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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

ESPECIALIZAÇÃO INDIVIDUAL NO USO DO ESPAÇO E DIETA NO MORCEGO FRUGIVORO STURNIRA LILIUM

PATRICIA KERCHES ROGERI

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia e Biodiversidade

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AUTORA: PATRÍCIA KERCHES ROGERI
ORIENTADOR: MARCIO SILVA ARAUJO
COORIENTADOR: MILTON CEZAR RIBEIRO

Aprovada como parte das exigências para obtenção do Título de Doutora em ECOLOGIA E BIODIVERSIDADE, área: BIODIVERSIDADE pela Comissão Examinadora:

Prof. Dr. MARCIO SILVA ARAUJO
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Profa. Dra. MARINA CORREA CORTES
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Prof. Dr. ARIOVALDO PEREIRA DA CRUZ NETO
Departamento de Zoologia / Instituto de Biociências de Rio Claro - SP

Prof. Dr. BERNARDO BRANDÃO NIEBUHR DOS SANTOS
CENAP / ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade - SP

Prof. Dr. LEONARDO CARREIRA TREVELIN
ITV / Instituto Tecnológico da Vale - PA

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Resumo

A maior parte dos estudos em ecologia trata indivíduos coespecíficos como equivalentes. No entanto, tem sido crescente o número de estudos que verificaram que os indivíduos de uma mesma população podem utilizar diferentes subconjuntos do total de recursos utilizados por sua população, o que foi definido como especialização individual. Morcegos frugívoros são importantes dispersores de sementes e a especialização individual no uso do espaço e na dieta traz consequências para essa função ecológica. No presente estudo verificamos a presença de variação interindividual no uso do espaço e de especialização individual na dieta no morcego frugívoro *Sturnira lilium* e investigamos possíveis mecanismos dessa variação. Para isso, 28 indivíduos adultos foram capturados em rede de neblina e marcados com radiotransmissores monitorados por meio de receptores fixos ("dataloggers") distribuídos pela área de estudo de acordo com características da paisagem. Estudamos a dieta desses mesmos indivíduos a partir de amostras fecais, com foco na análise das sementes presentes e amostras de pelos por meio de análise de isótopos estáveis de carbono e nitrogênio. Para investigar um possível mecanismo gerador dessa variação, estabelecemos a ordem de preferência dos itens alimentares para cada indivíduo, por meio da razão entre o conteúdo energético e o tempo de manipulação de cada recurso (Teoria de Forrageamento Ótimo). Para isso, realizamos experimentos com 30 indivíduos para medir o tempo de manipulação dos recursos. Também medimos o conteúdo energético dos frutos. Encontramos variação interindividual no uso do espaço e movimento sumarizada em síndromes de movimento: indivíduos generalistas de habitat associados com frutos de *Piper* e indivíduos especialistas em áreas abertas associados com frutos de *Solanum*. Verificamos que os indivíduos variam principalmente no consumo de insetos, com indivíduos muito frugívoros e indivíduos onívoros. A análise de isótopos estáveis indicou que o fruto mais consumido pelos indivíduos, *Solanum*, não foi o fruto mais rentável energeticamente segundo os experimentos para metade dos indivíduos, para os quais o fruto mais rentável foi *Piper*. Isso pode acontecer por competição interespecífica, uma vez que existem outras espécies de morcegos que consomem os mesmos recursos. Estes resultados sugerem que a diferença na ordem de preferência dos recursos, somada à competição interespecífica e características comportamentais parecem ser os mecanismos geradores dos padrões de movimento e uso do espaço observados nesta população do morcego frugívoro *S. lilium* em uma paisagem fragmentada.

Abstract

Most ecology studies treat co-specific individuals as equivalents. However, there has been a growing number of studies that have verified that individuals from the same population can use different subsets of the total resources used by their population, which has been defined as individual specialization. Fruit bats are important seed dispersers and individual specialization in space use and diet can have consequences for this ecological function. In the present study we verified the presence of interindividual variation in the use of space and individual specialization in the diet of the fruit bat *Sturnira lilium* and investigated possible mechanisms that trigger this variation. To that end, 28 adult individuals were captured in mist net and tagged with radio transmitters monitored by fixed receivers ("dataloggers") distributed in the study area according to landscape characteristics. We studied the diet of these same individuals from fecal samples, focusing on the analysis of the seeds present, and hair samples for stable isotope analysis of carbon and nitrogen. In order to investigate mechanisms that generate such variation, we established the rank preference for each individual, as the ratio between the energy content and handling time of each resource (Optimal Foraging Theory). For this, we performed experiments with 30 individuals to measure handling time. We also measured the energy content of the fruits. We found interindividual variation in space use and this variation was summarized in two movement syndromes: habitat generalist individuals associated with *Piper* fruits and individual specialized in open areas associated with *Solanum*. We found that individuals vary mainly in insect consumption, with extremely frugivorous individuals and omnivorous individuals. Stable isotope analysis indicated that the fruit most consumed by all individuals, *Solanum*, was not the most profitable fruit according to the experiments for half the individuals, for which the most profitable fruit was *Piper*. This can be pushed by interspecific competition, since there are other species of bats that consume the same resources. These results suggest that the difference in the rank preferences for resources, together with interspecific competition and behavioral characteristics, seem to be the mechanisms that generate the patterns of movement and space use observed in this population of the frugivorous bat *S. lilium* in a fragmented landscape.

Sumário

Capítulo 1 - Introdução Geral

A teoria de nicho tem sido usada para estudar a ecologia de espécies ou de populações locais, tratando indivíduos coespecíficos como ecologicamente equivalentes (LEIBOLD, 1995). Por exemplo, a maioria dos modelos de competição intraespecífica e dinâmica predador-presa supõe que indivíduos da mesma espécie atuam de maneira idêntica (ROUGHGARDEN, 1979). Essa simplificação teórica tem convivido com a percepção empírica de que indivíduos de uma mesma população podem diferir ecologicamente em função do sexo, da idade, e mesmo dentro desses grupos demográficos. Por exemplo, Estes *et al.* (2003) estudaram os hábitos alimentares de uma população de lontras marinhas, *Enhydra lutris*, na Califórnia - EUA, e observaram que a população consumia uma ampla variedade de recursos alimentares, incluindo abalones, ouriços-do-mar, caranguejos e estrelas-do-mar. No entanto, cada indivíduo preferia e consumia principalmente apenas um desses itens, sendo exigidas para isso habilidades específicas. Outro exemplo ocorre com o Tentilhão da Ilha de Cocos – Costa Rica, *Pinaroloxias inomata*. A população como um todo apresentava uma diversidade grande de comportamentos alimentares: ciscar nos galhos (insetos), extrair larvas do tronco, ciscar nas folhas (insetos), extrair minadores das folhas, ciscar na serapilheira (insetos), visitar nectários extra-florais, visitar flores (néctar) e comer sementes no chão. No entanto muitos indivíduos apresentavam apenas um desses comportamentos alimentares consistentemente ao longo do tempo (WERNER; SHERRY, 1987). Outros exemplos de variação no uso do recurso entre os indivíduos já foram observados em mais de 200 espécies, incluindo moluscos, insetos, crustáceos, peixes, anfíbios, aves e mamíferos (revisado em Bolnick *et al.* 2003 e Araújo, Bolnick & Layman 2011), em diferentes partes do mundo (ARAÚJO; COSTA-PEREIRA, 2013).

