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“INTERAÇÕES ENTRE O MORCEGO *STURNIRA LILIUM* (CHIROPTERA: PHYLLOSTOMIDAE) E PLANTAS DA FAMÍLIA SOLANACEAE”

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Orientador: Prof. Dr. Wesley Rodrigues Silva

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"Quando alguém busca, então acontece facilmente de seus olhos verem apenas a coisa buscada, de maneira a não ser capaz de encontrar, de admitir em si nada, porque ele pensa apenas no buscado, porque ele tem uma meta, porque ele está possesso pela meta. Encontrar, no entanto, quer dizer: estar livre, permanecer aberto, não ter meta."
(Hermann Hesse)

"Escrever um livro é uma aventura. Principia um brinquedo e um gosto. Vira uma amante. Depois um tutor, depois um tirano. Na fase final, já conformado em ser um escravo, você o mata e arremessa o corpo ao público."
(Winston Churchill)

ÍNDICE

ÍNDICE DE FIGURAS

ÍNDICE DE TABELAS

RESUMO

Morcegos têm grande importância ecológica nos Neotrópicos, por serem muito diversos, abundantes e interagirem com várias espécies de plantas e animais. Os morcegos filostomídeos da subfamília Stenodermatinae são frugívoros especializados e importantes dispersores de sementes, sendo que *Sturnira lilium* tem preferência por frutos de Solanaceae, uma família de grande valor ecológico e econômico. O objetivo do presente estudo foi investigar quatro aspectos principais e testar hipóteses relacionadas à maneira como essa interação ocorre e afeta ambos os grupos. De acordo com o esperado, a dieta de *S. lilium* foi inteiramente frugívora com uma forte dominância de solanáceas. A abundância de morcegos apresentou dois picos curtos ao longo do ano, ao contrário da produção de frutos que teve um pico único, porém mais longo. Os morcegos deixaram a área durante os meses mais frios e provavelmente migraram para altitudes mais baixas e quentes para escapar do clima severo e procurar por frutos de Solanaceae. A maioria das fêmeas de *S. lilium* se reproduziu durante os meses mais úmidos e quentes, durante a maior oferta de frutos. As solanáceas mostraram ser uma fonte de alimento confiável para *S. lilium* e sua fenologia pareceu regular a dinâmica populacional dos morcegos. *S. lilium* não apresentou fidelidade aos refúgios noturnos e diurnos, e usou uma grande distância de comutação e uma grande área de forrageio em comparação com outros pequenos mamíferos. A dispersão de sementes por *S. lilium* pareceu ser altamente benéfica para as plantas, de acordo com as hipóteses clássicas de fuga, colonização e dispersão limitada. Não observei evidências de fobia lunar em *S. lilium*, apesar de ter observado em outros dois filostomídeos frugívoros, *Artibeus lituratus* e *Carollia perspicillata*. As diferenças nas respostas à luz da Lua podem ser explicadas pelo habitat de forrageio, a dieta e distribuição espaço-temporal das plantas-alimento, e podem ter conseqüência para o sucesso reprodutivo das plantas-alimento. Os resultados do presente trabalho confirmam que a relação entre *S. lilium* e as solanáceas é muito forte, e que ela também é benéfica para ambos os grupos, afetando as populações de morcegos e plantas e consequentemente a estrutura de toda a comunidade.

ABSTRACT

Bats have a high ecological importance in the Neotropics for they are highly diverse, very abundant and interact with many plant and animal species. Phyllostomid bats of the subfamily Stenodermatinae are specialized frugivores and important seed dispersers, and *Sturnira lilium* prefers fruits of the Solanaceae, a family of high ecological and economical value. The goal of the present study was to investigate four main aspects and test hypotheses related to the way this interaction occurs and how it affects both groups. As expected, the diet of *S. lilium* was totally frugivore and Solanaceae prevailed. Bat abundance presented two short peaks throughout the year, while fruit production presented a single, but longer, peak. Bats left the area during colder months and probably migrated to lower and warmer altitudes to escape the severe climate and to search for Solanaceae fruits. Most *S. lilium* females reproduced during wetter and warmer months, during the highest fruit availability. The Solanaceae showed to be a reliable food source for *S. lilium*, and their phenology seemed to regulate bat population dynamics. *S. lilium* showed no roost fidelity, and used large commuting distances and foraging areas, if compared to other small mammals. Seed dispersal by *S. lilium* seemed to be highly beneficial for plants, according to the classical hypotheses of escape, colonization and limited dispersal. I observed no evidences of lunar phobia in *S. lilium*, despite having observed in other two frugivorous phyllostomids, *Artibeus lituratus* and *Carollia perspicillata*. Differences in response to moonlight may be explained by foraging habitat, diet and spatio-temporal distribution of food-plants, and may have consequences for the reproductive success of food-plants. Results of the present study suggest that the relationship between *S. lilium* and the Solanaceae is very strong, and that it is also beneficial for both groups, affecting populations of bats and plants, and consequently the structure of the whole community.

INTRODUÇÃO GERAL

A TEORIA DA DISPERSÃO DE SEMENTES

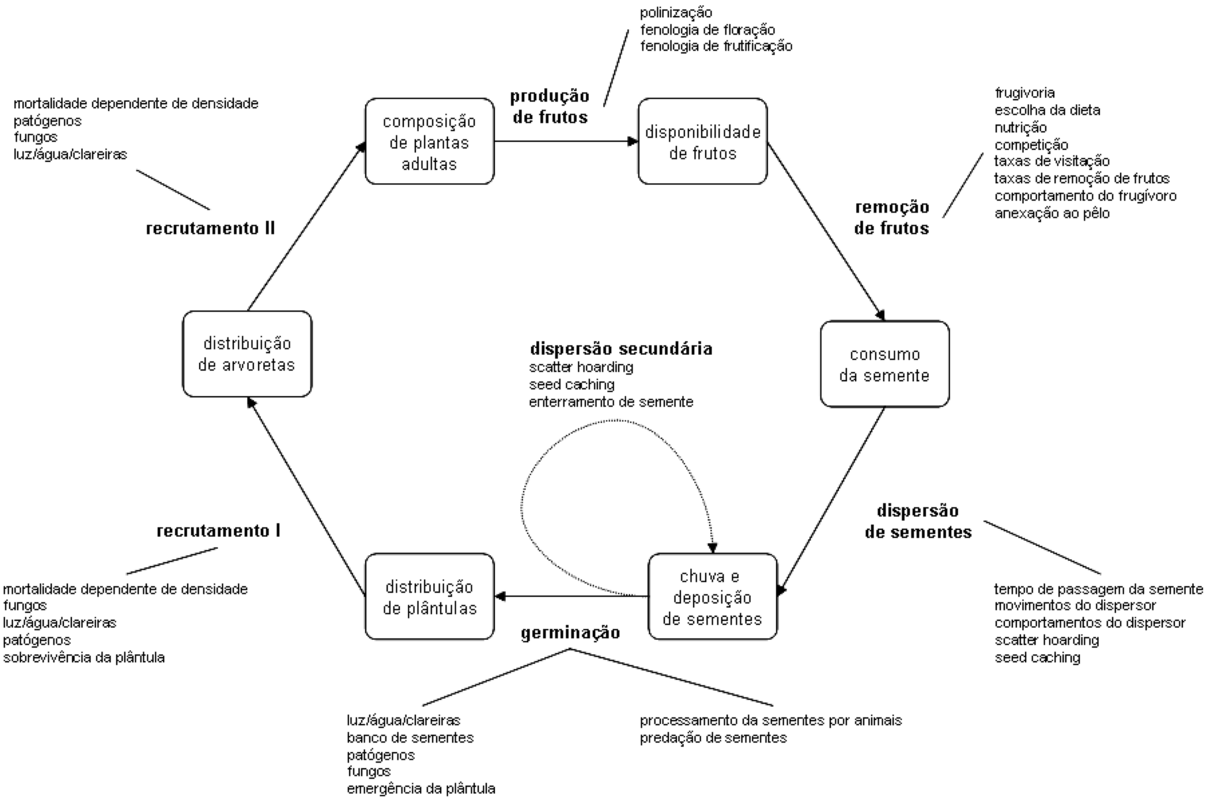
A dispersão de sementes é o processo de mover sementes para longe das plantas-mãe. Este processo pode ser realizado por diferentes agentes, incluindo o vento, a água, a gravidade, animais e a própria planta (Fleming & Estrada, 1993). Antes de falar sobre a dispersão de sementes, é interessante contextualizá-la dentro da teoria das interações ecológicas. Essas interações costumam ser classificadas de acordo com o balanço entre as perdas e ganhos de cada parte envolvida. Normalmente, usam-se quatro grandes categorias: antagonismo (perde-ganha), mutualismo (ganha-ganha), comensalismo (ganha-zero) e amensalismo (zero-zero) (Pianka, 1994). Mais especificamente, as antagônicas podem ser divididas em esclavagismo, competição, parasitismo, parasitoidismo e predação. Já as mutualistas podem ser de simbiose (obrigatória) ou protocooperação (facultativa). Por sua vez, as interações comensalistas podem ser de comensalismo alimentar, inquilinismo ou foresia. No amensalismo, não há perda nem ganho para ambos os lados.

A teoria da dispersão de sementes envolve principalmente interações entre animais e plantas e se enquadra na categoria do mutualismo. Apesar de naturalistas antigos como Darwin (1994) já reconhecerem sua importância, a teoria da dispersão de sementes ganhou mais impulso a partir da década de 1970. Boa parte do desenvolvimento deste campo foi proporcionada por Van der Pijl (1972), que propôs o modelo das “síndromes de interações”, uma sistematização do conhecimento acumulado até então enriquecida por um novo axioma central. Este axioma postula que as características das plantas interagem com determinado tipo de animal (por dispersão de sementes oi polinização) ocorreriam em “pacotes” característicos. Este se tornou um paradigma muito influente na Ecologia, servindo até hoje de base para elaboração de hipóteses que continuam gerando um grande número de evidências positivas e negativas.

Seguindo a terminologia de Van der Pijl (1972) e no que diz respeito à dispersão de sementes, as síndromes seriam categorizadas de acordo com o agente dispersor. Haveria então a baricoria, quando os frutos se abrem e as sementes simplesmente caem no solo; a autocoria, quando a planta “arremessa” suas sementes; a anemocoria, cujo agente é o vento; a hidrocoria, onde as correntes d’água causam a dispersão; e a zoocoria, onde animais fazem a dispersão. A zoocoria pode ainda ser subdividida de acordo com o táxon, por exemplo, em mamalocoria (mamíferos), ornitocoria (aves) e mirmecocoria (formigas), dentre outras.

Desta maneira, os animais dispersores atuam em diferentes níveis do processo e em diferentes escalas espaço-temporais. Os dispersores primários são aqueles que pegam as sementes diretamente dos frutos e têm grande influência sobre o padrão inicial da chuva de sementes (Wang & Smith, 2002). Por sua vez, os dispersores secundários são os que pegam as sementes que já foram dispersadas inicialmente e são responsáveis pelo segundo nível de arranjo espacial da chuva de sementes, gerando padrões diferentes dos iniciais, que por fim ainda podem ser modificados por predadores e patógenos de sementes e plântulas, antes de se traduzirem nos padrões finais das plantas adultas (Levine & Murrell, 2003). O comportamento de cada dispersor também influencia muito o padrão final de deposição das sementes, variando desde animais que estocam várias sementes em um determinado local (e.g. esquilos) até animais que as espalham mais uniformemente em uma grande escala (e.g. morcegos) (Guevara & Laborde, 1993).

Wang & Smith (2002) propuseram ainda um modelo gráfico (Fig.I) para explicar como se dá a dispersão de sementes. Esses autores dividiram os estudos entre aqueles que analisam o processo na seqüência em que ele ocorre na natureza (*onwards*), ou seja, da escolha dos frutos pelos animais até o estabelecimento das plântulas, e aqueles que o abordam ao contrário (*backwards*), inferindo os padrões de dispersão a partir da distribuição espacial de plantas jovens e adultas. Este diagrama nos dá uma boa idéia de quão complexo é o processo de dispersão e de quantos mecanismos estão envolvidos na determinação da distribuição espacial final de uma população de plantas. Ele também deixa claro que este processo forma um círculo de etapas a serem vencidas por cada semente individual, que “cumpre sua meta” e reinicia o ciclo assim que consegue crescer, produzir e dispersar suas sementes.



Fonte: Wang, B.C.; Smith, T.B. 2002. Closing de seed dispersal loop. TREE, 17(8): 379-385. (Fig.1)

Figura I: Modelo explicativo do processo de dispersão de sementes, adaptado e traduzido de Wang & Smith (2002). As setas indicam a ordem em que o processo ocorre na natureza. *Scatter hoarding* se refere ao comportamento de alguns dispersores em acumular sementes em diferentes depósitos, visando o consumo no futuro; *seed caching* é um comportamento similar, porém as sementes são armazenadas em um único depósito central.

Dentre os vários axiomas e hipóteses que compõem a teoria da dispersão de sementes (Howe & Smallwood, 1982), os trabalhos de Janzen (1970) e Connell (1971) vieram a se tornar um paradigma na Ecologia: o "modelo de Janzen-Connell" ou a "hipótese da fuga". Estes dois autores, de maneira independente, criaram modelos muito similares para explicar padrões de diversidade de plantas nos trópicos através das vantagens da dispersão das sementes em relação à planta-mãe. O modelo geral propõe que a mortalidade de sementes e plântulas (por predadores e patógenos) é fortemente dependente de densidade e, portanto, deve ser bem mais alta perto da planta-mãe, do que mais afastado dela. Este modelo foi amplamente aceito, apesar de na época não haver muitas evidências empíricas para suportá-lo, mas posteriormente foi fortalecido por diversos testes (Wright, 2002).

Várias espécies se enquadram neste modelo, de acordo com os estudos disponíveis (Santos, 1991). Augspurger (1983) gerou ainda um modelo, que não é mutuamente exclusivo em relação à hipótese da fuga, para explicar as vantagens da dispersão em relação à planta-mãe: a "hipótese da colonização". Esta segunda hipótese sugere que a dispersão aumenta a probabilidade de alguma parte da progênie ir parar em locais de perturbações no ambiente, como clareiras, que aumentam a chance de estabelecimento e sobrevivência das plântulas. A probabilidade de uma clareira ocorrer dentro da área de dispersão de uma planta-mãe aumenta com o aumento da distância de dispersão (Augspurger, 1984).

Cintra (1997) afirmou que a maioria dos estudos que se propuseram a testar o modelo de Janzen-Connell se limitaram a um mapeamento estático da população, focalizando apenas um estádio de desenvolvimento. No entanto, ao contrário desta tendência de se estudar apenas um estádio, sugerida na literatura, no estudo de Augspurger (1983), vários estádios foram estudados, acompanhando-se coortes. Os dados das nove espécies de árvores estudadas apoiaram a hipótese da colonização, enquanto que a hipótese da fuga foi suportada por oito delas. Já que em oito espécies não foi possível distinguir entre as hipóteses, é possível que ambos os processos sugeridos nos modelos sejam importantes para as populações estudadas. Especialmente a hipótese da fuga tem conseguido muitas evidências positivas (Wright, 2002).Contudo, ainda há controvérsias. Por exemplo, Hubbel (1980) não concordou que o recrutamento de plântulas tenderia a ser maior a uma dada distância da planta-mãe. Segundo este autor, a chuva de sementes é tão mais intensa perto da planta-mãe, que esta diferença compensaria os fatores de mortalidade dependentes de densidade, promovendo um recrutamento maior ao redor da mãe, a menos que a mortalidade de sementes e plântulas perto da mesma seja total.

Howe & Smallwood (1982) citam ainda a "hipótese da dispersão direcionada", segundo a qual alguns dispersores transportariam as sementes para locais não-aleatórios, de acordo com seu comportamento de forrageio. Este seria o caso das formigas e da síndrome da mirmecocoria, já que estes animais tendem a carregar as sementes para os formigueiros, o que muitas vezes aumenta a probabilidade de germinação das mesmas e de estabelecimento das plântulas, graças aos “serviços de jardinagem” das formigas (Pizo & Oliveira, 2000).

A dispersão de sementes pode ter ainda um papel-chave na manutenção da diversidade de espécies em florestas tropicais, de acordo com a “hipótese da dispersão limitada” (Fuentes, 2000; Wright, 2002). Segundo essa hipótese, já que a sair das proximidades da planta-mãe pode aumentar muito a sobrevivência das plantas, espécies com capacidade de dispersão mais limitada poderiam estar em desvantagem, em relação àquelas que contam com dispersores eficientes e confiáveis. Sendo assim, o balanço da competição por espaço entre diferentes espécies vegetais seria alterado pela dispersão de sementes (Levin *et al.*, 2003), tendo grandes conseqüências sobre os padrões de diversidade em florestas tropicais (Levine & Murrell, 2003).

A FRUGIVORIA EM MORCEGOS

No Mundo, os morcegos representam a segunda maior ordem de mamíferos com mais de 1.100 espécies (Wilson & Reeder, 2005). No Brasil, eles constituem um terço da fauna total de mamíferos (Marinho-Filho & Sazima, 1998), sendo ecologicamente muito importantes, porque se alimentam de uma grande variedade de espécies de animais e plantas. Por causa de sua diversidade alimentar e grande abundância local, morcegos agem como importantes dispersores de sementes, polinizadores e predadores (Findley, 1993; Kalko, 1997; Kunz, 1982).

Segundo Altringham (1998), os morcegos apresentam a maior diversidade de hábitos alimentares dentre os mamíferos, e com base nas idéias desse autor, seria possível classificar as espécies de acordo com sua dieta em três categorias principais e diversas subcategorias: 1. fitófagos, que são os consumidores de partes de plantas, incluindo frugívoros, nectarívoros, polinívoros, folívoros e granívoros; 2. animalívoros, que se alimentam de outros animais, englobando insetívoros, carnívoros generalistas, piscívoros, ranívoros e os sanguívoros (também chamados de hematófagos ou vampiros); 3. onívoros, que comem tanto plantas quanto animais, em proporções similares. No entanto, estas classificações não são estanques. Por exemplo, todas as espécies folívoras não dependem unicamente deste recurso, sendo também frugívoras; e quase todos os morcegos microquirópteros comem insetos, mesmo aqueles que são mais frugívoros (Kunz, 1982). Apesar disso, frutos infestados por larvas de insetos, embora consumidos, foram consistentemente evitados por *Carollia brevicauda* e *Sturnira ludovici* no estudo de Engriser (1995).

Nesse vasto universo alimentar, a fitofagia pode ser dividida nas seguintes categorias: frugivoria, nectarivoria, polinivoria, folivoria (Fleming, 1982) e granivoria, tendo sido essa última categoria descrita em morcegos por Nogueira & Peracchi (2003). A fitofagia ocorre principalmente nas famílias Phyllostomidae (Novo Mundo) e Pteropodidae (Velho Mundo). Espécies de outras famílias também podem consumir partes de plantas esporadicamente, com registros raros. Apesar de ambas as famílias serem fitófagas, os pteropodídeos (subordem Megachiroptera), são exclusivamente fitófagos, ao passo que a maioria dos filostomídeos (subordem Microchiroptera) é também animalivora. Dentre os microquirópteros, cerca de 70% das mais de 1.100 espécies se alimentam principalmente de insetos (Nowak, 1994; Simmons, 2005), e esta maioria de insetívoros pode ser explicada pelo fato de que este hábito é ancestral dentre os morcegos (Ferrarezzi & Gimenez, 1996).

A grande maioria dos morcegos filostomídeos é frugívora em diferentes graus, sendo que os membros das subfamílias Brachyphyllinae, Glossophaginae e Phyllonycterinae (Phyllostomidae) são especializados na nectarivoria (Fleming, 1982). No Mundo, aproximadamente 250 (26%) espécies de morcegos consomem frutos (Heithaus, 1982). No entanto, no Brasil, os frugívoros (Phyllostomidae) representam uma parcela bem maior dentre as 138 espécies listadas no último registro oficial (Aguiar & Taddei, 1995 – atualmente sabe-se que há pelo menos 164 espécies no país), 72 espécies (52%). Dentre estas, algumas são oficialmente confirmadas como frugívoras (em diferentes graus) e outras, sobre as quais não se sabe muito, são consideradas potencialmente frugívoras (por causa dos hábitos de espécies irmãs).

Poucas espécies de morcegos frugívoros são especializadas apenas neste hábito alimentar, sendo que muitas consomem também néctar, insetos e até vertebrados. A onivoria é o hábito mais comum dentre os filostomídeos (Gardner, 1977), sendo a insetivoria o hábito mais ancestral (Ferrarezzi & Gimenez, 1996). É interessante ressaltar que os frugívoros filostomídeos já foram até mesmo propostos como um grupo monofilético (Ferrarezzi & Gimenez, 1996), e que alguns estudos sugerem que as dietas de filostomídeos em geral combinam com suas filogenias (Cruz-Neto *et al.*, 2001; Guiannini & Kalko, 2004). Nos Neotrópicos, os filostomídeos perfazem um total de 160 espécies que apresentam todos os hábitos alimentares comentados anteriormente. Esta é uma das mais impressionantes radiações ecológicas e evolutivas dentre os mamíferos (Nowak, 1994; Simmons, 2005).

DISPERSÃO DE SEMENTES POR MORCEGOS

Seguindo o axioma de Van der Pijl (1972), Heithaus (1982) descreveu mais especificamente os sintomas pertencentes às duas ‘síndromes de interação’ entre morcegos e plantas, discutindo a possibilidade de as mesmas servirem como evidências de processos de coevolução. A primeira síndrome seria a quiropterofilia, ou síndrome da polinização por morcegos. A outra seria a quiropterocoria, relacionada ao consumo de frutos e à dispersão de sementes.

No caso da quiropterocoria, os frutos especializados na dispersão por morcegos, em sua maioria, possuem algumas características típicas e dentre elas podemos citar: são do tipo baga, são carnosos, permanecem verdes quando maduros, possuem odor forte ao amadurecerem, ficam bem expostos nos ramos e possuem grande número de sementes. Exemplos clássicos de frutos quiropterocóricos seriam os das famílias Piperaceae, Solanaceae, Cecropiaceae e Moraceae (Fig.II). Porém, vale à pena lembrar que há espécies que se enquadram em outras síndromes dentro destas famílias, podendo ser dispersas por aves ou pelo vento. Há frutos que não preenchem todas essas características e, no entanto, são dispersos por morcegos, por exemplo, os casos dos da gutífera *Andira* (angelim), da combretácea *Terminalia* (amêndoa), da anacardiácea *Mangifera* (manga) e da clusiácea *Calophyllum* (guanandí), que têm sementes únicas e grandes.

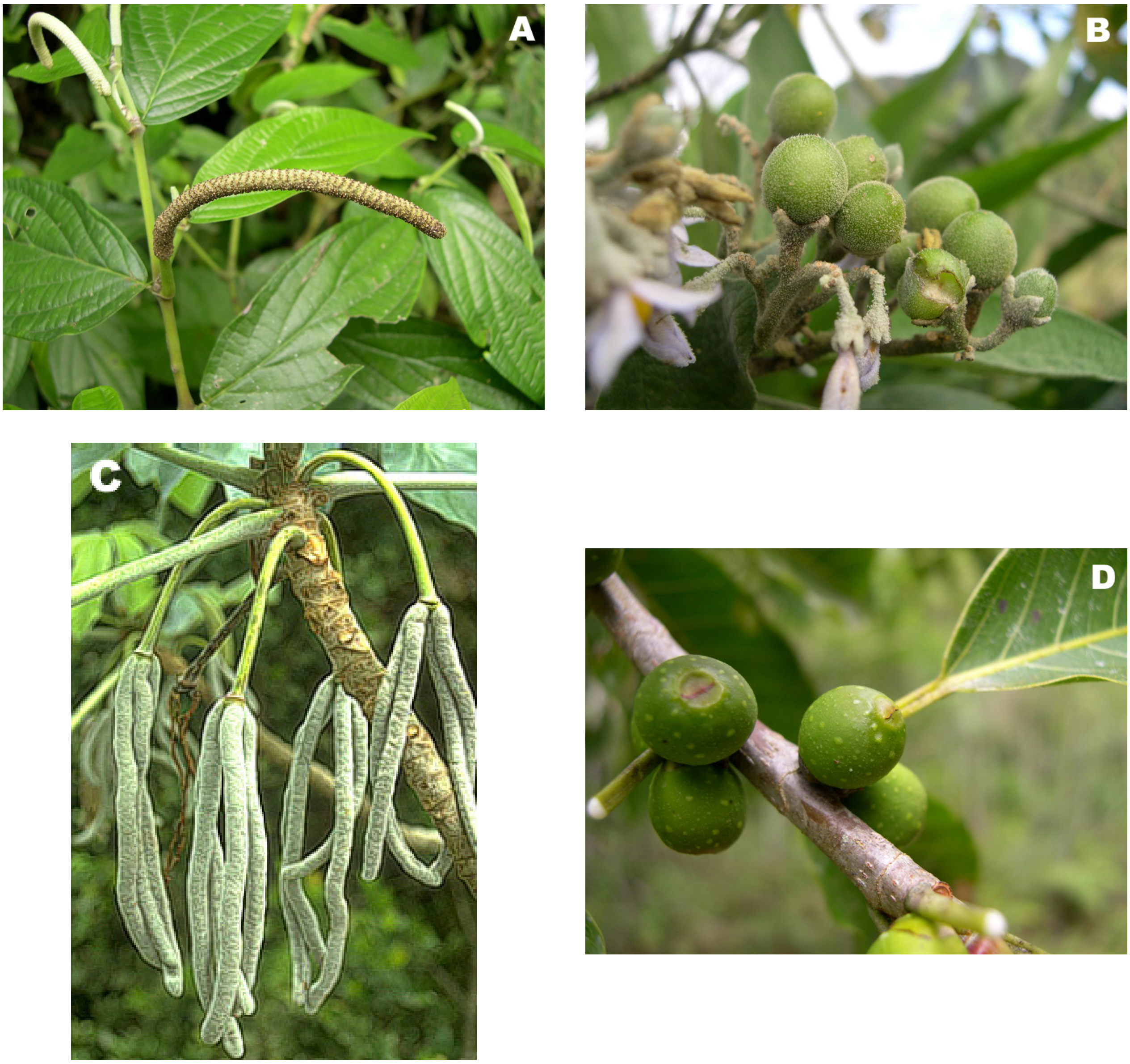


Figura II: Exemplos de frutos considerados tipicamente quiropterocóricos, segundo proposto por Heithaus (1982): a. Piperaceae, b. Solanaceae, c. Cecropiaceae e d. Moraceae. Fotos por Marco A.R. Mello.

Como frutos, ao contrário das flores, não têm tantos meios de restringir o acesso dos visitantes de modo a selecioná-los, vários outros vertebrados também utilizam os "frutos de morcegos", como, por exemplo, gambás (*Didelphis*), cuícas (*Marmosops*) e bugios (*Alouatta*), entre os mamíferos, além de diversas aves. Por isso, diz-se que a quiropterocoria seria uma síndrome mais "fraca" do que a quiropterofilia, pois apresenta muitas exceções. Considerando-se então que, em muitos casos, os frutos comidos por morcegos não se enquadram bem na síndrome da quiropterocoria, pode ser mais útil discutir a biologia dos morcegos frugívoros e de suas plantas-alimento em si, independente dos modelos de Van der Pijl (1972).

Com relação às características da dispersão por morcegos, algumas espécies frugívoras têm um comportamento alimentar relacionado ao uso de poleiros de alimentação (Kunz, 1982). Estes morcegos pegam os frutos nas plantas e, ao invés de consumi-los no mesmo local, levam-nos a abrigos de alimentação (geralmente em árvores). Devido a este comportamento, as sementes contidas nos frutos são, em sua maioria, descartadas ou defecadas em tais locais, gerando um padrão de agregação secundária nas plântulas. Contudo, apesar dessa agregação em poleiros, em uma escala maior, o padrão da chuva de sementes gerada por morcegos costuma ser aleatório, aumentando a chance de as sementes encontrarem locais adequados à germinação, de acordo com a hipótese da colonização (Ebigbo *et al.*, no prelo). Considerando as grandes distâncias voadas por morcegos em uma mesma noite (Bernard & Fenton, 2003), a maioria deles também proporciona benefícios às plantas de acordo com a hipótese da fuga.

