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A test of the effects of climate and fruiting of *Piper* species (Piperaceae) on reproductive patterns of the bat *Carollia perspicillata* (Phyllostomidae)

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Bats of the genus *Carollia* feed mainly on plants of the genus *Piper*, dispersing their seeds in all localities where they occur together. Interactions among these bats, their food plants, and the climate were studied in an Atlantic Forest area in Southeastern Brazil. Path analysis was used to estimate the strength of direct and indirect effects through which variables determine the timing of bat reproduction. Temperature had a small direct influence, but a strong indirect one. Rainfall affected bat reproduction through indirect ways. Although the consumption of *Piper* fruits by bats did not have a significant influence, the timing of production of *Piper* fruits was a strong variable directly affecting bat reproduction. We therefore suggest that *Piper* plants and climate may play a keyrole in the timing of reproduction in *C. perspicillata* bats.

Key words: Atlantic Forest, frugivory, *Carollia perspicillata*, indirect effects, path analysis, reproduction, seasonality

INTRODUCTION

Neotropical leaf-nosed bats (Chiroptera: Phyllostomidae) may be regarded as keystone-species in forests (Marinho-Filho and Sazima, 1998), because of their roles as seed dispersers and pollinators of many plants (Kunz, 1982; Fleming, 1988; Charles-Dominique, 1991; Nowak, 1994). Consequently they are important to the processes of ecological succession and forest regeneration (Fenton *et al*., 1992; Whittaker and Jones, 1994; Estrada and Coates-Estrada, 2001).

Among the Phyllostomidae, bats of the subfamily Carolliinae (genera *Carollia* and *Rhinophylla* — Wetterer *et al*., 2000) interact with plants mainly by fruit consumption (Heithaus, 1982; Fleming, 1988). These bats forage mainly at ground level in the understory (Bernard, 2001), focusing on shrubs and small trees, therefore being members of the guild ‘highly cluttered space gleaning frugivores’ (Kalko, 1998).

Mutualistic interactions between these bats and pioneer plants were extensively studied by Fleming (1982, 1988, 1991) and Charles-Dominique (1991), especially regarding the species *Carollia perspicillata* (Linnaeus, 1758), which is widespread in the Neotropics. These bats feed mainly on plants of the genus *Piper* (Linnaeus, 1737), which comprises the black pepper (*P. nigrum*), an economically important species (Fleming, 1988). *Carollia perspicillata* may also eat other kinds of food (see the review by Fleming, 1988), but it seems to show a preference for *Piper*, although not so very strong as in *C. castanea* (Thies and Kalko, 2004).

We propose that this interaction between bats and plants, influenced by variations in climate, might affect the timing of reproduction of both groups. Several authors have reported reproductive seasonality in *Carollia* bats (reviewed by Fleming, 1988). In many places, including the Atlantic Forest of southeastern Brazil, this species breeds mainly in rainy seasons, during highest fruit availability (Mello and Fernandez, 2000). Many species of *Piper* do also produce fruits seasonally, especially forest-dwellers, although patterns may differ between localities (Fleming, 1985; Greig, 1993; Thies and Kalko, 2004).

The present work aimed to study in detail how the availability of *Piper* and the climate might affect the timing of bat reproduction. We hypothesized that the climate might determine plant reproduction, which might determine bat reproduction.

MATERIALS AND METHODS

Study Site

This research was conducted in 'Reserva Biológica Poço das Antas' (RBPA), municipality of Silva Jardim, state of Rio de Janeiro, southeastern Brazil (22°30'–22°33'S, 42°15'–42°19'W). Situated in a flat area and covering about 6,100 ha, RBPA is the largest lowland Atlantic Forest remnant of the state (Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis, pers. comm.), including many permanently flooded forest areas (Scarano, 2002).

Regional climate is uniformly wet and hot, classified as Am according to Koeppen's system (Takizawa, 1995). From 1987 to 2001, the average annual temperature was 24.6°C. The hottest month was February with an average of 28.7°C, whereas June was the coldest with an average of 21.1°C. The average annual total rainfall was 2,121 mm. March was the wettest month, scoring 277 mm, while July was the driest, scoring 53 mm (see also Fig. 1). Data on climate were provided by Luis Fernando Morais (Programa Mata Atlântica, Jardim Botânico do Rio de Janeiro), and were obtained from the reserve's climate monitoring station.

