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Evidence of vertical migration in the Ipanema bat *Pygoderma bilabiatum* (Chiroptera: Phyllostomidae: Stenodermatinae)

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ABSTRACT. Migration is defined as a seasonal and cyclic population movement observed in all animal classes and studied mainly in vertebrates. A considerable part of the knowledge on migration comes from birds, for which migration is an important aspect of their biology. In the case of bats, females usually migrate larger distances than males in some species. The present study analyzes the seasonal occurrence of *Pygoderma bilabiatum* (Wagner, 1843) at different elevations, in order to test for a pattern that evidences migration, using data from the states of Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, Brazil. A total of 529 specimens of *P. bilabiatum* were captured. *Pygoderma bilabiatum* seems to be more frequent at intermediate and high elevations (over 80% of all captures were made above 250 m a.s.l.) and at latitudes above 22°S, where rainfall is high (over 1,500 mm) and temperatures are mild (16-23°C). Sex ratio varied with elevation; it was skewed towards males at lower elevations (N = 9, $r^2 = 0.60$, F = 12.311, P = 0.008, Sex ratio = 0.0004*elevation + 0.976), though females predominated at all altitudinal bands and in all states analyzed.

KEY WORDS. Atlantic Forest; Brazil; capture efficiency; seasonality; temperature.

Migration is defined as a seasonal and cyclic population movement (Alerstam & Hedenström 1998) observed in all animal classes and studied mainly in vertebrates. A considerable part of the knowledge on migration comes from birds, for which migration is an important aspect of their biology (Bisson *et al.* 2009). In some bat species, females usually migrate larger distances than males (Fleming & Eby 2003). Migratory movements may not occur in all populations of a species (McCraken *et al.* 1994, Russel *et al.* 2005).

Migration occurs mainly in species that live in temperate climates, and is more common in winter (SICK 1997). It is,

therefore, less frequently observed in the Neotropics (Fenton & Kunz 1977). Migration may occur over large distances, between localities in different continents or hemispheres. There is also migration that involves only altitudinal, latitudinal or longitudinal movements; these movements, which may be regional or local, are related to resource availability (ALVES 2007).

Even for birds, local and vertical migrations are the least known and the most difficult to record (Sick 1997, Maia-Gouveia *et al.* 2005). Some authors do not consider smaller spatial movements in bats as migration, because they do not require physiological adaptations (Fleming & Eby 2003, Bisson *et al.* 2009).

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However, local or regional movements in bats are also expected in the Neotropics (e.g., Passos *et al.* 2003, Mello *et al.* 2009), and many authors reported changes in bat assemblages between dry and rainy seasons (e.g., Marinho-Filho & Sazima 1989, Pedro & Taddei 2002, Aguiar & Marinho-Filho 2004, Camargo *et al.* 2009), based mainly on variations in capture rates or species richness. Horizontal, vertical and regional movements may be important to understand temporal variations in the abundance of some species, but they do not necessarily represent migration, because the whole population does not perform them in a cyclic way. Although partial migration can be more frequent than expect by this definition (Chapman *et al.* 2011).

Little is known about the biology of the Ipanema Broad-Nosed Bat, *Pygoderma bilabiatum* (Wagner, 1843), a frugivorous species (Gardner 1977) that feeds on species such as *Pouteria caimito* (Ruiz & Pav.) Radlk (Sapotaceae), *Miconia brasiliensis* (Spreng.) (Melostomataceae), *Maclura tinctoria* (L.) Don ex Steud (Moraceae), *Ficus insipida* Willd, *F. enormis* (Mart. ex Miq.)

(Moraceae), Solanum sanctae-catharinae, S. granuloso-leprosum Dunal (Solanaceae), and Eugenia (Myrtaceae) (Peracchi & Albuquerque 1971, Webster & Owen 1984, Faria 1997, Passos et al. 2003).

The present study analyzes the seasonal occurrence of *P. bilabiatum* at different elevations, in order to test for a pattern that evidences migration, using published and unpublished data from southern and southeastern Brazil.