Dentre as muitas espécies de filostomídeos fitófagos, o papel ecológico dos morcegos frugívoros é particularmente importante (Kunz, 1982). Morcegos frugívoros, junto com as aves, são responsáveis por uma grande quantidade de dispersão de sementes em florestas tropicais. Ambos os grupos podem gerar cerca de 80% da chuva de sementes em algumas localidades neotropicais (Galindo-Gonzáles *et al.*, 2000). Com base na revisão de Pyke (1984) sobre a "teoria do forrageio ótimo" (Emlen, 1966; MacArthur & Pianka, 1966), morcegos frugívoros se enquadrariam na categoria de "forrageio de lugar central", porque eles procuram comida dentro de uma dada área, mas sempre transportam os frutos para longe da planta até abrigos de alimentação temporários, onde eles finalmente os comem (Fleming, 1988).

A ECOLOGIA DO MORCEGO *STURNIRA LILIUM*

Dentre os filostomídeos frugívoros, os membros da subfamília Stenodermatinae destacam-se por serem os mais especializados na frugivoria (Nowak, 1994). *Sturnira lilium* (É. Geoffroy St.-Hilaire, 1810) (Fig.III) é um dos estenodermatíneos mais abundantes em diversas localidades, especialmente em florestas de montanha no sudeste do Brasil, sendo um importante dispersor de plantas pioneiras (Marinho-Filho & Vasconcellos-Neto; 1994). Em comparação a outros morcegos é uma espécie de pequeno porte, com massa corporal em torno de 20 g. Esta espécie é endêmica dos Neotrópicos e é encontrada do México até o Norte da Argentina, incluindo as Antilhas (Nowak, 1994). Esta espécie prefere florestas úmidas e ambientes abertos, incluindo bordas de florestas e clareiras, e vegetação secundária (Giannini, 1999; Tavares, 1999), sendo um membro da guilda dos “frugívoros catadores de espaço obstruído” (Kalko, 1998).

Figura III: O morcego filostomídeo *Sturnira lilium*, espécie principal do presente estudo. Foto por Marco A.R. Mello.

Na maioria dos casos, tem sido relatado que morcegos da espécie *S. lilium* se alimentam principalmente de frutos da família Solanaceae, especialmente do gênero *Solanum* L. (Nowak, 1994). Entretanto, *S. lilium* também consome menos freqüentemente frutos da família Piperaceae (especialmente do gênero *Piper* L.) e, raramente, de outras famílias como Cecropiaceae, Elaocarpaceae, Guttiferae e Moraceae, assim como néctar, pólen, e insetos (Dias, 1997; Faria, 1996; Gannon *et al*., 1989; Giannini, 1999; Marinho-Filho, 1991; Passos *et al*., 2003; Tavares, 1999; Uieda & Vasconcellos-Neto, 1985). Geiselmann *et al*. (2002) listaram 28 famílias e 76 espécies de plantas na dieta de *S. lilium* em toda sua distribuição geográfica.

Giannini (1999) observou em uma floresta ombrófila no noroeste da Argentina que a abundância relativa de *S. lilium,* revelada por capturas em redes-de-neblina, tende a ser maior durante a estação chuvosa, quando a abundância de frutos é maior, e menor durante a estação seca, quando a abundância de frutos é baixa. Em sua área de estudo, Sierra de San Javier (província de Tucumán), este padrão poderia ser provavelmente causado por migrações regionais ou altitudinais dos morcegos. Entretanto, para a maior parte da ampla área de distribuição de *S. lilium*, não é sabido se e como as populações de *S. lilium* respondem a variações estacionais, e como isto poderia estar relacionado à disponibilidade de frutos de Solanaceae.

Como em outros filostomídeos frugívoros – por exemplo, *Carollia perspicillata* (Fleming, 1988; Mello *et al*., 2004) e *Artibeus jamaicensis* (Handley *et al*., 1991), variações estacionais no item alimentar preferido podem também influenciar a atividade reprodutiva. Ambas as espécies, *C. perspicillata* e *A. jamaicensis*, têm dois picos reprodutivos anuais, onde a gravidez e a lactação coincidem com as estações de maior abundância de alimento.

Devido à sua ampla área de distribuição, alta abundância local, moderada mobilidade (Tavares, 1999), e especialização alimentar, *S. lilium* é um bom modelo para se estudar os possíveis benefícios mútuos da dispersão de sementes. Além disso, já que *S. lilium* come principalmente frutos de plantas pioneiras, estudos detalhados do seu comportamento de forrageio também revelarão mais informações sobre seu papel na regeneração de áreas degradadas.

FOBIA LUNAR EM MORCEGOS

Segundo alguns estudos, um fator importante restringe a atividade noturna de morcegos: a intensidade da luz da Lua (Kunz, 1982). Dois dos primeiros estudos a discutirem esta hipótese foram realizados por Morrison (1978) e Crespo *et al.* (1972). O primeiro estudo sobre a atividade noturna de um filostomídeo neotropical, *Desmodus rotundus*, foi feito por Málaga (1954, apud Crespo et al., 1972).

De acordo com o que foi proposto no estudo de Crespo *et al.* (1972), *D. rotundus* apresenta uma maior atividade durante períodos mais escuros da noite. De acordo com as observações em campo, o vampiro só saiu para se alimentar nos horários em que a Lua ainda não havia nascido, ou em que ela já havia se posto.

Ao que consta, Morrison (1978) foi o primeiro a empregar o termo “fobia lunar” (que já fora utilizado para outros animais) ao estudar a mudança no padrão de atividade do morcego *Artibeus jamaicencis*, na Ilha de Barro Colorado. O autor conta que havia uma dúvida com relação ao padrão de queda do número de capturas de morcegos em redes-de-neblina, quando em condições de luminosidade alta: os morcegos conseguiriam enxergar melhor as redes mais iluminadas, ou eles realmente reduziriam sua atividade em períodos ou locais mais claros? O autor fez monitoramento por redes e por radiotelemetria e, comparando os resultados de ambos os métodos, constatou a validade da hipótese de fobia lunar.

Esta hipótese continuou sendo testada em trabalhos posteriores, inclusive em outras famílias de morcegos, sendo aceita para algumas espécies e rejeitada para outras. Reith (1982) constatou que o morcego insetívoro *Myotis yumanensis* (Vespertilionidae), no Novo México, tende a voar em áreas sombreadas para evitar exposição na claridade excessiva. Elangovan & Marimuthu (2001) adicionaram mais uma evidência positiva para a hipótese da fobia lunar, ao constatarem que o megaquiróptero indiano *Cynopterus sphinx* (Pteropodidae) apresentou uma forte correlação negativa entre o número de vôos de alimentação e a intensidade da luz da Lua a cada noite. Mais recentemente, Singaravelan & Marimuthu (2002), também investigando o morcego *C. sphinx*, observaram que a luz da Lua inibiu a atividade de forrageio em um pomar, enquanto que durante um eclipse lunar a atividade foi significativamente aumentada.

Por outro lado, uma pesquisa feita com o filostomídeo *Stenoderma rufum* em Porto Rico demonstrou que este morcego não altera seu padrão de atividade em resposta à variação da luminosidade lunar (Gannon & Willig, 1997). Da mesma maneira, não foi observada fobia lunar em seis espécies de morcegos insetívoros da família Vespertilionidae, na Suécia (Karlsson *et al*., 2001). Ambos os estudos atribuíram estes padrões a uma menor riqueza de predadores, em comparação com áreas continentais e áreas de menor latitude, respectivamente.

Por fim, é importante ressaltar que outros fatores também contribuem para a escolha da estratégia de forrageio de cada espécie de morcego. Pode-se citar, por exemplo, a importância da dieta, do tamanho corporal, da habilidade de vôo e do habitat principal de forrageio (O'Donnell, 2000; Catto *et al*., 1995; Thies *et al*., 2006). Grandes diferenças com relação às estratégias de forrageio de morcegos insetívoros e frugívoros podem estar relacionadas à diferença nos padrões de disponibilidade destes dois alimentos durante a noite. Isto por que insetos apresentam atividade variada, enquanto frutos amadurecem em maior quantidade no começo da noite e ficam então disponíveis até serem colhidos, então os morcegos regulariam sua atividade de acordo com a disponibilidade de cada alimento (Lang *et al*., 2006). Já no caso de morcegos nectarívoros, seu recurso também pode estar limitado temporalmente, como no caso dos insetos, já que algumas flores apresentam um padrão concentrado de antese e produção de néctar em determinados períodos da noite (Dobat & Holle, 1995); desta maneira eles forrageariam nos horários de pico de produção, independente da luminosidade.

CARACTERÍSTICAS GERAIS DAS SOLANÁCEAS

Solanaceae (ordem Solanales) é uma família de dicotiledôneas, incluindo muitas plantas comestíveis e outras tóxicas. O nome da família vem do Latim *solanum*, que significa "sombra noturna", sendo que essas plantas são conhecidas como *nightshade* em países de língua inglesa. Provavelmente este nome deve ter sido dado por causa dos efeitos calmantes e alucinógenos de algumas espécies. São membros desta família a batata, o tomate, a berinjela, a páprica, a pimenta malagueta, o tabaco e a petúnia, dentre outras espécies comercialmente importantes. Esta família é tipicamente etnobotânica, sendo usada por humanos como alimento, tempero, fumo, remédio, cosmético, calmante ou alucinógeno. Algumas espécies possuem glicosídeos alcalóides que podem ser fatais para humanos e outros animais (Nee, 2004; Wikipédia, 2005).

Esta família compreende uma grande diversidade, possuindo aproximadamente 95 gêneros e 2.200 espécies no Mundo, sendo que nos Neotrópicos está representada por 63 gêneros e 1.575 espécies. A distribuição da família é cosmopolita, estando ausente apenas dos pólos e tendo sua maior diversidade da região tropical. Seus membros são encontrados em quase todos os tipos de habitat, desde os mais secos até os mais úmidos, e das planícies até as grandes altitudes (Nee, 2004).

Suas espécies têm folhas simples, alternas, inteiras, lobadas ou partidas, sésseis ou pecioladas, glabras ou pilosas, sem estípulas. São plantas arbóreas, arbustos, ervas, lianas ou mesmo árvores de grande porte. Seu floema é interno. As flores são andrógenas, ou diclamídeas, pentâmeras, com comprimento variando de 1 a 20cm, isoladas, aos pares, ou dispostas em inflorescências variadas extra-axilares. O cálice é persistente, às vezes ampliando-se no fruto. A corola é actinomorfa ou levemente zigomorfa, gamopétala, rotácea, campanulada, infundiforme, hipocrateriforme, tubulosa ou urceolada. O androceu tem 2, 4 ou 5 estames, com filetes livres ou parcialmente soldados entre si, com anteras poricidas (gênero *Solanum*) ou rimosas. O gineceu é constituído de ovário súpero, bilocular ou falsamente plurilocular, com muitos óvulos em cada lóculo. O fruto é do tipo baga, drupa ou cápsula (Nee, 2004; Wikipédia, 2005). Na Figura IV podem ser vistos alguns exemplos das solanáceas mais comuns encontradas na área de estudo.

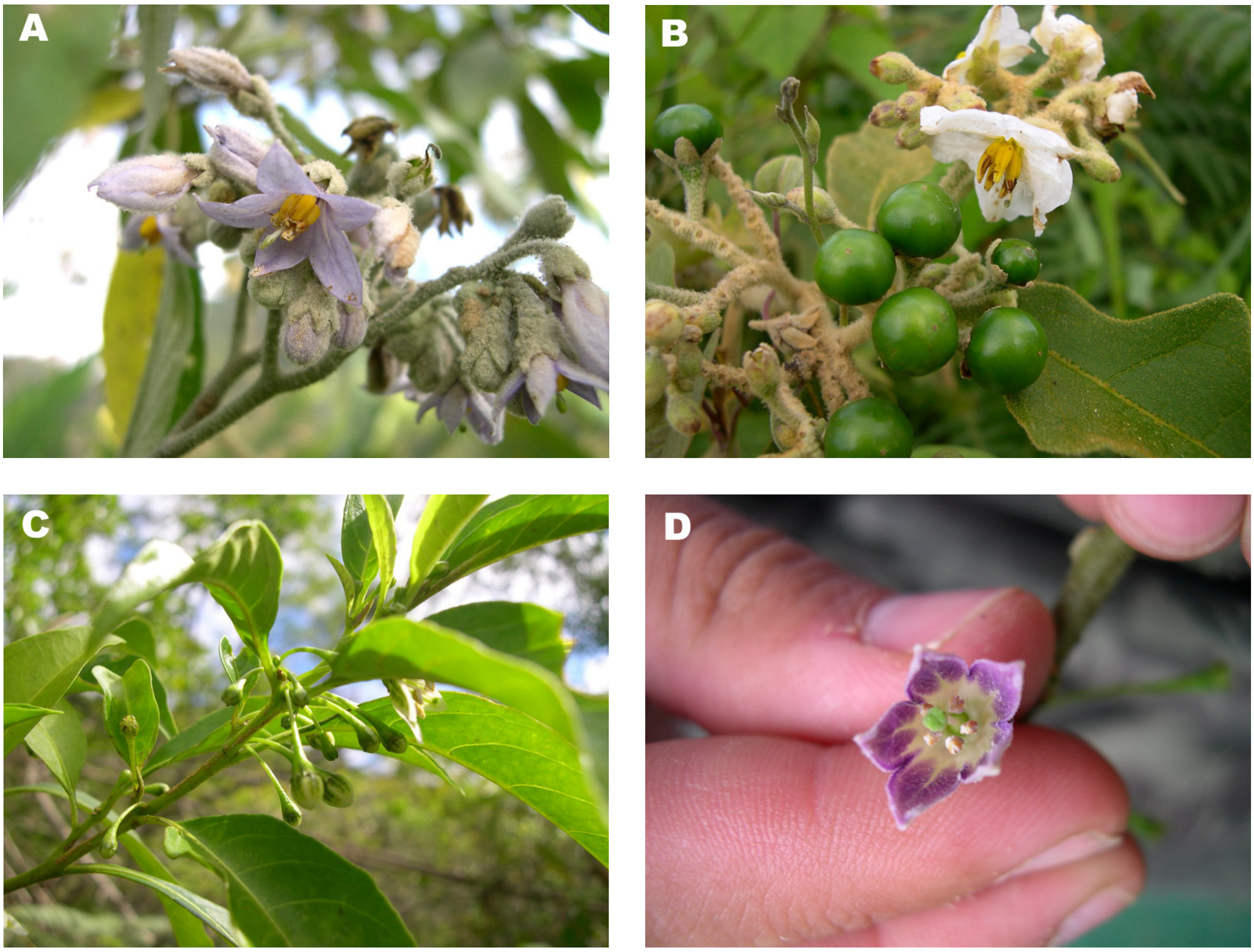


Figura IV: Algumas das solanáceas mais comuns observadas na área de estudo: a. flor de *Solanum granulosoleprosum*, b. flores e frutos de *S. variabile*, c. um ramo com frutos de *Aureliana* sp. e d. uma flor de *Vassobia breviflora*. Fotos por Marco A.R. Mello.

Há diversos registros de consumo de solanáceas por morcegos na literatura, sendo que esta família é apontada como o alimento principal dos morcegos do gênero *Sturnira* na maioria das localidades estudadas (Geiselmann *et al*., 2002). Há evidências de que elas são realmente preferidas e não apenas consumidas de maneira oportunista (Giannini, 1999; Hernández-Conrique *et al.*, 1997). Há algumas solanáceas, como *Dyssochroma viridiflorum*, que têm tanto sua polinização quanto sua dispersão feitas por morcegos (Sazima *et al*., 2003). Algumas espécies como *Solanum* *asperum* foram classificadas como tipicamente quiropterocóricas (Uieda & Vasconcellos-Neto, 1985), e a dispersão por morcegos foi observada em diversas outras espécies, como *S. granulosoleprosum* (Cáceres & Moura, 2003). Mais recentemente, foi observado até mesmo o consumo de folhas de algumas solanáceas por morcegos estenodermatíneos, como no caso da lobeira, *S. lycocarpum* (Aguiar, 2005), sendo que o consumo de folhas de outras plantas nesta subfamília já era conhecido há mais tempo (Zórtea & Mendes, 1993).

PERGUNTAS E HIPÓTESES GERAIS

Tendo em vista a teoria da dispersão de sementes e o papel dos morcegos neste processo, o presente trabalho teve como objetivo descrever algumas características do sistema formado pela espécie *Sturnira lilium* e as plantas da família Solanaceae, além de testar algumas hipóteses clássicas e outras mais específicas sobre a sua interação, descritas em cada capítulo. Quatro perguntas gerais nortearam os diferentes capítulos aqui apresentados:

1. Do que se alimenta o morcego *S. lilium*?

Há registros de mais de 70 espécies de plantas na dieta de *S. lilium* (Geiselmann *et al*., 2002) e, apesar da grande variação geográfica, as solanáceas costumam ser o item mais consumido na maioria das localidades. Portanto, meu objetivo foi descrever a dieta deste morcego na área de estudo e suas variações ao longo do ano. Testei se as solanáceas seriam o alimento preferido no geral e na maioria dos meses, se o consumo de frutos de solanáceas estaria relacionado à sua produção, e se o consumo de solanáceas afetaria o consumo de outros itens.

2. Qual é a relação entre a fenologia das solanáceas e a reprodução do morcego *S. lilium*?

Muitos mamíferos, especialmente aqueles que têm preferência ou são especializados em determinado tipo de alimento, costumam concentrar sua atividade reprodutiva na época do ano em que a abundância deste alimento é mais alta, a fim de suprir os altos requerimentos energéticos da gravidez e lactação (Kunz, 1982). Esse é o caso de outros morcegos filostomídeos, como *Carollia perspicillata* (Mello *et al.*, 2004), por exemplo. Sendo assim, testei a hipótese de que a população de *S. lilium* apresentaria uma maior atividade reprodutiva durante a estação de maior produção de frutos pelas solanáceas.

3. Como o comportamento de forrageio do morcego *S. lilium* afeta sua qualidade como dispersor de sementes de solanáceas?

A teoria da dispersão de sementes possui diversas hipóteses sobre a qualidade de animais como agentes dispersores. Dentre elas, destacam-se as hipóteses da fuga (Connell, 1971; Janzen, 1970) e da colonização (Augspurger, 1983), que também levam a induções sobre o papel da dispersão na manutenção da diversidade de plantas nos trópicos. De um modo geral, a teoria diz que para a interação ser estável, as plantas devem ser uma fonte de alimento confiável e, por sua vez, os morcegos devem ser consumidores e dispersores confiáveis (Snow, 1965). Portanto, testei as hipóteses de que as solanáceas produziriam frutos em baixa sincronia e por um longo tempo (estratégia do 'estado-estável'), elas seriam consumidas frequentemente por *S. lilium*, os morcegos concentrariam sua atividade perto delas, eles levariam as sementes para longe das plantas-mãe e das espalhariam por diversos locais em uma grande área.

4. A intensidade da luz da Lua afeta o comportamento de forrageio dos morcegos frugívoros?

Este capítulo, ao contrário dos outros três, não foi baseado em dados coletados no Parque Estadual Intervales, e trata de outras duas espécies de filostomídeos frugívoros além de *Sturnira lilium*. A hipótese da "fobia lunar" propõe que animais noturnos e pequenos diminuíram de alguma forma sua atividade durante períodos mais claros da noite ou em áreas mais iluminadas, a fim de evitarem serem mortos por predadores visualmente orientados (Crespo *et al.*, 1972). No caso dos morcegos, essa hipótese já foi aceita e rejeitada em diferentes casos, sendo que os padrões observados foram atribuídos a diferenças no hábito alimentar, nível trófico e habitat de forrageio principal. Considerando essa inconsistência na resposta à luz da Lua, decidi testar a ocorrência de fobia lunar em três espécies de morcegos filostomídeos frugívoros muito abundantes nos Neotrópicos, os estenodermatíneos *Artibeus lituratus* (Olfers 1818) e *Sturnira lilium* (E. Geoffroy, 1810), e o carolliíneo *Carollia perspicillata* (Linnaeus, 1758), que diferem entre si com relação à família de planta predileta e ao comportamento de forrageio (Bernard, 2001; Fleming, 1988; Handley *et al.*, 1991). Testei a hipótese de que a atividade desses morcegos seria reduzida durante períodos mais claros da noite.

1ª NOTA

Na seção “Anexos”, disponibilizei material adicional aos capítulos, que pode ser útil para os leitores da tese de diferentes formas. O primeiro anexo é a lista completa da fauna de morcegos do Parque Estadual Intervales registrada em trabalhos anteriores no presente estudo. No segundo anexo apresento dados sobre a amostra da comunidade de morcegos que eu obtive durante meu trabalho de campo, sendo que o terceiro anexo é composto de fotos dessas espécies. A lista das plantas-alimento estudadas, assim como o número de indivíduos de cada uma que eu marquei, estão no quarto anexo, ao passo fotos de algumas dessas plantas estão no quinto anexo. Ainda com relação às plantas, no sexto anexo mostro fotos de algumas das sementes encontradas nas fezes dos morcegos. O sétimo anexo é a lista completa de todas as espécies de plantas que já foram registradas como alimento de *S. lilium* na literatura, sendo que a maioria dos dados é oriunda da revisão feita por Geiselmann *et al.* (2002). Por fim, o oitavo e último anexo apresenta fotos de alguns dos equipamentos usados no estudo, que podem ser interessantes para estudantes interessados no tema.

2ª NOTA

Decidi escrever os capítulos da minha tese em Inglês, tendo em vista que o meio de comunicação científico principal são as revistas especializadas, nacionais ou estrangeiras, que têm circulação internacional. Acredito que não há sentido em restringir novas idéias, hipóteses, testes, observações e resultados a um pequeno público-alvo, devido a uma barreira lingüística, já que fazemos ciência para a humanidade e não para nós mesmos ou só para o nosso país.

Além disso, é extremamente importante submetermos nossos trabalhos à avaliação de revisores anônimos de fora do nosso círculo social, a fim de diminuir o viés cultural que recai sobre nossas interpretações da natureza. Escrevi as seções gerais de introdução e conclusões em Português, com o intuito de explicar melhor o contexto, os objetivos e minha interpretação sobre os resultados para as pessoas dentre o público nacional que não compreendem o inglês.

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CAPÍTULO I

Hábitos alimentares e variação na abundância do morcego *Sturnira lilium* (Chiroptera: Phyllostomidae)

Feeding habits and abundance variation of the bat *Sturnira lilium* (Chiroptera: Phyllostomidae)

RUNNING TITLE: Diet and dynamics of *Sturnira lilium.*

KEYWORDS: Atlantic Forest, diet, dynamics, interactions, frugivory, montane forest, population, seasonality.

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ABSTRACT

Bats of the family Phyllostomidae present the highest dietary diversity among mammals, including stenodermatines like *Sturnira lilium* that are specialized frugivores and important seed dispersers. We mist-netted *S. lilium* in the montane Atlantic Forest of Brazil and assessed its diet to understand the effects of climate and food availability on its population dynamics. Bats were captured throughout 15 monthly sessions to address possible seasonal fluctuations in relative abundance and to collect fecal samples for dietary analysis. We also monitored climate variability and documented phenology of the main food-plants of *S. lilium* to illustrate possible variations in resource availability. The diet of *S. lilium* consisted exclusively of fruits with a strong preference for Solanaceae, although the bats also fed on Piperaceae and Cecropiaceae with varying proportions depending on the season. The consumption of fruits of Solanaceae by bats was not related to the phenology of the plants. In our case, relative abundance of bats caught in mist-nets peaked three times in contrast to fruit production that peaked only once. Bats were almost absent in the area during colder months, probably migrating to lower and warmer altitudes in search of Solanaceae fruits.

INTRODUCTION

Worldwide, bats represent the second largest order of mammals with more than 1,100 recognized species (Simmons, 2005). In Brazil they constitute one third of the mammal fauna (Marinho-Filho & Sazima, 1998). Among phyllostomids, members of the subfamily Stenodermatinae feed almost exclusively on fruits, being important seed dispersers (Heithaus, 1982). The species *Sturnira lilium* (É. Geoffroy St.-Hilaire, 1810) is one of the most abundant stenodermatines in many localities of the Neotropics and has a broad distribution. It occurs from Mexico to Northern Argentina, including the Antilles (Nowak, 1994; Simmons, 2005), and prefers humid forests, open environments, and secondary vegetation (Giannini, 1999; Tavares, 1999). Geiselman *et al*. (2002) list 28 plant families and 76 plant species as food for *S. lilium* throughout its geographical range. In spite of the large numbers of fruits known to occur in its diet, *S. lilium* feeds mainly on fruits of the family Solanaceae. The Solanaceae comprises 63 genera and 1,575 species in the Neotropics and is very abundant in the Atlantic Forest (Nee, 2004). Patterns of low and continuous fruit production over an extended period ("steady-state" - Snow, 1965) and the presence of toxic secondary metabolites (Cipollini & Levey, 1997) suggest that this family may have specialized dispersers, and some species of Solanaceae do indeed depend on bats both for pollination and seed dispersal (Sazima *et al*., 2003). "Big-bang" plants may also have specialized frugivore interactions (e.g. Nogueira & Peracchi, 2003), but specialization seems to be more common among "steady-state" strategists (Snow, 1965).

Although there is extensive literature on the diet of *S. lilium*, knowledge of feeding habits of this species in montane forests is poor. Montane systems are characterized by different environmental conditions compared to lowland forests, in particular lower temperatures, lower food availability, and higher seasonality (Mantovani, 2001). This is likely to lead to differences in foraging behavior of bats, as observed by Giannini (1999) who studied diet composition and space use in conspecific *Sturnira* bats at different altitudes in Argentina. In Brazil, detailed studies on feeding habits of *S. lilium* are crucial to determine its importance as seed disperser at the higher altitudes of the Atlantic Forest, a biome with high research priority, as it has been almost totally destroyed or profoundly altered through fragmentation and human disturbance (Myers *et al*., 2000). Although some studies show that even small forest fragments still may comprise a surprisingly high level of biodiversity, the Atlantic Forest in general forms one of the most endangered "hot spots" of biodiversity worldwide as classified by IUCN (Myers *et al*., 2000).

We focused in our study on the composition and temporal variability of diet in *S. lilium* and the abundance variation of this bat in a selected area of the Brazilian montane Atlantic Forest. We wanted to find out whether the diet of *S. lilium* in the highlands is similar to the diet observed in lowlands, with Solanaceae as their main component. We expected temporal variations in the diet of *S. lilium* because of higher seasonality at higher altitudes assuming that plant species differ in fruit production throughout the year. Furthermore, if consumption of Solanaceae by *S. lilium* is related to fruit production, as it is the case for other small phyllostomids like *Carollia perspicillata* and their preferred food plants (e.g. Mello *et al*., 2004a), we propose that an increase in fruit production of Solanaceae should also lead to an increase in consumption of their fruit by *S. lilium*. Finally, we suggest that climate variations typical for the highlands, such as rather large drops in temperature during winter, might affect abundance variation of *S. lilium.*

METHODS

Time frame and study area

We conducted our study for a total of 36 nights in 15 monthly sessions from October 2003 to February 2005, except January and February 2004, at the state park “Parque Estadual Intervales” (hereafter “Intervales”), Ribeirão Grande municipality, São Paulo state, southeastern Brazil. Intervales and three neighboring conservation units form the “Contínuo Ecológico de Paranapiacaba” which represents the largest continuous remnant of the Atlantic Forest in Brazil.

Within Intervales, we worked in “Sede de Pesquisa” (24º16'24.7"S – 48º25'00.6"W), located 850 m above sea level, at the highest research base of the park. We covered an area of ca. 400 ha for our study, where we monitored both, bats and plants. The climate of the region classifies as temperate humid or Cwa in the system of Köppen (Mantovani, 2001), with average temperatures of 22ºC during the warmest months, and absolute minimum temperatures scoring -4ºC during winter at the highest parts of the park, including Sede de Pesquisa. There are one to five days of frost each year. The number of rainy days at Intervales varies from 125 to 150, and average annual total rainfall amounts to ca. 2,000 mm. It can be twice as much (4,000 mm) in the lowlands of the park. The main vegetation at Sede de Pesquisa classifies as montane dense rainforest or mist forest, a subsystem of the Atlantic Forest (Mantovani, 2001).