The study area in RBPA was a system composed of eight small forest patches located on small hills and surrounded by open vegetation, locally known as the 'Ilhas dos Barbados' (Souza *et al*., 2000). There are some ponds and a big swamp in this open area. In the southernmost portion of the system flows a medium-sized river, the 'São João' (2 m deep and 20 m wide). RBPA was extensively studied for some years. The inventory of its bat fauna was published by Baptista and Mello (2001), while its plant species were listed by Guimarães *et al*. (1988), which points out several species that are consumed by leaf-nosed bats, including the genera *Piper*, *Solanum*, *Cecropia* and *Ficus*.

Time Frame and Data Acquisition

Fieldwork was carried out from January 2000 to September 2001. With the exception of December 2000, January 2001 and May 2001, we conducted monthly sampling at the study area with each session lasting two consecutive nights, totalizing 18 months (sampling units). Detailed data on the demography of *C. perspicillata* in the area were published by Mello and Fernandez (2000).

Six mist-nets (7 m × 3 m – Ecotone, Inc.) were opened all night long, in forest edges, and each net was at least 30 m away from other nets. All individuals caught were marked with numbered metallic rings (A. C. Hughes, Inc.). We recorded the following data from each individual: species, sex, age, reproductive condition, body mass, and other body measurements (forearm, cranium and tibia length). Bat species were identified using keys provided by Taddei and Vizotto (1973), Cloutier and Thomas (1991), and Emmons and Feer (1997). A. Pol, M. R. Nogueira and A. L. Peracchi confirmed identification by checking voucher specimens at the Universidade Federal Rural do Rio de Janeiro, were bats were deposited.

Age of the bats was estimated using the method proposed by Kunz (1988) and Cosson *et al.* (1993), based on the degree of digital epiphyses ossification. External characters were used to analyze reproductive condition of females, following Kunz (1988), which were ranked into four categories: pregnant, lactating, post-lactating or inactive. Males were not included in the analysis, because their status could not be precisely determined by external characters.

About 90 individual *Piper* plants from all species found were marked and checked monthly for their phenology (some of them died and new individuals were added). We categorized individual plants according to their relative proportion of fruits and flowers: inactive, flowering, equally flowering and fruiting, and fruiting. We did not record the exact number of fruits and flowers of each individual, but made only an estimation of their proportion. Voucher *Piper* species were identified by Davyson Moreira (Universidade Federal do Rio de Janeiro) and Elsie Guimarães (Jardim Botânico do Rio de Janeiro).

The diet of *C. perspicillata* was studied through fecal analysis. Fecal pellets were washed, dried, and items were separated into four categories: seeds, pulp, arthropods, and unidentifiable parts. Seeds were classified according to genera or families, by comparison with seeds from fruits collected in the study area.

Statistical Analyses

Relationship between two or more variables was tested using simple or multiple linear regressions, and simple linear correlation (in the case of non-causal relationship). Data on reproduction (pregnant females), consumption of food items (presence in fecal samples), and plant phenology (reproductive status) were obtained by calculating the proportion of occurrence of each of the categories in relation to the monthly total of samples. Proportional data were arcsine transformed, as proposed in Zar (1996).

To analyze the relationship between variables, we used path analysis, following Kingsolver and Schemske (1991) and Sokal and Rohlf (1995). This technique tests for the respective strength of associations between variables and their mutual influence. Variable names were coded as follows: criterion variable (Y): 1. 'reproduction' — proportion of pregnant or lactating females of *C. perspicillata* on each month; 2. 'U_Y' — sum of the effects of variables (such as photoperiod) that were not measured explicitly, but that might influence the criterion variable 'reproduction' (Heideman *et al.*, 1992). Predictor variables (X_i): 3. 'rainfall' — monthly total rainfall (mm); 4. 'temperature' — monthly mean temperature (ºC); 5. 'fruit production' — monthly proportion of *Piper* individuals in the 'fruiting' category; 6. 'fruit consumption' — consumption of *Piper* plants by *C. perspicillata* bats, expressed by the proportion of fecal samples containing *Piper* seeds on each month.

