (Z, P)	Model	Population size (n ± SE)	1st Model, 2nd Model	LR test <sup>(a)</sup> (Chi, df, P)	AICc <sup>(b)</sup> ΔAICc <sup>(c)</sup>	Sw <sub>i</sub> <sup>(d)</sup>	K <sup>(e)</sup>	$\hat{c}^{(f)}$	P <sub>DOOF</sub> <sup>(g)</sup>	$\phi \pm SE^{(h)}$	Annual survival	
Anhangava, (13 <sup>(i)</sup> ), Aug1994–Sep1995 (3.56, < 0.05)	Rejected	Mth <sup>(j)</sup>	361 ± 42.8, 95%C.I. 289–476	$\phi(\cdot)p(t)^k, \phi(t)p(t)^l$	8.7, 10, 0.56	549.2	14.6	1586	13	0.84	0.046	0.9143 ± 0.0384	0.34
Anhangava, (8 <sup>(m)</sup> ), Nov1999–Jun2001 (1.12, > 0.05)	Supported	Mth	159 ± 100, 95%C.I. 98–644	$\phi(\cdot)p(t), \phi(t)p(t)$	6.4, 5, 0.27	222.8	5.7	17.5	8	1.12	0.277	0.9429 ± 0.0362	0.75
Capivari, (6 <sup>(n)</sup> ), Jul2000–Feb2002 (0.11, > 0.05)	Supported	Mth	187 ± 16.87, 95%C.I. 162–229	$\phi(\cdot)p(t), \phi(t)p(t)$	0.1, 3, 0.99	259.7	6.8	28.1	6	0.86	0.700	0.99 ± 0.02	0.96
Arenitos, (10 <sup>(o)</sup> ), Jan2000–Aug2002 (1.19, > 0.05)	Supported	Mth	1902 ± 213.3, 95%C.I. 1543–2386	$\phi(t)p(t), \phi(\cdot)p(t)$	16.4, 7, 0.02	1083.9	1.4	2.1	17	1.24	0.010	0.9592 ± 0.009	0.85
Furna 1, (8 <sup>(p)</sup> ), Jun2000–Aug2002 (0.0, > 0.05)	Supported	Mth <sup>(q)</sup> , Mh <sup>(r)</sup>	810 ± 50.5, 95%C.I. 719–917	$\phi(\cdot)p(\cdot)^r, \phi(t)p(t)$	3.9, 6, 0.69	19.1	8.95	88.0	2	1.95	0.162	1.0 ± 0.0	1.0

<sup>a)</sup> Likelihood Ratio (LR) test between models. <sup>b)</sup> Akaike's Information Criterion of the 1st model. <sup>c)</sup> Difference between AICc of the 1st and 2nd model. <sup>d)</sup> Superiority of the Akaike Weight. <sup>e)</sup> Number of parameters of the 1st model. <sup>f)</sup> Variance Inflation Factor of the 1st model. <sup>g)</sup> Probability of the bootstrapped GOF testing. <sup>h)</sup> Survival between samplings ± SE. <sup>i)</sup> Mean interval of one month between them. <sup>j)</sup> Mth = capture probabilities vary with time and individual animal. <sup>k)</sup>  $\phi(\cdot)p(t)$  = constant survival and recapture time dependent. <sup>l)</sup>  $\phi(t)p(t)$  = survival and recapture time dependent. <sup>m)</sup> Mean interval of two and a half months between them. <sup>n)</sup> Mean interval of three months between them. <sup>o)</sup> Mean interval of three and a half months between them. <sup>p)</sup> Mth = capture probabilities vary with behavioural response to capture, time, and individual animal (this model does not allow the estimation of any population parameter). <sup>q)</sup> Mh = capture probabilities vary with individual animal, it was the nearest "Mth" model for the Furna 1 data. <sup>r)</sup>  $\phi(\cdot)p(\cdot)$  = both survival and recapture constant.

of the population (Otis *et al.* 1978). Considering the overall annual survival estimates of the Anhangava, Capivari and Arenitos colonies that fit the models best, we obtain a general mean ( $\pm$  SD) value of  $0.88 \pm 0.07$ . This annual survival results in a mean life span (Mls) of 18 years.