The flora at this region is rather well known as it has been inventoried recently (Passos *et al.* 2003), facilitating identification of the bats' food plants. Our study species, *Sturnira lilium*, is abundant in Sede de Pesquisa (Passos *et al.* 2003).

Data collection

Daily data on climate, air temperature (°C) and rainfall (mm), were provided by Intervales' meteorological station. During our study, rainfall averaged a total of 176.2 mm per month and varied from a minimum of 3.3 mm (August 2004) to a maximum of 507.9 mm (January 2005), while monthly temperature averaged 16.8°C and ranged from 12.6°C (June 2004) to 19.7°C (January 2005). In winter, few days yielded values around 0°C. Following the known pattern for the area, there was a relatively dry and cold season between April and September, and a relatively rainy and hot season between October and March (Fig.1.1). Variations in rainfall and temperature were correlated with the long-term monthly means that had been registered in the area for the last seven years (rainfall: $r^2 = 0.76$, $p < 0.001$; temperature: $r^2 = 0.85$, $p < 0.001$).

We captured bats using 10 nylon mist-nets (7 x 3 m – Ecotone, Inc.) each night throughout 36 nights during 15 months to describe feeding habits of *S. lilium*. The nets were set on trails and dirt roads in the study area 30 m or more apart from each other and kept open for six hours after local sunset. Half of them were positioned near known patches of food plants and the other half set at random, to reduce bias caused by net placement that could result in overestimations of the proportion of those plants in fecal samples and of relative abundance of the bats. All captured bats were marked with numbered aluminum wing bands (A.C. Hughes, Inc.). We used the keys provided by Vizotto & Taddei (1973) and Emmons & Feer (1997) for identification of bat species. There were two species of *Sturnira* in the area, *S. lilium* that was the most abundant, and *S. tildae* that was seldom captured. We used the characters suggested by Gannon *et al.* (1989), Goodwin & Greenhall (1961) and Simmons & Voss (1998) for identification including forearm length, form of the lower maxilla, of the lower cusps of the molars, and of the lower incisors. The identification of some specimens was confirmed by Marcelo R. Nogueira (Universidade Estadual do Norte Fluminense, Brazil).

We studied the feeding habits of *S. lilium* by analyzing fecal samples, which we collected directly from bats captured in mist-nets using small plastic recipients and from individuals that we kept for at least one hour inside clean cloth bags. Each sample from each individual was collected separately into a plastic Eppendorf cup, and then stored frozen at about 0°C. For analysis, each sample was put in a fine-meshed sieve and carefully rinsed with water, to separate seeds from pulp and other materials including insect parts. Seeds were first classified to family, and in most cases also to genus. In some cases we identified the samples to species based on a reference collection of seeds eaten by birds and bats in the study area, which had been started in previous studies (Passos *et al*., 2003) and is being continued in subsequent studies. We also checked the bats' fur to see if there were pollen grains attached.

We marked 70 individual Solanaceae along the trails in our study area to describe the phenology of the main food plants of *S. lilium* and checked the phenology of the plants on a monthly basis. We distinguished between inactive, flowering, fruiting or flowering/fruiting. Furthermore, we counted total number of flowers and fruits in individuals that could be clearly observed and made estimates for other individuals, following the method proposed by Korine *et al.* (2000). For the Piperaceae, we counted infrutescences and inflorescences of 30 random individuals each month. Identification of plants was provided by Jorge I. Tamashiro (Universidade Estadual de Campinas), Rafael Fernando da Silva Possette (Embrapa Florestas), Osmar Ribas and Gerdt Hatschbach (Museu Botânico Municipal de Curitiba). Vouchers of studied plant species were deposited in the collection of the "Laboratório de Interações Vertebrados-Plantas" (Universidade Estadual de Campinas, Brazil).

Data analysis

Our total netting effort was 41,580 h.m^2. We calculated netting-effort as the total amount of m^2 of nets (each net has 21 m^2) opened each night multiplied by the total number of hours worked in the whole study, following Straube & Bianconi (2002). This permits comparisons between studies that used different sizes and quantities of mist-nets. Capture success was calculated as the number of captures divided by capture effort (captures/h.m²) and it was used to assess variations in bat population size in the area, We then tested the relationship between capture success, and temperature, and between capture success and average individual fruit crop of Solanaceae by a non-linear simple regressions.

We identified different items found in fecal samples and summarized their frequency of consumption. To address possible temporal variation in diet, we pooled dietary data of *S. lilium* on a monthly basis as the percentage of samples of each plant family. We tested the differences in the overall proportion of each plant family in fecal samples with the χ^2-test (whole dataset), and the monthly variation in this proportion with the G-test (months).

Concerning the phenology of food plants, we assessed the status of the population as the percentage of adult individuals in each category – inactive, flowering, fruiting - on a monthly basis. We also used the average number of fruits produced by individuals of each family in each month as a measure of fruit production (crop). To assess if variation in fruit production (% of individuals with fruits) of all Solanaceae species was related to air temperature and rainfall, we used a multiple linear regression. To test the hypothesis of a relationship between consumption (% in fecal samples) and production (average individual crop) of fruits of all Solanaceae we used a logarithmic model, to find out whether consumption remains constant when production reaches a high level, as proposed in Mello *et al*. (2004a).

We collected data on air temperature (°C) and rainfall (mm) daily and pooled them on a monthly basis (total sum for rainfall, and daily mean for temperature) to describe variations in climate in the area and to link them to the demography of both bats and plants. We used simple linear correlations to find out if the climate data from our study period followed the long-term yearly average from the last seven years. We further tested the relationship between temperature, rainfall, and fruit production with multiple linear regressions.

We based our statistical analyses on Zar (1999), and used the softwares Systat 9.0 (regular statistics) and Oriana 2.0 (circular statistics) for calculations. Percentual data were arcsine transformed, before being used in statistical tests.

RESULTS

We caught a total of 477 bats including recaptures, representing 15 species. The majority (13 species), were members of the family Phyllostomidae and two species belonged to the family of Vespertilionidae. The captures corresponded to about 40% of the bat species that had been recorded for the park (34 species - Anexo 2). This low local species richness is mostly due to size of the sampled area. It is much smaller and less diverse than the area of the whole park, which encompasses a variety of habitats and altitudes. This is also reflected in the overall capture success at our study site in the highland which was much lower (11.5×10^{-3} captures/h.m²) compared to studies in lowland Atlantic Forest areas (e.g. 37.3×10^{-3}, Mello, 2002).

Sturnira lilium was the dominant species and represented 70% of all captures (N = 333 individuals). Capture success of *S. lilium* varied strongly between months. It averaged $7.46 \times 10^{-3} \pm 6.64 \times 10^{-3}$ captures/h.m² with a maximum of 19.84×10^{-3} (Fig.1.2). We obtained three peaks with regard to capture success, one at the beginning of the dry season (April), the second at the end of the dry season (September) and the third in the middle of the rainy season (December). During the coldest months *S. lilium* was either not captured at all or at very low numbers. The variation in capture success was significantly and positively linked with temperature (model: $y = x^{8.76}$, n = 12, $r^2 = 0.51$, p = 0.009). However, there no association between capture success and average individual fruit crop of Solanaceae (model: $y = 0.02 \cdot x^{2.04}$, n = 12, $r^2 = 0.16$, p = 0.19).

To describe the diet of *S. lilium*, we analyzed 96 fecal samples from different individuals; each sample belonged to a single individual and contained only one kind of seed. 19 samples contained exclusively soft parts of fruits (pulp). 77 samples had seeds from different families in them. As we did not find any animal parts we conclude that *S. lilium* fed exclusively on fruits during our study, confirming the hypothesis of a frugivorous diet for this species. We found seeds of 22 plant species and morphospecies (unidentified seed with differences in morphology) in the feces of *S. lilium* including Solanaceae, Piperaceae, and Cecropiaceae (Tab. 1.1). *Sturnira lilium* fed mostly on fruits of Solanaceae, which represented 84% of all seed samples ($n = 96$, $\chi^2 = 94.92$, $p < 0.001$). Bats also ate Piperaceae that were present in 13% of all samples with seeds and to a lesser extent also on Cecropiaceae (3%). Pulp and seeds from unidentified fruits represented 19% of all samples. Most of the unidentified seeds were likely to stem from Solanaceae or Piperaceae, because their form matched the form of seeds in our reference collection: tiny cylinder-shaped green and black seeds for Piperaceae, and tiny dish-shaped brown to yellow seeds for Solanaceae. Overall we found seeds of 22 plant species and morphospecies in the fecal samples of *S. lilium*: *Aureliana fasciculata, Aureliana* sp.2, *Cecropia glaziovii*, *P. corintoanum, P. gaudichaudianum, P. hoehenei, Piper* sp., *Solanum capsicum, S. granulosoleprosum, S. sanctacatharinae, Vassobia breviflora* and 11 non-identified different morphospecies (one or two samples each). Among the identified Solanaceae, *S. granulosoleprosum* was consumed most frequently (40% of all samples) by *S. lilium*, and among the Piperaceae, *P. gaudichaudianum* prevailed (6% of all samples). The proportions of each plant family in the bats' diet varied during the months ($n = 96$, $G = 66.66$, $p = 0.019$) (Tab.1.2). However, Solanaceae dominated throughout the study period and were present in more than half (59 ± 33%) of all fecal samples. Fruit production of Solanaceae varied from month to month from 0% to 100% (percentage of adult plants producing fruits). During the middle of the rainy season, *S. lilium* fed on a higher number of plant species than during the dry season.

In our phenological part of the study, we documented 13 species of Solanaceae and four species of Piperaceae, three of which did not produce fruits during the study period. The majority of species of Solanaceae revealed a steady-state strategy and continuously produced fruits over several months (Tab.1.3). Despite the extended fruiting season of Solanaceae, fruit production varied with time (Rayleigh's $Z = 17081.78$, $p < 0.001$) and was highest in the first half of the rainy season. Fruit production was negatively related to air temperature (standardized partial coefficient of the multiple regression (b') = -0.659, p = 0.034). However, it was not associated with rainfall (b' = -0.183, p = 0.505). Contrary to what we expected, there was no relationship between fruit production of Solanaceae and consumption of those fruits by *S. lilium* (model: $y = 0.42 + 0.13 \cdot \ln x$, n = 7, r^2 = 0.39, p = 0.13) (Fig.1.3).

DISCUSSION

Sturnira lilium is a specialist in our study area as its diet consisted entirely of fruits, mostly of Solanaceae. This is in accordance to most studies, but in contrast to a few observations where animalivory and nectarivory have also been reported for this species (Gannon *et al*., 1999; Nowak, 1994). Thomas (1984) suggested that phyllostomid frugivorous bats should supplement their diets with insects, because plants contain low protein levels. On the other hand, Delorme & Thomas (1996) observed that at least *Carollia perspicillata*, which supposedly eats animals more frequently than *S. lilium* (Fleming, 1988), may meet its nutritional requirements by feeding only on fruits. Although we cannot exclude the possibility of rare animalivory or nectarivory in *S. lilium* in our area, these habits may not be important to this species, as Herrera *et al*. (2001) observed experimentally that a pure fruit diet may allow *S. lilium* to meet all its energetic and nitrogen needs.

Fruits of Solanaceae were the main food of *S. lilium*, but Piperaceae and Cecropiaceae were also consumed, albeit to a much lesser degree. This dietary pattern is consistent with findings reviewed in Geiselmann *et al*. (2002), referring to the whole geographic range of this species. The dominance of Solanaceae in the diet of *S. lilium* has been reported at a wide range of other localities in the Neotropics (e.g. Cáceres & Moura, 2003; Iudica & Bonaccorso, 1997; Passos *et al*., 2003; Uieda & Vasconcellos-Neto, 1985).

The diet of *S. lilium* varied throughout the year. Although *S. lilium* continued to feed mainly on Solanaceae, during the middle of the rainy season, it ate a larger variety of fruits. The opportunistic use of bat fruits other than the species' preferred ones is common in phyllostomids, when the latter are scarce during some particular season (Giannini, 1999). This pattern is consistent with predictions of the "optimal foraging theory", which states that a species of forager has a ranking of preferred items, according to cost/benefit relationships, and may go top-down this list according to spatio-temporal variations in food availability (Pyke, 1984; Schoener, 1971). Similar changes in diet have already been observed in other phyllostomids, like the frugivores *Carollia* (Mello *et al*., 2004a) and *Artibeus* (Handley *et al*., 1991), and the nectarivore *Leptonycteris* (Howell & Hartl, 1980).

We conclude from the overall and monthly high proportions of Solanaceae in the bats diet that the individuals actively selected those fruits, because a range of other plant species that are also known to be part of *S. lilium*'s diet produced large fruit crops during the same time (for the phenology of other families see Leiner, 2005). If bats were to react opportunistically to fruit abundance, they could have eaten for instance more fruits of Piperaceae. Evidences that Solanaceae is actually preferred by *Sturnira* have also been observed by Giannini (1999) and Hernández-Conrique *et al*. (1997). Fruits of other families may supplement energetic needs of *S. lilium*, when the fruit crop of Solanaceae is low.

Contrary to our expectation that fruit consumption of Solanaceae by *S. lilium* should be positively related to fruit production, this relationship was not significant. The main reason for this pattern is likely to be the low abundance or even absence of *S. lilium* in the study area during the cold season. This weakened the relationship between consumption and production of fruits. We assume that the bats migrated to the lowland forests in search of Solanaceae. This finding contrasts with another shrub frugivore, *C. perspicillata,* in a lowland Atlantic Forest, where the bats started to feed on other plant families and included also insects in their diet, when their preferred food was not available (Mello *et al*., 2004a).

We observed that air temperature played a major role in determining local abundance of *S. lilium* and its dietary patterns. Maybe the low temperatures during the cold season (with a mean of 12°C and even some days of frost per year) affected *S. lilium* (Stones & Wiebers, 1965) and made them undergo "facultative hypothermia" as it is known for other phyllostomid bat species (Audet & Thomas, 1997). Temperature plays an important role in the demography of tropical bats, as for instance *C. perspicillata* tends to peak its reproduction during warmer months (Mello *et al*., 2004b). At high altitudes temperature may play even a bigger role, because low temperatures may not be tolerated well by small phyllostomids.

In addition to temperature, crop production of the preferred fruit plants may also play an important role, although the relationship between fruit production of Solanaceae and capture success of *S. lilium* was not significant. Generally, we captured more bats during the season when fruits were more abundant. Possibly the regression model was not significant, because there were three peaks in bat abundance and only one in fruit availability. It is probable that most individuals of *S. lilium* make a seasonal altitudinal migration as observed by Giannini (1999), to harvest other species of Solanaceae at different altitudes in Intervales, that produce fruits at different seasons (pers. obs.).

We conclude that *S. lilium* relies heavily on Solanaceae, a finding consistent with most studies available on this species, in contrast to a wide range of other stenodermatine bats that feed mainly on Moraceae and Cecropiaceae (Giannini & Kalko, 2004; Heithaus, 1982; Handley *et al*., 1991). Furthermore, *S. lilium* responds differently to temporal variation in resource availability compared to similar-sized frugivorous bats like *C. perspicillata* (Mello *et al*., 2004a) that occur sympatrically in the same area In contrast to the mostly sedentary *C. perspicillata*, *S. lilium* probably migrates from the highlands to the lowlands in search of Solanaceae fruit instead of changing its diet from a Solanaceae-dominated composition to other plants, and, as observed in *C. perspicillata*, adding nectar and arthropods (Marinho-Filho, 1991; Mello *et al*., 2004a).

The evidence of migration observed in the present study underlines the importance of suitable habitats along elevational gradients. Regarding conservation strategies, *S. lilium* seems to be well-protected in such large parks as Intervales. Nevertheless, populations of this important seed disperser bat may be endangered if habitats are seriously altered along the vertical gradient.

Therefore, parks situated mainly in montane environments should be connected with areas in the lowlands via continuous habitat, in order to ensure the viability of altitudinal migrants and thus the ecological services provided by them, reinforcing the suggestions proposed by Loiselle (1991) for the first time in the Neotropics with regard to birds.

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TABLES

Table 1.1: Diet composition of *S. lilium* based on fecal samples. Fecal samples that contained only pulp or other unidentifiable material were excluded (n = 21).

morphospecies	family	species	# samples	% samples
s.01	Solanaceae	*Solanum granulosoleprosum*	31	41%
s.07	Solanaceae	unidentified	8	11%
p.01	Piperaceae	*Piper gaudichaudianum*	5	7%
s.21	Solanaceae	*Solanum sanctacatharinae*	4	5%
s.06	Solanaceae	unidentified	3	4%
s.09	Solanaceae	unidentified	3	4%
c.02	Cecropiaceae	*Cecropia* sp.	2	3%
p.04	Piperaceae	*Piper corintoanum*	2	3%
p.05	Piperaceae	*Piper hoehenei*	2	3%
s.03	Solanaceae	*Vassobia breviflora*	2	3%
s.13	Solanaceae	*Aureliana fasciculata*	2	3%
s.26	Solanaceae	unidentified	2	3%
p.02	Piperaceae	*Piper* sp.	1	1%
s.05	Solanaceae	unidentified	1	1%
s.08	Solanaceae	unidentified	1	1%
s.10	Solanaceae	unidentified	1	1%
s.11	Solanaceae	unidentified	1	1%
s.12	Solanaceae	unidentified	1	1%
s.23	Solanaceae	*Solanum capsicum*	1	1%
s.27	Solanaceae	Solanaceae	1	1%
s.28	Solanaceae	*Aureliana* sp.2	1	1%
	subtotals	Solanaceae	63	84%
		Piperaceae	10	13%
		Cecropiaceae	2	3%
		total	**75**	
		pulp and other plant material	21	

Table 1.2: Monthly variation in the diet of *S. lilium*, represented as the number of fecal samples (cells different from zero are grey-colored). Seeds that could not be identified to the genus level are represented as morphospecies of Piperaceae (p.02) or Solanaceae (all others). All fecal samples contained only one kind of seed.

species	**oct.03**	**nov.03**	**dec.03**	**interval**	**mar.04**	**apr.04**	**mai.04**	**jun.04**	**jul.04**	**aug.04**	**sep.04**	**oct.04**	**nov.04**	**dec.04**	**jan.05**	**feb.05**
Cecropiaceae																
Cecropia glaziovii			1													
Piperaceae																
Piper gaudichaudianum													1	3		
p.02			1													
Piper corintoanum														1		
Piper hoehenei						2		period with almost no captures of *S. lilium*								
Solanaceae																
Aureliana fasciculata			1													1
Aureliana sp2																
Solanum capsicum														1		
Solanum granulosoleprosum	7	10	1									6	5			
Solanum sanctacatharinae						1							1	1		1
Vassobia breviflora			2													
s.05	1															
s.06	1				1									1		
s.07		2	5		1											
s.08		1														
s.09			1										1	1		
s.10			1													
s.11			1													
s.12			1													
s.26			1			1										
s.27						1										
total	**9**	**13**	**16**	**0**	**2**	**5**	**0**	**0**	**0**	**0**	**0**	**6**	**8**	**8**	**0**	**2**

Table 1.3: Fruiting phenology of Solanaceae and Piperaceae in the study area. Number inside brackets after species' names represent sample size for each species. Grey cells represent months when monitored plants were producing fruits. Plants of the Solanaceae were permanently marked, while plants of the Piperaceae were randomly sampled each month.

morfo (N)	**mar.04**	**apr.04**	**mai.04**	**jun.04**	**jul.04**	**aug.04**	**sep.04**	**oct.04**	**nov.04**	**dec.04**	**jan.05**	**Feb.05**
Solanaceae												
Aureliana cf. *fasciculata* (1)											100%	100%
Aureliana sp.1 (13)	23%	8%	8%								8%	15%
Aureliana sp.3 (1)											100%	
Solanum granulosoleprosum (22)				5%	45%	59%	68%	68%	5%			
Solanum phyllosepalum (11)					9%	9%		27%	18%			
Solanum santaecatherinae (3)	33%	67%	67%				33%	33%				
Solanum variabile (14)	21%		14%	7%		7%	7%	36%	29%	36%		21%
Vassobia breviflora (3)	33%							33%	100%	33%		
Piperaceae												
Piper gaudichaudianum (10)					50%	46%	33%	64%	100%	71%		10%
Piper hispidum (10)					14%	12%	33%	21%		7%	7%	23%
Piper mosenii (10)									50%			86%

FIGURES

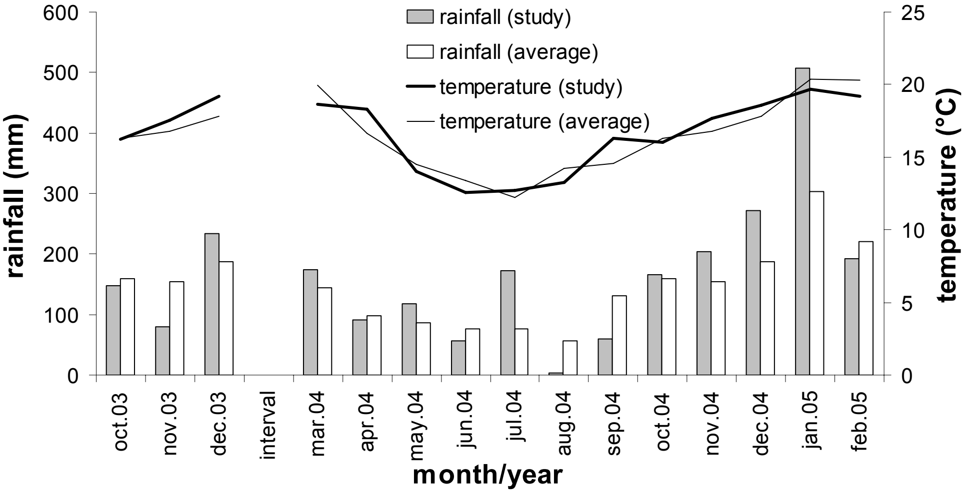

Figure 1.1: Monthly variation in rainfall (mm) and mean air temperature (°C) in the study area. We present data from the sampling period (study) and the average for the past seven years (average).

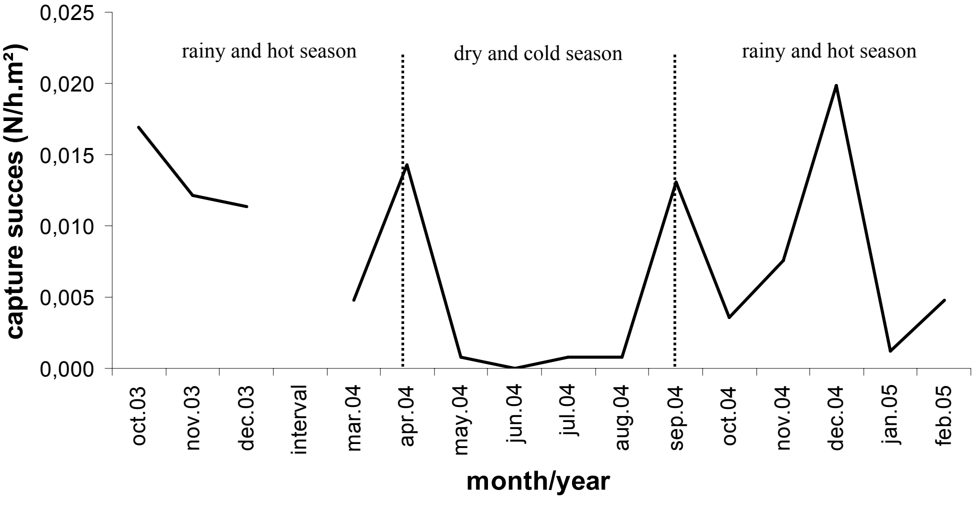

Figure 1.2: Monthly variation in capture success of the bat *Sturnira lilium* in the study area. “Interval” represents two months when we did not carry out sampling.

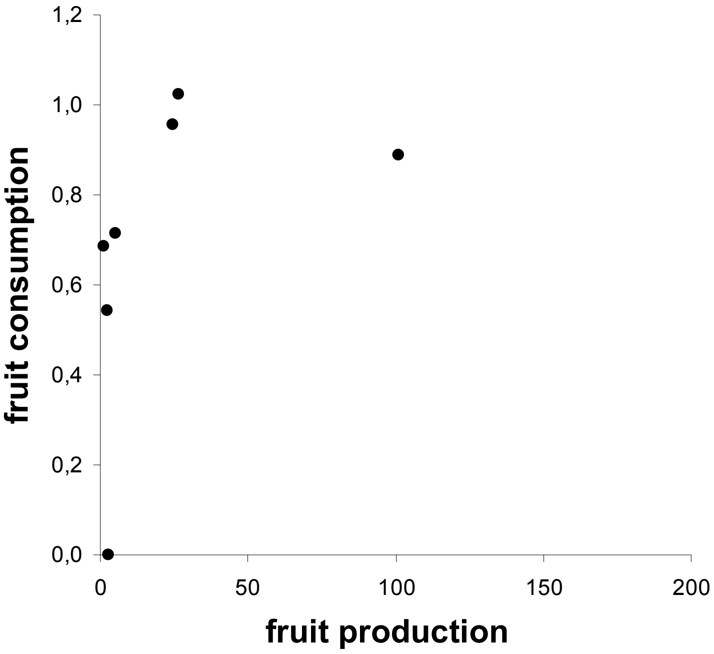

Figure 1.3: Relationship between consumption rate of Solanaceae fruits by *S. lilium*, expressed as percentage of samples that contained seeds of this family on a monthly basis (values were arcsine transformed), and fruit production of Solanaceae, expressed as monthly average fruit crop for each individual plant.

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CAPÍTULO II

Influência do clima e da disponibilidade de alimento na reprodução do morcego *Sturnira lilium* (Mammalia: Chiroptera)

Influence of climate and food availability on the reproduction of the bat *Sturnira lilium* (Mammalia: Chiroptera)

RUNNING TITLE: Reproductive ecology of *Sturnira lilium*.

KEYWORDS: reproduction, dynamics, interactions, frugivory, phenology, Stenodermatinae, Solanaceae, Atlantic Forest.

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ABSTRACT

Frugivorous bats are crucial for the dynamics of tropical forests, especially because of their interactions with plants. In the Neotropical family of leaf-nosed bats (Phyllostomidae), Stenodermatines represent specialized frugivores that tend to breed twice a year. Several factors are known to affect the timing of their reproduction including food availability, climate, and day length. *Sturnira lilium* is a stenodermatine bat with a broad geographic distribution ranging from lowlands to highlands and a strong preference for Solanaceae. This makes it a good model to study how variations in climate and food availability affect timing of reproduction. We studied a population of *S. lilium* in the montane Atlantic Forest of Brazil, by sampling bats with mist-nets and analyzing their reproductive status and diet for 15 months, as well as monitoring fruit production of their main food-plants at the same time. We hypothesized that reproduction would coincide with peaks in fruit abundance coupled with higher temperatures. As found in other studies, *S. lilium* was characterized by an entire frugivorous diet dominated by Solanaceae. As predicted, a higher proportion of females was observed breeding (pregnant or lactating) during wetter and warmer months, when fruits were abundant. We conclude that reproduction of *S. lilium* is strongly linked to plant phenology, particularly Solanaceae.

INTRODUCTION

Bats are highly diverse all over the world and also in Brazil, where they constitute one third of the country's mammal fauna (Marinho-Filho & Sazima, 1998). They are mammals with very interesting life-history characteristics, because they are small (most weigh less than 100 g) but are long-lived (many live more than 30 years) and slowly-breeding (most have one or two offspring a year) (Barclay *et al.*, 2004). The highly diverse and strong trophic interactions between bats and plants are likely to influence life-history and population dynamics of both (e.g. Fleming, 1988). More specifically regarding reproduction, bats are characterized by four basic patterns: 1. seasonal monoestry with a single reproductive peak during the year; 2. seasonal polyoestry with two or three reproductive peaks during the year; 3. a long reproductive period with a short period of reproductive inactivity; and 4. reproduction throughout the year (Fleming *et al.*, 1973; Myers, 1977; Taddei, 1980). A wide range of factors are regarded as determinants of the timing of reproduction, including diet and resource availability, day length, rainfall, and temperature (e.g. Arlettaz *et al.*, 2001; Handley *et al.*, 1991; Kalko, 1998; Kunz, 1982 and 2003).