MATERIAL AND METHODS

In the present study, 26 samples from 21 localities were analyzed within the *sensu strictu* Atlantic Forest Biome (Ururahy *et al.* 1983). Geographic coordinates and elevation of sampling sites are given in Tab. I and Fig. 1. The reproductive condition of females was assessed at the moment of capture and each specimen was assigned to one of the following categories: inactive female, female with palpable fetus and lactating female (e.g., Costa *et al.* 2007).

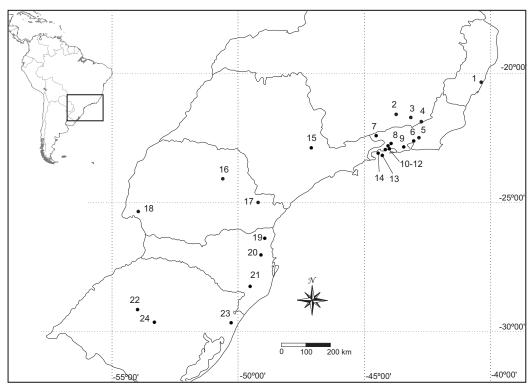


Figure 1. The study area in Brazil and the states where sampling was carried out. Few sampling sites were added. (1) Parque Estadual Paulo Cezar Vinha; (2) Ibitipoca; (3) Juiz de Fora; (4) Rio Preto; (5) Reserva Biológica de Araras; (6) Estação Ecológica Estadual Paraíso; (7) Serra da Concórdia; (8) Reserva Biológica do Tinguá; (9) Maciço da Tijuca, including sampling in the municipality of Rio de Janeiro (Parque Nacional da Tijuca, Parque da Gávea, Parque do Penhasco Dois Irmãos); (10-12) Seropédica and surroundings, Fazenda Portobello and Reserva Rio das Pedras; (13) Ilha Grande; (14) Ilha da Gipóia; (15) Santa Genebra Forest; (15) Fazenda Monte Alegre; (17) Parque Estadual do Campinho; (18) Parque Nacional de Iguaçú; (19) Parque Municipal Natural Nascentes do Garça; (20) Reserva de Sassafrás; (21) Pedras Grandes; (22) Parque Estadual do Turvo; (23) Agudos; (24) Maquiné.

Table I. Percentage of captures of *Pygoderma bilabiatum* in different municipalities and states in southeastern and southern Brazil. For each site we inform its geographical coordinates, elevation (m), sampling period, and number of sampling nights. Parentheses indicate years with sampling at monthly intervals; other years were sampled irregularly.