Para entender melhor essa variação entre indivíduos, Roughgarden (1974) propôs que o nicho total de uma população (*total niche width* - TNW) pode ser decomposto em dois componentes, o componente intraindividual (*within-individual component* – WIC, que é a variação média dos recursos encontrados dentro do nicho dos indivíduos) e o componente interindividual (*between-individual component* – BIC, que é a variação entre os indivíduos; Fig. 1). Geralmente se espera que indivíduos de diferentes idades ou sexo sejam diferentes. Por exemplo, a variação entre macho e fêmeas pode surgir por diferentes necessidades nutricionais durante a fase reprodutiva (CLUTTON-BROCK; ALBON; GUINNESS, 1985). Da mesma forma, mudanças no nicho podem ocorrer

devido a mudanças no tamanho corporal, de forma que a variação entre os indivíduos pode ser um artefato de fatores ontogenéticos (SPECZIÁR; REZSU, 2009). No entanto, indivíduos do mesmo sexo ou idade podem possuir nichos diferentes. Usando esta ideia, Bolnick et al. (2003) definiram como especialista um indivíduo cujo nicho é substancialmente mais estreito do que o nicho da sua população, devido a razões não atribuíveis ao sexo ou à idade. Desta forma, a especialização individual ocorre quando os indivíduos usam apenas um subconjunto dos recursos usados pela população como um todo.

Assim, surgiu uma importante questão destacada por Bolnick et al. (2003): por que diferentes indivíduos da mesma população, que possuem o mesmo conjunto de recursos disponíveis, selecionam recursos diferentes? Macarthur & Pianka (1966) propuseram que os organismos, ao escolherem a sua dieta, maximizam seu retorno energético. Essa teoria recebeu o nome de Teoria do Forrageamento Ótimo (TFO - Stephens & Krebs (1986). Segundo esta teoria, os indivíduos ordenariam os itens alimentares de acordo com a razão entre conteúdo energético e tempo de manipulação (*e*/*h*) de cada item alimentar. Os indivíduos devem ignorar itens alimentares menos rentáveis quando o tempo que seria gasto consumindo-os for melhor aproveitado na procura de um item mais rentável. À medida que os itens mais rentáveis se tornam escassos, os indivíduos passariam a adicionar os itens menos rentáveis a sua dieta.

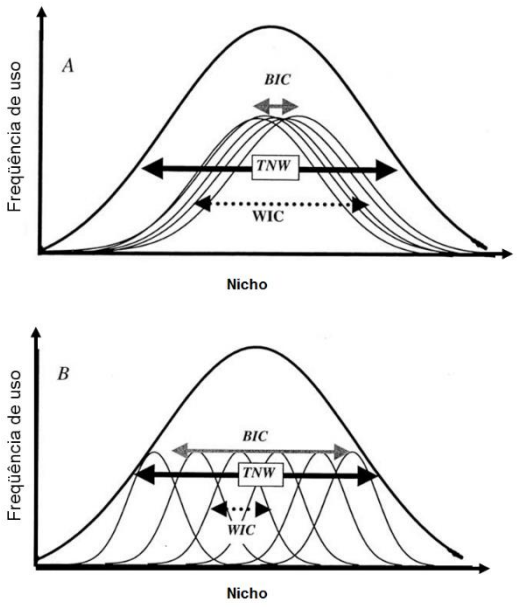

Figura 1: O nicho de uma população (curva grossa) pode ser subdividido nos nichos de cada um dos indivíduos que a compõem (curvas finas). A amplitude do nicho da população (*total niche width* - TNW) é a variação no uso dos recursos por todos os

indivíduos. TNW = WIC + BIC, onde WIC (*within-individual component*) é a média da amplitude dos nichos individuais e BIC (*between-individual component*) é a variação entre as médias individuais. Em uma população de indivíduos generalistas (*A*), WIC representa a maior parte de TNW, enquanto que em uma população de indivíduos especialistas (*B*) BIC representa a maior parte de TNW (modificada a partir de Bolnick et al. 2003).

Uma importante suposição da TFO clássica é que todos os indivíduos de uma população possuem a mesma ordem de preferência pelos diferentes recursos alimentares e possuem a mesma propensão para incorporar os recursos alternativos, quando o item mais rentável está escasso (STEPHENS; KREBS, 1986). Svanbäck & Bolnick (2005) relaxaram essa suposição, propondo que diferentes fenótipos de uma população podem possuir ordens de preferência distintas se diferirem em suas habilidades de manipulação dos recursos. Assim, eles propuseram três modelos, destacados a seguir. No modelo de "preferências compartilhadas", indivíduos com diferentes fenótipos têm a mesma ordem de preferências alimentares, mas diferem na propensão de incluir os recursos alternativos na dieta. Neste caso, quando não há competição, os indivíduos se especializam no recurso preferido; à medida que a competição aumenta, alguns indivíduos adotam uma estratégia generalista enquanto outros mantêm a especialização no recurso preferido (Tabela 1). No modelo de "refúgio competitivo", os diferentes fenótipos possuem o mesmo recurso preferido, mas diferem nas preferências pelos recursos alternativos. Neste caso, quando a competição é baixa, os diferentes fenótipos possuem dietas similares, ao passo que suas dietas divergem à medida que a competição aumenta (Tabela 1). Finalmente, no modelo de "preferências distintas", o recurso preferido difere entre os fenótipos, mas as preferências pelos recursos alternativos se assemelham em algum grau. Neste caso, as dietas diferem entre os fenótipos para baixos níveis de competição, tornando-se mais semelhantes à medida que a competição aumenta (Tabela 1).

As diferenças entre as preferências alimentares de diferentes fenótipos em geral resultam de *trade-offs* funcionais (Bolnick et al. 2003) e fortes *trade-offs* funcionais estão implícitos nos modelos propostos por Svanbäck & Bolnick (2005). A ideia de *trade-off* é que se um fenótipo é eficiente no uso de um recurso, ele é necessariamente ineficiente no uso de um outro recurso e vice-versa. Os *trade*-offs podem ser morfológicos, comportamentais ou fisiológicos (SCHLUTER, 1995; ESTES et al.,

2003; OLSSON et al., 2007). Por exemplo, Robinson (2000) estudou a eficiência de forrageio de uma população morfologicamente variável do peixe esgana-gatos (*Gasterosteus aculeatus*). Os indivíduos coletados na zona litorânea dos lagos tendiam a ser morfologicamente divergentes dos indivíduos coletados na zona pelágica. Uma das hipóteses testadas foi a de que as formas litorâneas e pelágicas enfrentam *trade-offs* envolvendo o consumo de recursos específicos de cada habitat. Para testar essa hipótese, o pesquisador mediu a eficiência de forrageio em dois tipos de recursos, um bentônico e outro pelágico, e verificou que a eficiência de forrageio estava relacionada a diferenças morfológicas entre os dois fenótipos. A forma pelágica consumiu náuplios de *Artemia*, uma presa pelágica, a uma taxa maior do que a forma litorânea. Inversamente, a forma litorânea foi mais eficiente no consumo de anfípodes bentônicos do que a forma pelágica.