Among Neotropical bats, members of the endemic family Phyllostomidae are generally characterized by a bimodal reproductive cycle with two peaks per year (Cosson & Pascal, 1994). As our knowledge on reproductive patterns is still limited to a few species (Mello *et al.*, 2004), we selected *S. lilium* as an example to better understand the relationship between reproduction, food availability, and climate. Members of the subfamily Stenodermatinae, which feed almost exclusively on fruits, generally follow the bimodal pattern of phyllostomids.

Sturnira lilium (É. Geoffroy St.-Hilaire, 1810) is one of the most abundant stenodermatines in many localities and has a very broad distribution. It occurs from Mexico to Northern Argentina, including the Antilles (Simmons, 2005), and prefers humid forests, open environments, and secondary vegetation (Giannini, 1999; Tavares, 1999). Geiselman *et al.* (2002) list 28 plant families and 76 plant species as food for *S. lilium*, but this bat has a remarkable preference for the Solanaceae. Therefore, due to its broad distribution and dietary specialization, *S. lilium* is a good model to study the effects of variations in climate and food availability on the timing of reproduction.

The objective of the present study was to describe the reproductive ecology of a *S. lilium* population during a full cycle in the wild, and to test if the pattern found was consistent with the bimodal pattern known from other frugivorous phyllostomids (Kunz, 1982). We specifically wanted to test if reproduction was influenced by variations in fruit availability of Solanaceae and by variations in climate (rainfall and temperature), as it has been demonstrated for other small frugivore and nectarivore bats (Mello *et al.*, 2004; Tschapka, 2005). Special emphasis is given to our study area in the Brazilian montane Atlantic Forest, where climate variations, in particular fluctuations in temperature tend to be more severe than in lowlands (Mantovani, 2001), where most studies on *S. lilium* have been conducted so far. We hypothesized that the main reproductive peak of *S. lilium* should occur in the season of high fruit abundance and high temperatures so that recruitment and weaning of juveniles would take place at high food availability and favorable climatic conditions. Additionally, we hypothesized that the typical bimodal pattern would be less marked in our study area, because its harsher climate would make the bats' reproductive season to be shorter.

METHODS

Time frame and study area

We carried out field work during 36 nights in 15 monthly sessions from October 2003 to February 2005 (except January and February 2004) at the state park "Parque Estadual Intervales" (hereafter "Intervales"), Ribeirão Grande municipality, São Paulo state, southeastern Brazil. Intervales is part of the "Contínuo Ecológico de Paranapiacaba", which represents the largest continuous remnant of Atlantic Forest in Brazil.

Inside the park, we chose the area known as "Sede de Pesquisa" (24º16'24.7"S – 48º25'00.6"W) for sampling bats and plants. This area is located 850 m above sea level and represents the highest research base of the park. In the region, climate is classified as temperate humid (Mantovani, 2001). Average temperatures score 22ºC during the warmest months, while absolute minimum temperatures may reach -4ºC during winter in the highlands. There are one to five days of frost each year, and the number of rainy days at Intervales varies from 125 to 150, with an average annual total rainfall of 2,000 mm. Rainfall can be twice as much (4,000 mm) in the lowlands of the park. At Sede de Pesquisa, the main vegetation consists of Atlantic Forest, and more specifically known as montane dense rainforest (Mantovani, 2001).

Our study species, *Sturnira lilium,* is the most abundant bat species in the area (Passos *et al.* 2003). Some researchers have been inventorying the flora of this region and seeds found in feces of bats and birds, which formed the basis for our dietary study.

Data collection

Intervales' meteorological station provided data on air temperature (°C) and rainfall (mm). Variation in climate followed the general trend of the last seven years (Capítulo I, Fig.1.1).

We captured bats using 10 nylon mist-nets (7 x 3 m – Ecotone, Inc.) each night, which were set on trails and dirt roads in the study area to describe the reproductive cycle and feeding habits of *S. lilium*. Nets were set at a distance of 30 m or more from each other and were kept open for six hours after local sunset. All captured bats were marked with numbered aluminum wing bands (A.C. Hughes, Inc.).

We used the keys provided by Vizotto & Taddei (1973) and Emmons & Feer (1997) to identify bat species. The genus *Sturnira* was represented by two species in the area: *S. lilium*, which was dominant and *S. tildae* that was rarely captured. We based our identification on the characteristics published by Gannon *et al.* (1989), Goodwin & Greenhall (1961) and Simmons & Voss (1998) including forearm length, form of the lower maxilla, of the lower cusps of the molars, and of the lower incisors. For a full species list see Anexo 1. Marcelo R. Nogueira (Universidade Estadual do Norte Fluminense) confirmed the identification of new vouchers.

We used external characters to determine reproductive conditions of adult males and females. For the females, we followed Kunz (1988) and classified the bats into five categories: 1. apparently inactive, 2. pregnant, 3. lactating, 4. pregnant and lactating, and 5. post-lactating. Males were categorized according to the position of their testes, inside the abdomen or inside the scrotum. Because the position of the testes may vary according to non-reproductive effects (fear of the researcher, protection against cold temperatures etc.), we also analyzed the condition of their shoulder glands, which could be active (bright reddish and with strong smell) or inactive, following

Gannon *et al*. (1989). Age was estimated using the method proposed by Kunz (1988) and Cosson *et al*. (1993), based on the ossification of the digital epiphyses.

We studied the feeding habits of *S. lilium* by analyzing fecal samples, which we collected directly from bats captured in mist-nets using small plastic recipients and from individuals that we kept for at least one hour inside clean cloth bags (Capítulo I). In order to estimate food availability for *S. lilium*, we marked 70 individual Solanaceae of 13 species along the trails transverse to our study area and checked the plants on a monthly basis (Capítulo I).

Data analysis

We collected and analyzed climatic data, in order to describe variations in rainfall and temperature in the area and to link them to the demography of both bats and plants (Capítulo I).

The total netting effort during our study was 41,580 h.m² (see Capítulo I for calculations). We described the reproductive status of the *S. lilium* population for each month 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. For some analyses, we pooled all data on reproductively active females and males and did not discriminate between the subcategories. We tested for differences in the proportions of reproductive females and males between the rainy and dry seasons, as well as between abundant and scarce food seasons, using a *t*-test.

We identified seeds from 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. Concerning the phenology of food plants, we assessed the status of the population as the percentage of adult individuals in each category – inactive, flowering, fruiting - on a monthly basis. We also used the average number of fruits produced by individuals of each family in each month as a measure of fruit production (crop).

We based our statistical analyses on Zar (1996), and used the softwares Systat 9.0 (regular statistics) and Oriana 2.0 (circular statistics) for calculations. Percentual data were arcsine transformed, before being used in statistical tests.

RESULTS

We caught a total of 477 bats including recaptures, representing 15 species, which correspond to about 40% of the bat species that had been recorded for the park (34 species). *Sturnira lilium* represented 70% of all captures (N = 333 individuals). The observed sex ratio was biased towards females and scored 1.3:1 (189 females and 142 males: $\chi^2 = 6.39$, $p = 0.01$), and varied only little between months ($G = 21.61$, $p = 0.06$). The population of *S. lilium* showed a marked trend towards seasonal demographic fluctuations.

Capture success varied strongly between months, with the highest number of captures in the middle of the rainy season (December). During the coldest months, *S. lilium* was either not captured at all or at very low numbers (Capítulo I, Fig.1.2). We captured far more adults (n = 287) than subadults (n = 25) or juvenile bats (n = 19), resulting in an age structure dominated by adults ($\chi^2 = 424.48$, $p < 0.001$). Age structure did also present monthly variations and there were two periods of juvenile recruitment on the same year, one in the middle of the rainy season and another between the wet and the dry seasons (Fig.2.1).

The detailed reproductive patterns of females (Fig. 2.2) and males (Fig.2.3) are consistent with a bimodal reproductive pattern. We should notice that as only very few individuals were captured during the colder months, data from this period are less detailed than data of the rainy season. The occurrence of females that are pregnant and lactating at the same time, together with the highest proportion of reproductive females (pregnant + lactating), followed by a decrease in that proportion, and the subsequent short reproductive peak at the beginning of the dry season, and with the pattern of bimodal juvenile recruitment may be regarded as strong evidences of post-partum estrus in *S. lilium*. The proportion of reproductive females was significantly higher in the rainy and hot than in the dry and cold season (n = 15, t = -2.93, p = 0.01), and also higher in the season of high food abundance, although this difference was significant only at a 10% level (n = 15, t = 1.79, p = 0.09). In the case of males, there was no difference between the dry and the rainy seasons (n = 15, t = -1.74, p = 0.10), as well as no difference between seasons of abundance and scarcity of food (n = 15, t = -0.03, p = 0.98). Males also differed from females with regard to synchrony of reproduction, because the proportion of reproductive active adults varied widely during dry and cold season as well as in relation to food abundance (Fig.2.4). Anyway, males did also present their reproductive peaks during the rainy season, as well as females.

The diet of *S. lilium* was entirely frugivorous during the study, and was dominated by Solanaceae (Capítulo I, Tabela 1.1). The proportions of each plant family in the bats' diet varied during the months, but Solanaceae was the preferred family throughout the year (Fig.2.5). The majority of species of Solanaceae revealed a steady-state strategy and continuously produced fruits over several months, with a peak in the first half of the rainy season (Fig.2.6).

DISCUSSION

Although there is a lot of information for frugivorous bats of the subfamily Carolliinae (Fleming, 1988), reports of reproductive activity among the Stenodermatinae have been anecdotal, and seldom as detailed as in Handley *et al.* (1991). In our study, we observed that the reproductive cycle of the local population of *Sturnira lilium* was consistent with the pattern of seasonal bimodal polyoestry (*sensu* Fleming *et al.*, 1973), which is frequently found in frugivorous phyllostomids. Although the pattern observed was not as markedly bimodal as in other case studies (Mello & Fernandez, 2000; Tschapka, 2005; Zortéa, 2003), because the pause between both reproductive peaks of females was not complete, there were two distinct periods of higher juvenile recruitment within a year. Maybe this pattern is influenced by food availability, because the fruiting season tends to be shorter and the fruit crop tends to be lower in the highlands than in the lowlands, and thus bats have to concentrate their reproductive cycle during the most favorable months (as suggested by Barclay *et al*., 2004).

The temporal pattern of a longer reproductive peak followed by a shorter one has been attributed to post-partum estrus in a large number of females, because they get pregnant again when they are still nursing their newborns, and thus there are two periods of juvenile recruitment in the same year (Kunz, 1982). This could be a strategy to increase the number of offspring per year and therefore fitness of females that breed twice a year, when they are in good health condition due to high food abundance and favorable climate (Cosson & Pascal, 1994; Tschapka, 2005). This kind of ecological plasticity, i.e. to reproduce twice in the same year even including the season of lower food abundance, could be responsible for the wide geographic distribution of some phytophagous phyllostomids like *Glossophaga* (Tschapka, 2005). As discussed by Zortéa (2003), even in bimodal cycles of species that are not completely synchronous, most births tend to occur during the rainy season, when food is more abundant. Males showed a more complex reproductive pattern, and it is possible that the method of external evaluation by checking the position of the testes is not fully trustable. In the case of *S. lilium*, we should pay more attention to the condition of the shoulder glands than to the testes, because the former seem to present a more precise clue to the real breeding status of males. It would be interesting in a future study to investigate if *S. lilium* also exhibits delayed embryonic development, as it has been demonstrated for other phyllostomids, in particular the frugivorous *Artibeus jamaicencis* (Kalko, 1998). This strategy permits females to give birth at the most favorable season with high fruit availability.

Our hypothesis of the relationship between climate and reproductive cycle was supported, because *S. lilium* tended to reproduce more during the rainy season, when rainfall and temperature are higher. This pattern was observed for females and males, because both sexes presented reproductive peaks during the rainy season. A positive relationship between reproduction and temperature has also been observed in *Carollia perspicillata*, another small frugivorous phyllostomid (Mello & Fernandez, 2000). Especially in montane forests, like our study area, severe decreases in temperature may beget unfavorable conditions for bats like *S. lilium*, where evidence accumulates that they migrate to lower altitudes during the coldest months. This migration makes it important for us to consider that we captured few bats during the dry and cold season, and therefore we can not know for sure their reproductive pattern during some months. It would be interesting to study *S. lilium* population at lower altitudes in the same park, which we suppose do not undergo seasonal migration, and test if they do really cease to reproduce during the season of fruit scarcity.

Similarly, the variation in food availability showed to be another strong influence on reproduction. Fruits of Solanaceae accounted for 84% of the diet of *S. lilium*. This preference has been observed all over the geographic range of this bat (Geiselmann *et al*., 2002), and thus our data confirmed the importance of this food source. This strong dietary preference probably affects the timing of reproduction in *S. lilium*, because we observed that pregnancy and lactation were concentrated during the months of highest Solanaceae availability, leading to a high reproductive synchrony among females. With this timing, young are born during high fruit availability, in particular by the time they are weaned, as has been shown for other fruit-eating bats, including *Artibeus jamaicensis* (Handley *et al*. 1991; Kalko, 1998) and *Carollia perspicillata* (Mello *et al*., 2004) as well as for bats with a mixed diet (nectar, fruit), including *Anoura geoffroyi* (Heideman *et al.,* 1002) and *Glossophaga commissarisi* (Tschapka, 2004). Timing of reproduction determined by variation in food abundance has also been observed in bats with other diets, like insectivorous vespertilionids (Arlettaz *et al*., 2001).

We conclude from the relative high synchrony in reproduction observed especially among females that *S. lilium* adjusts its reproductive cycle to the specific environmental conditions of montane forests and takes advantage of the relatively short, but favorable season when food availability is higher. For further studies, it would be interesting to compare *S. lilium* populations in the lowlands of the park, where temperature and rainfall are higher than in the highlands, to see if reproductive season is longer and population synchrony lower. There is also the possibility that some part of the reproductive cycle of migratory highland populations of *S. lilium* take place in lowlands, when they move to those areas.

Overall, we conclude that the tight interactions between *S. lilium* and the Solanaceae with a high degree of specialization similar to the ones found as an example for *Carollia castanea* and fruits of Piperaceae (Thies & Kalko, 2004) to a strong dependence of *S. lilium* on this plant family, and to a population dynamic that is largely regulated by plant phenology.

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FIGURES

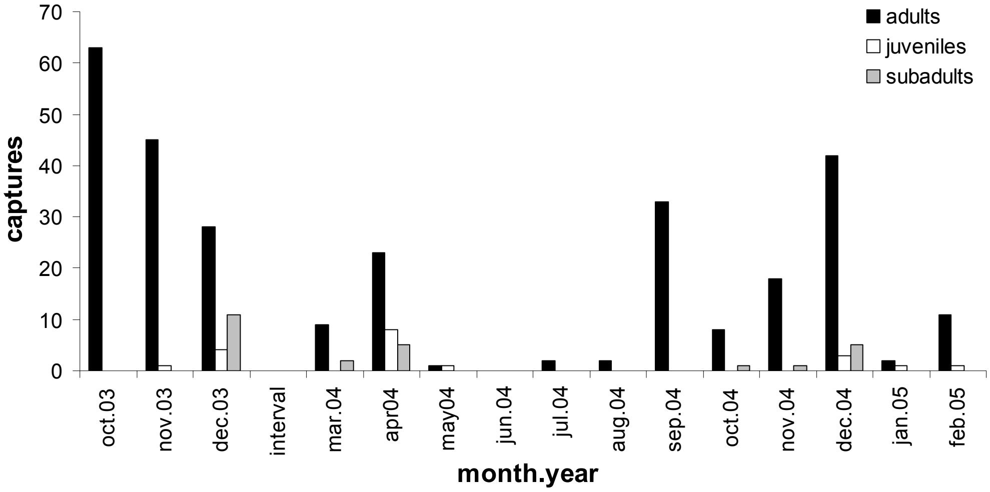

Figure 2.1: Monthly variation in age structure of the population of *Sturnira lilium* in the study area. "Interval" represents two months when we did not carry out sampling.

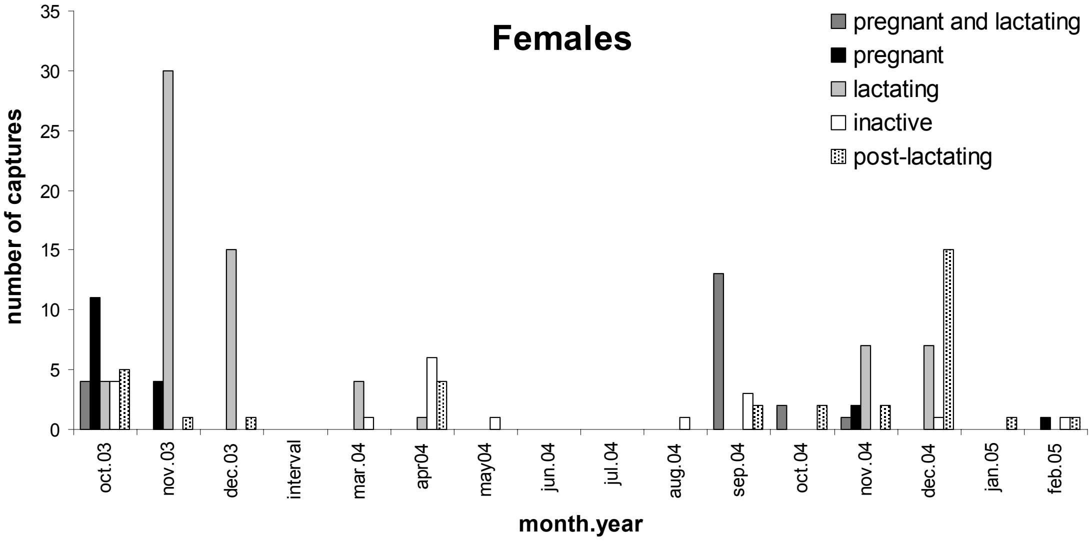

Figure 2.2: Monthly variation in the number of adult females of *Sturnira lilium* in different reproductive status in the study area. "Interval" represents two months when we did not carry out sampling.

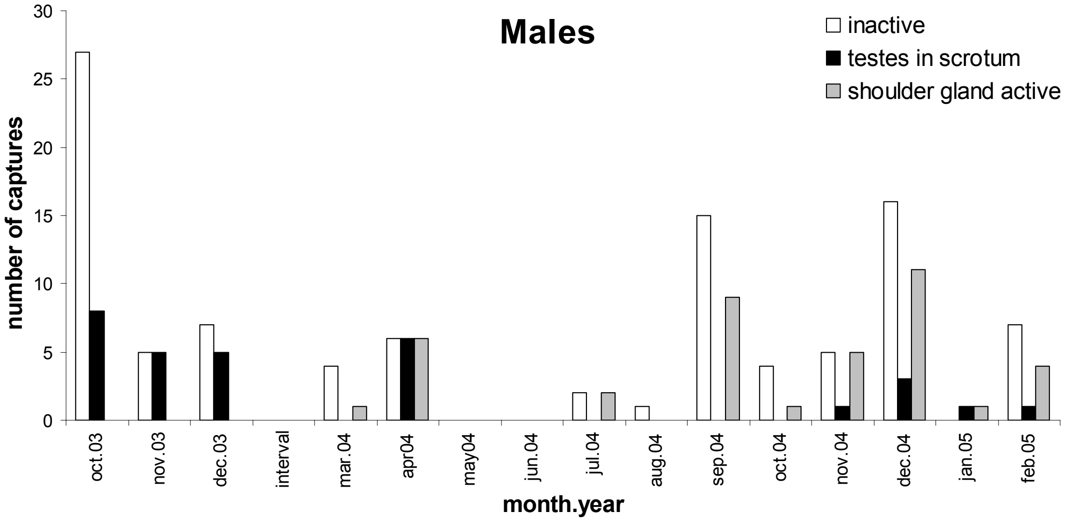

Figure 2.3: Monthly variation in the number of adult males of *Sturnira lilium* in different reproductive status in the study area. “Interval” represents two months when we did not carry out sampling.

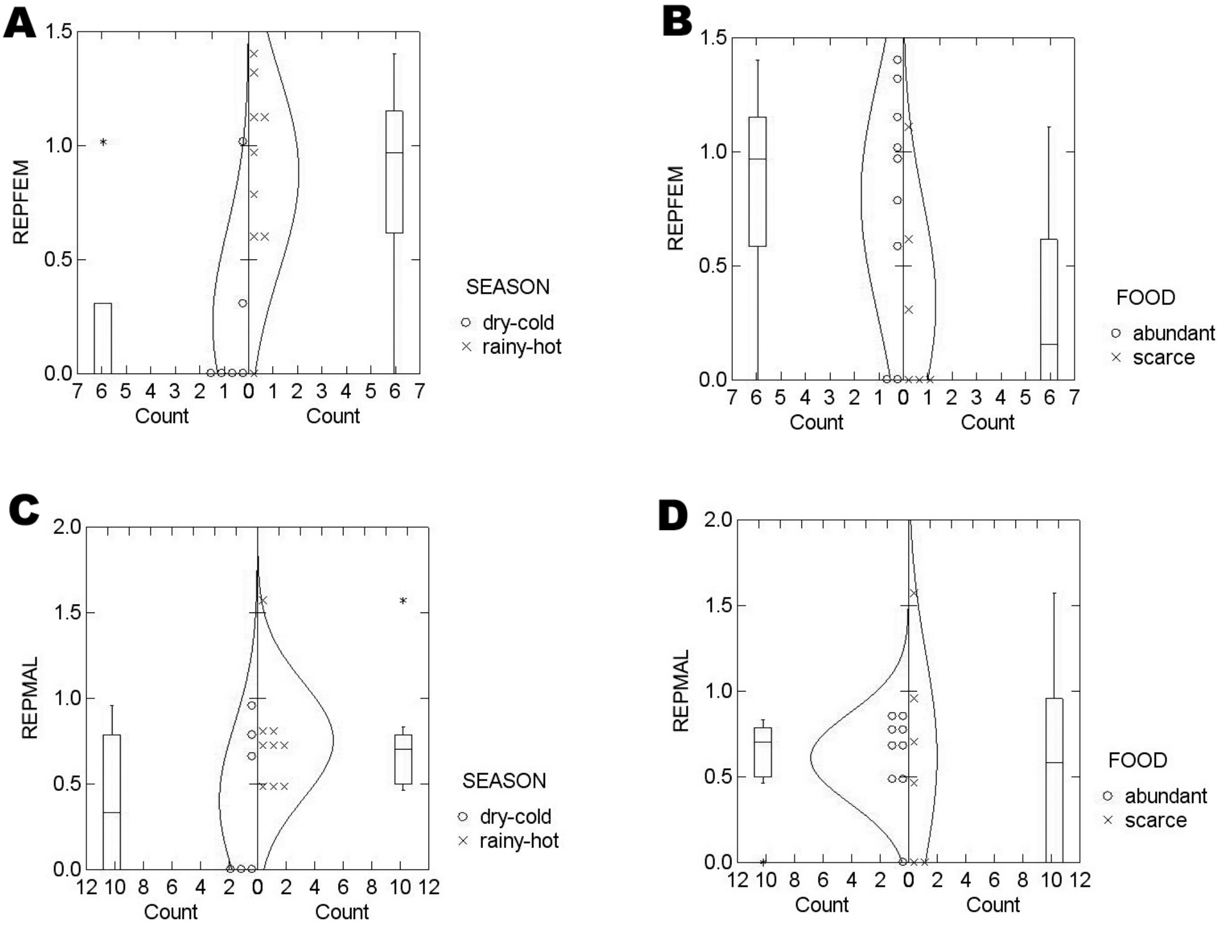

Figure 2.4: Differences between seasons in the proportion of reproductive adults of *Sturnira lilium*. A: proportion of reproductive females (repfem) between the dry-cold and the rainy-hot seasons; B: proportion of reproductive females (repfem) between the seasons of abundance and scarcity of Solanaceae; C: proportion of reproductive males (repmal) between the dry-cold and the rainy-hot seasons; D: proportion of reproductive males (repmal) between the seasons of abundance and scarcity of Solanaceae. Three displays are combined for each group in the graphs: a box plot displaying the sample median, quartiles, and outliers (if any), a normal curve calculated using the sample mean and standard deviation, and a dit plot displaying each observation.

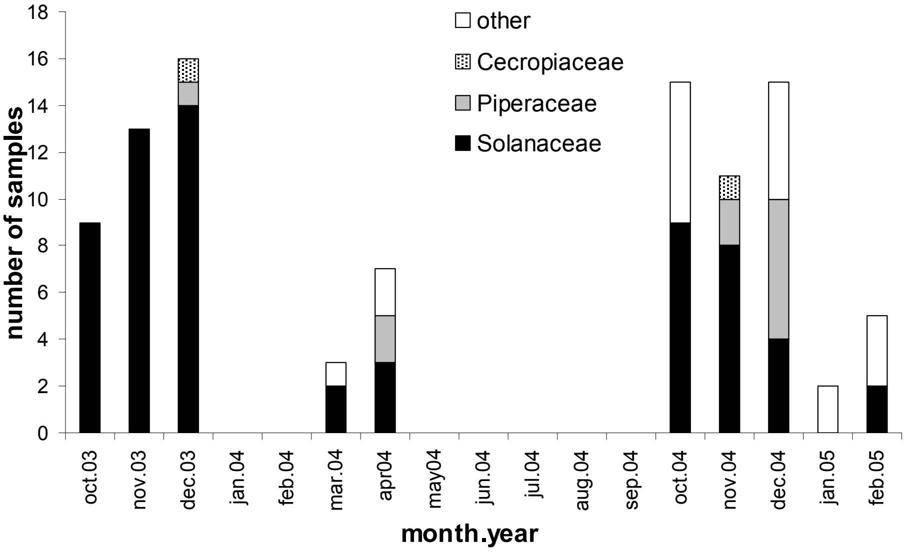

Figure 2.5: Monthly variation in the number of fecal samples that contained different plant families eaten by *S. lilium*. "Other" refers to seeds from unidentified families and plant material other than seeds (e.g. pulp).

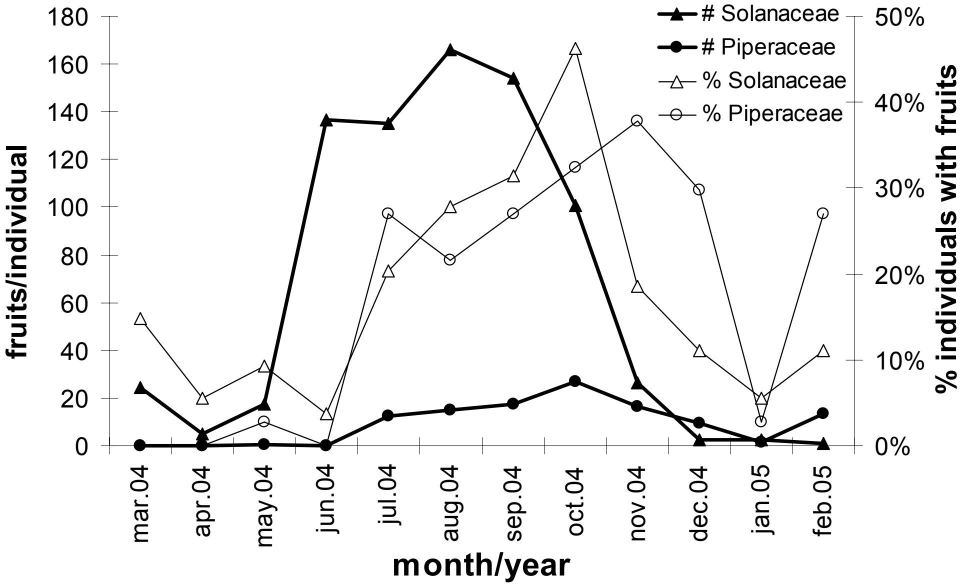

Figure 2.6: Monthly variation in the proportion of individual plants that were producing fruits (thin lines) and in the average individual amount of fruits (thick lines) of Solanaceae (△) and Piperaceae (X).