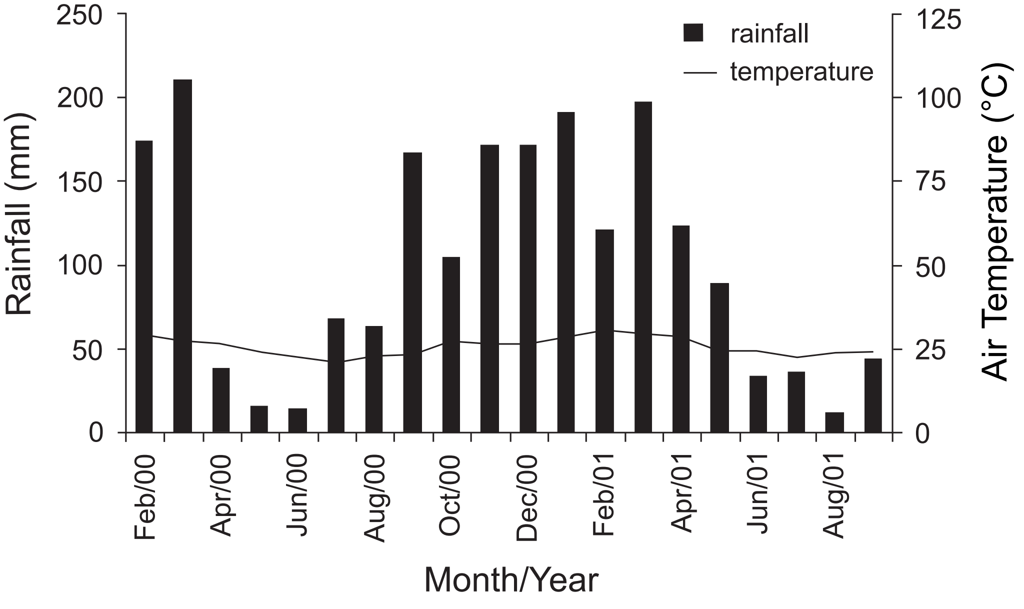

FIG. 1. Monthly variations in total rainfall and mean air temperature in the study area

7. 'U_{PIP}' (U_{X4}) — sum of the effects of variables such as insect consumption that were not measured explicitly, but that might influence the variable 'diet'.

We created a path diagram — the graphical representation of our working hypothesis, suggesting how variables might interact with each other (see Fig. 5). These relationships guided our step-by-step statistical analyses. The relationship or 'path' between two adjacent variables in the diagram is called 'direct'; the relationship between two variables that are not adjacent, therefore including intermediate variables, is called 'indirect'. The strength of each relationship, causal or not, was estimated by calculating its standardized regression or correlation coefficient. Total value of indirect paths was estimated by multiplying standardized coefficients of direct paths. The total path coefficient for each variable was estimated by summing all possible partial path coefficients. Microsoft Excel XP and the statistical package Systat 7.0 were used to make calculations.

RESULTS

A total of 2,046 individuals (excluding recaptures) of *C. perspicillata* were caught during a total sampling of 432 nets × nights, which represent 78% of the total for all bat species (2,596). Recapture rate of this species was 11%. Total adult females included in reproductive analyses were 1,014.

In the study area, about 100 patches of *Piper* plants were found, many of which were clonally grown. Seven species of the genus *Piper* were identified: *P. arboretum* var. *arboreum*, *P. arboreum* var. *latifolium*, *P. mollicomum*, *P. vicosanum*, *P. cernuum* var. *cernuum*, *P. divaricatum*, and *P. caldense*. Nearly 90% of the individuals studied were *P. arboreum* var. *arboreum*, and seeds of this species could be identified in bat feces. One individual of *Potomorphe umbellata* (Piperaceae) was also found, but this species was not included in this analysis due to its low abundance.