Tabela 1: Modelos de forrageamento ótimo propostos por Svanbäck e Bolnick (2005). São apresentadas as ordens de preferência dos diferentes fenótipos e a dieta realizada em um cenário de baixa e um de alta competição. A razão entre o conteúdo energético e o tempo de manipulação (e/h) é o retorno energético dos itens alimentares, enumerados de 1 a 4. A dieta realizada corresponde aos recursos consumidos pelos fenótipos sob cenários de competição baixa ou intensa.

Modelo	**Fenótipo**	**Ordem de Preferência**	**Dieta realizada**	
			Baixa competição	Competição intensa
Preferências compartilhadas	I	$e_1/h_1 > e_2/h_2 > e_3/h_3 > e_4/h_4$	1	1,2,3
	II	$e_1/h_1 >> e_2/h_2 >> e_3/h_3 >> e_4/h_4$	1	1,2
	III	$e_1/h_1 >>> e_2/h_2 >>> e_3/h_3 >>> e_4/h_4$	1	1
Refúgio competitivo	I	$e_1/h_1 > e_2/h_2 > e_3/h_3 > e_4/h_4$	1	1,2,3
	II	$e_1/h_1 > e_3/h_3 > e_4/h_4 > e_2/h_2$	1	1,3,4
	III	$e_1/h_1 > e_4/h_4 > e_2/h_2 > e_3/h_3$	1	1,4,2
Preferências distintas	I	$e_1/h_1 > e_2/h_2 > e_3/h_3 > e_4/h_4$	1	1,2,3
	II	$e_2/h_2 > e_1/h_1 > e_3/h_3 > e_4/h_4$	2	2,1,3
	III	$e_4/h_4 > e_3/h_3 > e_2/h_2 > e_1/h_1$	4	4,3,2

Araújo et al. (2010) aplicaram vários métodos baseados na teoria de redes complexas para investigar os padrões intrapopulacionais de uso de recurso na espécie de

marsupial *Gracilinanus microtarsus*. Eles encontraram que as dietas dos indivíduos especialistas são um subconjunto da dieta dos generalistas, padrão conhecido como aninhado. Esse padrão encontrado é consistente com o modelo de "preferências compartilhadas" (SVANBÄCK; BOLNICK, 2005), pois, de acordo com este modelo, indivíduos possuem a ordenação de recursos alimentares idêntica, mas diferem em suas habilidades de incluir novos itens a suas dietas. Em tal cenário, para um dado conjunto de recursos, alguns indivíduos na população devem se comportar como generalistas enquanto outros ainda se especializam no recurso preferido. Como os indivíduos possuem os itens alimentares ordenados da mesma forma, eles devem adicionar novos recursos a sua dieta em uma ordem previsível, o que gera o aninhamento.

Um estudo com lontras marinhas testou os três modelos de como a especialização individual na dieta pode surgir. A variação entre os indivíduos era ausente quando a densidade era baixa, mas aumentava com a densidade de lontras. Os autores encontraram que quando se considera todos os recursos utilizados, o resultado encontrado é consistente com o modelo preferências compartilhadas. No entanto, quando se consideram apenas os principais recursos favoritos, os resultados corroboram o modelo de "refúgio competitivo" (TINKER et al., 2012). Já o "modelo de preferências" distintas é consistente com os resultados encontrados para a análise da dieta em uma população do molusco *Nucella emarginata*, na qual os indivíduos possuíram dieta diferente e essa diferença não estava relacionada com a abundância relativa dos recursos disponíveis ou distribuição de recursos nos diferentes micro-habitat utilizados por cada um (WEST, 1986).

Assim, a TFO prevê que a competição intraespecifica pode aumentar ou diminuir a especialização individual, dependendo da variação nos ordem dos recursos. No entanto, a competição interespecífica, a oportunidade ecológica e a predação também podem afetar o grau de especialização individual em populações naturais (Araújo et al 2011, Fig. 2).

A ideia de que a competição interespecífica interfere na especialização individual vem da Hipótese da Variação de Nicho, que afirma que quando uma população é ecologicamente liberada de competição interespecífica, a amplitude do nicho total da população (TNW) aumenta principalmente pelo aumento da variação entre os indivíduos (BIC, Van Valen 1965). Se a competição interespecífica enfraquece a especialização individual, espera-se que a especialização individual seja fraca em comunidades ricas em espécies, onde a competição interespecífica deve ser mais forte

(ARAÚJO; BOLNICK; LAYMAN, 2011). Por exemplo uma população de Truta do Ártico *Salvelinus alpinus*, em um lago com poucas espécies, apresenta maior variação interindividual no uso do recurso do que outra população da mesma espécie em um lago que possuía mais espécies de peixes competidoras (KNUDSEN et al., 2007).

Competição interespecífica e oportunidade ecológica são conceitos relacionados, mas distintos (ARAÚJO; BOLNICK; LAYMAN, 2011). A oportunidade ecológica pode ser entendida como a diversidade de recursos disponíveis para uma espécie. Presume-se que a competição interespecífica reduza a oportunidade ecológica de uma espécie, mas ela também pode depender de fatores como o tamanho do ecossistema, a diversidade de micro-habitats e a estabilidade ambiental. Por exemplo, no morcego frugívoro *Rousettus aegyptiacus*, o grau de especialização individual foi maior na primavera, quando o número de plantas frutificando também é maior (HERRERA et al., 2008). Uma revisão encontrou uma correlação entre grau de especialização individual e a latitude. Uma explicação plausível para isso seria que a maior diversidade de recursos (oportunidade ecológica) em regiões tropicais pode promover maior variação intraespecífica no nicho (ARAÚJO; COSTA-PEREIRA, 2013).

Os predadores podem influenciar no grau de especialização individual das presas ao regular a densidade populacional (influenciando a densidade de indivíduos e consequentemente os padrões de competição intraespecíficas citados acima). Além disso, a presença de um predador em um determinado micro-habitat pode fazer com que as presas se refugiem em outro micro-habitat, mesmo que o custo disso seja que todos os indivíduos precisem convergir no uso dos mesmos recursos (ARAÚJO; BOLNICK; LAYMAN, 2011; CAMP et al., 2017). Os indivíduos podem também divergir com relação a aversão ou exposição ao risco, de forma que os indivíduos avessos ao risco mudam para habitats menos lucrativos ou possuem área de vida menor do que os indivíduos mais ousados (COLEMAN; WILSON, 1998; DUBOIS; GIRALDEAU, 2014).