We recorded only five movements between the colonies. The longest distance covered was 120 km; this individual, a nestling, was banded in the Anhangava colony (16 December 1999) and recaptured in the Furna 1 colony (31 August 2001). The other movements occurred exclusively in the Vila Velha State Park (VVSP). An individual banded in the Arenitos colony on 26 June 2000 was recaptured 4 km away in the Furna 1 colony on 13 April 2002. Another individual banded in the Arenitos colony on 2 December 2000 was recaptured in the Furna 1 colony 20 days later. Movements in the opposite direction also took place between these two colonies. A Furna 1 individual, banded on 27 June 2000 was recaptured in the Arenitos colony on 4 December of the same year. Another individual, banded in Furna 1 on 20 July 2001, was recaptured in Arenitos two days later.

In each subsequent year of the study, the birds occupied their shelters in a different manner. During the breeding periods, the birds were more scattered at each colony site, occupying many secondary rifts and small grottos. In the Arenitos colony we recaptured 13 individuals in different rifts from those in which they were ringed. During the non-breeding season the birds were more concentrated and occupied fewer sites. One

of these sites, in the Arenitos colony, is located behind the main grotto of the VVSP and near the natural formation called "Pedra Suspensa", a type of rift (around 14 m high, 16 m deep, and 0.8 m wide) that shelters a large part of the colony in June and July. For two years, we counted the birds that entered this rift during the late afternoon to rest overnight (Table 3). Between spring and fall the mean number ( $\pm$  SD) of individuals was  $160 \pm 35$  (12 censuses), and in the winter the mean ( $\pm$  SD) was  $913 \pm 612$  (4 censuses), with a maximum count of 1620 birds in July. We observed similar behavior in the Capivari colony. In the winter, almost all the birds entered a single portion of the overnight rift (mean  $\pm$  SD =  $113 \pm 30$  individuals, 5 censuses), while in the spring narrower parts of the rift were used and access through the main entry point decreased (mean  $\pm$  SD =  $98 \pm 31$  individuals, 5 censuses).

In the Anhangava colony, the birds entered and left the shelter by two independent rocky rifts (Pichorim 2002). Some of the individuals captured in one of the rifts were recaptured in another, showing that there is no route segregation. We recaptured 19 birds at different entry points from where they were first captured. The number of birds that entered the shelter via the main rift varied with season, showing low numbers in the winter (mean  $\pm$  SD =  $122 \pm 43$  individuals, 6 censuses) and higher numbers in the other seasons (mean  $\pm$  SD =  $184 \pm 55$  individuals, 10 censuses). The highest numbers of birds in this colony (mean  $\pm$  SD =  $236 \pm 36$

**Table 3.** Counts of biscutate swift individuals that arrived to rest at each colony site during the study. Data are presented in the following sequence: mean  $\pm$  SD, day of the respective month and year of the counts.

Month	Arenitos	Anhangava	Capivari
January	95 $\pm$ 14, 11–12/2002	173 $\pm$ 3, 27–28/2000	–
March	187 $\pm$ 5, 16–18/2001	205 $\pm$ 1, 8–9/2001	–
April	171 $\pm$ 33, 14–15/2002	268 $\pm$ 3, 1–2/2000	–
May	–	110 $\pm$ 5, 31/1995 and 21/2001	–
June	560 $\pm$ 28, 14–16/2001	83 $\pm$ 13, 1/1995 and 4/2001	88 $\pm$ 4, 29–30/2001
July	1620, 06/2002	158 $\pm$ 38, 1 and 20/2000	–
August	–	126 $\pm$ 14, 20–21/2001	130 $\pm$ 27, 3, 18 and 26/2001
September	188 $\pm$ 4, 1–2/2001	168 $\pm$ 8, 10–11/2001	–
October	165 $\pm$ 2, 13–14/2001	–	100 $\pm$ 7, 6/2000, 26–27/2001
November	–	–	72 $\pm$ 14, 23–24/2000
December	153 $\pm$ 10, 12–13/2001	–	–

individuals, 4 censuses) were observed in March and April. In the Furna 1 colony, birds were not counted in the afternoon as they returned to rest, because they were in large polyspecific flocks (with white-collared swifts), making it impossible to correctly identify the species in flight.