Rainfall and mean air temperature varied as usual during the study period: summer was the wettest season, while winter was the driest (Fig. 1). Both variables were significantly correlated ($r^2 = 0.63$, $n = 17$, $P < 0.01$), and due to this one of them should be eliminated from the path analyses, following assumptions of this test. We decided to remove the 'rainfall', because we did not expect it to directly influence bat reproduction, as it does in insects. Reproduction of *C. perspicillata* bats, fruit production in *Piper* plants and consumption of *Piper* by *C. perspicillata* did also present marked monthly variations (Fig. 2).

Regarding the path analysis, first the effects of predictor variables (x_i) 'diet', 'fruit production' and 'temperature' on the criterion variable 'reproduction' (y) were evaluated. The model [reproduction = cnt + fruit consumption + fruit production + temperature], where 'cnt' is a constant, was used for the first multiple linear regression ($r^2 = 0.76$, $n = 17$, $P < 0.001$). The variables fruit production [standardized coefficient (SC) = 0.652, $P < 0.01$] and temperature (SC = 0.377, $P < 0.05$), explained most of the variation in reproduction, while fruit consumption (SC = -0.161, $P = 0.31$) did not present a significant effect at the 0.05 confidence level after accounting for the effect of the other variables (Fig. 3).

The effect involving the direct path from 'fruit production' to 'fruit consumption' was evaluated by the model [fruit consumption = cnt + fruit production], and was only nearly significant ($r^2 = 0.43$, $n = 17$, $P = 0.08$; Fig. 4). However, this relationship could be significant, if it were tested by a non-linear model, because fruit consumption tends to reach a 'plateau'. In the present work, a linear model had to be used due to path analysis requirements.

The values of standardized coefficients were added to the path diagram and relationships between all variables, as indicated by values of their respective partial paths, presented (Fig. 5). The final step of this analysis was to estimate the total path

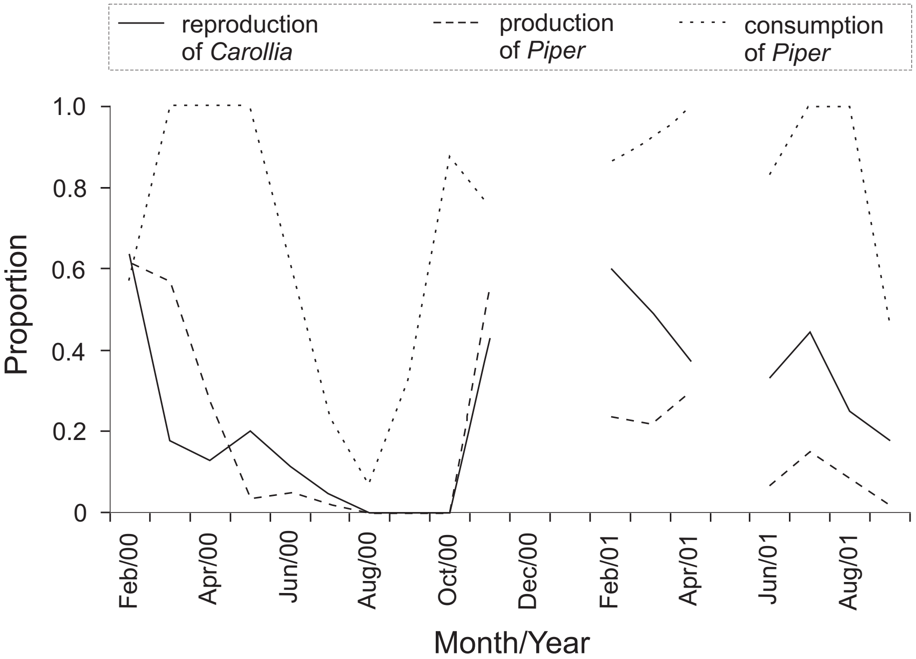

FIG. 2. Monthly variations in the three main parameters studied: percent of adult reproductive females of *Carollia perspicillata* (reproduction of *Carollia*), percent of fruiting *Piper* individuals (production of *Piper*), and percent of fecal samples that contained *Piper* seeds (consumption of *Piper*)

coefficients for all predictor variables (X_i), in order to compare their total effects on the criterion variable 'reproduction'. 'Temperature' had the highest coefficient (0.637), followed by 'fruit production' (0.582), and 'fruit consumption' (-0.161).