Além da competição intra e interespecífica, predação e oportunidade ecológica (Araújo et al 2011), diferenças consistentes no comportamento entre os indivíduos (personalidade animal) pode ser um fator adicional que contribui para a existência e persistência da especialização individual (TOSCANO; GOWNARIS; HEERHARTZ, 2016). A personalidade animal pode promover especialização individual por proporcionar diferenças interindividuais no comportamento de forrageio. Um dos

mecanismos que podem conectar a personalidade animal e a especialização individual está relacionado com o aspecto espacial do forrageio. Traços de personalidade animal frequentemente covariam com tendências à dispersão, migração, tamanho da área de vida e fidelidade de habitat em populações naturais, sugerindo que a personalidade pode levar à especialização individual quando os recursos são distribuídos de maneira heterogênea pela paisagem. Por exemplo, o comportamento de exploração de indivíduos de Chapim-real (*Parus major*) está relacionado com a resposta espacial a experimentos de mudança na disponibilidade de comida. Após a comida ser removida dos alimentadores, todos os indivíduos aumentaram o tamanho de suas áreas de vida. Mas indivíduos mais lentos permaneceram relativamente próximos ao alimentador, mudando para o recurso alternativo, enquanto que indivíduos mais rápidos imediatamente mudaram para áreas de forrageio mais longe buscando o recurso preferido (VAN OVERVELD; MATTHYSEN, 2010).

Dessa forma, variação na ordem de recursos, competição intra e interespecifica, aversão ao risco, oportunidade ecológica e personalidade podem ser os mecanismos geradores da variação entre os indivíduos no uso do recurso e também nos padrões de movimento e uso do espaço em paisagens heterogêneas observados em populações naturais. Ainda, esses mecanismos ecológicos também podem auxiliar na compreensão de como a especialização individual no recurso se relaciona com o uso do espaço e movimento animal.

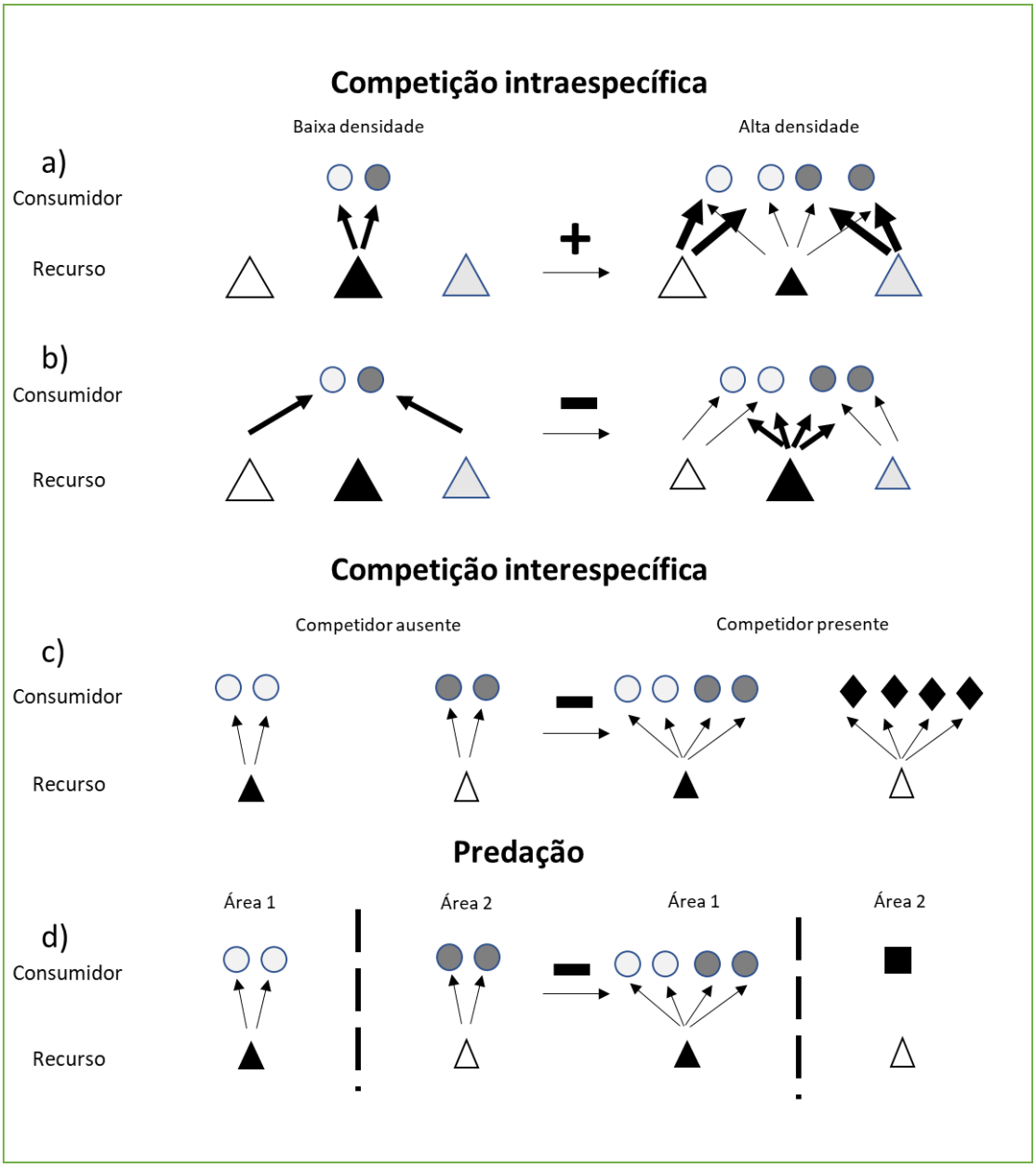

Figura 2: Ilustração de como os mecanismos ecológicos podem afetar o grau de especialização individual. Setas ligando recursos a consumidores individuais indicam consumo de recursos (espessura relativa indica contribuição proporcional). Setas horizontais indicam o sinal (positivo ou negativo) do efeito no grau de especialização individual. a) Consumidores com fenótipos diferentes (diferentes tons de cinza) compartilham o mesmo recurso preferido (triângulo cinza escuro), mas diferem nos recursos alternativos (triângulos brancos e cinza claro). Quando ambos os fenótipos estão com baixa densidade, eles consomem o recurso preferido; em maior densidades, à medida que o recurso preferido torna-se escasso (triângulo de tamanho menor) devido à alta competição intraespecífica, os consumidores adicionam os recursos alternativos a

suas dietas, aumentando o grau de especialização individual. (b) Alternativamente, os consumidores com diferentes fenótipos podem ter os recursos preferidos distintos, de modo que, em baixa densidade, há dietas distintas. Em densidades mais altas, todos os indivíduos convergem para o mesmo recurso alternativo (triângulo cinza escuro), reduzindo a variação na dieta. (c) Na ausência de uma espécie concorrente (diamantes negros), os consumidores com diferentes fenótipos exploram recursos diferentes e a especialização individual é alta. Na presença de um concorrente, o nicho populacional é restrito a um recurso (triângulo cinza escuro) que limita o grau de especialização individual. (d) se os recursos ocorrem em diferentes micro-habitat, a presença de um predador em um dos micro-habitat pode restringir os consumidores à área segura, reduzindo o escopo para a especialização individual (adaptação de Araújo et al 2011).

