Ambient temperature is more important than food availability in explaining reproductive timing of the bat *Sturnira lilium* (Mammalia: Chiroptera) in a montane Atlantic Forest

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Abstract: Reproduction of bats is determined by a suite of endogenous and exogenous factors. Among exogenous influences, special attention has been given to the influence of food availability. However, in highland forests, severe decreases in temperature during the cold and dry season may also play an important role. In the present study we tested the influence of ambient temperature and food availability on the timing of reproduction in the frugivorous bat *Sturnira lilium* (E. Geoffroy, 1810). We conducted a 15-month mist-netting sampling in a mountain area of the Brazilian Atlantic Forest during which time we assessed the bats' diet through fecal samples, monitored fruit production of the main food plants, and recorded variations in ambient temperature. *Sturnira lilium* fed almost exclusively on Solanaceae. Similarly to the lowlands, reproduction was bimodal, but reproductive season tended to be shorter in the highlands and peaked in the warmer months of the year. Overall, 44% to 53% of the reproductive pattern was explained by variations in ambient temperature, while the relationship with food availability was nonsignificant. We conclude that variations in ambient temperature in tropical mountains may be a stronger selection pressure than food availability in determining reproductive timing of bats.

Résumé : La reproduction des chauves-souris est déterminée par une série de facteurs endogènes et exogènes. Parmi les facteurs exogènes, on a porté une attention particulière à l'influence de la disponibilité de nourriture. Cependant, dans les forêts des terres hautes, les grandes chutes de température durant la saison froide et sèche peuvent aussi jouer un rôle important. Dans notre recherche, nous testons l'influence de la température ambiante et de la disponibilité de la nourriture sur le calendrier de la reproduction chez la chauve-souris frugivore *Sturnira lilium* (E. Geoffroy, 1810). Nous avons fait une échantillonnage pendant 15 mois dans une région montagneuse de la Forêt atlantique brésilienne; nous avons déterminé le régime alimentaire des chauves-souris par prélèvement de fèces, suivi la production de fruits des principales plantes nourricières et enregistré les variations de la température ambiante. *Sturnira lilium* se nourrit presque exclusivement de Solanaceae. Comme dans les basses terres, la reproduction est bimodale, mais la saison de reproduction tend à être plus courte dans les terres hautes et elle atteint un sommet durant les mois plus chauds de l'année. Les variations de la température ambiante expliquent globalement 44 % à 53 % du patron de reproduction, alors que la relation avec la disponibilité de nourriture n'est pas significative. Nous en concluons que dans les montagnes tropicales, les variations de la température ambiante peuvent exercer une pression de sélection plus grande que la disponibilité de nourriture dans la détermination du calendrier de reproduction des chauves-souris.

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Introduction

Bats (Mammalia: Chiroptera) are highly diverse worldwide including Brazil (Simmons 2005), where they constitute one third of the country's mammal species (Marinho-Filho and Sazima 1998). They have an unusual combination of life-history characteristics (Barclay and Harder 2003). Most bats are small compared with other mammals (<50 g) but are long-lived, as some individuals in the temperate zone have been recorded to live more than 40 years. They are also slow-breeding, mostly with one or two offspring a year, which makes every reproductive season very important (Barclay and Harder 2003). A variety of factors are regarded as determinants of reproductive timing, including endogenous causes, especially the hormonal cycle (Klose et al. 2006), and exogenous causes, represented mainly by diet, food availability, day length, rainfall, and temperature (Kunz 1982; Handley et al. 1991; Kalko 1998; Arlettaz et al. 2001; Barclay et al. 2004).

Regarding reproductive timing, bat populations are characterized by four basic patterns (Fleming et al. 1972): continuous reproduction throughout the year, a single reproductive season a year, two or more well-defined reproductive seasons a year, and no clearly defined reproductive

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pattern. Differences in those patterns have been linked mainly to differences in diet and temporal availability of food (Crichton and Krutzsch 2000). Whereas ambient temperature is well known to influence reproductive pattern of bats in the temperate zone (Crichton and Krutzsch 2000), it may also be more important in the tropics than previously thought (Mello et al. 2004).