DISCUSSION

Our results, using path analysis, suggest that several factors influence the timing of reproduction in *C. perspicillata*. They also suggest that indirect effects may be as important as direct effects, and should not be overlooked.

Seasonality of reproduction (Fleming, 1988), of local abundance (Stoner, 2001), and also of diet (Charles-Dominique, 1991), are common phenomena in *C. perspicillata*. The response of this species to variation in environmental conditions, especially food abundance, suggests that breeding in *C. perspicillata* takes place during more favorable seasons (Stoner, 2001).

Consistently with this hypothesis, *C. perspicillata* is known to reproduce twice each year, but the second peak is usually weaker in intensity, because it is a consequence of post-partum estrus (Cloutier and Thomas, 1991). This phenomenon was observed in *C. perspicillata* at our study site (Mello and Fernandez, 2000) and also at other locations (Charles-Dominique, 1991; Ramirez-Pullido *et al.*, 1993), as well as in other phyllostomids (e.g., *Artibeus jamaicensis* — Gardner *et al.*, 1991).

Now regarding the climate, we should consider the relationship between temperature and rainfall in tropical areas. The ultimate and strongest cause of temperature variation in tropical localities is the variation in the relative inclination of the Equator Line, what makes the seasonality of this variable relatively independent of rainfall. However, cloud coverage and

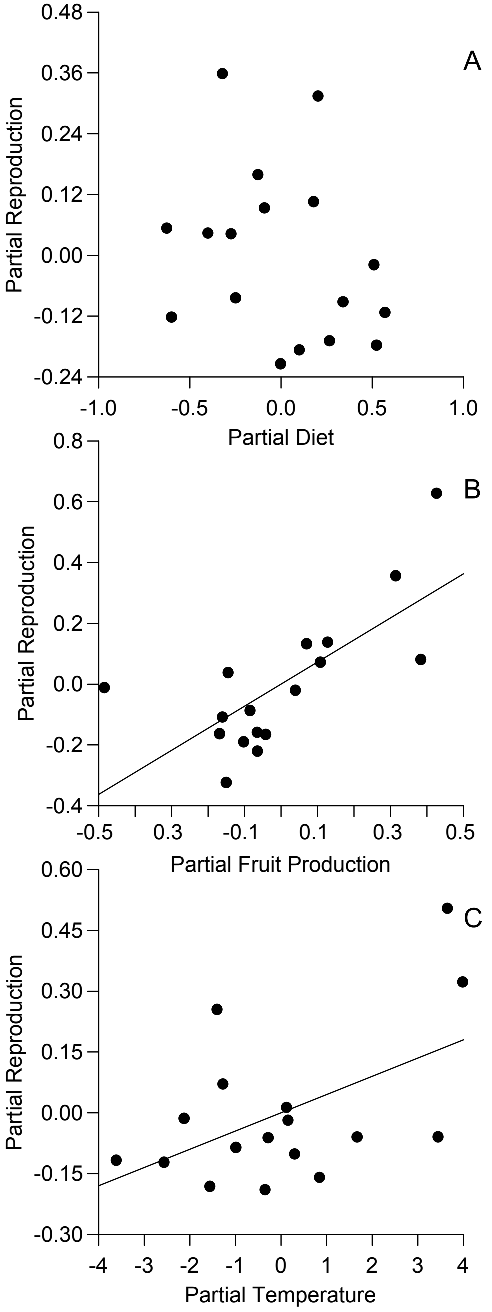

Fig. 3. Diagrams of the partial regressions of the first multiple linear regression. A. Partial regression between variables diet and reproduction, discounting the effects of fruit production and temperature; B. Partial regression between fruit production and reproduction, discounting the effects of diet and temperature; C. Partial regression between temperature and reproduction, discounting the effects of diet and fruit production

rainfall may reduce temperature levels. But only cold air masses may reduce temperature to lowest levels during the rainy season. Therefore, the absence of rainfall in our model is justifiable, although *Piper* plants depend on the availability of water for fruit production, because some species of this genus reproduce based on day length. Furthermore, we could not analyze temperature and rainfall together, due to path analysis' assumptions.