## Discussion

The best-fit models for the Anhangava, Capivari and Arenitos colonies are characteristic of closed populations or constant survival, and with capture probabilities that are time and individual dependent. Constant survival and population closure mean the absence of any significant mortality, recruitment or movement events. The Mth model provided different population sizes between colonies and large confidence intervals (see Table 2). The jackknife estimation procedure in the CAPTURE program is a robust technique when recaptures are high, but the procedure does not seem particularly useful in providing a satisfactory estimate of the confidence intervals, so the results must be considered only as a rough indication and not as a valid statement of inference (Otis *et al.* 1978). The recaptures in the Anhangava, Capivari and Arenitos colonies corresponded to 47%, 43% and 35% of the total number of captured birds, respectively. These results provide a reliable population estimate, despite the large confidence intervals.

The best-fit models for the Anhangava, Capivari and Arenitos colonies reflect the complexity of these populations, given that capture probabilities vary as a function of more than one factor, which act independently in each population. For example, during the sampling events, we found temporal variation in the captures as a function of climatic changes, mostly during rainy periods. In these situations, the birds took longer to leave the shelters, or they left the sites from different rifts from those normally used and formed smaller flocks. During rainy periods the birds sometimes did not leave the rifts, remaining in the shelters throughout the day. However, we also recorded situations in which the whole colony left the shelter even in bad weather, and on other occasions, despite good weather, some individuals remained in the rifts all day. There

were cases in which the birds left the rifts in unfavorable weather, returning to the shelter after about one hour. Based on the observed data, we conclude that individuals of a biscutate swift colony somehow evaluate if the weather is favorable or not at the moment of leaving the shelter in the morning. When the first individuals decide to leave the shelter they are followed by others, forming relatively cohesive flocks, generally flying in circles and vocalizing. We also observed that when capture of the first flocks was detected by the rest of the colony, likely due to vocalizations, the remaining birds took longer to leave the shelter or they left via routes not commonly used. It is important to point out that the sheltered birds could not see the nets and the captured birds. Thus, we believe that the behavior of the first flocks may stimulate the birds that are still sheltered to leave the site. Another factor that showed the complex dynamics of the colonies was the practice of using secondary rifts during certain parts of the year, mostly during the breeding season. This diversity of environmental and behavioral variables acting on the colonies explains the complexity of the best-fit models for the colonies.

In the Furna 1 colony, the best-fit models were more complex than in the other colonies. All three factors that may affect capture probabilities (capture, time, and individual animal) are assumed to be operating. We ignore the exact reasons for these results, but believe that they are related to the peculiar physical and biological characteristics of this shelter. It is wider than the others, enabling many birds to avoid the nets when exiting. Thus, in the local system, the probability of recapture may vary as a function of previous captures. Moreover, this shelter is also used by white-collared swifts, which are likely more numerous than biscutate swifts (M. Pichorim pers obs.). We observed that white-collared swifts start to leave the shelter before biscutate swifts. The capture of the first birds (generally white-collared swift) may change the capture probability of the subsequent birds (biscutate swift individuals). Owing to the interaction with other species with relatively similar biological characteristics in the same shelter, the behavior of this biscutate swift population is likely different from that observed in the other

colonies. We believe that emigration and immigration occur more frequently in this shelter due to the probable competition for space or in response to seasonal events. The movements observed reinforce this idea, given that the Furna 1 colony received more individuals than the other colonies.

The populations of the Anhangava and Capivari colonies are relatively small compared to other studied colonies of the same species and of other species of the genus, while the Arenitos and Furna 1 colonies have similar population sizes to those found in the southeast of Brazil (*see* Introduction). The estimates reported by other studies were obtained through counting methods, and not by using the capture-recapture technique. Counts are useful for general estimates, because they provide immediate results. However, it is very difficult to perform accurate counts, mostly during the reproductive period when birds nest in large numbers of rifts. Moreover, in the areas where white-collared swifts and biscutate swifts co-occur it is not possible to separate the species when counting flying flocks. Thus, the figures shown here are the first and best estimates for a species from this genus to date.