Municipality (States)	Sampling Sites	Coordinates	Elevation (m)	Sampling period	Nights	%
Guarapari (ES)	Paulo Cesar Vinha	20°34.0′S, 40°24.5′W	1	2004-2005	28	0.56
Angra dos Reis (RJ)	Ilha Grande	23°09.4′S, 44°14.3′W	1-120	1997-2003	58	0.06
Angra dos Reis (RJ)	Ilha Grande	23°09.4′S, 44°14.3′W	240	2004-2006	35	2.86
Angra dos Reis (RJ)	Ilha da Gipóia	23°02.4′S, 44°22.3′W	1-40	2003-2010	40	0.05
Nova Iguaçu (RJ)	Reserva Biológica do Tinguá	-	1-1,270	2000-2006	31	1.53
Nova Friburgo (RJ)		22°16.9′S, 42°31.9′W	790	_	-	-
Guapimirim (RJ)	Estação Ecológica Paraíso	22°29.8′S, 42°54.5′W	80	1996, 1997-1998, 2000, 2004	43	0.65
Itaguaí, Mangaratiba, Seropédica, Cacaria (RJ)	Banana plantations and surrounding forests	-	1-120	2008-2010	48	0.17
Mangaratiba (RJ)	Reserva Rio das Pedras	22°59.7′S, 24°06.3′W	40	1995, 1997-1998, 2004-2008, 2009	41	0.08
Mangaratiba (RJ)	Fazenda Portobello	22°56.5′S, 44°00.9′W	1-110	1994,1995, 2005-2010	19	0.18
Petrópolis (RJ)	Reserva Biológica de Araras	22°26.0′S, 43°15.2′W	1,100	1993-1995	47	1.28
Rio de Janeiro (RJ)	Parque Nacional da Tijuca	22°57.4′S, 43°17.7′W	535	1995-1997, 1998-2002	46	0.29
Rio de Janeiro (RJ)	Alto da Boa Vista	22°54.2′S, 23°15.6′W	565	2001-2003	7	0.67
Rio de Janeiro (RJ)	Parque Penhasco Dois Irmãos	22°59.1′S, 43°14.1′W	440	1996-1997, 1999-2001	21	0.12
Teresópolis (RJ)	Parque Nacional da Serra dos Órgãos	22°29.5′S, 43°00.8′W	410	-	-	-
Seropédica (RJ)		22°45.9′S, 43°41.3′W	40	_	_	-
Rio de Janeiro (RJ)	Parque da Cidade	23°58.8′S, 43°14.8′W	480	1992-1994,1995 – 1999	31	0.10
Valença (RJ)	Serra da Concórdia	22°22.2′S, 43°47.2′W	600	2005 and 2010	15	1.69
Rio Preto (MG)		22°01.7'S, 43°52.5'W	400-900	1997	56	_
Descoberto (MG)		21° 27′S, 42°58.0′W	400-500	_	-	-
Lima Duarte (MG)		21°50′S, 43°48.0′W	750-800	_	-	-
Juiz de Fora (MG)		21°46.3′S, 43°22.1′W	900	2003-2010	104	-
Lima Duarte (MG)	Parque Estadual do Ibitipoca	21°51′S, 43°48′W	1,430	2010-2011	14	-
Campinas (SP)	Santa Genebra	22°49.2′S, 47°07.0′W	650	1994*	35	6.16*
Telêmaco Borba (PR)	Fazenda Monte Alegre	21°13.4′S, 50°32.5′W	885	2004-2007	84	2.97
Céu Azul (PR)	Parque Nacional do Iguaçú	25°23′S, 54°09′W	200-400			
Tunas do Paraná (PR)	Parque Estadual de Campinhos	25°02.2′S, 49°05.5′W	890	2003-2004	24	2.13
Florianópolis (SC)	Nascentes do Garça	27°03.6′S, 49°06.7′W	320	2004-2006	81	6.68
Florianópolis (SC)	Nascentes do Garça	-	640	2004-2006	81	27.3
Joinville (SC)		-	1-200	1989-1997	_	
Pedra Grande (SC)		-	330	2009-2010	39	2.27
Doutor Pedrinho (SC)	Reserva de Sassafrás	26°42.7′S, 49°40.5′W	915	2010-2011	21	10.77
Derrubadas (RS)	Parque Estadual do Turvo	27°11.5′S, 53°56.0′W	485	1990-1992	31	4.16
Maquiné (RS)		29°40.5′S, 50°12.4′W	83	_	_	_
Agudos (RS)		29° 38.7′S 53°15.0′W	50		_	_

^{*} Only phyllostomid species are considered.

Captures were grouped according to states and altitudinal bands (1-1,600 m a.s.l., in 200 m intervals). Each altitudinal band had at least 24 months of continuous sampling, with a minimum sampling effort of two nights per month, except for the bands over 1,200 m a.s.l., which were only occasionally sampled.

To test for differences in average temperatures between months when the species was present and months when the species was absent in the samples, we used a Student t test (α = 0.05). To test for the effect of rainfall on the local seasonality of *P. bilabiatum* a linear regression between average rainfall and

the number of months when the species was captured was calculated for the 11 localities with higher number of captures.

To test whether males and females prefer different elevations, we calculated a linear regression between sex ratio, expressed as the total number of males divided by the total number of females, and elevation for nine samples with at least ten captures.