Temperature turned out to have the strongest total path coefficient. However, it is important to note that its influence was almost doubled when summing the strengths of other variables. Seasonal fluctuations in temperature levels influence seasonality of bat reproduction in temperate zones (Kunz, 1982; Neuweiler, 1993), but it is not clear if this generalization holds for tropical frugivorous species.

Surprisingly, the consumption of *Piper* fruits, as indicated by fecal analysis, did not show a significant relationship (although $P < 0.10$) with the reproduction of *C. perspicillata* bats. Considering that this is the preferred food of *C. perspicillata* in many places (Fleming, 1988), it seems strange that the variation in fruit availability did not significantly influence the bats' breeding activities. Heithaus *et al.* (1975), Fleming (1985) and Thies and Kalko (2004) showed that different *Piper* species produce fruits at different times of the year, and that there is a difference between forest and gap guilds of *Piper*. Marinho-Filho (1991) and Mello *et al.* (2004) also reported that *C. perspicillata* bats might undergo seasonal changes in diet, reacting to variations in *Piper* availability.

This was also proposed by Thies and Kalko (2004), but for a sister species, *C. castanea*. Our results are partially consistent with this evidence, because in the first year of the analysis *Piper* was consumed most, when it was most abundant — suggesting

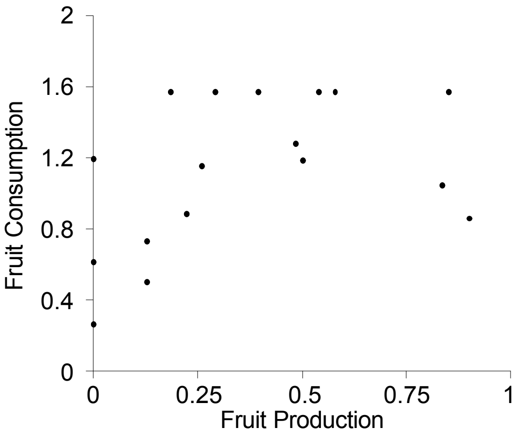

FIG. 4. The relationship between two variables: fruit consumption (diet) and fruit production

a generalist strategy. On the other hand, Bizerril and Raw (1997) suggested that C. *perspicillata* bats select *Piper* fruits mainly because of their spatial and temporal predictability, which could be related to a specialist strategy. The lack of statistical significance in the relationship between consumption and reproduction could be explained by the constancy of consumption in the subsequent year (see Fig. 2) — contrary to our expectations, as happened with *C. castanea*, but not with *C. perspicillata*, in the study of Thies and Kalko (2004). Nevertheless, we could have found a more significant pattern, if we have identified *Piper* seeds to the species level, because we do not know for sure which of the seven *Piper* species of the area were consumed by *C. perspicillata*, and in which were the dominant species in its diet.

Shifts in diet have been observed by other authors (Heithaus *et al.*, 1975), as in the present study, when bats started eating fruits of the genus *Solanum* and insects during the dry season of 2000 when the availability of fruit of *Piper* fruits was very low (Mello *et al.*, 2004). However this pattern was not repeated in 2001, for unknown reasons. Maybe the bats found fruiting *Piper* outside of the study area, which is likely, considering the small area of the system that was sampled, and the ability of this species to change its foraging areas seasonally (Charles-Dominique, 1991). This unexpected pattern reduced the strength of the variable 'fruit consumption'.