In the Neotropics, fruit-eating leaf-nosed bats are a very interesting study group, because they feed on an easily-trackable resource, fruits, making the monitoring of food availability much less difficult than for instance in insect-eating bats (Kunz 1988). This permits linkage of seasonal variation in food over time with reproductive seasonality, thus allowing accurate assessment of the relative strength of this and other exogenous factors such as ambient temperature. Thus far, our knowledge on the reproductive ecology of frugivorous leaf-nosed bats is still limited, encompassing only a few species, which is remarkable little given the high diversity and ecological importance of this group (Zortéa 2003; Mello et al. 2004; Klose et al. 2006).

We selected one of the most widespread and common neotropical bat species (Simmons 2005), the stenodermatine little yellow-shouldered bat (*Sturnira lilium* (E. Geoffroy, 1810)), as an example to better understand the relationship between reproduction and exogenous factors, namely food availability and ambient temperature. Members of the subfamily Stenodermatinae feed almost exclusively on fruits, encompassing 28 plant families and 83 plant species that have been listed as food for *S. lilium* (Mello et al. 2008*a*). This species has a strong preference for fruits of the family Solanaceae, which represent usually over 80% of its diet (Mello et al. 2008*a*). Despite this preference, *S. lilium* can be considered a generalist to some degree, because local population feed on a great number of Solanaceae species (Mello et al. 2008*a*). *Sturnira lilium* seems to follow the bimodal reproductive pattern of stenodermatines and phyllostomids in general (Handley et al. 1991). However, most studies on *S. lilium* have been conducted in tropical lowlands, and little is known about the ecology of this species in montane regions (Mello et al. 2008*b*). It is known that, on average, plant diversity and abundance is lower in highlands if compared with lowlands of the Atlantic Forest (Mantovani 2001), thus it is reasonable to suppose that food availability for frugivorous leaf-nosed bats may be lower in highlands.

Although the tropics are often regarded as stable environments with low seasonality and nearly constant food availability (Ricklefs and Wikelski 2002), variations in some factors, especially ambient temperature, may have ecologically important consequences (Speakman and Thomas 2003; Mello et al. 2004). Palearctic and Nearctic bat species are well adapted to a wider range of decreases in ambient temperature if compared with tropical bar species (Speakman and Thomas 2003). As an example, in the case of moderate drops in temperature, species such as trawling Daubenton's bats (*Myotis daubentonii* (Kuhl, 1817)) temporarily increase food intake, form larger aggregations in nursery colonies, and reduce the use of torpor to prioritize reproductive demands during colder seasons (Dietz and Kalko 2006). Other temperate species like European free-tailed bats (*Tadarida teniotis* (Rafinesque, 1814)) may achieve a stronger drop in body temperature and hibernate (Arlettaz et al. 2000). However, their neotropical counterparts differ in thermoregulatory strategies and do not cope well with severe drops in environmental temperature (Speakman and Thomas 2003). When faced with low temperatures during winter, leaf-nosed bats like *S. lilium* can only resort to suboptimal strategies such as facultative hypothermia (Audet and Thomas 1997) or probably migration (Mello et al. 2008*b*). Therefore, taking into account that *S. lilium* does not cope well with big drops in temperature, and that this bat species is able to feed on a wide range of fruits (even considering the preference for Solanaceae) and even other items like pollen and nectar, environmental temperature may be more important than food availability in determining reproductive timing of frugivorous leaf-nosed bats in highlands of the Atlantic Forest. This is a reasonable hypothesis, because even during seasons of overall fruit scarcity, especially during winter, there are always some fruits and flower products available, thus the diet limitation is less important than the temperature limitation.