RESULTS

For the entire dataset the total sampling effort was 1,141 nights and 9,296 hours in 24 localities (Fig. 1); 529 specimens of *P. bilabiatum* were captured (0.47 specimens/night and 0.06 specimens/hour), at elevations that varied from 1 to 1,430 m a.s.l.

In Espírito Santo, three individuals were captured in July and August 2005: two males and one female (Tab. II). In 16 localities of Rio de Janeiro, *P. bilabiatum* was observed in all altitudinal bands. Three bands had few captures: 601-800 m a.s.l., 801-1,000 m a.s.l. (one capture each) and 1,200-1,400 m a.s.l. (two captures). At 1,001-1,200 m a.s.l., 17 animals were collected from January to April and from September to December, a rate of 0.03 captures/hour. In the intermediate bands, the presence

of *P. bilabiatum* was confirmed by 21 captures at 401-600 m a.s.l. (0.010 captures/hour) and four captures at 201-400 m a.s.l. (0.01 captures/hour). Bats were captured during all months, except for February, March, June and November. At the lower band, the species was only captured in March and from May to September, with a total of 20 individuals (0.006 captures/hour).

During the dry season, *P. bilabiatum* was absent from elevation bands at 1,100 m a.s.l. or higher (six months), except for two individuals captured in July at 1,270 m a.s.l. However, it was found during the same period at 1-200 m a.s.l.; at this elevation there are also dry months (five months), but they are warmer. The sex ratio was 1.00 males/females at 1-200 m a.s.l, but at the other bands there was a higher frequency of females: 0.50 males/females at 201-400 m a.s.l., 0.63 males/females at 401-600 m a.s.l. and 0.42 males/females at 1,001-1,200 m a.s.l.

Out of 62 individuals analyzed, 10 females were reproductive and among them, four were pregnant: one in September, two in October and one in November. Five lactating females were found: one in August, one in October, two in November and one in December. None of the females captured at 1-200 m a.s.l. were reproductive.

Table II. Captures of *Pygoderma bilabiatum* in the states (UF) of Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, according to month and elevation. Latitude (LAT) is given in degrees and elevation (ELE) in meters above sea level. Numbers in parentheses represent the number of nights in which the species was captured, when it differed from the total of nights.

	9														
UF	LAT	ELE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AGO	SEP	ОСТ	NOV	DEC	Captures
ES	20	1	0	0	0	0	0	0	1	2(1)	0	0	0	0	3
MG	21	401-600	1	0	0	0	0	0	0	0	0	0	0	0	1
MG	21	601-800	0	0	0	0	0	0	0	0	0	0	1	0	1
MG	21	801-1000	1	5 (4)	4 (3)	0	0	0	0	0	1	1	1	0	4
MG	21	1401-1600	0	0	0	0	0	0	0	0	0	2	0	0	2
RJ	22	1-200	0	0	0	0	2	3	10 (5)	3	2	0	0	0	20
RJ	22	201-400	0	0	0	1	0	0	3 (1)	0	0	0	0	0	4
RJ	22	401-600	1	0	0	5 (3)	7 (3)	4 (2)	1	1	1	1	0	1	21
RJ	22	601-800	0	0	0	0	0	0	0	0	0	1	0	0	1
RJ	22	801-1000	0	0	0	0	0	0	0	1	0	0	0	0	1
RJ	22	1001-1200	1	1	1	2	0	0	0	0	1	3 (1)	5 (3)	3 (2)	17
RJ	22	1201-1400	0	0	0	0	0	0	2 (1)	0	0	0	0	0	2
SP	23	650	0	0	0	1	1	1	0	0	0	0	23 (3)	1	27
PR	24	201-400	2 (1)	0	1	13 (4)	1	1	1	1	1	1	1	1	21
PR	24	801-1000	9	6 (4)	3	0	0	0	0	0	1	3	2	5(4)	20
SC	27	1-200	0	10 (5)	12 (8)	3 (3)	1	5 (3)	0	0	0	0	0	0	31
SC	27	201-400	1	6 (4)	5 (3)	1	1	6 (2)	14 (3)	32 (5)	9 (5)	2	2	1	80
SC	27	601-800	36 (8)	10 (4)	0	5 (4)	39 (5)	42 (3)	43 (6)	59 (4)	2	2 (1)	1	6 (4)	247
SC	27	801-1000	8 (3)	3 (3)	2 (2)	1	0	0	0	0	0	0	0	1	15
SC	28	201-400	0	0	2	4	0	0	1	1	0	0	0	0	11
RS	27	1-200	0	0	0	0	0	0	0	0	1	0	0	1	2
RS	27	401-600	0	0	1	2	1	2	1	0	0	0	5 (3)	0	12