A forma como um animal explora a paisagem desempenha um papel crucial para a sua persistência. O movimento animal é definido como a mudança na localização espacial no tempo. Mesmo que o movimento seja baseado no indivíduo, tem um papel central na estrutura e dinâmica da população, comunidade e ecossistema. Nathan et al. (2008) propuseram que o movimento de qualquer organismo móvel é o resultado da interação entre quatro componentes: estado interno, capacidade de movimento, capacidade de navegação e fatores externos. Esses componentes estão relacionados com as questões por que, como e onde se mover. Com base nessas ideias, propuseram o paradigma da Ecologia do Movimento para unificar as pesquisas sobre movimento animal e cunhou definitivamente essa área da ciência (Figura 3).

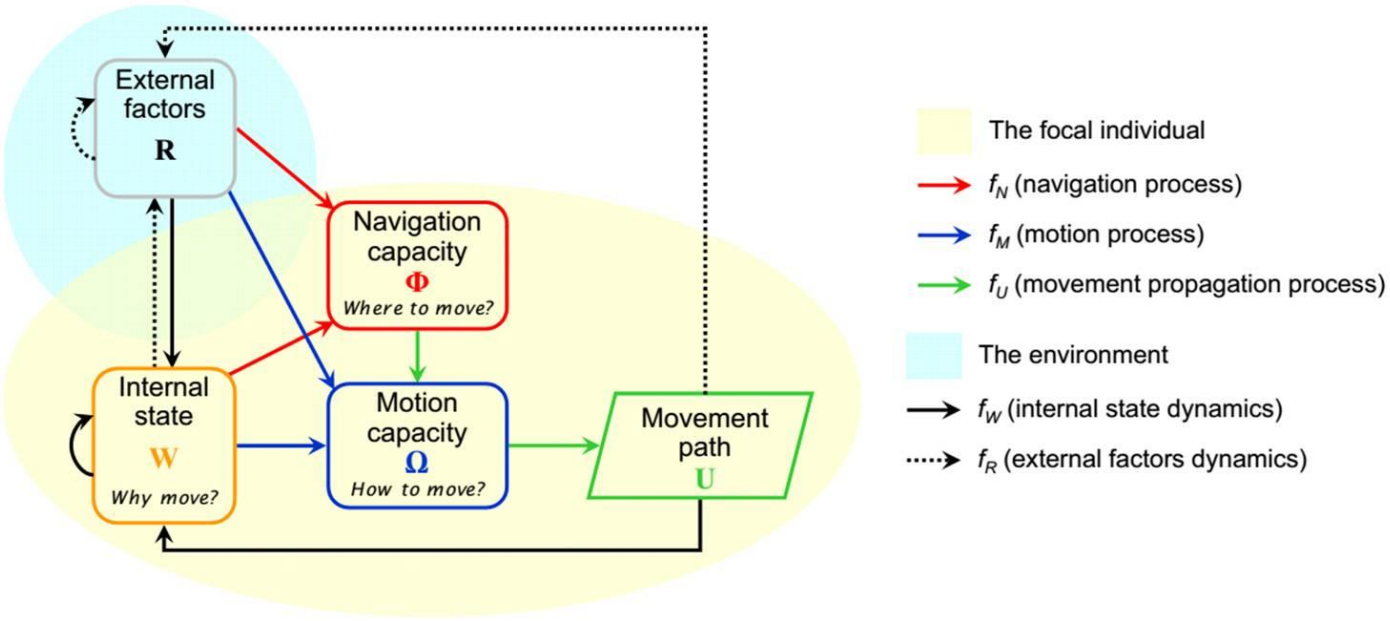

Figura 3. Uma estrutura conceitual para a ecologia do movimento, composto por três componentes básicos (fundo amarelo) relacionado ao indivíduo focal (estado interno, capacidade de movimento, e capacidade de navegação) e um quarto componente básico (fundo azul claro) que se refere a fatores externos que afetam o movimento. A relação entre os componentes relacionados com os processos pelos quais eles afetam um ao outro, com setas indicando a direção do impacto. A trajetória resultante alimenta novamente os componentes externos e internos (Modificado de Nathan et al. 2008).

A fragmentação do habitat, o padrão de uso da terra e as mudanças climáticas destacam a conexão entre o movimento dos animais e as mudanças na paisagem. Uma melhor compreensão sobre as causas, padrões, mecanismos e consequências do movimento animal e uso do espaço são centrais para o gerenciamento e restauração de paisagens fragmentadas (Nathan et al 2008).

A análise do uso de espaço e seleção de habitat é crucial para identificar os fatores que determinam a distribuição de espécies (Pulliam & Danielson, 1991). O movimento e o uso do espaço estão diretamente relacionados à paisagem, uma vez que as características dela promovem diferentes quantidades de recursos, riscos e facilidades ou dificuldades de locomoção (Fahrig 2007).

Como os ambientes naturais, como a Mata Atlântica, estão cada vez mais impactados e muito do que sobra são pequenos fragmentos (Ribeiro et al., 2009), tornou-se cada vez mais importante para a conservação entender como as espécies respondem a características distintas da paisagem. Atualmente, muitas abordagens espacialmente explícitas têm buscado acoplar os modelos de movimento e uso do espaço à ecologia da paisagem (Ovaskainen 2004). Por exemplo, com modelos de seleção de habitat, que consideram a preferência ou predisposição de uma espécie em usar um habitat particular (Morales et al. 2004; Capra et al.2017). Como essa dinâmica ocorre no nível individual, e o indivíduo são os agentes que interagem com a paisagem e realizam o movimento, muitos modelos tentam inserir a variação entre os indivíduos nos modelos (Jønsson et al. 2016, Delgado et al 2014, Patterson et al 2008). Geralmente, esses modelos usam caminhos individuais para encontrar um padrão de movimento para uma população inteira.

Austin et al (2004) estudaram uma população de focas cinzentas. Eles modelaram o movimento como uma caminhada aleatória correlacionada (CRW) para os individuais. Eles usaram o comprimento médio do passo, o ângulo de virada e o

deslocamento (R2n: a taxa de mudança na área ao longo do tempo) em movimentos sucessivos. As focas cinzentaas exibiam três tipos de movimento, conforme determinado pelo ajuste do modelo CRW: motores direcionados (animais exibindo viagens de longa distância direcionadas significativamente subpredicados pelo CRW); moradores (animais remanescentes na área circunvizinha que foram superestimados pelo modelo); e caminhantes aleatórios correlacionados (aqueles em que o movimento foi previsto pelo modelo CRW). A variação intraespecífica no comportamento de forrageamento reflete diferentes táticas usadas por indivíduos ou sexos dentro de uma espécie ou população para sobreviver. Dado que a seleção natural opera no nível individual, os modelos ecológicos que consideram todos os indivíduos dentro da mesma categoria de comportamento, efetivamente desconsideram essa variação. Consequentemente, o exame das respostas médias para uma população obscurece a variabilidade na ecologia comportamental. O movimento animal geralmente se torna mais intrigante quando se examina como os indivíduos não conseguem se ajustar às previsões dos modelos (Austin et al. 2004).

Um animal que explora o espaço amplamente são os morcegos. Por serem os únicos mamíferos com voo verdadeiro, eles podem sobrevoar dezenas de quilômetros em uma única noite (BERNARD; FENTON, 2003). Essa é uma das características que os tornam importantes dispersores de sementes nos Neotrópicos (MELLO; KALKO; SILVA, 2008a). Herrera *et al.* (2008) encontraram variação interindividual na dieta do frugívoro *Rousettus aegyptiacus* (Chiroptera: Pteropodidae). Considerando a distribuição heterogênea das plantas que os morcegos se alimentam, eles também exibiriam especialização individual no uso do espaço?