Thus, considering that (*i*) our study population of *S. lilium* lives in a montane region with a severe winter by subtropical standards, (*ii*) this species does not cope well with low temperatures, and (*iii*) that ambient temperature may be important in determining reproductive timing (Mello et al. 2004), our objective was to test the hypothesis that *S. lilium* exhibits a relatively short reproductive season compared with patterns observed for the same species in the tropical lowlands. We expected the main reproductive peak of *S. lilium* to occur during summer, when temperatures are warmer, so that recruitment and weaning of juveniles, two very costly activities, would take place when it is easier to maintain normothermic body temperatures. Furthermore, we predicted that the typical bimodal reproductive pattern usually documented for stenodermatine bats would be less marked or even unimodal in our study area, because of the harsh climatic seasonality that may force bats to reproduce within a shorter time window.

Materials and methods

Time frame and study area

Fieldwork was conducted during 15 monthly sample periods from October 2003 to February 2005 (except January and February 2004) in the protected area Parque Estadual Intervales (hereafter Intervales), São Paulo state, southeastern Brazil. Intervales is part of the "Paranapiacaba Ecological Continuum", which comprises more than 100 000 ha and is the largest continuous remnant of Atlantic Forest in Brazil, one of the hotspots of the International Union for the Conservation of Nature and Natural Resources (Myers et al. 2000).

Inside the park, we chose the area known as Sede de Pesquisa (24°16′24.7″S, 48°25′00.6″W). This area is located 850 m above sea level and represents the highest elevation in the park. The climate of this region is classified as temperate humid (Mantovani 2001). Mean temperatures of 22 °C during the warmest months (October–March), and during the coldest months absolute minimum temperatures may reach –4 °C during the colder months (April–September) in the highlands. There are 1–5 days of frost each year. At

Sede de Pesquisa, the main vegetation consists of montane Atlantic Forest (Mantovani 2001).

Sturnira lilium is the most abundant bat species in the area (Passos et al. 2003). Extensive inventories of the local flora, as well as reference collections for seeds found in the feces of bats and birds, are available (Passos et al. 2003). For other aspects of the ecology of *S. lilium* in the area see Mello (2006) and Mello et al. (2008*a*, 2008*b*).

Data collection

The staff at Intervales' meteorological station provided us with data on ambient temperature. We did not include rainfall because its influence is reflected indirectly in fruit availability (Mello et al. 2004). Variation in climate followed the general trend of the previous 7 years (Mello et al. 2008*a*).

Capture and handling of bats were carried out in accordance to guidelines for animal care and use approved by the American Society of Mammalogists (Gannon and Sikes 2007). We captured bats on a monthly basis in two consecutive nights, using 10 nylon mist nets (7 m × 3 m, mesh 36 mm; Ecotone, Inc., Sopot, Poland). Nets were set on trails and dirt roads at a minimum distance of 30 m and kept open for 6 h after local sunset. Every 30 min we checked nets for bats. Between capture and release bats were kept in individual cloth bags for 1–4 h, so we could get fecal samples for dietary analysis. Bats were banded with aluminum rings with individual markings (A.C. Hughes Inc., Middlesex, England), always using ring sizes that were 30% larger than the bat's forearm diameter to minimize injuries. We identified the bat species with a combination of keys (Vizotto and Taddei 1973; Gannon et al. 1989; Emmons and Feer 1997; Simmons and Voss 1998). Marcelo R. Nogueira (Universidade Estadual do Norte Fluminense) confirmed the identification of two voucher specimens (one male and one female). We followed Kunz (1988) in estimating age of bats, considering juveniles to be those with at least one unossified epiphysis in the bones of wing fingers and adults to be those with all epiphyses ossified. We used external characters to determine reproductive condition of adult bats. Females were classified into five categories according to the status of the nipples (hair cover, color, and size) and the presence of a palpable embryo following Kunz (1988): 1, inactive; 2, pregnant; 3, lactating; 4, pregnant and lactating; 5, postlactating. Males were categorized according to the position of their testes, either inside the abdomen or inside the scrotum. Because the position of the testes may vary according to other effects as well (i.e., fear, cold temperatures), we also documented the condition of the males' shoulder glands, which were either active (bright reddish, sticky fur around glands with a strong, terpentine-like smell) or inactive following Gannon et al. (1989). Males were assigned as "reproductive", considering both testes and shoulder gland condition. Age was estimated using the method proposed by Kunz (1988), based on the ossification of the digital epiphyses.