CAPÍTULO III

Comportamento de forrageio do morcego Sturnira lilium (Chiroptera: Phyllostomidae) e suas implicações para a dispersão de sementes de Solanaceae

Foraging behavior of the bat *Sturnira lilium* (Chiroptera: Phyllostomidae) and its implications for seed dispersal of Solanaceae

RUNNING TITLE: Seed dispersal of Solanaceae by *Sturnira*.

KEYWORDS: interactions, frugivory, seed dispersal, foraging, seasonality, Atlantic Forest.

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ABSTRACT

Seed dispersal may have different consequences on plant species, both at the population and at the community level. Phyllostomid bats are good models for testing some of the hypotheses regarding mutual benefits of this interaction. Within phyllostomids, *Sturnira lilium* plays a particularly important role in this process, because it is widespread, locally very abundant and feeds on a large variety of fruits, mainly of the family Solanaceae. The present study focused on some aspects of the interaction between Solanaceae and *S. lilium* in the Brazilian montane Atlantic Forest, in order to test the quality of seed dispersal delivered by bats, in the context of the 'escape' and the 'colonization' hypotheses. We monitored bat diet and foraging behavior by mist-net captures and radiotelemetry, and simultaneously assessed spatial distribution and phenology of plants. Results suggest a steady-state strategy in fruit production by the Solanaceae, a strong preference of *S. lilium* for those fruits, low roost fidelity both during night and day, and large commuting distances and foraging areas in comparison to other small mammals. We observed also a seasonal variation in bat activity mainly related to air temperature but also to fruit crop production, and a probable seasonal migration. We conclude that seed dispersal by *S. lilium* is highly beneficial to the plants, because those bats are reliable consumers, carry fruits away from the parent-plant, transport them over a large area and drop the seeds unharmed in multiple sites. Consequently, feeding behavior of *S. lilium* is likely to affect distribution of plants in local communities and therefore species diversity.

INTRODUCTION

Seed dispersal is the process of moving seeds away from parent-plants. It can be carried out by different agents, including wind, water, gravity, animals or the plant itself (Fleming & Estrada, 1993). The basis for modern dispersal theory has been formulated by Van der Pijl (1973), who introduced the key concept of "dispersal syndromes". It is widely accepted that seed dispersal greatly influences plant populations and communities (Fuentes, 2000), and contributes to maintenance of diversity in tropical forests (Levine & Murrell, 2003). Two main models have been suggested in terms of benefits for plant populations and increase of plant diversity provided by seed dispersal (Howe & Smallwood, 1982): the “escape hypothesis” (Janzen, 1970; Connell, 1971), which supposes that dispersal from the parent plant increases survival due to escape from species-specific predators and pathogens, and the “colonization hypothesis” (Augspurger, 1984), which states that the availability and effective finding of safe sites for germination is also of major importance for successful dispersal. Both hypotheses are not mutually exclusive and have a large body of empirical evidences, most of them positive (Fuentes, 2000; Levin *et al.*, 2003; Wright, 2002).

Considering those hypotheses and studies that investigated dispersal sequences as they happen in nature, starting with fruit removal and ending with seed deposition (Wang & Smith, 2002), frugivorous bats of the Neotropical family Phyllostomidae, together with birds, are good models for studying those processes because they feed on a variety of fruits, eat large amounts each night, are highly mobile because of their ability to fly, and, among bats, do not harm seeds with the exception of *Chiroderma* (Kunz, 1982; Kalko, 1998; Nogueira & Peracchi, 2003). Bats and birds may be responsible for about 80% of the seed rain in some Neotropical localities (Galindo-Gonzáles *et al.*, 2000). Overall, bats are of paramount importance as models for understanding vegetation dynamics (due to general seed dispersal and pollination), maintenance of diversity (due to alteration of competition balance between dispersed and non-dispersed plants), and regeneration of tropical forests (due to their preference for pioneer plants) (Whittaker & Jones, 1994).

Among frugivorous phyllostomids, *Sturnira lilium* (É. Geoffroy St.-Hilaire, 1810) has a broad distribution area, high local abundance, and flies over several hectares each night (Gannon *et al.*, 1989; Marinho-Filho, 1991; Tavares, 1999). This species occurs from Mexico to Northern Argentina, including the Antilles (Nowak, 1994; Simmons, 2005), and prefers humid forests and open environments including forest edges and gaps, and secondary vegetation (Giannini, 1999;

Tavares, 1999). Geiselman *et al*. (2002) list 28 plant families and 76 plant species as food for *S. lilium* throughout its geographical range. However, most of those items are seldom eaten as *Sturnira lilium* feeds mainly on fruits of Solanaceae, especially of the genus *Solanum* L. (Nowak, 1994). Because of this strong dietary preference, *Sturnira lilium* is likely to play an important role in the dispersal of Solanaceae.

The Solanaceae comprise 63 genera and 1.575 species in the Neotropics and are very abundant in the Brazilian Atlantic Forest. Some species are of considerable economic value as they are used as food, spices, medicines, cosmetics, fume, and narcotics (Nee, 2004). Fruits are harvested by many animals, with some degree of specialization between genera and species of Solanaceae and particular animal taxa (Nee, 2004). Patterns of low and continuous fruit production over an extended period ("steady-state" - Snow, 1965) and the presence of toxic secondary metabolites suggest that this family may have specialized dispersers (Cipollini & Levey, 1997). Some species of Solanaceae interact strongly with bats, depending on them both for pollination and seed dispersal (Sazima *et al*., 2003). "Big-bang" plants may also have specialized frugivory interactions (e.g. Nogueira & Peracchi, 2003), but specialization seems to be more common among "steady-state" strategists (Snow, 1965).

The main objective of the present study was to investigate the foraging behavior of *S. lilium* and to assess its quality as a seed disperser of Solanaceae in the Brazilian Atlantic Forest. This biome is a research priority, because it is almost totally destroyed through human activities. The remaining patches, however, still comprise a surprisingly high biodiversity, and are considered as a "hot spot" by the IUCN (Myers *et al*., 2000). We focused on the following hypotheses in order to evaluate if seed dispersal of Solanaceae by *S. lilium* is effective, i.e. if transport by bats is likely to improve seed survival and seedling establishment. First, the Solanaceae consumed by bats should produce fruits over longer periods of time with a 'steady-state' strategy (Fleming, 1982), thus being a reliable food source during most of the year. Second, bats should feed mainly on those plants, so they would be reliable consumers and potential dispersers. Third, according to the escape hypothesis, bats should pick up fruits from the parent-plants, eat their pulp and drop the seeds away from the parent plants. Fourth, as proposed by the colonization hypothesis, the bats should fly over a large area and use different night roosts, so that seeds would be widely scattered throughout the landscape, increasing their chance to find 'safe sites'.

METHODS

Time frame and study area

We conducted our study during 36 nights in 15 monthly sessions from October 2003 to February 2005, except January and February 2004, at the conservation area "Parque Estadual Intervales" (hereafter referred to as "Intervales"), Ribeirão Grande municipality, São Paulo state, southeastern Brazil. Intervales and three neighboring conservation units form the "Contínuo Ecológico de Paranapiacaba" which represents the largest continuous remnant of Atlantic Forest in Brazil.

Within Intervales, we worked in "Sede de Pesquisa" (24º16'24.7"S – 48º25'00.6"W), located at 850 m above sea level. We covered an area of ca. 400 ha for our study, where we monitored bats and plants. The climate of the region classifies as temperate humid or Cwa in the system of Köppen (Mantovani, 2001), with average temperatures of 22ºC during the warmest months, and minimum temperatures scoring -4ºC during winter at the highest altitudes. There are one to five days of frost each year. The number of rainy days at Intervales varies from 125 to 150. Average annual total rainfall amounts to ca. 2,000 mm, and can be double (4,000 mm) in the lowlands of the park. The main vegetation at Sede de Pesquisa classifies as montane dense rainforest or mist forest.

Sturnira lilium, our study species, is abundant in Sede de Pesquisa (Passos *et al.* 2003). Furthermore, the flora at this region is rather well known as it has been inventoried recently (Passos *et al.* 2003), facilitating identification of the bats' food plants.

Data collection

Data on climate - air temperature (°C) and rainfall (mm) - were provided by the Intervales' meteorological station on a daily basis. We pooled data together on a monthly basis to compare them with biological data from bats and plants.

To describe the phenology of the main food-plants of *S. lilium*, we marked 70 individual Solanaceae from 13 species that we found at trails dissecting our study area, and checked their phenology monthly following Korine *et al*. (2000). We distinguished between inactive, flowering, fruiting or flowering/fruiting. Furthermore, we counted total number of flowers and fruits in individuals that could be completely observed and made estimates for individuals that were not totally observable. This applied to about 10 % of all sampled individuals that were either too high or covered by vegetation. Because Piperaceae were much more abundant than Solanaceae, occurred in clumps and usually died more quickly and frequently, we randomly picked 30 individuals of four species scattered along the same trails as the Solanaceae, and checked their phenological status on a monthly basis by counting number of flowers and fruits for each plant. Identification of plants was made by Jorge I. Tamashiro (Universidade Estadual de Campinas), Rafael Fernando da Silva Possette (Embrapa Florestas), Osmar Ribas and Gerdt Hatschbach (Museu Botânico Municipal de Curitiba). Vouchers were deposited in the collection of the "Laboratório de Interações Vertebrados-Plantas" of the Universidade Estadual de Campinas.

To describe patterns of feeding habits and use of space in *S. lilium*, we captured bats on a nightly basis with 10 nylon mist-nets (7 x 3 m – Ecotone, Inc.), set on trails and dirt roads in the study area. They were kept open for six hours after sunset. Mist-nets were set at least 30 m apart from each other, and half of them were positioned near known patches of food plants and the other half at random points, to reduce bias caused by net placement. We used a fixed number of netting-points that we mapped with a Garmin GPS 12 (error < 8 m). All captured bats were marked with numbered aluminum wing bands (A.C. Hughes, Inc.), to identify recaptures and derive movement patterns.

We used the keys provided by Vizotto & Taddei (1973) and Emmons & Feer (1997) for identification of bat taxa. There were two species of *Sturnira* in the area, *S. lilium* was the most abundant and *S. tildae* was seldom captured. We used the morphological characters suggested by Gannon *et al*. (1989), Goodwin & Greenhall (1961) and Simmons & Voss (1998) to identify them. The identification of some bat species was confirmed by Marcelo R. Nogueira at the Universidade Federal Rural do Rio de Janeiro. We kept one voucher of *Phylloderma stenops* (Phyllostomidae) as a new record for the area, and it was deposited in the collection of the Laboratório de Interações Vertebrados-Plantas of the Universidade Estadual de Campinas.

We studied the feeding habits of *S. lilium* by analyzing fecal samples, which we collected directly from bats captured in mist-nets and from individuals that we kept for at least one hour inside clean cloth bags. Each sample was put in a fine-meshed sieve and carefully rinsed under a faucet, to separate seeds from pulp and other materials like insect parts. Seeds were first classified onto family level, and in most cases also to genus. In some cases we were able to identify the seeds based on a reference collection of seeds eaten by birds and bats in the study area, which had been started in previous studies (Passos *et al*., 2003).

To study patterns of space use by *S. lilium*, we conducted two telemetry monitoring sessions including 10 consecutive nights, one in October 2004 when fruit abundance of Solanaceae was high and the other on February 2005 when fruit abundance of Solanaceae was low. We followed six adult, non-reproductive *S. lilium* in each session, leading to a total of 12 tagged individuals (six males and six females). The bats were equipped with small radio-transmitters (models LB-2 and BD-2N, Holohil Systems, Inc.) attached to their backs between the shoulder blades (scapula). They were glued onto the bats' backs with a drop of surgical glue. All transmitters were below the 5 % limit with regard to the bat's body mass (4.3±0.4%) addressed by Aldridge & Brigham (1988), who found that bats might be somewhat affected in their mobility if transmitters exceed 5 % of their body mass. We used one radio-receiver (model TRX-1000S, Wildlife Materials, Inc.) to monitor individuals by triangulation, and recorded signals from all six tagged bat first from one previously mapped point in the study area, and then moved on to the next nearest point. Intervals between consecutive bearings at the fixed points were shorter than three minutes. We excluded data from analysis when bearings did not intersect or when the interval between records was longer than three minutes. Our method did not allow precise localization of bats in flight, but it permitted a decent estimate of the size of foraging and roosting areas. According to previous field tests, where we compared locations estimated by triangulation with previously known GPS-mapped locations, the error of our position estimates is around 20 m.

Data analysis

We used simple linear correlations to test if the climate data from the study period (temperature, rainfall) followed a pattern similar to the average variation in the area based on seven years or if the weather pattern of our study period was atypical. Variations in rainfall and temperature corresponded to the long-term monthly means that had been registered in the area for the last seven years (rainfall: $r^2 = 0.76$, $p < 0.001$; temperature: $r^2 = 0.85$, $p < 0.001$) (Capítulo I, Fig.1.1).

Concerning phenology of food plants, we assessed the status of the population as percentage of adult individuals in each category – inactive, flowering, fruiting - on a monthly basis. To compare phenology and bat movement data, we used the monthly average amount of fruits in individual crops of each family and the total amount of fruits in the crops of individual Solanaceae throughout each telemetry session. We tested the relationship between fruit production and climate (air, temperature, and rainfall) by multiple linear regressions. To determine whether fruit production is randomly distributed or is bound to a specific season, we used Rayleigh's circular test. To assess whether Solanaceae and Piperaceae differ in their phenologies, we used Watson-Williams circular test.

To address feeding habits, we pooled the dietary data of *S. lilium* on a monthly basis based on the number of plant species and the percentage of samples that contained seeds of each taxon.

We tested the feeding preferences of *S. lilium* with a χ^2-test (whole dataset) and a G-test (months). We investigated the relationship between consumption and production of fruits of Solanaceae with a logarithmic model, to find out whether consumption remains constant when production reaches a high level, as proposed in Mello *et al*. (2004a).

To study demographic patterns of *S. lilium*, both in space and time, we calculated netting-effort during our study as the total number of m^2 of nets opened each night multiplied by the total number of hours worked in the whole study (Straube & Bianconi 2002). Our total netting effort was 41,580 $h.m^2$. For estimating flight distances, we plotted locations of bats, obtained by radiotelemetry or mist-netting, in the software ArcView 3.2a. We treated data from radio-tracking and mist-netting separately, because they are not directly comparable due to different time scales and methods of estimation. We then used the extensions "Animal Movement", "Spatial Analyst" and "X-Tools" for calculating areas, perimeters of the polygons, and flight distances. Values are given in meters and hectares. For calculating areas used by individual bats, we used the method of "minimum convex polygon", which is proper for comparisons with other studies in the literature and also for situations where the number of located positions is small. We also calculated the maximum distances flown by individual bats from its day roost to a foraging location ("commuting distance"), and also between two different foraging locations during the night (linear distance). We tested the relationship between capture success (number of captures / effort), climate (air temperature and rainfall) and fruit production by Solanaceae by a multiple linear regression. Hypotheses concerning foraging areas, flight distances, and roost fidelity were tested by checking if observed patterns matched our expectations qualitatively.

We based our statistical analyses on Zar (1999), and used the softwares Systat 9.0 (regular statistics) and Oriana 2.0 (circular statistics) for calculations. Percentual data were arcsine transformed, before being used in statistical tests.

RESULTS

Concerning the phenological study, we found 12 species of the family Solanaceae in the area: *Aureliana* cf. *fasciculata, Aureliana* sp.1, *Aureliana* sp.2*, *Aureliana* sp.3, *Solanum americanum*, S. granulosoleprosum, S. phyllosepalum, S. santaecatherinae*, *S. swartzianum*, S. variabile, Solanum* sp.1, and *Vassobia breviflora.* The Piperaceae were represented by four species: *Piper gaudichaudianum, P. hispidum*, *P. mosenii*, and *P. xylosteoides*.* We also observed one member of the Cecropiaceae, *Cecropia glaziovii,* and one member of the Moraceae, *Ficus luschnatiana*, that could be bat-food in the area. Species marked with an * did not produce fruits during the study and were therefore omitted from further analysis.

The majority of Solanaceae and Piperaceae presented a steady-state strategy, because they produced a few ripe fruits per day over several months (Capítulo II, Fig.2.7). Despite the extended fruiting season, fruit production was characterized by peaks (Solanaceae: Rayleigh's Z = 17081.78, $p < 0.001$; Piperaceae: Z = 1,009.63, $p < 0.001$). Fruiting peak of the Piperaceae (October) occurred two months after the Solanaceae (August) (F = 2,560.554, $p < 0.001$). Fruit production in the Solanaceae was negatively related to air temperature (standardized partial coefficient of the multiple regression (b') = -0.659, p = 0,034), but was not explained by rainfall (b' = -0.183, p = 0.505), indicating that fruit production was higher during colder months. In the Piperaceae, rainfall (b' = -0.154, p = 0.724) and temperature (b' = 0.004, p = 0.992) were not related to fruit production. Fruiting varied also among and within species. Within the Solanaceae and the Piperaceae, respectively, the species with largest crops during the studied year were *Solanum granulosoleprosum* (total = 35,136 fruits, mean = 171.4±527.5) and *Piper gaudichaudianum* (total = 2,452 fruits, mean = 13.9±25.9).

In our study, we obtained 477 captures (including recaptures) from 15 bat species: 13 were members of the Phyllostomidae and two of the Vespertilionidae. Overall capture success was low (11.5×10^{-3} captures/h.m²) in comparison with studies in lowland areas of the Brazilian Atlantic

Forest (e.g. 37.3 x 10^{-3}, Mello, 2002). *Sturnira lilium* dominated with 70% of all captures (N = 333 captures). We analyzed 96 fecal samples from *S. lilium* throughout the study to assess its diet. Only one kind of seed was present in each fecal sample. 21 samples contained only soft parts of the fruits or unidentified seeds. No animal parts were observed. As expected, *S. lilium* bats fed mostly on fruits of Solanaceae throughout the year with an average of 59 ± 33% among months (n = 96, G = 66.66, p = 0.019) (Capítulo II, Fig.2.5). They represented 84% of all identified seed samples, compared to Piperaceae, Cecropiaceae, and other unidentified plant families (n = 96, $\chi^2 = 94.92$, $p < 0.001$). Despite this strong preference, bats ate also Piperaceae (13%) and Cecropiaceae (3%). Among Solanaceae, *S. granulosoleprosum* dominated with 40% of all samples, and among Piperaceae, *P. gaudichaudianum* prevailed (6%). Fleshy material from unidentified fruits represented 19% of all samples, and most of them seemed to be Solanaceae or Piperaceae.

We analyzed temporal and spatial patterns of capture success of *S. lilium* in order to understand its population dynamics and use of space. Capture success varied a lot among months with an average value of 7.46 x 10^{-3} ± 6.64 x 10^{-3} captures/h.m² (Capítulo I, Fig.1.2). During the coldest months *S. lilium* was not captured at all, or only very rarely. Capture success of *S. lilium* at the netting-points was in average 7.46 x 10^{-3} ± 6.64 x 10^{-3} captures/h.m², varying from 0 to 19.8 x 10^{-3} captures/h.m². Bats were seemed to be captured in higher frequencies around some species of Solanaceae, and not necessarily around any productive individual (Fig.3.1). Unfortunately, this relationship could not be tested statistically, because of the sampling design along trails. We could not establish a grid design due to topographic irregularities and very dense understory in the area. Our captures comprised 306 individuals of *S. lilium* and a recapture rate of 8% (N = 27). The low recapture rate suggests a higher mobility in comparison to other similar-sized phyllostomids in the area, including the primarily frugivorous *C. perspicillata* with a recapture rate of 44% (36 recap. / 81 cap.). We also recaptured 12 individuals of *S. lilium* that had been marked in a previous study (Passos et al., 2003) up to two years ago. These results suggest rather high site fidelity of *S. lilium* in the study area (Fig.3.2).

Unfortunately, bats could be monitored by radiotelemetry only for 10 days, at the season of highest food abundance (October 2004). In the season of low food abundance (February 2005), we were unable to monitor the bats' behavior in greater detail because we consistently received only a few very weak signals for all of the individuals the night after tagging although all transmitters were working well before the release of the bats. This pattern suggests to us that the tagged bats must have flown far away from our study area.

During high fruiting season, we obtained several data from the six radio-tagged bats (Tab.3.1). Areas used by individual bats (MCP) varied between 1.31 and 13.67 ha (Fig.3.3), while the maximum distance flown by a single bat from a day roost to the foraging area (commuting distance) during the monitored period varied from 480 to 760 m. All bats foraged in almost the same core area every night, where many Solanaceae trees were available, and used more than one nocturnal feeding roost. Furthermore, tagged bats roosted at different locations during different days, showing no day-roost fidelity (Figs. 3.4 and 3.5).

DISCUSSION

In our study on foraging habits of *S. lilium* and its relationship with its main food source, Solanaceae, we conclude that *S. lilium* fulfills a range of prerequisites that makes it an effective disperser.

The Solanaceae showed a phenological pattern that is consistent with the 'steady-state' strategy (Altringham, 1998; Snow, 1965), typical of plants that attract 'reliable' consumers, i.e. animals with a particular feeding preference or specialization, which depend on the plant to meet their nutritional requirements and therefore concentrate their foraging activities on selected target-species in a given area (Altringham, 1998; Fleming, 1982; Snow, 1965). Indeed, *S. lilium* was a reliable consumer of Solanaceae, because fruits of Solanaceae represented 84% of its diet. This pattern is consistent with findings on the diet of *S. lilium* reviewed in Geiselmann *et al.* (2002)

referring to the whole geographic range of *S. lilium*. The dominance of Solanaceae in the diet of *S. lilium* has also been reported at several other localities in South and Central America (Iudica & Bonaccorso, 1997; Marinho-Filho, 1991; Passos *et al*., 2003; Uieda & Vasconcellos-Neto, 1985).

Foraging activity of *S. lilium* was concentrated on patches with many trees and shrubs of Solanaceae, a pattern revealed both through a comparatively high number of captures in mist-nets and our tracking data. The concentration of foraging activity of *S. lilium* on particular species, like *Solanum granulosoleprosum* (one of the most common in the study area), was also reported by Cáceres & Moura (2003). Data on spatial use combined with data on diet suggest that Solanaceae plants affect spatial distribution of *S. lilium* in the study area. However, we found this pattern of concentrated use only in the season of high fruit availability. During the season of fruit scarcity, radio-tagged bats most probable used a much larger area and did not concentrate their foraging activity at a specific site. This is corroborated by the very low capture success during this time of year.

Furthermore, there is increasing evidence that *S. lilium* conducts a seasonal altitudinal migration (Giannini 1999; Capítulo I) probably to harvest fruits of Solanaceae at lower altitudes. Interestingly, our recaptures suggest that the bats return to the same individual foraging sites every year, because some individuals have been repeatedly recapture inside the same 400 ha area since three years.

Regarding the 'escape hypothesis', we found evidence that S. lilium indeed contributes to the movement of the seeds away from the parent plant. Night-roosts of individual *S. lilium* were scattered all over within and also outside the common core foraging area of all tagged bats, suggesting that bats plucked fruits from trees and bushes and brought them to temporary night roosts to consume them (Fleming, 1988; Kunz, 1982). This "shuttling" foraging behavior is well known from other frugivorous phyllostomids including *Carollia perspicillata* (Fleming, 1988) and is interpreted in part as predator-avoidance as predators might concentrate around fruiting trees and lay in wait for foraging bats (Handley *et al*., 1991). As the seeds of Solanaceae are tiny, *S. lilium* probably swallows them whole when processing fruit. As gut passage is rapid in phyllostomid bats (Kunz, 1982; Thies *et al.*, in press) and as small seeds pass through the gut unharmed (Iudica & Bonnacorso, 1997) except in *Chiroderma* where seeds are chewed (Nogueira & Peracchi, 2003), *S. lilium* is likely to disperse viable seeds at the various night roosts and probably also during flight. With this behavior, *S. lilium* may increase the reproductive success of Solanaceae in the area, by reducing density-dependent mortality near parent-plants.

Similarly, the 'colonization hypothesis' was also supported, because bats showed no fidelity to night and day roosts, and flew at least several hundred meters in the dry season and more in the rainy season between day roosts and feeding areas, and also between temporary night roosts inside their foraging areas. This behavior is similar to other small phyllostomids (Bernard & Fenton, 2003; Charles-Dominique, 1991; Fleming *et al.*, 1972; Thies *et al.*, in press). The bats frequently changed location of night-roosts, so it is reasonable to suppose that *S. lilium* delivers seeds not always at the same site, what may increase its efficiency as a seed disperser. This behavior probably generates a scattered seed rain, and increases the possibility of depositing seeds at 'safe sites', i.e. sites favorable for germination and establishment of seedlings (Augspurger, 1983), like in the systems studied by Ebigbo *et al*. (in press) and Thies *et al*. (in press). This is especially important because *S. lilium* seems not to use caves as roosts as other frugivorous bats such as *C. perspicillata* (hier ein oder zwei Fleming Referenzen angeben), therefore delivering all of the seed rain to the forest (Fenton *et al.*, 2000). However, this requires further study, particularly to identify the microsites and the plants used by *S. lilium* as feeding perches (night roosts), in order to better evaluate the chances of seeds for successful germination.

Interestingly, *S. lilium* used a different area for foraging at night than for roosting during the day. Perhaps environmental characteristics requested for roosting are not the same as for feeding areas, because *S. lilium* may require large trees for roosting (Evelyn & Stiles, 2003), which were more abundant in the main roosting area at Intervales than in the main foraging area of the bats, whose physiognomy is more of a second-growth open area. However, roost use in *S. lilium* is not fully clear as Fenton *et al*. (2000 and 2001) reported in their study areas that *S. lilium* bats may roost also within vegetation underneath palm leaves and in vine tangles.

All these evidences lead us to conclude that *S. lilium* plays an important role as seed disperser of Solanaceae in our study area. Overall, the interaction with *S. lilium* is likely to be highly beneficial for Solanaceae, because bats may increase gene flow between different plant populations due to the use of different night roosts and areas over which they fly and most likely drop viable seeds, therefore increasing fitness of some Solanaceae species. Nevertheless, as not all Solanaceae species in the area seem to be eaten by *S. lilium,* and some present actually typical signs of bird dispersal (according to Van der Pijl, 1972), benefits of bat dispersal may be restricted to a few species, improving their ability to reach suitable germination sites and probably altering the balance of interspecific competition for space. It would be interesting to compare the density and spatial distribution of bat and bird-dispersed Solanaceae in the area, in order to test if services delivered by bats and birds result in different outcomes for sympatric plant populations.