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In Minas Gerais, 22 specimens from three localities were analyzed, at elevations that varied from 400 to 1,430 m a.s.l. However, only at 801-1,000 m a.s.l. more than two captures of *P. bilabiatum* were obtained. There was a predominance of females: 0.47 males/females in the entire sample and 0.42 males/females at 801-1,000 m a.s.l. (N = 17 individuals). Reproductive activity was observed in February, March and April, with pregnant and lactating females captured at 900 m a.s.l. and a lactating female captured at 1,430 m a.s.l. in October.

In Campinas, state of São Paulo, 27 animals were captured; 19 were captured during a single night close to a M. tinctoria in fruit. Captures were carried out from April to June and from November to December. Lactating (N = 16) and pregnant (n = 5) females were observed in November.

In the Parque Nacional do Iguaçú, state of Paraná, 21 specimens were captured every month except for February (12 females and 9 males). Lactating females were observed in January, March and April. In the Fazenda Monte Alegre, a total of 20 specimens were collected at 885 m a.s.l. (nine males and 11 females), with captures concentrated from January to March and from October to December (0.06 captures/hour). Pregnant females were observed in January and lactating females in March. In the Parque Estadual de Campinho, nine individuals were captured in September, January, February and March.

In Santa Catarina, 91 individuals were captured at 201-400 m a.s.l. and 241 animals at 601-800 m a.s.l., resulting in rates of 0.12 and 0.50 captures/hour, respectively. This species was present in all months at these elevation bands. In Joinville and surroundings, 31 animals were captured at 1-200 m a.s.l. from February to June, and in the Reserva Estadual de Sassafrás 14 animals were captured from January to April. Reproductive females were observed in March, April and June at 1-200 m a.s.l.; in January, July and August at 201-400 m a.s.l.; in September, October and December at 601-800 m a.s.l.; and from January to April at 915 m a.s.l. The sex ratio observed was 0.81 males/females at 1-200 m a.s.l., 0.89 males/females at 320 m a.s.l., 0.63 males/females at 640 m a.s.l., and 0.56 males/females at 915 m a.s.l.

In Rio Grande do Sul, 12 specimens were collected at $401\text{-}600\,\mathrm{m}$ a.s.l. (sex ratio = $0.50\,\mathrm{males/females}$) in March, April, May, June, July and November; a pregnant female was observed in November.

Pygoderma bilabiatum was present in higher sites in months with temperatures over 16°C, as shown in Tab. III for Araras (Rio de Janeiro), Telêmaco Borba (Paraná) and Juiz de Fora (Minas Gerais). At intermediate elevations in Campinas and Rio de Janeiro (401-800 m a.s.l.) there were no differences in average temperature between months when the species was present or absent. In these localities the low density of this species probably results from the lack of specimens captured in other months of the year. At low elevations, such as Rio de Janeiro at 80 m a.s.l. and Espírito Santo at 1 m a.s.l., the species was present in months with temperatures below 23°C. In Santa Catarina, where the species was present throughout the year, it occurred at average temperatures below 21°C.

All localities at intermediate and high elevation (over 600 m a.s.l.) have high rainfall (over 1,500 mm). We observed a positive relationship between the number of months in which the species was captured in each locality and its average rainfall (N = 11 localities, $r^2 = 0.41$, F = 6.361, p = 0.033, occurrence = 0.0928*rainfall – 4.3539).