We investigated the feeding habits of *S. lilium* by analyzing fecal samples, which we collected directly from 96 bats captured in mist nets using small plastic vials and from individuals that we kept for 1–4 h inside clean cloth bags.

Seventy individual Solanaceae of 13 species were marked and monitored on a monthly basis to estimate food availability for *S. lilium* (Mello et al. 2008*a*).

Data analysis

Data on climate were analyzed on a monthly basis (Mello et al. 2008*a*). Total netting effort during our study was 41 580 h·m^2 (total area of nets opened multiplied by the total number of hours sampled) following Straube and Bianconi (2002). We characterized the reproductive status of the population of *S. lilium* on a monthly basis as the proportion of females and males in each reproductive class in relation to total numbers of captures of adult females and males in the respective month. We tested the relationship between ambient temperature, fruit production of Solanaceae, and proportions of reproductive females and males using simple nonlinear regressions (model: $y = a{\cdot}x^b$). We chose this geometric model because we predicted that the response of bats to the variation in ambient temperature should be nonlinear, first exhibiting a fast increase in reproductive activity when temperature increases and then reaching a plateau when the percentage of reproductive females approaches the maximum of 100%.

We identified seeds from 96 fecal samples and pooled dietary data of *S. lilium* on a monthly basis as the percentage of samples for each plant family to assess possible temporal variation in diet (for details on dietary analysis see Mello et al. 2008*a*). Concerning phenology of food plants, we assessed the status of each population of Solanaceae species as the percentage of adult individuals producing fruits on a monthly basis (details in Mello et al. 2008*a*). We based our statistical analyses on Zar (1996), and used SPSS version 16.0 (SPSS Inc., Chicago, Illinois, USA) for regular statistics and Oriana version 2.0 (Kovach Computing Services, Anglesey, Wales) for circular statistics in our calculations. Percent data were arcsine-transformed.

Results

We captured a total of 477 bats including recaptures, representing 15 species. This corresponds to about 40% of the bat species that have been recorded for the park (34 species; see Mello 2006). *Sturnira lilium* represented 70% of all captures (333 captures with 8% recaptures). The observed sex ratio was biased towards females (189 females and 142 males: $\chi^2 = 6.39$, $p = 0.01$) with little variation among months ($G = 21.61$, $p = 0.06$).

The population of *S. lilium* showed a marked trend towards seasonal fluctuations. Capture success varied strongly between months, with a concentration of captures in the middle of the rainy and warm season (October–March), especially during summer (Rayleigh's $Z = 18.58$, $p < 0.001$) (Fig. 1). During the cold and dry months (April–September), *S. lilium* was either not captured at all or at very low numbers. Overall, we captured far more adults ($n = 287$) than subadults ($n = 25$) or juveniles ($n = 19$), resulting in an age structure dominated by adults ($\chi^2 = 424.48$, $p < 0.001$). Age structure revealed two distinct peaks of juvenile recruitment per year, one in the middle of the rainy season and another one between the rainy and dry seasons (Rayleigh's $Z = 7.33$, $p < 0.001$) (Fig. 1). This finding is in accordance with the results on the reproductive patterns of females (Rayleigh's

Fig. 1. Monthly variation in the age structure of populations of the little yellow-shouldered bat (*Sturnira lilium*) in Intervales, southeastern Brazil. "Interval" stands for a 2-month period when we could not carry out our sampling because of logistic problems.