Um bom modelo para se estudar a especialização individual no uso do espaço e na dieta são os morcegos da família Phyllostomidae. Esta família constitui grande parte da fauna de morcegos, possui ampla distribuição e é fundamental para processos ecológicos, como a polinização e a dispersão de sementes (HEITHAUS; FLEMING; OPLER, 1975). Entre os morcegos da família Phyllostomidae, uma das espécies mais abundantes na Mata Atlântica é *Sturnira lilium*. Indivíduos de *S. lilium* são conhecidos por terem uma forte preferência por frutos do gênero *Solanum*, mas também por consumirem frutos de *Piper* e *Cecropia* entre outros (MELLO; KALKO; SILVA, 2008b). Alguns estudos sugerem que existem variações espaciais na dieta dessa espécie, como por exemplo um aumento no consumo de *Solanum* correlacionado com o aumento na altitude (SÁNCHEZ; DOS SANTOS, 2015). Com relação ao uso do espaço e

movimento, *S. lilium* utiliza amplas áreas, e, por sua capacidade de se locomover, conecta fragmentos florestais (LOAYZA; LOISELLE, 2008; MELLO; KALKO; SILVA, 2008a), e, por se alimentar de plantas consideradas pioneiras, sugere-se que não é, aparentemente, afetada pela fragmentação (FENTON et al., 2000). Além disso, o modelo de "refúgio competitivo" pode ser útil para compreender o padrão de uso de recursos alimentares por morcegos *S. lilium*. Em um estudo experimental realizado por Muylaert, Matos & Mello (2014) foram oferecidos frutos em uma tenda de voo, sendo observada uma forte preferência de morcegos *S. lilium* por frutos de *Solanum*. Entretanto, os indivíduos de morcegos diferiram na escolha do fruto secundário. No entanto, em outra população de *S. lilium*, os indivíduos forrageram constantemente em diferente áreas que diferiam na disponibilidade de recursos (ROGERI, 2011), o que sugere que os indivíduos preferem diferentes recursos, em linha com o modelo de "preferências distintas". Compreender se esse padrão ocorre por diferenças na habilidade de cada indivíduo na manipulação dos frutos, e, consequentemente, na ordem de preferência alimentar é fundamental, pois tem consequências diretas sobre a escolha dos frutos dispersados por esses morcegos e, portanto, no processo de dispersão de sementes.

Justificativa

A especialização individual na dieta e no uso do recurso pode ter implicações ecológicas importantes, como na forma como morcegos *S. lilium* prestam serviços ambientais de dispersão de sementes e como conectam elementos de paisagens fragmentadas. Com relação à dispersão de sementes, ao utilizarem áreas com qualidades diferentes para as espécies de plantass das quais se alimentam (por exemplo, áreas de borda podem possuir uma qualidade melhor para plantas pioneiras), os indivíduos podem diferir na efetividade como dispersores de sementes de diferentes plantas, sendo alguns melhores dispersores que outros. Além disso, sabe-se da importância dos morcegos em áreas fragmentadas como "elos móveis" (LUNDBERG; MOBERG, 2003), permitindo que as populações das espécies que dispersam mantenham contato reprodutivo (HENRY; PONS; COSSON, 2007). Se os indivíduos estão conectando os fragmentos de formas distintas, essa conectividade pode afetar o fluxo gênico das plantas de uma forma diferente do que ao se considerar apenas os indivíduos como equivalentes. Por exemplo, se um determinado indivíduo utiliza apenas um fragmento, não está conectando-o a outros e também não está dispersando as sementes a grandes

distâncias. Assim, a especialização individual no uso do espaço pode comprometer este serviço ecológico. Por fim, se os indivíduos utilizam diferentes áreas, projetos de conservação devem levar em consideração a heterogeneidade da paisagem. Manter um fragmento e não outro, pode selecionar indivíduos dentro da população e diminuir a variabilidade dentro dela (HAMMERSCHLAG-PEYER; LAYMAN, 2010).

Objetivos

O presente estudo teve como objetivo verificar a presença de variação interindividual no uso do espaço e de recursos alimentares no morcego frugívoro *S. lilium* e investigar uma possível causa imediata dessa variação. Para isso, propusemos as seguintes perguntas que serão exploradas nos próximos capítulos:

I. Há especialização individual na dieta?

II. Os indivíduos possuem diferentes ordens de preferência pelos recursos?

III. O uso do espaço pelo morcego frugívoro *S. lilium* é influenciado pela estrutura da paisagem (cobertura e configuração)?

IV. Os indivíduos diferem no uso do espaço em função da estrutura da paisagem?

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Capítulo 2 – Interindividual variation in a frugivorous bat: an optimal foraging theory approach

Patricia Kerches-Rogeri[1,2], Milton Cezar Ribeiro[1], Márcio Silva Araújo[1]
[1] Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, SP, Brazil
[2] corresponding author: parogeri@gmail.com

Abstract

1. Most ecology studies treats co-specific individuals as equivalent. However, there has been a growing number of studies that have found that individuals from the same population can use different subsets of the total resources used by their population. Interindividual variation in resource use may reflect intrapopulational variation in a number of individual characteristics that determine specific efficacy and preferences of a particular resource, such as the difference between individuals in the ability to handle prey of different sizes and shapes.

2. This study aims to verify the presence of interindividual variation in diet in fruit bat *Sturnira lilium* and investigate whether individuals have different rank preference for the resources.

3. Data collection was carried out in two steps: diet assessment and experiments in flight tent. We accessed the diet of the individuals through fecal samples, focusing on the analysis of the present seeds, and hair samples for the analysis of stable isotopes of carbon and nitrogen. In order to investigate a possible mechanism for this variation, we established an ordering of the food items for each individual, by the ratio between the energy content and handling time of each resource (Optimal Foraging Theory). To that end, thirty individuals underwent experiment in a flight tent, where we measured the handling time for each fruit, and the energy content of the fruits was established in a calorimetric bomb.

5. We found that individuals have different rank preferences with different optimal resources. According to the individual rank preferences, for most individuals, the optimal fruit is *Piper*. However, the realized diet by individuals is very similar, with the main consumption of *Solanum*, as indicated in the literature.
6. Intra and interspecific competition decrease the difference between individuals in the diet, especially in a fragmented environment, where abundance of the optimal resource can be scarce. Thus, we provide a further level of complexity to understand the partition of resources among neotropical frugivorous bats.

Introduction

In the last few years, many studies have shown that an apparently generalist population can be actually composed of relatively specialized individuals (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011). For example, in a population of sea otters, *Enhydra lutris*, consuming a wide variety of food resources, including abalones, sea urchins, crabs and starfish, each individual consumes preferentially only one of these items, and specific skills are required for foraging on each item (Estes *et al.* 2003). Other examples of variation in resource use among individuals have already been observed in more than 200 species, including mollusks, insects, crustaceans, fish, amphibians, birds and mammals (reviewed in Bolnick *et al.* 2003 and Araújo *et al.* 2011) in different parts of the world (Araújo & Costa-Pereira 2013).