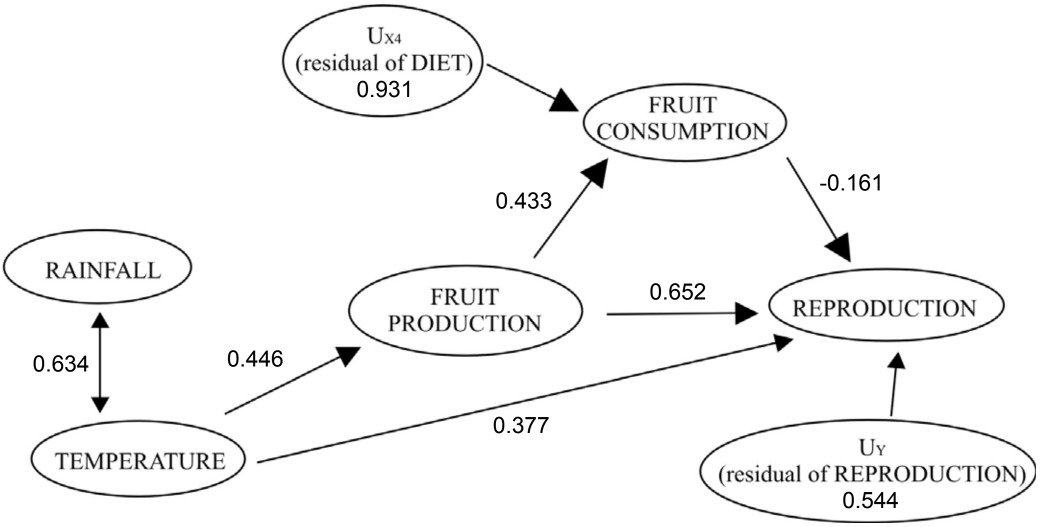

FIG. 5. Path diagram presenting the path coefficients for all predictor variables, including the coefficients for the two residual variables, UX4 and UY

However, we should not forget that the relationship between these variables was nearly significant. It is also possible that another method of consumption estimation could have provided a better estimation of the intensity of the interaction. Maybe in future studies we should quantify *Piper* seeds in bat feces, therefore acquiring another parameter for diet that could be interpreted together with proportion of occurrences in samples. Therefore, we would consider the importance of *Piper* in *Carollia*'s diet as a product of its presence and quantity in feces, because it is important to know both how many bats are consuming *Piper* fruits and how many ripe fruits they are finding in average.

The last of the predictor variables, production of *Piper* fruits, had the second strongest indirect and the strongest direct influences on bat reproduction. Perhaps breeding in *C. perspicillata* starts early during the fruiting season, and is not triggered by the highest availability of *Piper* fruits. This quickness of response would be advantageous, if it made possible for juveniles to be born during highest fruit availability, as in *Artibeus jamaicensis* (Gardner *et al*., 1991) and other bats (Kalko, 1998), considering that pregnancy lasts four months in average for *C. perspicillata* (Cloutier and Thomas, 1991). It is also the case of other phyllostomid bat, *Anoura geoffroyi*, which synchronizes parturition with highest food abundance (Heideman *et al*., 1992).

Finally, we suggest that the strong influence observed for fruit production is not necessarily contradictory to the relatively weak influence of fruit consumption. If the beginning of fruiting influences the start of breeding in *C. perspicillata*, one could suppose that plants might produce some substance, probably not nutritive, which could act as a stimulus for the beginning of estrus. It has already been reported that *Carollia* bats use volatile substances produced by *Piper* plants as a clue to find mature fruits (Thies *et al*., 1998; Mikich *et al*., 2003). Besides, Dechaud *et al*. (1999) and Breinholt *et al*. (2000) suggested that flavinoids might be strong stimulants for mammalian reproduction, because they contain estrogen-like substances. Santos *et al*. (2001) recorded the presence of many kinds of flavinoids in Piperaceae plants in the state of Rio de Janeiro. Taking this into account, it could be helpful to study the pattern of flavinoid production by *Piper* species, in order to see if there are differences between maturation stages, which could result in differential effects on *Carollia* bats on each fruiting season.

Considering that C. *perspicillata* seems to be relatively independent of *Piper* fruits at other locations, especially in the presence of other *Carollia* species (Thies and Kalko, 2004), there may be other relevant factors that we did not take into account in the present study. For instance, it could be also interesting to study rates of fruit production and consumption by counting the number of fruits that become mature and are removed by bats each night, and how these variables change between seasons. Nevertheless, our data point to the importance of analyzing multiple factors that might determine reproduction, and also their direct and indirect influences, in order to avoid misinterpretations caused by looking at only small parts of the whole system.

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