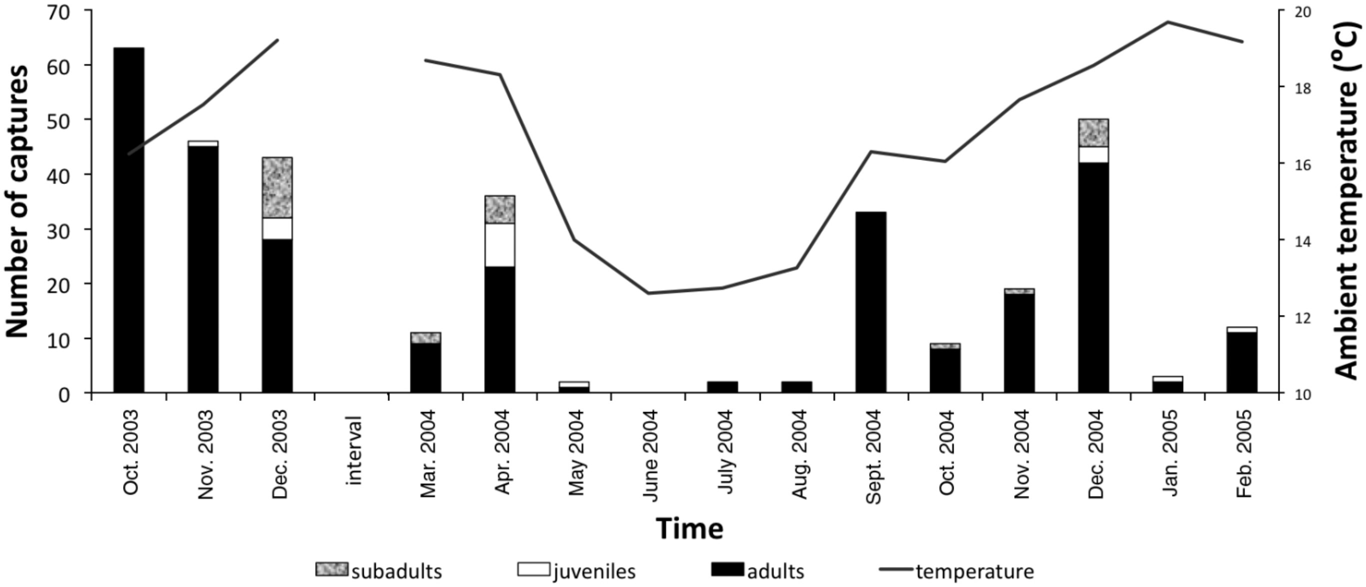
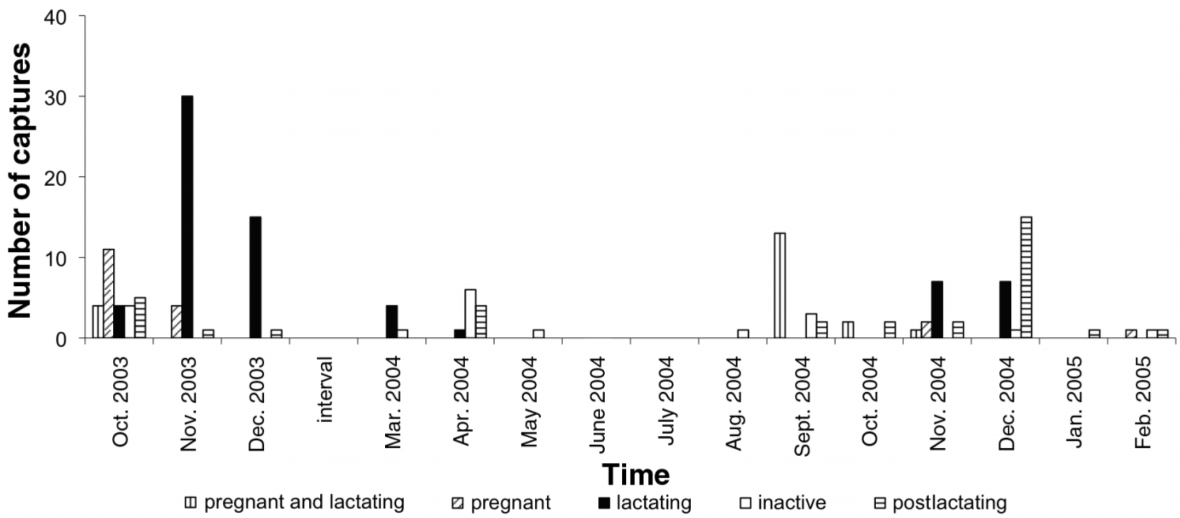