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TABLES

Table 3.1: Summary of data obtained by radiotracking six adult non-reproductive *S. lilium* during 10 days in October 2004.

transmitter #	**23**	**24**	**25**	**26**	**27**	**28**
Sex	male	female	female	male	Male	male
body mass (g)	20	21	21	23	22	25
transmitter mass (g)	0.9	0.9	0.9	0.9	0.9	0.9
% load carried by bat	4.5%	4.3%	4.3%	3.9%	4.1%	3.6%
days of contact (out of a total of 10 days)	5	5	6	6	6	6
# positions triangulated	2	5	5	11	6	5
# different resting positions located by day (day roosts)	0	0	0	3	2	0
# different resting positions located at night (night roosts)	0	1	2	1	1	2
total area used MCP (ha)		1.31	0.89	13.67	10.56	1.50
maximum linear flight distance (m)	140	220	190	250	470	400
maximum linear commuting distance (m)				760	480	

FIGURES

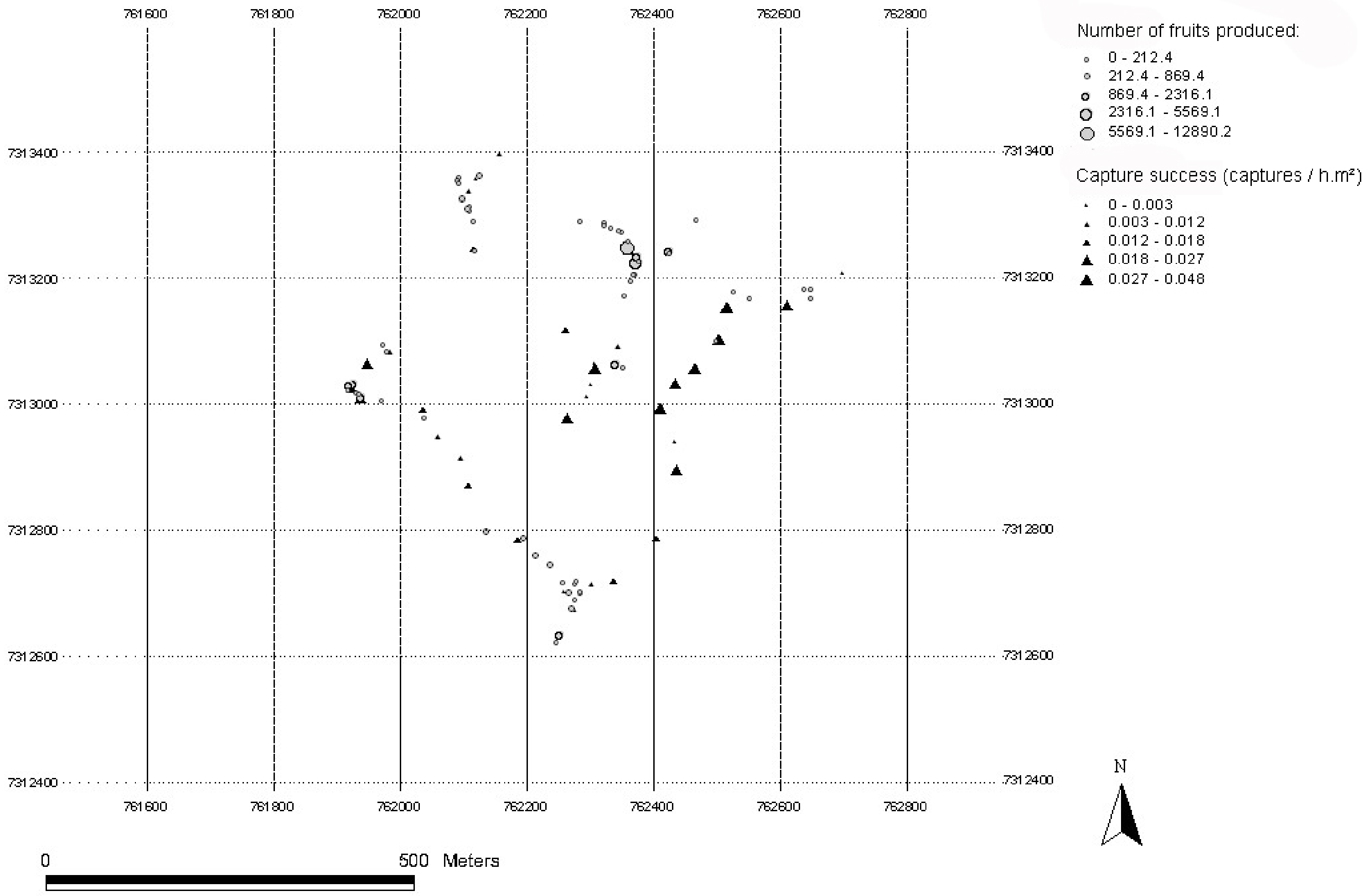

Figure 3.1: Spatial distribution of captures of *S. lilium* at different netting-points (triangles) combined with spatial distribution of Solanaceae plants (circles) with their total number of fruits produced during the study. Coordinates are in UTM.

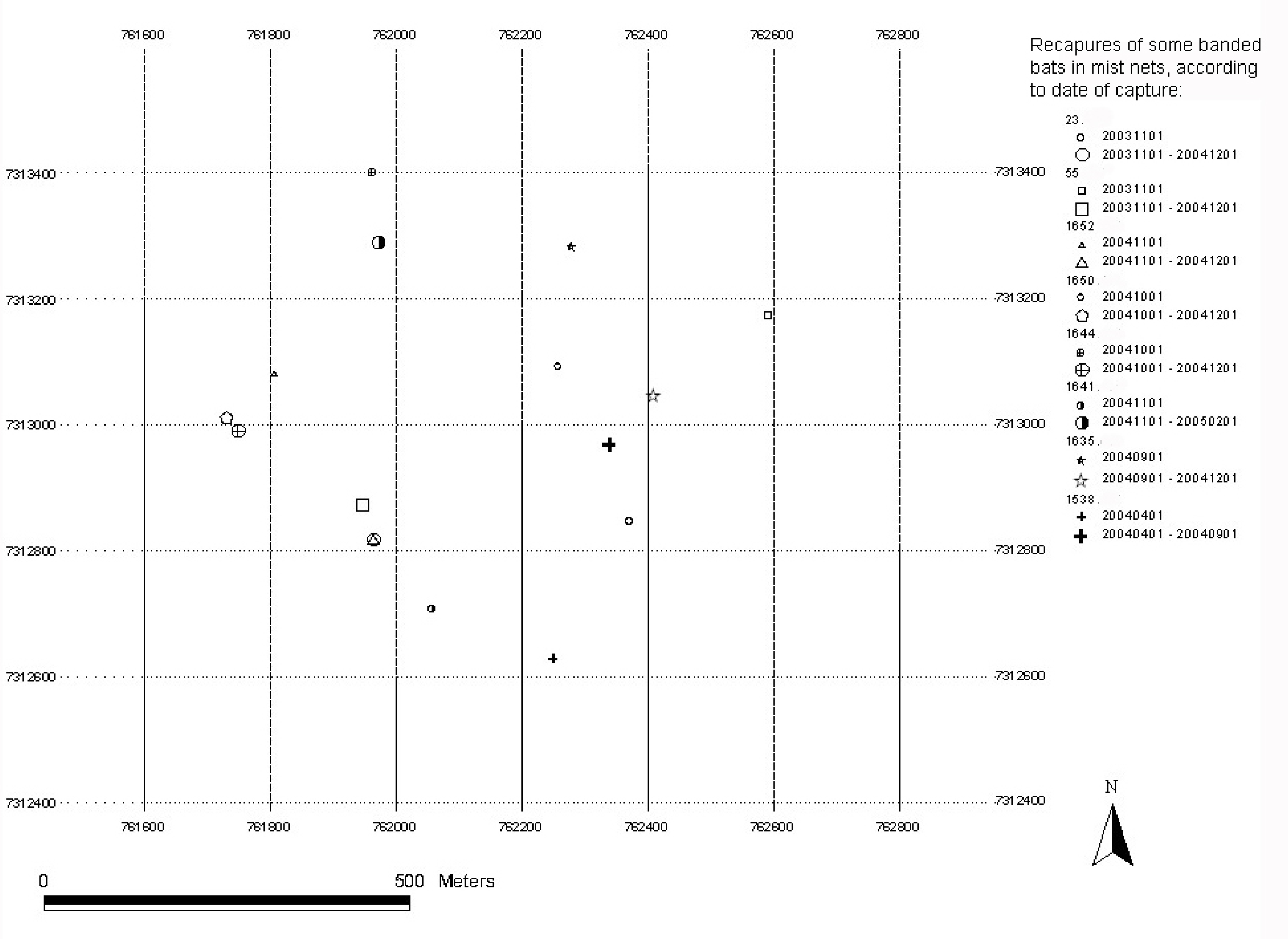

Figure 3.2: Recaptures of *S. lilium* in mist-nets (positions were the same during the whole study). In the codes of dates, the four first digits stand for the year (e.g. 2004), the fifth and sixth digits stand for the month (e.g. 09, September), and the seventh and eighth digits stand for the day (e.g. 01). Coordinates are in UTM.

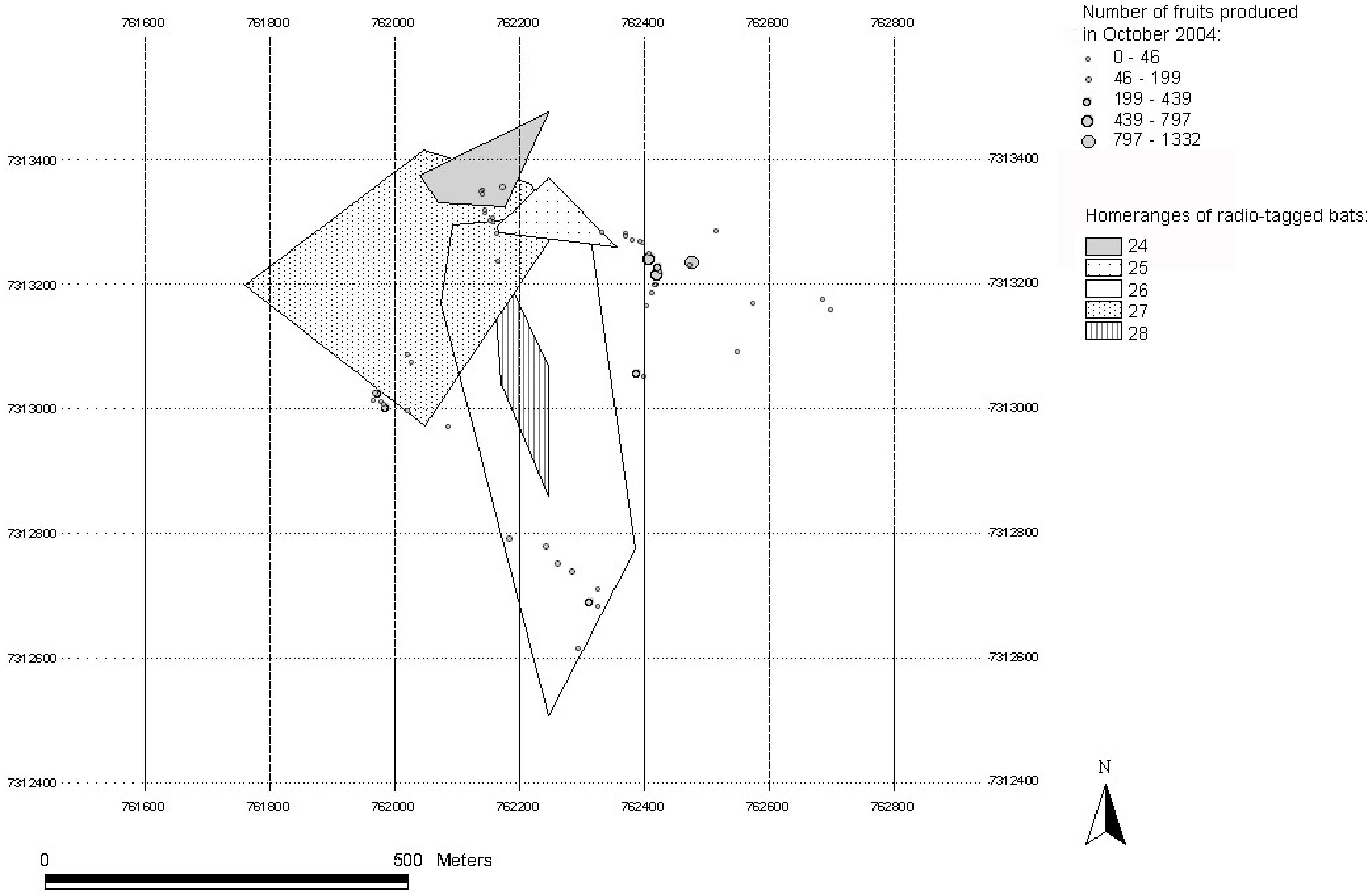

Figure 3.3: Areas used (Minimum Convex Polygon) by five *S. lilium* radiotracked for 10 days in October 2004. Gray circles stand for individual Solanaceae plants and their total number of fruits produced in October. Numbers in the legend stand for the individual codes of individuals (see details in Table 3.1). Coordinates are in UTM.

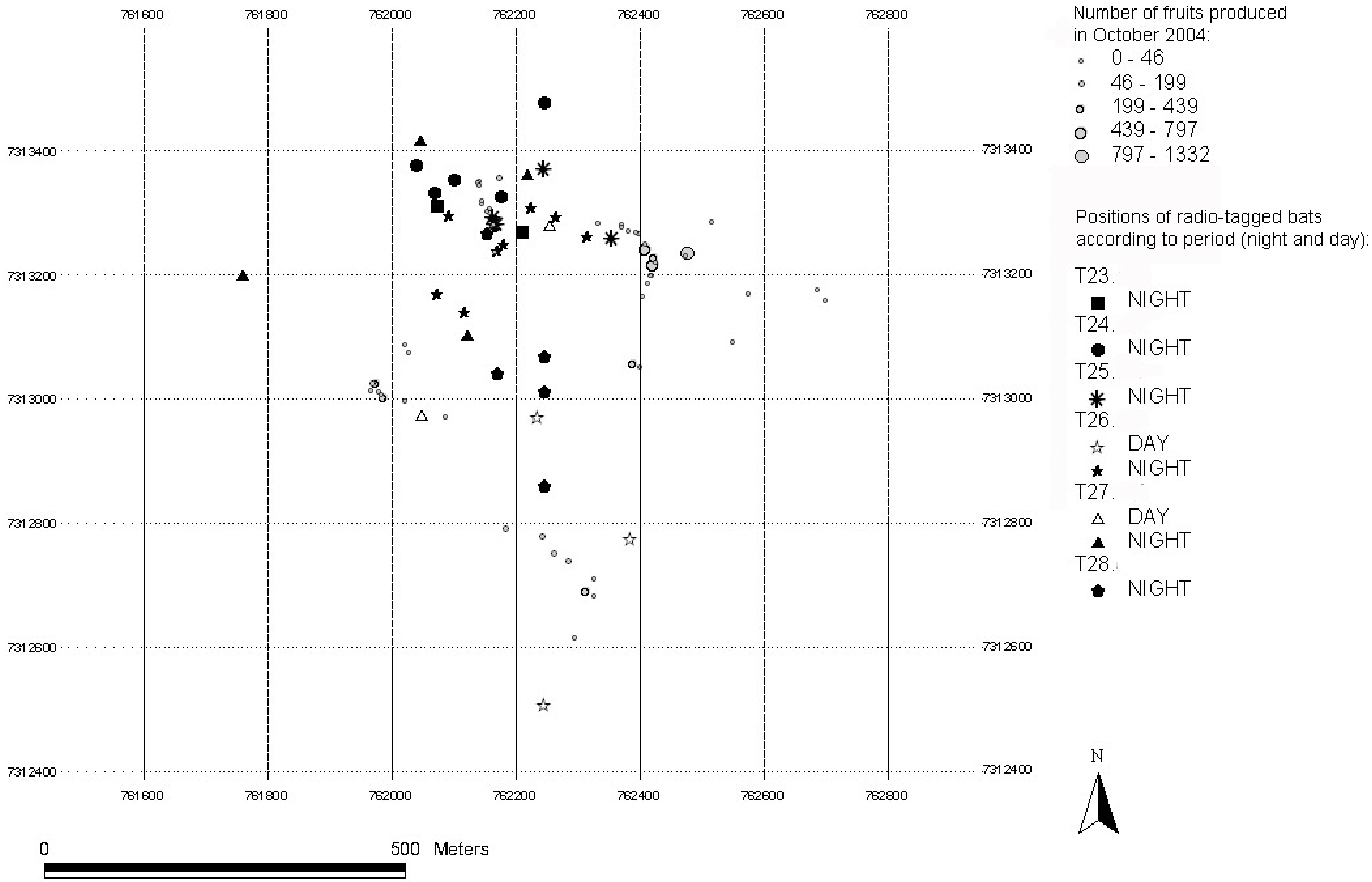

Figure 3.4: Positions of six *S. lilium* radiotracked for 10 days in October 2004, during day (white symbols) and night (black symbols). Gray circles stand for individual Solanaceae plants and their total number of fruits. Coordinates are in UTM.

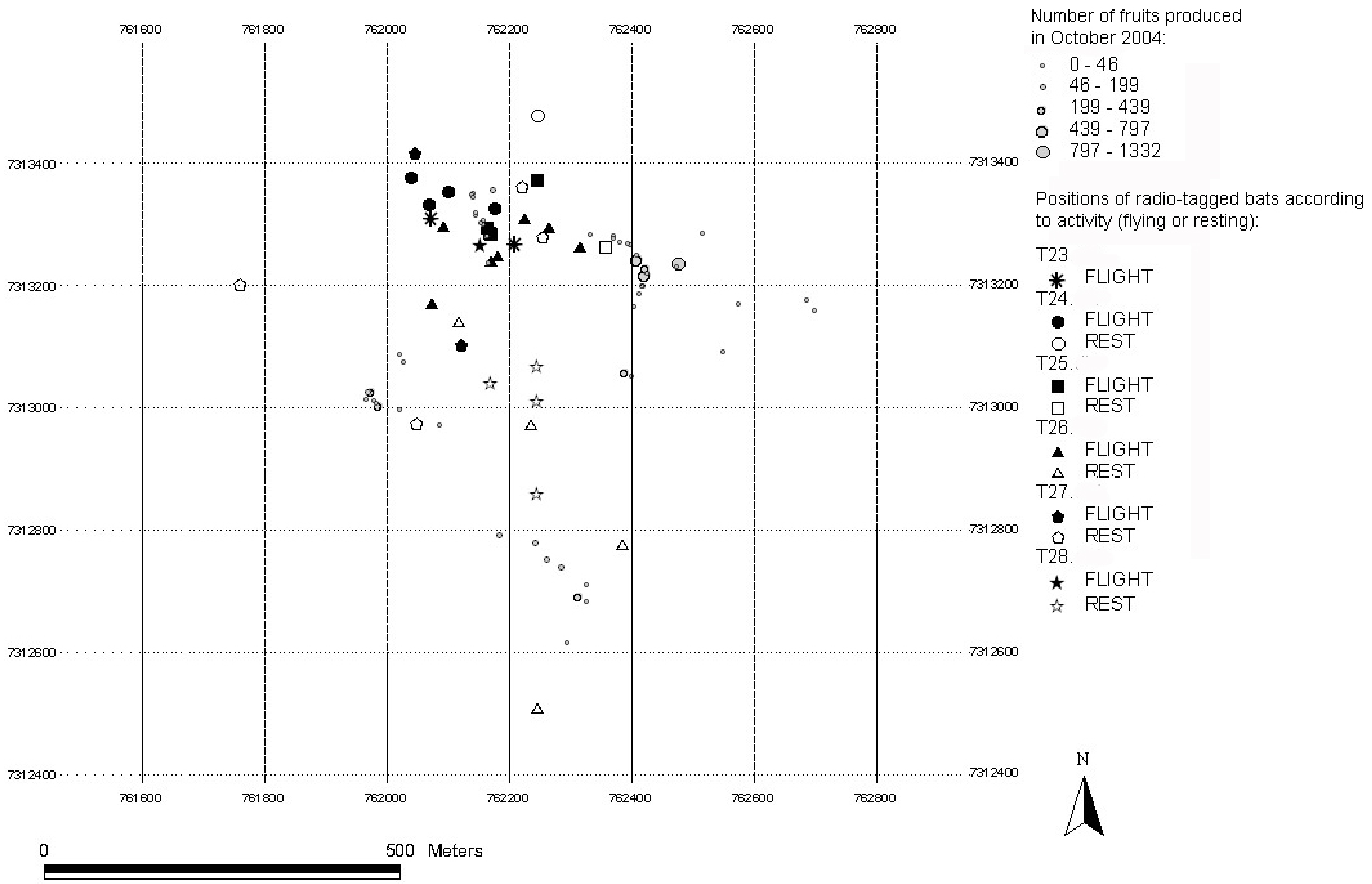

Figure 3.5: Positions of the six *S. lilium* bats tracked for 10 days in October 2004 while flying (filled symbol) or resting (open symbol). Gray circles stand for individual Solanaceae plants and their total number of fruits in October 2004. Coordinates are in UTM.

CAPÍTULO IV

Um teste da fobia lunar usando morcegos frugívoros (Chiroptera: Phyllostomidae) como modelo de estudo

A test of lunar phobia using frugivorous bats (Chiroptera: Phyllostomidae) as study models

RUNNING TITLE: Lunar phobia in frugivorous bats

KEY-WORDS: foraging, activity, behavior, ecology, Chiroptera, *Artibeus*, *Carollia*, *Sturnira*.

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ABSTRACT

‘Lunar phobia’, or the avoidance of brighter areas and periods with intense moonlight, has been proposed as a major influence on the behavior and activity pattern of nocturnal foragers, including insects, reptiles and mammals. The present study aimed to test the hypothesis that lunar phobia restricts time available for foraging by using three frugivorous phyllostomid bats as study models: *Artibeus lituratus, Carollia perspicillata* and *Sturnira lilium*. We mistnetted bats and tested for a relationship between capture success and moonlight measured as illuminance. We observed evidence for lunar phobia in *A. lituratus* and *C. perspicillata*, but not in *S. lilium*. Differences in response to moonlight may be explained by diet, foraging habitat, and spatial distribution of food-plants.

INTRODUCTION

Among nocturnal foragers, intensity of moonlight might restrict foraging time because a brighter environment may facilitate detection by visually-oriented predators. Therefore, some nocturnal small animals tend to avoid gaps and forest edges during brighter periods, often combined with a strong reduction in foraging activity. This behavior is named ‘lunar phobia’, and has been observed in a range of taxa, including insects (Skutelsky, 1996) and mammals (Clarke, 1983).

Among mammals, some bat species (Mammalia: Chiroptera) are known to exhibit lunar phobia. Málaga (1954, apud Crespo *et al.*, 1972) observed for the first time for phyllostomids that captures were fewer during brighter nights. Subsequently, Morrison (1978) coined in his study on the frugivorous bat *Artibeus jamaicensis* (Phyllostomidae) the term “lunar phobia”. In the meantime, positive (e.g. Elangovan & Marimuthu, 2001) as well as negative evidence for lunar phobia (e.g Gannon & Willig, 1997) has been found. Explanations for these differences between species include, for instance, feeding habits (Lang *et al*., 2006) and differential predation pressure in relation to locality and foraging habitat (Thies et al., 2006).

We selected three frugivorous bat species as study models to compare the influence of moon light on foraging activity. The three species belong to the ecologically diverse Neotropical family Phyllostomidae: the stenodermatines *Artibeus lituratus* (Olfers 1818) and *Sturnira lilium* (E. Geoffroy, 1810), and the carolliine *Carollia perspicillata* (Linnaeus, 1758). Although those species are mainly frugivorous and include a wide range of plant species in their diet, they differ in their preference for particular plant taxa and microhabitat (Bernard, 2001; Fleming, 1988; Handley *et al*., 1991; Kalko, 1998; Kunz, 1982).

We hypothesized that the three bat species would differ in their response to moonlight because of differences in foraging behavior and habitat use. Considering that the large *A. lituratus* forages mainly in the canopy and feeds usually on plants that fruit in a ‘big-bang’ pattern (short fruiting period and large number of fruits available per night) (Geiselmann *et al*., 2002; Passos & Graciolli, 2004), this bat is likely to be more exposed to predators lurking in the trees, such as owls and snakes, than the other two species. In contrast to *A. lituratus, S. lilium* and *C. perspicillata* fly mostly in the understory and feed on ‘steady-state’ fruits (long fruiting period and low number of fruits per night) (Fleming, 1988; Geiselmann *et al*., 2002), what is likely to reduce predator pressure because it is difficult for a predator to detect and pursue prey in the mostly dense vegetation, and it may not pay to wait at a fruiting bush with few ripe fruits per night and thus few opportunities to get near potential prey (Thies *et al*., 2006). Therefore, we expected to observe strong lunar phobia in *A. lituratus* and less or no lunar phobia in *S. lilium* and *C. perspicillata*.

METHODS

Study area

This research took place in the “Reserva Biológica Poço das Antas” (RBPA), municipality of Silva Jardim, state of Rio de Janeiro, southeastern Brazil (22º30’-22º33’ S, 42º15’-42º19’ W). Situated in a flat area and covering about 6,100 hectares, RBPA is the largest lowland Atlantic Forest remnant of the state (Scarano, 2002). Regional climate is uniformly wet and hot, classified as “Am” according to Koeppen’s system (Mello, 2002). From 1987 to 2001, the average annual temperature was 24.6ºC, and the annual total rainfall averaged 2.121mm.

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” (Mello, 2002). Bat ecology was intensively studied in RBPA for some years (e.g. Mello *et al*., 2004). The most recent inventory of its mammal fauna is given by Brito *et al*. (2004), while its plant species are summarized by Guimarães *et al*. (1988). There are many known and potential nocturnal predators of small bats in the area: the carnivore bats *Chrotopterus auritus* and *Phyllostomus hastatus*; the owls *Tyto alba* and *Speotyto cunicularia*; the marsupials *Didelphis aurita* and *Philander frenata*; the small cats *Leopardus pardalis* and *L. wiedii*; the coati *Nasua nasua* and the raccoon *Procyon cancrivorous* (Brito *et al*., 2004; pers. obs.).

Time frame and data collection

We carried out fieldwork monthly from February 2000 to September 2001 (except for December 2000, January and May 2001), totaling 29 nights of sampling. We measured activity as the number of net captures for each two-hour interval of each night. Bats were captured with 6 mist-nets (7 x 3 m – Ecotone, Inc.) that were opened all night long in different habitats ranging from closed to open areas. Using the calculation proposed by Straube & Bianconi (2002) (area of each net x number of nets opened each night x total number of hours worked), total sampling effort amounted to 43,848 m².hours. We recorded the time of capture for all individuals. Bat species were identified using several keys (Cloutier & Thomas, 1991; Emmons & Feer, 1997; Gannon *et al.*, 1989; Vizotto & Taddei, 1973), and confirmed by André Pol, Marcelo R. Nogueira and Adriano L. Peracchi (Universidade Federal Rural do Rio de Janeiro).

Many studies in the literature tested the effect of moon light on bat activity by summing total captures on bright versus dark nights and comparing them according to moon phases, but this categorization conceals the real variability between nights and periods of the same night. Therefore we used illuminance as a measure of moonlight intensity on each time interval as in Lang *et al.* (2006). Illuminance is defined as the amount of sunlight reflected by the moon, considering its relative position to the earth and the sun (phase), as well as its position in the sky (elevation) (João L. K. Moreira, pers. com.). Data on astronomical ephemeris (moon phase, sunset, sunrise) are available in the site of the "Observatório Nacional do Rio de Janeiro" (http://euler.on.br/ephemeris/index.php), and we also used a calculation worksheet for moon illuminance provided by João L.K. Moreira (Observatório Nacional do Rio de Janeiro).

Data analysis

We followed statistical procedures proposed in Zar (1999), and used the software Systat 9.0 for calculations. Percentual data were arcsine transformed, before being used in statistical tests. We regarded the number of hours after sunset in an area to characterize activity patterns for each night, because local time of sunset varied from 17:12 (winter) to 18:29 (summer), and frugivore phyllostomids tend to become active just after sunset (Thies *et al.*, 2006). Our main assumption was that the higher the number of bats flying, the higher is the chance of capturing them in mist nets.

To test the relationship between moon illuminance and bat captures with a linear regression, we grouped capture data according to two-hour intervals for each sampling night. Illuminance values for each period were calculated as arithmetic means of values at the beginning and at the end of the period. We excluded data from the second half of the night, because foraging activity of frugivore phyllostomid bats tends to be unimodal and strongly reduced during this period (Aguiar & Marinho-Filho, 2004; Kunz, 1982; Thies *et al.*, 2006).

In the illuminance data, 100% means that the moon received full light from the sun resulting in total reflection to the earth; 0% and negative values mean no reflection to the earth. We transformed raw illuminance values with arcsine to meet requirements of the regression analysis (Zar, 1999).

For all analysis we used capture data, collected during different moon phases and under different environmental conditions (air temperature, rainfall, and cloud cover), as a measure for bat activity. We aimed to conduct an unbiased sampling that comprised different natural conditions of the studied system, in order to avoid pseudoreplication, which would have been the case, for instance, if all data had been collected only during full moon nights.

Calculated illuminance of the moon averaged 13.4 ± 25.5, varying from 0.0 to 98.4%. This large variability is caused by the combination of moon phase and elevation in the sky, which vary greatly throughout the night. For instance, depending on the moon phase, the moon was sometimes fully visible during the day and absent during the night. In other nights, the full moon was in the zenith. We classified the time between new moon and third quarter as dark phase, and the time between full moon and first quarter as bright phase.