Sex ratio varied with elevation. It was skewed towards males at lower elevations (N = 9, r^2 = 0.60, F = 12.311, p = 0.008, Sex ratio = 0.0004*elevation + 0.976), though females predominated at all elevation bands and in all states analyzed (Fig. 2).

DISCUSSION

Pygoderma bilabiatum seems to be more frequent at intermediate and high elevations (over 80% of all captures were observed above 250 m a.s.l.) and at latitudes above 22°S, where rainfall is high (over 1,500 m) and temperatures are mild (16-23°C). For instance, in the state of Santa Catarina (27°S), where it was the third most frequent frugivorous bat in the Parque Nacional Serra de Itajaí (313 out of 2,252 captures) at 320 and

Table III. Temperature (average value and variance) in sites in different states and at different elevations, where *Pygoderma bilabiatum* was present of absent, number of months when the species was captured (N) and t test results.

States	Elevation (m a.s.l.)	Average Tem	perature (°C)	N	t-test	n	
states	Elevation (m a.s.i.)	Absent	Present	IN	t-test	р	
ES	36	24.6 (22.8-26.7)	21.9 (22.8-26.7)	2	2.233	0.005*	
MG	940	17.4 (16.1-19.5)	20.5 (18.0-22.4)	7	-2.183	0.054*	
RJ	820	15.5 (14.0-15.9)	20.1 (17.7-21.7)	8	-6.160	>0.001*	
RJ	535	24.9 (21.8-26.6)	23.0 (21.3-25.3)	8	-2.193	0.053*	
RJ	80	25.1 (22.9-26.4)	21.1 (19.5-21.4)	5	4.756	0.001*	
SP	650	21.0 (17.3-22.4)	20.2 (17.2-23.4)	5	0.593	0.566	
PR	885	14.5 (14.0-16.5)	19.4 (17.1-20.4)	6	4.546	0.001*	
SC	2	19.9 (16.5-23.0)	21.0 (16.7-24.6)	5	-3.970	0.700	
SC	2	-	18.7 (14.1-22.9)	11	_		

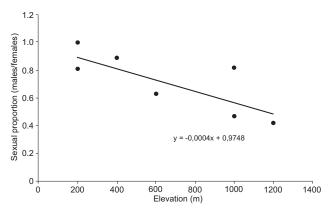


Figure 2. Sex ratio (males/females) of *Pygoderma bilabiatum* at different elevations. We considered only samples with 10 or more captures.

640 m a.s.l. In Paraguay (24°S), it was also the third most frequent species (522 out of 7,725 captures (Gorresen & Willig 2004, Stevens *et al.* 2004), and it was more frequent in sites located between 100 and 300 m a.s.l. (Willig *et al.* 2000). At latitudes below 22°S, this species has been rarely captured (Peracchi & Albuquerque 1993, Oprea *et al.* 2007, Faria *et al.* 2006). All these sites have high average temperatures and low rainfall. In Santa Catarina and Rio Grande do Sul, where total rainfall is high and monthly variations are small, this species can be found at all elevations throughout the year.

Vertical migration can only be proved through recaptures of previously marked animals. However, inferring from these data, *P. bilabiatum* probably moves from higher regions during colder months in the states of Rio de Janeiro and Paraná; it is found at intermediate elevations throughout the year and also at sea level in the months when it is absent from the highlands. These movements of *P. bilabiatum* may not cover large distances, since from the base to the top of Serra do Mar in Rio de Janeiro the linear distance is shorter than 30 km. Similarly, smaller densities of *Sturnira lillium* (E. Geoffroy, 1810) were observed in a high locality in southeastern Brazil during the colder months, though food-plant availability was not reduced when temperatures were lower (Mello *et al.* 2008).