Fig. 2. Monthly variation in the number of adult females of the little yellow-shouldered bat (*Sturnira lilium*) classified into different reproductive conditions in Intervales, southeastern Brazil.



$Z = 12.75$, $p < 0.001$) (Fig. 2) and males (Rayleigh's $Z = 5.32$, $p = 0.005$) (Fig. 3), which both exhibited a bimodal pattern in reproduction with peaks very close to each other.

As predicted, ambient temperature explained a large portion of variation in reproductive timing of females ($r^2 = 0.44$, $p = 0.02$, $n = 12$,) and males ($r^2 = 0.53$, $p = 0.01$, $n = 12$,) in contrast to fruit production that did not explain the variation in the percentage of reproductive females ($r^2 = 0.04$, $p = 0.95$, $n = 12$,) or males ($r^2 = 0.02$, $p = 0.70$, $n = 12$,) (Fig. 4).

The diet of *S. lilium* was entirely frugivorous during the study with a clear dominance of Solanaceae (Mello et al. 2008*a*). Although the proportions of each plant family in the bats' diet varied during the months, fruits of Solanaceae dominated throughout the year (detailed dietary analysis in Mello et al. 2008*a*). The majority of species of Solanaceae (9 from 12 species) revealed a steady-state strategy and continuously produced fruits over several months, with a peak between the dry and the rainy seasons (details in Mello et al. 2008*a*). Therefore, fruits of Solanaceae in general were available during most of the year, but the largest abundance of those fruits occurred during the beginning of the rainy season. However, bats could choose from more Solanaceae species during the dry season than in the rainy season.

Discussion

In our study, we confirmed our hypothesis that ambient temperature affects reproductive seasonality of the frugivorous *S. lilium* more than food availability in a montane region of the Atlantic Forest. Although we observed a bimodal reproductive pattern for *S. lilium* as it is known from lowland locations (Stoner 2001; De Knegt et al. 2005), reproduction was concentrated in a shorter period in the highlands and the first (main) and the second reproduc-

Fig. 3. Monthly variation in the number of adult males of the little yellow-shouldered bat (*Sturnira lilium*) classified into different reproductive conditions in Intervales, southeastern Brazil.