This individual specialization has important implications for both ecological interactions and evolutionary processes (Bolnick *et al.* 2003, 2011). However, little is known about the mechanistic basis of variation in diet. Classical Optimal Foraging Theory (OFT), predicts that organisms, when choosing their diet, maximize their energy return (Macarthur & Pianka 1966). According to this theory, individuals would rank

food items according to the ratio between energy content and handling time (e/h) of each food item. Individuals should ignore less profitable food items when the time that would be spent consuming them is best allocated in looking for a more profitable item. As more profitable items become scarce, individuals would add less profitable items to their diet.

An important assumption of classical OFT is that all individuals in a population have the same rank preference for different dietary resources (Stephens & Krebs 1986). Svanbäck & Bolnick (2005) have relaxed this assumption by proposing that different phenotypes may have distinct ranks if they differ in their handling times. In the "shared preferences" model, phenotypes have the same rank preference but differ in the likelihood to utilize alternative resources; in the "competitive refuge" model, phenotypes have the same optimal resource but differ in how they rank alternative resources; and in the "distinct preferences" model, phenotypes have different rank preferences, including the optimal resources.

At a proximate level, differences in food preferences between individuals generally result from functional trade-offs (Bolnick *et al.* 2003). The idea of a functional trade-off is that if a phenotype is efficient in the use of a resource A, it is necessarily inefficient in using resource B and vice-versa. Trade-offs may be morphological, behavioral or physiological. A morphological trade-off occurs when there are biomechanical limitations in the use of resources among phenotypes. For example, in a morphologically variable population of sticklebacks (*Gasterosteus aculeatus*), individuals collected in the coastal zone of the lakes tended to be morphologically divergent from the individuals collected in the pelagic zone, and the two phenotypes had different foraging efficiency with respect to two different types of resources (Robinson 2000). A trade-off is considered behavioral when it involves the

ability to search and manipulate resources, so that when an individual becomes very efficient in manipulating a given resource, it loses the ability to manipulate efficiently another resource. For example, in the above-mentioned sea otters, different prey require specific sensory and motor skills to be manipulated. Because these skills are difficult to learn it is impossible for an individual to learn all different skills, resulting in a large interindividual variation in diet (Estes *et al.* 2003). A trade-off is physiological when it occurs after ingestion, involving digestive conditions, enzymes and detoxification mechanisms. For example, a population of Eurasian perch (*Perca fluviatilis L.*) presents plasticity in the gut length when exposed to different types of food. Individuals who fed on low digestible resources developed longer guts compared to individuals who fed on highly digestible resources. Although there is plasticity, individuals switching to a new food item may experience an initial cost in fitness (Olsson *et al.* 2007).

Neotropical frugivorous bats (Phyllostomidae) are known to feed on a wide variety of fruits. In addition, there is a strong association between genera of bats and plants. For example, bats in the genus *Carollia* consume mostly fruits in the genus *Piper*; *Sturnira* spp. consume preferentially *Solanum* fruits; and *Artibeus* spp. consume *Cecropia* and *Ficus* fruits (Fleming 1986; Marinho-Filho *et al.* 1991; Lobova, Geiselman & Mori 2009). Results from a field experiment supported those preferences, since bats of those three genera selected first the fruits of their preferred plant genera, even when secondary fruits were offered in higher abundance, which indicates that those patterns of diet selection are real preferences (Andrade *et al.* 2013). In spite of these preferences, *Sturnira* bats also consume fruits of the genus *Piper* (Giannini 1993; Parolin, Bianconi & Mikich 2016), followed by smaller proportions of fruits of *Cecropia*, *Ficus*, and *Vismia* among other genera (Muscarella & Fleming 2007). In an experiment in which different fruits were offered, individuals of *S. lilium* preferred

Solanum, but differed in the choice of less preferred fruits (Muylaert, Matos & Mello 2014), in line with Svanbäck and Bolnick's (2005) "competitive refuge" model. Finally, in one population of *S. lilium*, individuals foraged consistently in different areas differing in the availability of resources (Rogeri 2011). This latter finding suggests that individuals prefer different resources, in line with Svanbäck and Bolnick's (2005) "distinct preferences" model.

Because the fruits consumed by *S. lilium* are different in shape and size (Aguirre *et al.* 2003) and bats need to manipulate them during consumption, it is reasonable to assume that individuals need to learn how to manipulate these resources. This in turn would generate differences in handling times and ultimately in preferences for different resources. Here, we aim to answer two questions: (i) whether there is interindividual variation in diet as suggested by previous studies and (ii) whether individuals have different rank preferences for resources. Our model species is *S. lilium*, one of the most abundant fruit bats of the neotropics (Muylaert *et al.* 2017). We used fecal samples and stable isotopes to investigate interindividual variation in diet, and observations in an experimental setting to determine the rank preferences of each individual.

Methods

1. Data Sampling

1.1. Study Area

The Vassununga State Park (Parque Estadual de Vassununga - PEV) is a state conservation unit with 2070 ha, divided into six fragments, all of them located in the city of Santa Rita do Passa Quatro, state of São Paulo (21º 42' 37" S, 47º 28' 41" W). The main vegetation types of the PEV is Atlantic Forest (858.5ha) and Cerrado (1212.92ha), surrounded by sugar cane and natural vegetation.

1.2. Bat sampling

Bat sampling was carried out from June 2015 to September 2016 during waning crescent and new moon phases. Bats were caught in mist nets which were open 30 minutes before the sunset. We closed the mist nets as soon as the first apt adult *S. lilium* were caught. We consider apt adults as males and non-reproductive females without wounds and in good condition. Then, this individual where taken to the field basis where a routine procedure was conducted, measuring its forearm with a caliper (precision 0.01 mm) and its weight with portable dynamometer (0.1 g precision) to confirm the species identification in the field. After the confirmation, a hair sample was taken and the individual was taken to the tent experiment (explained below). In order to capture the variability of individuals (Kerches-Rogeri manuscript – Thesis Chapter 3) within the population, we sampled individuals in different sites, contemplating forest and open physiognomies.

1.3. Diet data

1.3.1 Fecal sample analysis. - After being removed from the mist net, the bats were placed in cotton bags waiting for the routine of exams. During this period, it is common for them to deposit feces into the bag. In addition, we put plastic underneath the nets so that if the bat defecated while it was still trapped, the feces would remain in the plastic to be collected. In the laboratory, each sample was observed in a stereomicroscope. Seed samples were identified up to the genus level using mature fruits collected in the study area and collection of seeds present in the Department of Zoology for comparison.

1.3.2 Stable isotopes. - In addition to the fecal sample, we used stable isotopes for the study of interindividual variation in diet because when we infer the diet through feces, we are considering only a snapshot in the food habit of organisms, subject for example

to the influence of the heterogeneous distribution of resources in space (Araújo *et al.* 2007). In fact, food transit in the digestive system varies between 10 and 40 minutes in frugivorous bats (personal observation during the experiments; Maccarini *et al.* 2018).