Although the inferred partial migration (Chapman *et al.* 2001) of *P. bilabiatum* populations of southeastern Brazil and Paraná from highlands to lowlands occurs during the driest four months of the year, when less than 25% of the annual rainfall occurs, rainfall seems to be less important than temperature at this latitude (22 to 24°S). Phenology of food-plants and foraging strategies of bats seem to be more important than rainfall (Mello 2009).

If *P. bilabiatum* moves to intermediate or low elevations, it finds higher average temperatures of up to 9.0°C in southeastern Brazil (Ramos *et al.* 2009). *Pygoderma bilabiatum* seems to prefer elevations with average temperatures equal or above 16-17°C

and to avoid temperatures above 22-23°C in southeastern Brazil and Paraná. In Santa Catarina, the t test did not show significant differences; minimum temperatures were around 16°C both in months with and without captures. Migration to lowlands in this state would lead the population to areas with temperatures only 2°C higher. Temperature has been pointed out as a critical factor for frugivorous (Speakman & Thomas 2003) and non-frugivorous phyllostomids (McNab 1973). Temperature shortens the reproductive season at higher elevations (Mello *et al.* 2009). Capture rates are directly related to local density of bats (e.g., Fleming 1988), and lower rates are observed in the coldest months, in winter (e.g., Mello *et al.* 2009).

There is probably latitudinal variation in migration; it may not occur in localities with high average temperatures or it may last longer in colder climates, such as in high elevations. Further data are needed to test for latitudinal variation. There are differences between data collected in Santa Catarina and in southeastern Brazil and Paraná, as *P. bilabiatum* shows no seasonality at lower elevations, whereas captures in low-lands of Paraná and Rio de Janeiro were restricted to the period between March and September.

Our evidence on migration in *P. bilabiatum* is only circumstantial. However, the low capture frequency of *P. bilabiatum* observed above 800 m a.s.l. in Rio de Janeiro during the coldest months together with its high capture frequency observed at 1-200 m a.s.l. during the same period may be considered as indirect evidence of migration. The absence of *P. bilabiatum* above 800 m a.s.l. in winter should not be attributed to insufficient sampling effort, since even in the least sampled altitudinal band in Rio de Janeiro (1,000-1,200 m a.s.l.) sampling comprised more than 42 nights and 550 hours, and at 1-200 m a.s.l. it comprised more than 2,500 hours.

Similar migration patterns are known for birds, such as *Turdus albicollis* Vieillot, 1818, *Platycichla flavipes* (Vieillot, 1818) and *Aburria jacutinga* (Spix, 1825), which exchange highlands in summer for lowlands in winter (Sick 1997). The pattern described here fits the model described by Cohen (1967), in which migration is motivated by less favorable climate and by lower local food availability.

The lower the elevation the more the sex ratio is skewed towards males. This is evidence that males and females use different strategies, be it vertical migration in different seasons or preference for different elevations. Other bat species exhibit similar patterns, with samples skewed towards one sex in different seasons and in different localities, as was observed in *Lasiurus cinereus* (Beauvois, 1796) and *Lasionycteris noctivagans* (La Conte, 1831) (e.g., Cryan 2003, Kurta 2010). Among bats there are species in which females move more than males; one explanation is that females have higher nutritional requirements and need environments with proper conditions to breed (Cryan 2003). Elevation segregation has been already described in some insectivorous bat species (Barclay 1991, Cryan *et al.* 2000). In the Rocky Mountains, male *Myotis lucifugus* (Le Conte, 1831) are more fre-

quent in summer at proportions that reach 93% of the population, whereas females predominate in the lowlands (Barclay 1991). In *P. bilabiatum*, males seem to be more abundant at low elevations and females at intermediate and high elevations.

Different strategies adopted by each sex can be of advantage if mating occurs at lower elevations, where males are more abundant, as observed in the present study. Migration can only be considered an evolutionary advantage for the species if the benefit obtained is higher than the costs (e.g., costs of the movement itself, search for new roosts, time spent to adapt to a new foraging site) (RICHTER & GUMMING 2006).

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