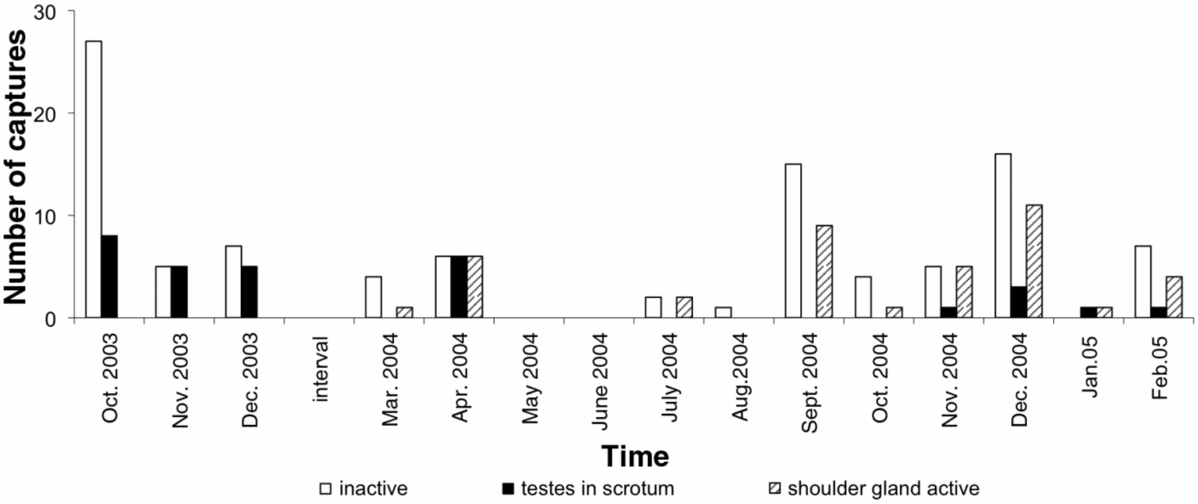
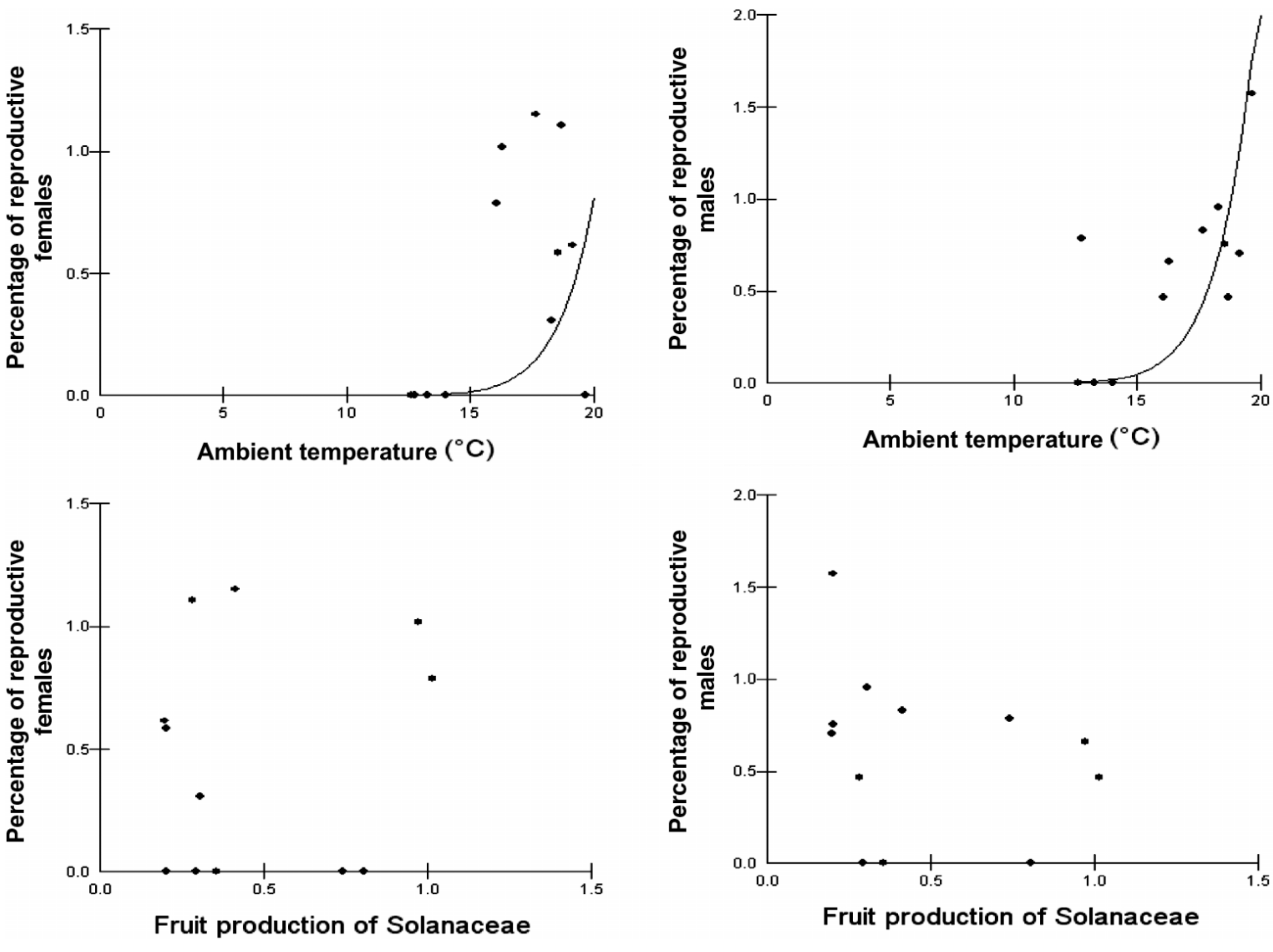