RESULTS

We captured a total of 1,054 bats of 14 species. This corresponds to 56% of the known bat fauna of the reserve (25 spp., Brito *et al.*, 2004). The family Phyllostomidae accounted for 97% of all captures (1,019 captures) and 64% of all species (9 species). Among the nine phyllostomids, seven ate fruits to varying degrees including the three species chosen for this study that were primarily frugivores (Cloutier & Thomas, 1991; Gannon *et al.*, 1989; Passos & Gracioli, 2004).

Carollia perspicillata dominated the assemblage by far and accounted with 816 captures for 77% of all captures, followed by *A. lituratus* with 99 captures (9%) and *S. lilium* with 68 captures (6%).

Average (± standard-deviation) capture success (captures/effort) of phyllostomid bats per night was $23 \times 10^{-3} \pm 18 \times 10^{-3}$ captures/h.m². It varied between 7×10^{-3} and 79×10^{-3} captures/m².h. Considering all of the frugivorous phyllostomids, capture success was significantly higher in the dark phases of the moon than capture success during phases with bright moon (d.f. = 25.0, t = 2.871, p = 0.008).

Throughout a night, we also calculated the patterns of hourly captures (although we used periods of two hours for statistical analyses) of the three bat species, in order to facilitate comparison to patterns described in other studies. Patterns of all three species were similar, with most captures during the first half of the night. The capture pattern of *A. lituratus* differed somewhat from the other two species suggesting a somewhat longer activity period throughout the night in contrast to the activity pattern of *C. perspicillata* and *S. lilium* that were most active during the first half of the night. Overall, capture success varied a lot between nights (Fig.1).

On the species level, there was a strong negative relationship between captures of *C. perspicillata* and illuminance of the moon (n = 87, a = 8.84, b = -9.35, F = 9.76, p = 0.002). In *A. lituratus* this relationship was not significant (n = 54, a = 1.61, b = -1.09, F = 2.98, p = 0.09). We did also not find such a relationship for *S. lilium* (n = 57, a = 0.87, b = -0.50, F = 1.16, p = 0.29) (Fig.2).

DISCUSSION

General activity patterns observed for the three bat species studied were consistent with patterns of other species of the same family (Aguiar & Marinho-Filho, 2004). Indeed, most frugivore phyllostomids tend to concentrate foraging activity in the first half of the night (e. g. Fleming, 1988; Handley *et al.*, 1991; Thies *et al.*, 2006). Frugivore bats have to find and ingest a large amount of fruits per night to meet their energy demand (Delorme & Thomas, 1996). They may need to do this early if they eat fruits that ripen in low numbers during the night as is the case with plants that have adopted the ‘steady-state’ strategy and are searched for by a number of animals that feed on them. This contrasts strongly with fruits that ripen during the day or in larger numbers each night, as in the ‘big-bang’ strategy (Thies *et al*., 2006). Fruits of some *Piper* species (Piperaceae) in the forest that ripen in low numbers late in the afternoon will not be replenished during the night. Field studies have shown that most of the fruits are already taken in the first night hours. This leads to a more or less unimodal pattern in foraging bats such as *Carollia castanea* (Thies *et al*., 2006). We also observed a high variation in capture success among nights. This kind of information is not given by many other studies, where captures from different nights were pooled together for analyses, leading to a more or less uniform pattern. However, this nightly variation is important for a better understanding of foraging ecology, including phenomena like lunar phobia.

Before interpreting the data acquired in the present study, it is necessary to consider possible limitations of the sampling method. Some studies carried out with mist-netting and radiotelemetry suggest that lower capture success goes hand in hand with less activity of the bats, which renders mist-netting a valuable tool for investigating lunar phobia (Elangovan & Marimuthu, 2001). However, there is also evidence for other bats that activity patterns do not differ between bright and dark nights based on radio-tracking data, as is the case for *C. castanea*, whereas other studies document reduced capture success in mist nets of this species during bright nights (Thies *et al*., 2006). This makes it questionable whether mist-netting is the adequate tool to address lunar phobia in bats. Several propositions have been made to explain the different results obtained from mist-netting and radiotracking. First, it is possible that frugivorous phyllostomids, like those studied in the present work, might detect mist-nets better when moonlight is more intense as they all have good eye sight (Altringham & Fenton, 2003). Second, maybe lunar phobic bats do not decrease activity time, but restrict their foraging areas to shaded microhabitats (Reigh, 1982), which could lead to fewer captures in mist-nets placed at forest edges, in gaps, and along trails. Given that the hypotheses of visual detection of mist-nets in brighter nights has not yet been tested, and that bat predators may predate all three species, we conclude that the interspecific differences that we observed in the three species are mainly explained by differences in their main diet and foraging habitat, as proposed by Thies *et al*. (2006).

So, we found no evidence for the first hypothesis that the larger species *Artibeus lituratus* reduces activity in bright nights. *Artibeus lituratus* feeds mainly on fruits of Cecropiaceae in the study area (unpub. data), a common fruit among stenodermatine bats (Lobova *et al*., 2003). This differs from other studies where *A. lituratus* is also known to feed heavily on figs (*Ficus*, Moraceae) (e.g., Handley *et al*. 1991, Wendeln *et al*. 2001). However, figs are not very abundant in the area (Guimarães *et al*., 1988). There is only one species, *Cecropia pachystachya,* in the area with a few scattered trees (> 10m high). Both Cecropiaceae and Moraceae show the typical 'big-bang' phenological strategy (Kalko, 1998; Snow, 1965; Wendeln *et al*., 2000), where each individual tree offers large numbers of fruits over a short period. Mass-fruiting trees that form the preferred food of *A. lituratus*, where often dozens or hundreds of bats forage simultaneously on huge fruit crops, are likely to attract a wide range of predators. As individual *Cecropia* and *Ficus* trees fruit asynchronously, *A. lituratus* may be subjected to higher predation pressures, because it probably has to fly over large areas including open habitats in fragmented landscapes, like the "Ilhas dos Barbados", to obtain enough food. Nevertheless, as observed in some mist-netting studies, *Artibeus* bats seem to forage in groups (Altringham, 1998; Handley *et al*., 1991). This "group foraging" could be a strategy to dilute the predation risk for each single individual, a behavior known to be presented by some bird and fish species, for instance. Therefore, the high exposure to predators due to the spatio-temporal distribution of the main food-plants could be balanced by the predation dilution behavior in this species, resulting in no lunar phobia.

In contrast to our expectations we found that *Carollia perspicillata* was very lunar phobic. *Carollia perspicillata* forages mostly at ground level in the forest understory, where they might be less exposed to predators, and also at edges and in gaps where vegetation might make it more difficult for predators to reach them easily (Fleming, 1988; Gannon *et al.*, 1989). As most small-sized phyllostomids, this species usually can not afford fasting for consecutive nights (Audet & Thomas, 1997). This imposes the need on its energy budget to search for food every night to avoid starvation. Thus, we did not expect lunar phobia in this species, because it would be a "waste of time" and put fasting individuals in risk.

Contrary to *C. perspicillata*, the results for *S. lilium* were in line with our initial hypothesis that it would not be lunar phobic. Although both species are similar in size, they have different diets whereby *Carollia perspicillata* prefers Piperaceae and *S. lilium*, Solanaceae (Marinho-Filho, 1991). Those plant families differ strongly in local densities and spatial distributions in the study area (Mello, 2002; and pers. obs.). Whereas Piperaceae occur in large numbers and show a clumped distribution at forest edges, Solanaceae are much less abundant and are scattered in space, occurring both in open and closed microhabitats. Considering these spatial differences in food availability, it is probable that *S. lilium* has to search for food over larger areas than *C. perspicillata*. Thus, *S. lilium* would not have enough time each night to wait for darker periods, because the risk of starvation would be higher than the risk of predation. Besides, we do not know if predation pressure is equal for both species; maybe *C. perspicillata* is killed more frequently by nocturnal animals, what could also make it worthy waiting for darkness.

Although all three bat species are frugivorous, we can assign them to different 'ecological regions', as expressed by the diagram in Fig.3. *C. perspicillata* feeds mainly on the Piperaceae, which are "steady-state" and "clumped". *S. lilium* feeds mainly on the Solanaceae, which are "steady-state" and "scattered". And *A. lituratus* feeds mainly on the Cecropiaceae and Moraceae, which are "big-bang" and "scattered". Together with the main foraging habitat (canopy/understory, open/closed) and the foraging behavior (gregary/solitary), those factors help us understand why different phyllostomid species respond differently to lunar phobia.

Furthermore, it is interesting to notice that a study has shown for an assemblage of figs (Moraceae) that species that are highly attractive to bats have significantly lower fruit removal rates and higher proportions of undispersed fruits when they ripen during full moon. Thus, we conclude that bats react differently to moon light and that lunar phobia in turn affects their foraging behavior with probable consequences on their interactions with plants, especially on fruit harvest and seed dispersal. One interesting line for future studies could be to further deepen our understanding of the link between foraging strategy of the bats, phenology of the plants and moon light by comparing the effect of moonlight on the foraging behavior of frugivorous bat species that differ in foraging habitat and phenological strategy of the main food-plant. We suppose that bat species that fly mostly at canopy level and open space would be more exposed to predators, and thus would be more lunar phobic than species that forage in the understory or cluttered-space. Bats that feed mainly on fruits that are abundantly available throughout each night would have the opportunity not to rush for collecting them and to wait for darker periods, and so could be more lunar phobic than specialists of fruits that ripen in low numbers and at the same time of the night and must forage even at brighter periods.

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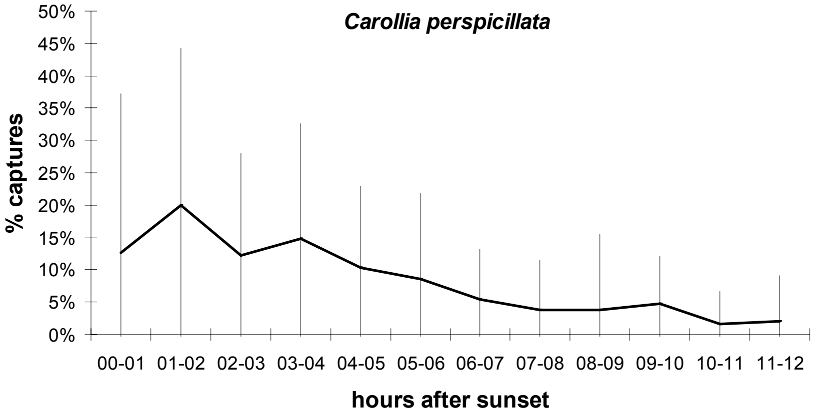
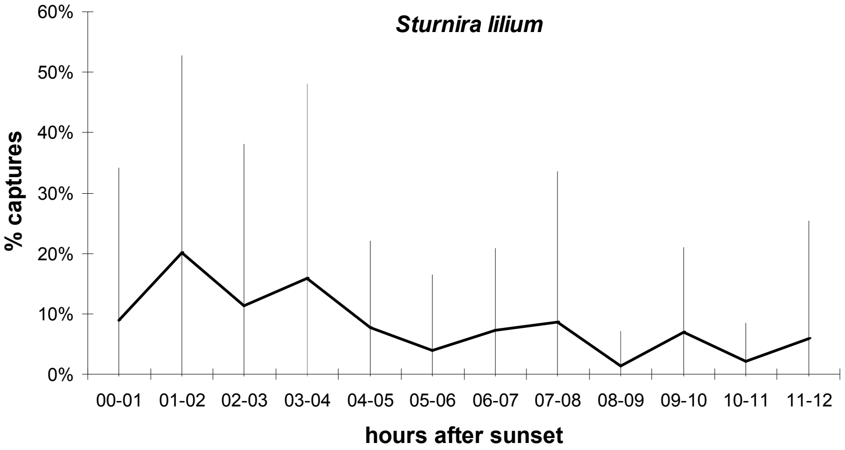
FIGURES





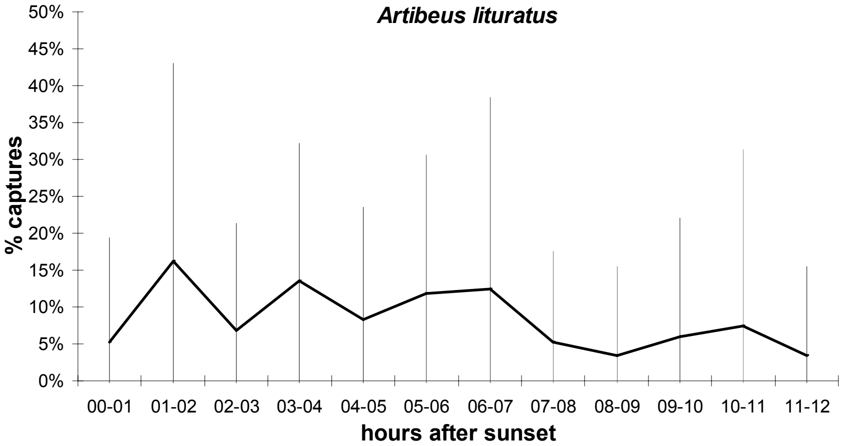


Figure 4.1: Activity patterns of *Carollia perspicillata*, *Sturnira lilium*, and *Artibeus lituratus*, given as the proportion of captures at hourly time intervals after local sunset, in relation to total capture of each different night. Data are given as average values and standard deviations.

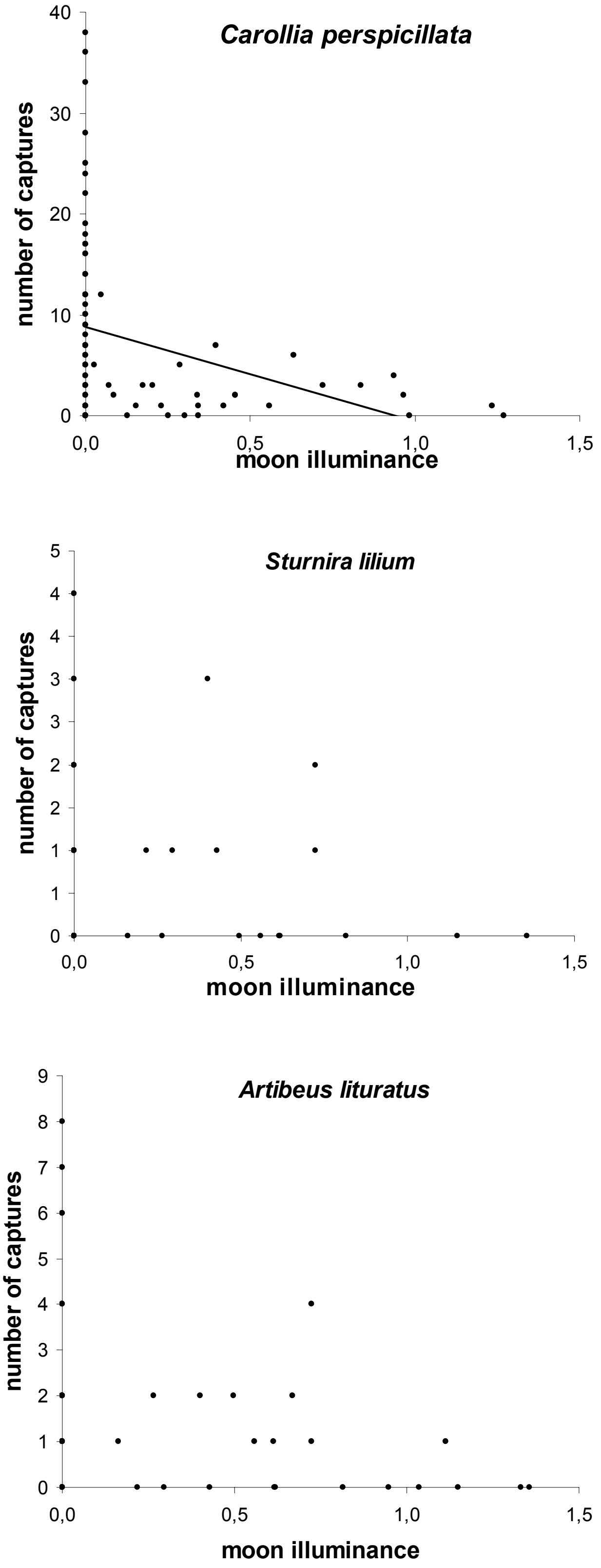


Figure 4.2: Relationship between moon illuminance (arcsine transformed) and number of captures for the three phyllostomid bat species: *Carollia perspicillata* (p = 0.002), *Sturnira lilium* (p = 0.29)*,* and *Artibeus lituratus* (p = 0.09).

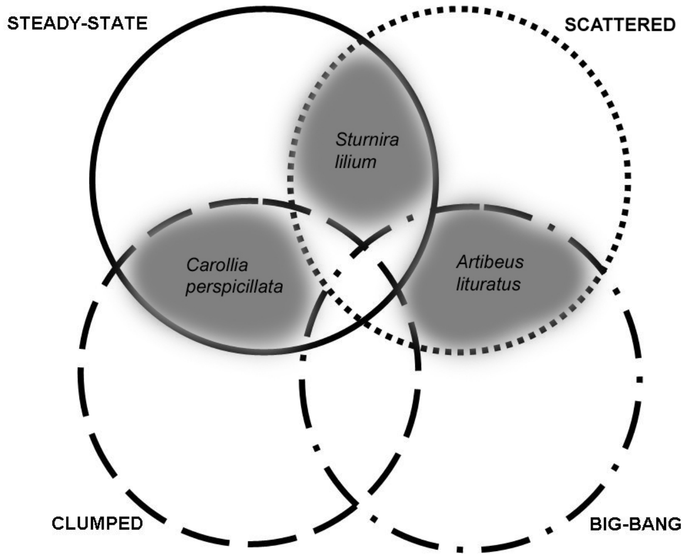


Figure 4.3: Diagram representing four groups with the spatial and temporal distributions of the main food plants of the three studied bat species, and the ecological regions (group intersections) that each bat species occupies. The first circle at the upper left corner represents the group of food-plants with the "steady-state" phenological strategy (i.e. plants that produce a few ripe fruits each night for a long periods); the second circle at the lower right corner represents food-plants with the "big-bang" phenological strategy (which produce several ripe fruits a night for a short period). The third circle at the upper right corner represents food-plants with a scattered spatial distribution, and the fourth circle at the lower left corner represents food-plants with a clumped spatial distribution.

CONCLUSÕES GERAIS

O presente estudo confirma a hipótese de que a interação entre os morcegos da espécie *Sturnira lilium* e as plantas da família Solanaceae é forte e especializada. Os quatro capítulos aqui apresentados reforçam essa conclusão principal sob diferentes pontos-de-vista.

Os morcegos *S. lilium* mostraram ser altamente especializados na frugivoria, dependendo das solanáceas como seu principal alimento durante quase o ano todo. Este grau de dependência também foi observado ao se analisar a sazonalidade reprodutiva dos morcegos, que parece ser regulada pela fenologia das plantas-alimento, já que a estação reprodutiva principal ocorre no auge da abundância de frutos.

O clima da área de estudo, que é uma região montanhosa e, portanto, mais fria e seca do que as regiões de baixada (mais intensamente estudadas), também pareceu influenciar a dinâmica populacional dos morcegos. Um dos reflexos dessa influência do clima pôde ser observado no grau de sincronia da população, já que no auge da estação reprodutiva 100% das fêmeas estavam envolvidas em alguma fase do ciclo, fosse a gravidez , a lactação ou a pós-lactação. O frio mais intenso e a escassez de frutos durante seis meses do ano podem ser fatores determinantes desta sincronia, já que seria vantajoso para os morcegos concentrarem as atividades reprodutivas, que são muito custosas energeticamente, no auge da estação favorável, de modo a não colocarem em risco seu balanço energético ou não investirem em um prole que teria poucas chances de sobreviver.

Essa estação fria e seca pareceu ser realmente uma época severa para *S. lilium*, já que há também fortes evidências de que os morcegos migram da região de estudo durante o período, retornando após o término do inverno. Provavelmente, como já proposto em outros trabalhos, esta migração é feita de modo que os morcegos possam viver temporariamente em áreas mais baixas, onde as temperaturas são maiores, e haveria outras espécies de plantas-alimento frutificando durante a época de escassez nas regiões mais altas.

Sturnira lilium se beneficia muito da interação com as solanáceas, que são uma fonte confiável de alimento durante o ano todo, graças à sua frutificação longa e estratificada. Por sua vez, essas plantas também recebem um “serviço ecológico” de alta qualidade por parte dos morcegos. As evidências coletadas no presente estudo mostram que *S. lilium* é um eficiente dispersor de solanáceas, já que consome regular e preferencialmente os frutos que elas produzem, leva as sementes para longe das plantas-mãe de acordo com a "hipótese da fuga" e as espalha por uma grande área em diversos locais na floresta de maneira consistente com a "hipótese da colonização". Esses fatores combinados tendem a aumentar a sobrevivência das sementes e favorecer o estabelecimento das plântulas e adultos jovens das diferentes espécies de solanáceas dispersadas. Além disso, já que os morcegos se concentram apenas em algumas das espécies que ocorrem na área, estas plantas escolhidas podem ter uma vantagem competitiva sobre as demais plantas dos mesmos gêneros, alterando assim a seu favor o balanço da competição por espaço no sistema natural.

Além disso, esta forte interação com as solanáceas parece também explicar a ausência de fobia lunar em *S. lilium*, que ao contrário de *Artibeus lituratus* e *Carollia perspicillata*, não mostrou redução de atividade em períodos mais iluminados da noite. Parece que a dependência de *S. lilium* em relação às solanáceas e a distribuição espacial delas, que é menos agregada que a das piperáceas (o alimento principal de *C. perspicillata*) e mais agregada que a das cecropiáceas (preferidas por *A. lituratus*), obrigam *S. lilium* a procurar alimento mesmo em períodos mais vulneráveis à predação. A relação custo-benefício parece favorecer uma exposição maior aos predadores do que em *C. perspicillata*, a fim de evitar o jejum prolongado.

Por isso, sugiro como possibilidade para futuros trabalhos, que se pesquisem mais detalhadamente outras populações de *S. lilium*, tanto em localidades de montanha quanto de baixada, a fim de se testar a consistência dos padrões aqui observados e avaliar a validade das interpretações feitas. Seria interessante verificar se mudanças em fatores locais, como o clima e a composição de espécies de solanáceas e outras plantas-alimento, poderiam levar a uma diferença na dieta, no comportamento de forrageio e no ciclo reprodutivo de cada população. Por exemplo, eu esperaria que: 1. o ciclo reprodutivo de *S. lilium* fosse menos sincronizado em áreas mais quentes, tendo em vista que a época favorável seria maior; 2. não houve migração em áreas de baixada, onde a oferta de frutos de solanáceas não sofre tão drástica redução durante uma época do ano, ao contrário das áreas montanhosas. Também poderiam ser feitos estudos de cativeiro, a fim de determinar se a regulação do ciclo reprodutivo de *S. lilium* é feita por fatores endógenos puramente hormonais, se depende de quão bem nutrido o animal está ou se possui algum "gatilho ambiental" externo (como o fotoperíodo). Por fim, seria importante comparar a filogenia de Stenodermatinae com uma classificação das espécies desta subfamília em guildas (baseadas na preferência alimentar, no modo de forrageio e no habitat principal), a fim de entender melhor os padrões evolutivos das grandes diferenças ecológicas observadas entre morcegos tão aparentados.

É preciso adquirir mais conhecimento científico sobre morcegos como *S. lilium*, que é uma das espécies mais abundantes nos Neotrópicos, mas cuja Ecologia é pouco conhecida. Menos ainda é sabido sobre suas interações com as solanáceas, que são plantas de grande valor ecológico e econômico no mundo todo, inclusive no Brasil. *Sturnira lilium* é um excelente modelo para se testar hipóteses ecológicas e evolutivas mais gerais relacionadas à interação entre animais e plantas e sua coevolução, e o conhecimento gerado através do estudo desta espécie poderia servir de base para planos de manejo de áreas degradadas através da manipulação do processo de dispersão de sementes.

ANEXOS

Anexo 1: Lista geral das 34 espécies de morcegos registradas no Parque Estadual Intervales, Ribeirão Grande, SP, até o momento. Espécies com o número 1 foram registradas pela primeira vez por De Vivo & Gregorin (2001), as com o número 2 por Passos *et al*. (2003), as com o número 3 por Portfors *et al.* (2000), e a com o número 4 no presente estudo.

Emballonuridae
Peropteryx macrotis1

Phyllostomidae
Anoura caudifer [1]
Anoura geoffroyi [1]
Artibeus fimbriatus [1]
Artibeus jamaicencis [2]
Artibeus obscurus [1]
Artibeus lituratus [1]
Carollia perspicillata 1
Chrotopterus auritus [1]
Desmodus rotundus [1]
Diphylla ecaudata [1]
Glossophaga soricina [1]
Lonchorina aurita [1]
Micronycteris megalotis [1]
Micronycteris microtis [2]
Mimon bennetti [1]
Phyllostomus hastatus [1]
Phylloderma stenops [4]
Platyrrhinus lineatus [1]
Platyrrhinus recifinus [2]
Tonatia bidens [1]
Trachops cirrhosus [1]
Pygoderma bilabiatum [1]
Sturnira lilium [1]
Sturnira tildae [1]

Furipteridae
Furipterus horrens [1]

Vespertilionidae
Eptesicus brasiliensis [1]
Histiotus velatus [1]
Lasiurus blossevilli [1]
Lasiurus ega [1]
Myotis nigricans [1]
Myotis aff. riparius [3]
Myotis ruber [1]

Molossidae
Tadarida brasiliensis [1]

Anexo 2: Lista das espécies de morcegos capturadas em redes-de-neblina durante o estudo, com número total de capturas, número total de indivíduos, número de indivíduos marcados, número de recapturas e taxa de recaptura.

espécie	**capturas**	**indivíduos**	**marcados**	**recapturas**	**% recapturas**
Sturnira lilium	333	306	208	27	8%
Carollia perspicillata	81	45	43	36	44%
Anoura caudifer	14	12	11	2	14%
Desmodus rotundus	11	11	8	0	0%
Artibeus fimbriatus	8	5	6	3	38%
Chrotopterus auritus	7	6	6	1	14%
Artibeus lituratus	5	5	4	0	0%
Pygoderma bilabiatum	5	5	3	0	0%
Myotis nigricans	3	3	3	0	0%
Eptesicus brasiliensis	2	2	2	0	0%
Mimon bennettii	2	2	2	0	0%
Phylloderma stenops	2	2	1	0	0%
Sturnira tildae	2	2	2	0	0%
Artibeus obscurus	1	1	1	0	0%
Trachops cirrhosus	1	1	1	0	0%
total	**477**	**408**	**301**	**69**	**14%**

Anexo 3: Fotos das espécies de morcegos capturadas durante o estudo. Fotos por Marco A. R. Mello (há duas exceções).

Anoura caudifer

Artibeus fimbriatus

Artibeus lituratus

Artibeus obscurus

Carollia perspicillata

***Chrotopterus auritus* (foto por Bruno Buzatto)**

Desmodus rotundus

Eptesicus brasiliensis

Mimon bennettii

Myotis nigricans

***Phylloderma stenops* (foto por Bruno Buzatto)**

Pygoderma bilabiatum

Sturnira lilium **(o modelo principal do estudo)**

Sturnira tildae

Trachops cirrhosus

Anexo 4: Lista das plantas-alimento encontradas e na área de estudo, com famílias, espécies e quantidade de indivíduos marcados.

família	morfotipo	individuos marcados	nome popular	espécie
Solanaceae	1	22	vitinga	*Solanum granulosoleprosum*
Solanaceae	2	14	jurubeba	*Solanum variabile*
Solanaceae	3	3	espora-de-galo	*Vassobia breviflora*
Solanaceae	4	1	quina coreana	*Aureliana* cf. *fasciculata*
Solanaceae	5	13	quina branca	*Aureliana* sp.1
Solanaceae	6	11	quina amarela	*Solanum phyllosepalum*
Solanaceae	7	3	quina	*Solanum santaecatherinae*
Solanaceae	8	1	quina preta	*Aureliana* sp.2
Solanaceae	9	1	pimenta-brava	*Solanum* sp.1
Solanaceae	10	1	quina	*Aureliana* sp.3
Solanaceae	11	0	joá-de-porco	*Solanum swartzianum*
Solanaceae	12	0	maria-pretinha	*Solanum americanum*
Solanaceae	13	0		*Tibouchina fothergillae*
Cecropiaceae	1	0	imbaúba	*Cecropia glaziovii*
Moraceae	1	0	figueira preta	*Ficus luschnatiana*
Piperaceae	1	0	jaborandí	*Piper gaudichaudianum*
Piperaceae	2	0	jaborandí	*Piper hispidum*
Piperaceae	3	0	cava-cava	*Piper mosenii*
Piperaceae	4	0	cava-cava	*Piper xylosteoides*

Anexo 5: Fotos de algumas das espécies de plantas-alimento encontradas durante o estudo. Fotos por Marco A.R. Mello.