The known shelters in the southeast and northeast of Brazil are used seasonally by the birds. In the northeast (Rio Grande do Norte) the birds arrive in February and leave in October (Andrade & Freitas 1987, Sick *et al.* 1988, Sick 1991). In the southeast (Minas Gerais) the shelters are occupied from August to February (Andrade & Freitas 1987, Vasconcelos & Ferreira 2001). In southern Brazil, the species occurs throughout the year with few movements between the colonies studied. Based on our observations so far, we have no concrete evidence of migration in the populations from eastern Paraná state, and in the state of Rio Grande do Sul its occurrence was confirmed in the winter, spring and summer (Belton 1994, Bencke 2001). We do not know the causes of this complex dynamic, where some populations migrate to and why others do not migrate. However, we suggest some mechanisms that could be triggering this process. Our data show that in the areas with comparatively harsher winters (southern Brazil) the birds do not migrate, whereas in areas with milder

winters (southeast and northeast) migration does take place, in contrast to what is expected. The biscutate swift probably stays in southern Brazil because food is more constantly available throughout the year than in the other regions. The regular abundance of flying insects in a tropical region is mainly associated with flora and rainfall rather than temperature (Wolda 1988, Poulin *et al.* 1992). The migrant colonies of biscutate swift are situated in regions with well defined wet and dry seasons, whereas the non-migrant colonies are in areas with more constant rainfall. The extreme seasonal variability of insect abundance observed in temperate zones forces long-distance migration of the majority of species breeding outside the tropics (Koskimies 1950, Chantler 1999). Furthermore, in these temperate regions, low winter temperatures reduce prey abundance considerably and this likely stimulates migration (*see* Cucco & Malacarne 1996). In Brazil, winter does not have the same effect, because winter temperatures do not decrease considerably, and insect density varies mainly due to changes in humidity between wet and dry seasons (Pinheiro *et al.* 2002).

Swifts have high annual survival and life span (Collins 1985) and our data show that biscutate swifts follow this tendency, with annual survival from 34%–100% among the colonies. It should be pointed out that survival estimates based on capture-recapture data should be considered as minimum values, owing to the possibility of permanent dispersion of some marked individuals (Boano *et al.* 1993). In pallid swifts (*Apus pallidus*), the annual survival reported varies between 74%–76% (Boano *et al.* 1993), in chimney swifts (*Chaetura pelagica*) between 62%–81% (Henny's results as cited in Collins 1973, Dexter 1979), in Alpine swifts (*Tachymarptis melba*) 79% (Glutz & Bauer's results as cited in Boano *et al.* 1993), in white-throated swifts 80% (Collins 1973), in common swifts (*Apus apus*) between 76%–85% (Perrins 1971, Dobson's results as cited in Boano *et al.* 1993, Chantler 1999) and in chestnut-collared swifts (*Streptoprocne rutila*) between 83%–85% (Collins 1974). However, survival during the first year of life is much lower in most species (Boano *et al.* 1993, Chantler & Driessens 1995).



We did not obtain estimates of subadult survival in biscutate swifts; however, we observed that they weighed less than the adults for nearly the entire first year of life. They likely face some type of food stress and survival rate during this developmental stage is expected to be low for this species. These high rates of annual survival and life span lead us to believe that the age of six years observed in some individuals from the Anhangava colony represents only a quarter of the maximum life expectancy of these birds. The largest interval between capture and recapture of an individual was six years and eight months. We captured the bird for the first time in October, when it was at least 11 months old (if it hatched in the previous reproductive season), corresponding to a minimum age of seven years and seven months. For other swifts the oldest ringed individuals reported were older than those of biscutate swifts (e.g. Alpine swift = 26 years, common swift = 21 years, chimney swift = 11–14 years, horus swift (*Apus horus*) = 13 years, chestnut-collared swift = 10.5 years, white-rumped swift (*Apus caffer*) and black swift = 10 years, Hight 1953, Dexter 1956, Arn-Willi's results as cited in Chantler & Driessens 1995, Dexter 1969, Collins 1974, Rydzewski 1978, Dexter 1979, Cramp 1985, Fry's results as cited in Chantler & Driessens 1995, Chantler & Driessens 1995, Collins & Foerster 1995). It is therefore important to monitor *Streptoprocne* colonies to determine the maximum life span of individuals in this genus.

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