Fig. 4. Relationships between the percentage of reproductive adult females and males of the little yellow-shouldered bat (*Sturnira lilium*), ambient temperature (°C), and fruit production of the plant family Solanaceae (%). Percentages were arcsine-transformed.



tive peaks were less distinct compared with the pattern registered for other neotropical leaf-nosed bats, like carolliines and glossophagines in the lowlands of rain forests, whose reproductive peaks last longer (Mello and Fernandez 2000; Zortéa 2003; Tschapka 2005). As an example, most pregnant female *S. lilium* at a study site in the lowlands of Costa Rica were registered in a 5-month period (Stoner 2001), whereas pregnancy was concentrated in only 2 or 3 months in our study area in the mountains.

The pattern of two reproductive peaks has been attributed to a postpartum estrus in New World leaf-nosed bats, where females mate again shortly after giving birth (while they are still nursing pups; Crichton and Krutzsch 2000). This is seen as a strategy of a large number of tropical bat species to increase the number of offspring per year from one to two per female depending on their fitness (Cosson and Pascal 1994; Tschapka 2005).

Our prediction of a positive relationship between temperature and reproductive cycle was fully supported, as ambient temperature explained the largest portion of reproductive timing of females (44%) and males (53%). At high altitudes, as in our study area, temperature is a critical factor, because low winter temperatures may not be tolerated well as they generate unfavorable conditions for bats like *S. lilium* (Speakman and Thomas 2003; Willis et al. 2006), whose thermoregulatory ability is not as efficient as in other groups with a global distribution such as vespertilionids (Audet and Thomas 1997). Interestingly, evidence accumulated that *S. lilium* and probably also other fruit-eating bats may circumvent this difficulty by migrating to lower altitudes during the coldest months (Giannini 1999; Mello et al. 2008*b*). This may explain the absence or very low numbers of *S. lilium* bats in highlands during winter, as they tend to remain abundant throughout the year in lowlands (Giannini 1999; Aguiar and Marinho-Filho 2004). It is unknown whether *S. lilium* reproduces during this time in lower altitudes, and this possibility should be tested in future studies.

We conclude from the short reproductive period that *S. lilium* has adjusted its reproductive cycle to the specific environmental conditions of highlands by limiting its main reproductive activity to the short but favorable season in summer. This supports the proposition that despite the lower seasonality of the tropics compared with the temperate zone, small variations in environmental factors, such as ambient temperature, may exert rather strong pressures that force tropical species, for instance, to adjust their reproductive pattern. In future studies, it will be interesting to investigate whether highland species, provided they migrate, add a third reproductive phase. Probably, this might not happen, as the effect of highland immigrants on lowland residents should increase competition for food and shelter.

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