SOLANACEAE


***Aureliana* sp.1 (quina coreana)**


***Aureliana* sp.2 (quina branca)**


***Solanum americanum* (maria-pretinha)**


***Solanum granulosoleprosum* (vitinga)**


***Solanum phyllosepalum* (quina amarela)**


***Solanum swartzianum* (juá de porco)**

Solanum variabile **(juá)**

Vassobia breviflora **(espora de galo)**

CECROPIACEAE

Cecropia glaziovii **(imbaúba)**

MORACEAE

Ficus luschnatiana **(figueira branca)**

Piper gaudichaudianum **(jaborandí, cava-cava)**

Piper hispidum **(jaborandí, cava-cava)**

Piper mosenii **(jaborandí, cava-cava)**

Anexo 6: Fotos das sementes de algumas das espécies de plantas consumidas pelo morcego *S. lilium* na área de estudo. Fotos por Marco A. R. Mello. A escala da lupa está em décimos de milímetros.

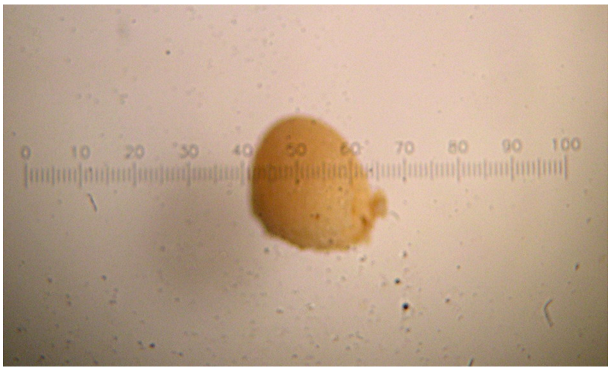
CECROPIACEAE

Cecropia glaziovii

PIPERACEAE

Piper gaudichaudianum

MORACEAE

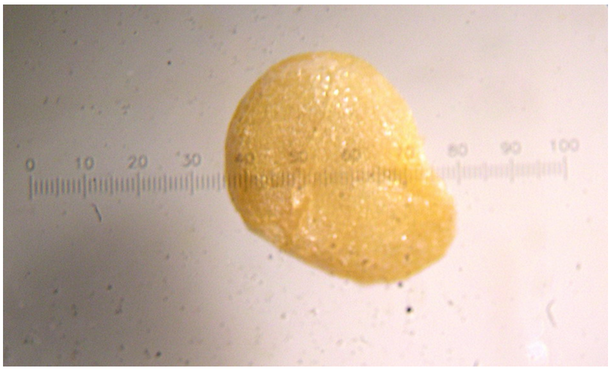


Ficus luschnatiana

SOLANACEAE

Aureliana fasciculata

Solanum americanum



Solanum granulosoleprosum

Solanum variabile

Solanum sanctacatharinae

Vassobia breviflora

Anexo 7: Lista das espécies de plantas consumidas pelo morcego *Sturnira lilium* em toda a sua distribuição geográfica (Neotrópicos), atualizada a partir da revisão de Geiselmann *et al*. (2002), com base na literatura mais recente e no presente estudo. Em negrito estão as espécies observadas no presente estudo.

Família	**espécie**	**nectarivoria**	**frugivoria**	**referência**
Amaranthaceae	*Cyathula prostrata*		x	Lobova & Mori, 2004
Anacardiaceae	*Anacardium excelsum*		x	Heithaus et al., 1975
Anacardiaceae	*Anacardium rhinocarpus*	x		Dobat & Peikert-Holle, 1985
Anacardiaceae	*Mangifera indica*		x	Heithaus et al., 1975
Anacardiaceae	*Mangifera indica*	x		Dobat & Peikert-Holle, 1985
Annonaceae	*Rollinia exsucca*		x	Maas et al., 1992
Apocynaceae	*Couma utilis*		x	Reis & Peracchi, 1987
Araceae			x	Cockle, 1997
Araceae			x	Charles-Dominique & Cockle, 2001
Arecaceae			x	Gannon et al., 1989
Arecaceae	*Phoenix dactylifera*		x	Gardner, 1977
Bignoniaceae		x		Gardner, 1977
Bignoniaceae		x		Heithaus et al., 1975
Bignoniaceae		x		Dobat & Peikert-Holle, 1985
Bignoniaceae	*Crescentia cujete*	x		Butanda-Cervera et al., 1978
Bignoniaceae	*Crescentia cujete*	x		Dobat & Peikert-Holle, 1985
Bombacaceae	*Bombacopsis fendleri*	x		Heithaus et al., 1975
Bombacaceae	*Bombacopsis fendleri*	x		Dobat & Peikert-Holle, 1985
Bombacaceae		x		Gardner, 1977
Bombacaceae		x		Howell & Burch, 1974
Bombacaceae		x		Butanda-Cervera et al., 1978
Bombacaceae		x		Dobat & Peikert-Holle, 1985
Bombacaceae	*Ceiba aesculifolia*	x		Heithaus et al., 1975
Bombacaceae	*Ceiba aesculifolia*	x		Dobat & Peikert-Holle, 1985
Bombacaceae	*Ceiba pentandra*	x		Gardner, 1977
Bombacaceae	*Ceiba pentandra*	x		Butanda-Cervera et al., 1978
Bombacaceae	*Ceiba pentandra*	x		Heithaus et al., 1975
Bombacaceae	*Ceiba pentandra*	x		Dobat & Peikert-Holle, 1985
Bombacaceae	*Ochroma lagopus*	x		Heithaus et al., 1975
Bombacaceae	*Ochroma lagopus*	x		Gardner, 1977
Bombacaceae	*Ochroma lagopus*	x		Butanda-Cervera et al., 1978
Bombacaceae	*Ochroma lagopus*	x		Dobat & Peikert-Holle, 1985
Bombacaceae	*Pseudobombax septenatum*	x		Dobat & Peikert-Holle, 1985
Bombacaceae	*Pseudobombax septenatum*	x		Heithaus et al., 1975
Bombacaceae	*Pseudobombax septenatum*	x		Gardner, 1977
Bombacaceae	*Pseudobombax septenatum*	x		Butanda-Cervera et al., 1978
Cactaceae			x	Simmons & Wetterer, 2002
Cactaceae	*Neobuxbaumia tetetzo*		x	Simmons & Wetterer, 2002
Cactaceae	*Pachycereus weberi*	x		Valiente-Banuet et al., 1997
Cactaceae	*Pachycereus weberi*	x		Simmons & Wetterer, 2002
Cactaceae		x		Ruiz et al., 2000
Cactaceae	*Pilosocereus chrysacanthus*	x		Valiente-Banuet et al., 1997
Cactaceae	*Stenocereus griseus*	x	x	Ruiz et al., 2000
Caesalpiniaceae		x		Pedro & Taddei, 1997
Caesalpiniaceae	*Bauhinia pauletia*	x		Heithaus et al., 1975
Caesalpiniaceae	*Bauhinia pauletia*	x		Dobat & Peikert-Holle, 1985
Caesalpiniaceae	*Bauhinia pauletia*	x		Gardner, 1977
Caesalpiniaceae	*Bauhinia pauletia*	x		Butanda-Cervera et al., 1978
Caesalpiniaceae	*Bauhinia pauletia*	x		Heithaus et al., 1974
Caesalpiniaceae	*Bauhinia ungulata*	x		Dobat & Peikert-Holle, 1985

Família	espécie	nectarivoria	frugivoria	referência
Caesalpiniaceae	*Bauhinia ungulata*	x		Heithaus et al., 1975
Caesalpiniaceae	*Copaifera langsdorfii*		x	Pedro & Taddei, 1997
Caesalpiniaceae	*Hymenaea courbaril*	x		Dobat & Peikert-Holle, 1985
Caesalpiniaceae	*Hymenaea courbaril*	x		Gardner, 1977
Caesalpiniaceae	*Hymenaea courbaril*	x		Butanda-Cervera et al., 1978
Caesalpiniaceae	*Hymenaea courbaril*	x		Heithaus et al., 1975
Caricaceae	*Carica papaya*		x	Reis & Peracchi, 1987
Cecropiaceae			x	Willig et al., 1993
Cecropiaceae			x	Muller & Reis, 1992
Cecropiaceae			x	Gannon et al., 1989
Cecropiaceae			x	Gardner, 1977
Cecropiaceae			x	Heithaus et al., 1975
Cecropiaceae	*Cecropia adenopus*		x	Marinho-Filho, 1991
Cecropiaceae	*Cecropia distachya*		x	Gorchov et al., 1995
Cecropiaceae	*Cecropia ficifolia*		x	Gorchov et al., 1995
Cecropiaceae	***Cecropia glaziovii***		**x**	**o presente estudo**
Cecropiaceae	*Cecropia obtusa*		x	Charles-Dominique, 1986
Cecropiaceae	*Cecropia obtusa*		x	Foresta et al., 1984
Cecropiaceae	*Cecropia obtusa*		x	Lobova et al., 2003
Cecropiaceae	*Cecropia obtusifolia*		x	Herrera M. et al., 2001a
Cecropiaceae	*Cecropia pachystachya*		x	Pedro & Taddei, 1997
Cecropiaceae	*Cecropia peltata*		x	Fleming, 1988
Cecropiaceae	*Cecropia peltata*		x	Fleming & Williams, 1990
Cecropiaceae	*Cecropia peltata*		x	Fleming et al., 1977
Cecropiaceae	*Cecropia peltata*		x	Fleming, 1986
Chrysobalanaceae			x	Gardner, 1977
Chrysobalanaceae			x	Howell & Burch, 1974
Clusiaceae			x	Gorchov et al., 1995
Clusiaceae			x	Reis & Peracchi, 1987
Clusiaceae			x	Willig et al., 1993
Clusiaceae			x	Gannon et al., 1989
Clusiaceae			x	Foresta et al., 1984
Clusiaceae			x	Reis & Peracchi, 1987
Clusiaceae			x	Foresta & Lescure, 1989
Clusiaceae			x	Charles-Dominique, 1986
Clusiaceae	*Vismia duckei*		x	Reis & Gillaumet, 1983
Clusiaceae	*Vismia duckei*		x	Reis & Peracchi, 1987
Clusiaceae	*Vismia guianensis*		x	Charles-Dominique, 1993
Clusiaceae	*Vismia guianensis*		x	Reis & Peracchi, 1987
Icacinaceae	*Poraqueiba sericea*		x	Reis & Gillaumet, 1983
Icacinaceae	*Poraqueiba sericea*		x	Reis & Peracchi, 1987
Malpighiaceae			x	Reis & Peracchi, 1987
Malvaceae	*Abutilon niveum*	x		Giannini, 1999
Melastomataceae			x	Gardner, 1977
Melastomataceae			x	Howell & Burch, 1974
Moraceae	*Chlorophora tinctoria*		x	Fleming, 1986
Moraceae	*Chlorophora tinctoria*		x	Fleming, 1988
Moraceae	*Chlorophora tinctoria*		x	Fleming et al., 1977
Moraceae	*Chlorophora tinctoria*		x	Heithaus et al., 1975
Moraceae			x	Fleming, 1986
Moraceae			x	Herrera M. et al., 2001a
Moraceae			x	Willig et al., 1993
Moraceae			x	Marinho-Filho, 1991
Moraceae			x	Muller & Reis, 1992
Moraceae			x	Cockrum & Bradshaw, 1963
Moraceae			x	Gannon et al., 1989

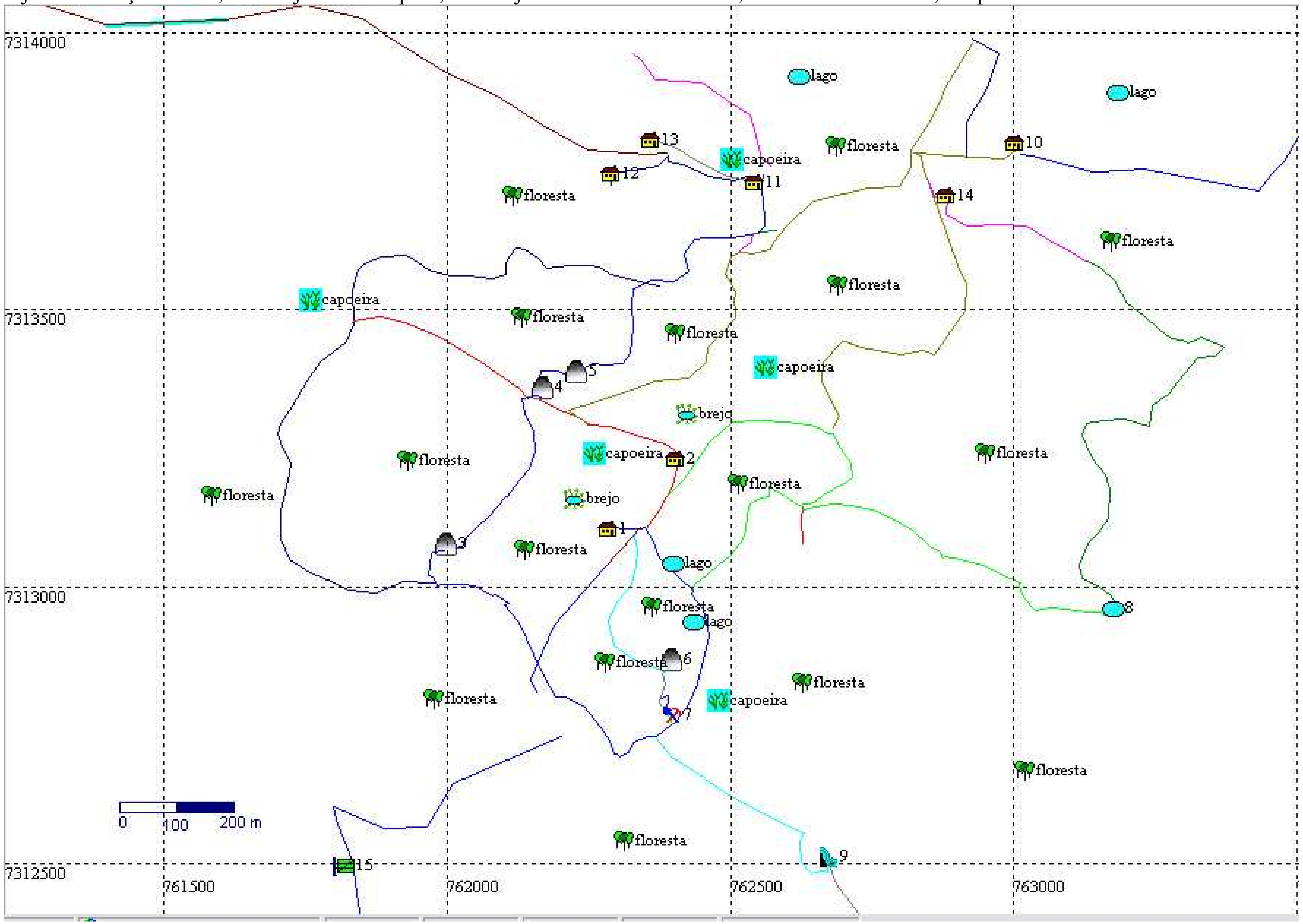
Família	espécie	nectarivoria	frugivoria	referência
Moraceae			x	Gardner, 1977
Moraceae			x	Pedro & Taddei, 1997
Moraceae	*Ficus luschnatiana*		x	Figueiredo, 1996
Moraceae	*Ficus ovalis*		x	Bonaccorso & Gush, 1987
Moraceae	*Maclura tinctoria*		x	Mikich, 2002
Muntingiaceae			x	Gardner, 1977
Muntingiaceae			x	Howell & Burch, 1974
Muntingiaceae	*Muntingia calabura*		x	Fleming, 1988
Muntingiaceae	*Muntingia calabura*		x	Bonaccorso & Gush, 1987
Muntingiaceae	*Muntingia calabura*		x	Gardner, 1977
Muntingiaceae	*Muntingia calabura*		x	Fleming et al., 1985
Muntingiaceae	*Muntingia calabura*		x	Heithaus et al., 1975
Muntingiaceae	*Muntingia calabura*		x	Fleming, 1986
Musaceae			x	Willig et al., 1993
Musaceae			x	Gannon et al., 1989
Musaceae			x	Gardner, 1977
Musaceae			x	Hernandez & Mart□z del Rio, 1992
Musaceae			x	Villa-R & Villa Cornejo, 1969
Myrtaceae			x	Acosta y Lara, 1950
Myrtaceae			x	Garcia, Rezende & Aguiar, 2000
Passifloraceae			x	Acosta y Lara, 1950
Passifloraceae	*Passiflora amethystina*		x	Marinho-Filho, 1991
Piperaceae			x	Heithaus et al., 1975
Piperaceae			x	Pedro & Taddei, 1997
Piperaceae			x	Herrera M. et al., 2001a
Piperaceae			x	Willig et al., 1993
Piperaceae			x	Muller & Reis, 1992
Piperaceae			x	Gannon et al., 1989
Piperaceae			x	Gardner, 1977
Piperaceae			x	Foresta et al., 1984
Piperaceae			x	Howell & Burch, 1974
Piperaceae			x	Charles-Dominique, 1986
Piperaceae			x	Marinho-Filho, 1991
Piperaceae	*Piper aduncum*		x	Reis & Gillaumet, 1983
Piperaceae	*Piper aduncum*		x	Marinho-Filho, 1991
Piperaceae	*Piper aduncum*		x	Gorchov et al., 1995
Piperaceae	*Piper aduncum*		x	Reis & Peracchi, 1987
Piperaceae	*Piper aduncum*		x	Garcia, Rezende & Aguiar, 2000
Piperaceae	*Piper amalago*		x	Fleming, 1988
Piperaceae	*Piper amalago*		x	Fleming et al., 1977
Piperaceae	*Piper amalago*		x	Fleming, 1985b
Piperaceae	*Piper amalago*		x	Pedro & Taddei, 1997
Piperaceae	*Piper amalago*		x	Fleming, 1986
Piperaceae	*Piper arboreum*		x	Bizerril & Raw, 1997
Piperaceae	*Piper arboreum*		x	Pedro & Taddei, 1997
Piperaceae	***Piper corintoanum***		**x**	**o presente estudo**
Piperaceae	***Piper gaudichaudianum***		**x**	**Marinho-Filho, 1991; o presente estudo**
Piperaceae	*Piper glabratum*		x	Marinho-Filho, 1991
Piperaceae	*Piper glabratum*		x	Pedro & Taddei, 1997
Piperaceae	***Piper hoehenei***		**x**	**o presente estudo**
Piperaceae	*Piper hostmannianum*		x	Reis & Gillaumet, 1983
Piperaceae	*Piper hostmannianum*		x	Charles-Dominique, 1993
Piperaceae	*Piper hostmannianum*		x	Reis & Peracchi, 1987
Piperaceae	*Piper jacquemontianum*		x	Fleming et al., 1977
Piperaceae	*Piper jacquemontianum*		x	Fleming, 1985b
Piperaceae	*Piper jacquemontianum*		x	Fleming, 1986

Família	**espécie**	**nectarivoria**	**frugivoria**	**referência**
Piperaceae	*Piper jacquemontianum*		x	Fleming, 1988
Piperaceae	*Piper pseudofuligineum*		x	Fleming, 1988
Piperaceae	*Piper pseudofuligineum*		x	Fleming et al., 1977
Piperaceae	*Piper pseudofuligineum*		x	Fleming, 1985b
Piperaceae	*Piper pseudofuligineum*		x	Fleming, 1986
Piperaceae	*Piper tuberculatum*		x	Heithaus et al., 1975
Piperaceae	*Piper tuberculatum*		x	Gardner, 1977
Piperaceae	*Piper tuberculatum*		x	Fleming, 1986
Piperaceae	*Piper tucumanum*		x	Iudica, 1995
Piperaceae	*Piper tucumanum*		x	Giannini, 1999
Rubiaceae			x	Reis & Peracchi, 1987
Sapotaceae	*Manilkara zapota*	x		Gardner, 1977
Sapotaceae	*Manilkara zapota*	x		Butanda-Cervera et al., 1978
Sapotaceae	*Manilkara zapota*	x		Heithaus et al., 1975
Sapotaceae	*Manilkara zapota*	x		Dobat & Peikert-Holle, 1985
Solanaceae			x	Gardner, 1977
Solanaceae			x	Gardner, 1977
Solanaceae			x	Howell & Burch, 1974
Solanaceae	*Capsicum baccatum*		x	Iudica, 1995
Solanaceae			x	Pedro & Taddei, 1997
Solanaceae			x	Foresta & Lescure, 1989
Solanaceae			x	Marinho-Filho, 1991
Solanaceae			x	Charles-Dominique, 1986
Solanaceae			x	Gorchov et al., 1995
Solanaceae			x	Willig et al., 1993
Solanaceae			x	Muller & Reis, 1992
Solanaceae			x	Gardner, 1977
Solanaceae			x	Howell & Burch, 1974
Solanaceae			x	Peracchi & de Albuquerque, 1971
Solanaceae			x	Heithaus et al., 1975
Solanaceae			x	Fleming, 1986
Solanaceae	***Aureliana fasciculata***		**x**	**o presente estudo**
Solanaceae	*Dyssochroma viridiflorum*	x	x	Sazima et al., 2003
Solanaceae	*Solanum argentinum*		x	Iudica, 1995
Solanaceae	*Solanum asperum*		x	Foresta et al., 1984
Solanaceae	*Solanum caavurana*		x	Reis & Peracchi, 1987
Solanaceae	***Solanum capsicum***		**x**	**o presente estudo**
Solanaceae	*Solanum chaetophorum*		x	Giannini, 1999
Solanaceae	*Solanum erianthum*		x	Marinho-Filho, 1991
Solanaceae	*Solanum grandiflorum*		x	Reis & Gillaumet, 1983
Solanaceae	*Solanum grandiflorum*		x	Reis & Peracchi, 1987
Solanaceae	*Solanum grandiflorum*		x	Conceição, 1977
Solanaceae	***Solanum granulosoleprosum***		**x**	**Cáceres & Moura, 2003; o presente estudo**
Solanaceae	*Solanum grossum*		x	Giannini, 1999
Solanaceae	*Solanum hazenii*		x	Fleming, 1986
Solanaceae	*Solanum hazenii*		x	Fleming, 1988
Solanaceae	*Solanum hazenii*		x	Fleming et al., 1977
Solanaceae	*Solanum hirtum*		x	Heithaus et al., 1975
Solanaceae	*Solanum inaequale*		x	Marinho-Filho, 1991
Solanaceae	*Solanum lanceolatum*		x	Gorchov et al., 1995
Solanaceae	*Solanum lanceolatum*		x	Ascorra & Wilson, 1992
Solanaceae	*Solanum ochraceo-ferrugineum*		x	Fleming, 1986
Solanaceae	*Solanum paniculatum*		x	Peracchi & de Albuquerque, 1971
Solanaceae	*Solanum paniculatum*		x	Reis & Peracchi, 1987
Solanaceae	*Solanum paniculatum*		x	Pedro & Taddei, 1997
Solanaceae	*Solanum riparium*		x	Giannini, 1999

Família	espécie	nectarivoria	frugivoria	referência
Solanaceae	*Solanum riparium*		x	Iudica, 1993
Solanaceae	*Solanum riparium*		x	Iudica & Bonaccorso, 1997
Solanaceae	*Solanum riparium*		x	Iudica, 1995
Solanaceae	*Solanum rugosum*		x	Reis & Gillaumet, 1983
Solanaceae	*Solanum rugosum*		x	Charles-Dominique, 1993
Solanaceae	*Solanum rugosum*		x	Foresta et al., 1984
Solanaceae	*Solanum rugosum*		x	Reis & Peracchi, 1987
Solanaceae	***Solanum sancthae-catarinae***		**x**	**Muller & Reis, 1992; o presente estudo**
Solanaceae	*Solanum subinerme*		x	Foresta et al., 1984
Solanaceae	*Solanum surinamense*		x	Foresta et al., 1984
Solanaceae	*Solanum torvum*		x	Lobova & Mori, 2004
Solanaceae	*Solanum trichoneuron*		x	Giannini, 1999
Solanaceae	*Solanum umbellatum*		x	Fleming, 1986
Solanaceae	*Solanum variabile*		x	Marinho-Filho, 1991
Solanaceae	*Solanum verbascifolium*		x	Peracchi & de Albuquerque, 1971
Solanaceae	*Solanum versabile*		x	Giannini, 1999
Solanaceae	***Vassobia breviflora***		**x**	**o presente estudo**
Ulmaceae	*Celtis iguanaea*		x	Giannini, 1999
	total de famílias	**28**		
	total de espécies	**83**		

Anexo 8: Mapa da área de estudo, feito usando em campo um GPS 12 Garmin e posteriormente plotando os dados no programa GPS Trackmaker 13. As coordenadas estão em UTM.

Legenda: 1. Sede de Pesquisa, 2. casa abandonada, 3. Gruta Colorida, 4. Gruta do Tatu, 5. Gruta do Cipó, 6. pedreira, 7. antigo britador, 8. Lago Negro, 9. Cachoeira do Mirante, 10. restaurante, 11. Alojamento Onça Pintada, 12. Alojamento Esquilo, 13. Alojamento Mono Carvoeira, 14. viveiro de mudas, 15. porteira do Carmo.



Anexo 9: Fotos e descrições dos equipamentos e técnicas usadas no trabalho de campo.

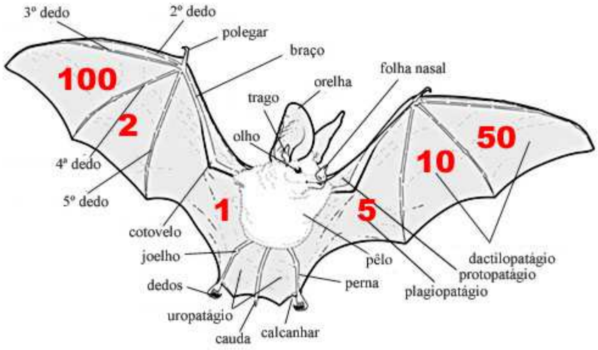
Conjunto usado para radiotelemetria: receptor TRX-1000S (Wildlife Materials), antena (Yagi 3 elementos), cabos, bolsa e fone de ouvido.

Transmissor LB-2N (Holohil Systems) colado às costas de um morcego *Sturnira lilium*.

Fezes, contendo sementes de piperáceas, coletadas nos sacos de algodão onde os morcegos aguardavam a análise em campo.

Modo como as redes de neblina (Ecotone, nylon, 7 x 3 m) eram armadas nas trilhas de estudo.

Foto mostrando o local onde as anilhas metálicas de marcação foram posicionadas nos morcegos: na parte mais fina do antebraço, pela faca dorsal e cobrindo a parte superior do propatágio. As anilhas possuíam um diâmetro bem maior que o do antebraço, a fim de minimizar ferimentos. A numeração era pintada e feita em baixo relevo, a fim de que fosse mais difícil as anilhas ficarem ilegíveis devido a mordidas.



Código de marcação de morcegos através de furos nos patágios. Usado em espécies às quais o tamanho da anilha não era adequado. Eram feitos três furos em forma de triângulo em uma determinada área, dependendo do valor desejado. Podiam ser feitos furos em até três áreas de um mesmo indivíduo.

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