Thus, during the battery of exams, we collected hair samples from 58 adult individuals (of which 30 were individuals who underwent the following experiments) using sterile scissors. The samples were frozen in the field until they were taken to the laboratory at the Ecology Department, UNESP. In the laboratory, we extracted the lipids using a solution of methanol-chloroform (2: 1 by volume), because the lipids are depleted in ^{13}C when compared to the whole organism and the lipid content of animal tissue samples is variable, and this may bias the result (Peterson & Fry 1987; Post 2002). After the lipid extraction, the samples were then dried at 60° C for 48 hours (Voigt *et al.* 2003) and macerated until a fine and homogeneous powder was obtained, encapsulated and sent to the UC Davis Stable Isotope Facility in Davis, CA, United States. The same procedure was done with samples of *Solanum*, *Piper* and *Cecropia* fruits, and 30 fruits of each species were collected. The resources collected in the study area were determined by the resources present in the feces of the individuals, and we had not found insects in the first samples evaluated. Besides that, *S. lilium* can have an entire frugivore diet (Herrera M. *et al.* 2001). At the end of data sampling, we found some insects in the feces of some individuals, so we considered the isotopic values of a study done in a similar area relatively close to our area (Kruszynski, Diniz-Reis & Pedrozo 2016). All stable isotope values are reported in δ notation, and expressed as ‰, where $\delta^{13}C$ or $\delta^{15}N = ([R_{sample} / R_{standard}] - 1) * 1000$, where R is the ratio $^{13}C:^{12}C$ or $^{15}N:^{14}N$. The standard for carbon is PeeDee Belemnite (PDB) and the standard for nitrogen is atmospheric N_2 air. Replicate measurements of internal laboratory standards (which are selected to be compositionally similar to the samples being analyzed and

have been previously calibrated against NIST Standard Reference Materials) indicate errors of 0.2 for $\delta^{13}C$ and 0.3 for $\delta^{15}N$.

1.4 Experiments - establishing the e/h ratio

To establish the in individual rank preferences according to each fruit energetic return determined by the ratio e/h, where *e* is the energy content and *h* is the time of manipulation, the bats were submitted to experiments in flight tent to estimate handling time and the energy content was established in calorimetric bomb analysis.

1.4.1 Energy content (e)

First, 30 fruits of each plant genus (*Piper, Solanum* and *Cecropia*) were collected throughout the experiment period. In the laboratory, they were oven dried at 60°C for 48h and then each sample was macerated for homogenization. Then, each sample was analyzed in a Parr 1425 Semimicro Calorimeter calorimetric bomb. As the calorimetric bomb quantifies the energy content of only dried fruits and we offer fresh fruits to the bats, we need to establish the relationship between the masses of these fruits to obtain the energetic content of the fresh fruit. For this, we weighed 10 fruits of each species using a precision balance (accuracy of 0.01 g) before and after being dried in the oven. We established a regression and thus an equation that allows us to calculate the dry mass from the fresh mass, and consequently, we can infer the energetic content of the fresh fruit (supplementary material).

The fruits were collected on the same day of the experiment. Before being offered to bats, they were weighed using precision balance (accuracy of 0.01g). The remains of the bitten fruits, pieces dropped and spats (fibrous material chewed) were collected. The energy content of the spats was also established in the calorimeter bomb. In order to establish the energetic content of what was ingested by the bat, we calculated

the difference between the initial mass of the fruit and the final mass of the rest of the fruits, correcting this value considering the mass of dried fruit ingested, and multiplied by the energy content of the dried fruit, which is the value of the energy content per fruit established in the calorimetric bomb minus the energy of the spat (see supplementary material for more details).

1.4.2 Handling time (h)

From May 2015 to August 2016 we realized experiments in flight tent with 30 individuals to establish the time of manipulation of each fruit by each individual. After the capture and examination routine, the individual was placed in a flight tent located near the base. Similar to that used by Dumont (1999) and Bonaccorso & Gush (1987), we used a tent made of shaded canvas and canvas ceiling, of dimensions 3 x 3 x 2m (length x width x height) in a dark area near the edge of the forest. We placed a large branch inside the tent where the fruits were placed to be offered to the bats. On the opposite side of the fruits, a researcher was inside the tent observing the behavior of the individuals with binoculars of night vision and measuring the handling time (Dumont 1999). Handling time was defined as the time spent from when the bat holds the fruit and begins to eat until the whole edible part is ingested and the inedible parts are discarded (adapted from Bonaccorso & Gush 1987).

The experiment consisted in offering fruits of one genus (order randomly determined) for two consecutive nights. As a way to standardize satiety, from capture to the beginning of the experiment we take 1h, as well as the interval between feeding (when the individual consumed the fruit offered) and the beginning of the next round with the next fruit. As soon as the individual ate the fruit, that round was closed, the interval of 1 hour started, and then the next one was offered. If the individual did not feed within the first hour of capture, he was taken to the laboratory and fed with banana.

After that, the experiment would restart after 1h. If he still did not feed, he was immediately released.

2. Data Analysis

2.2 Interindividual variation in diet

2.2.1 Fecal sample analysis

For feces analysis, we used mean proportions (average proportion) to calculate the proportion of use of the whole population. We did this because a single sample can have hundreds of seeds, and that does not necessarily mean that the individual has consumed hundreds of fruits. Thus, we estimated how many seeds are in 1 fruit and correct for numbers of fruits and insects ingested, so we could have the closest values of "foraging event". Then we calculate the proportion of consumption of each individual, and we averaged over the individuals to have the proportion for the whole population. The criteria for choosing the main food items were to be present in more than 10% of the individuals in the population or if they are consumed by fewer individuals, to have the proportion of consumption by the population above 10%. Based on this corrected table, we test if there is a difference between males and females using a MANOVA.

2.2 Stable isotope analysis

We first tested the influence of sex on the isotopic signature of carbon and nitrogen of each individual using a MANOVA with the values of δ13C and δ15N as response variable and sex as a categorical explanatory variable.

Reconstruction of diet using stable isotopes requires that the source values be corrected for a discrimination factor appropriate for the tissue used prior to analysis. As there is no specific factor in the literature for S. lilium, we calculated the mean and standard deviation of specific literature on available Phyllostomidae bats (Voigt *et al.*

2003; Voigt & Matt 2004; Miron *et al.* 2006): 3.75‰ (sd:0.57) for nitrogen and 1.56‰ (sd: 1.3) for carbon.

2.2.2 Individual Trophic Position

The stable isotope approach can elucidate some interactions within ecological communities allowing the assignment of an ecological position to different components (Peterson & Fry 1987; Post 2002). This is possible mainly by analyzing nitrogen isotopes because of fractionation, consumers have isotopic compositions enriched in relation to their food sources and while carbon has generally 1‰ nitrogen enrichment, nitrogen usually varies between 2 and 5‰ (Peterson & Fry 1987). The simplest way to calculate the trophic position is $\lambda + (\delta^{15}N$ secondary consumer - $\delta^{15}N$ baseline) / ΔN, where λ is the trophic position of the organism considered as baseline (eg. $\lambda = 1$ for producers) and ΔN is the enrichment of nitrogen by trophic level (discrimination factor; Post 2002). Thus, we consider by baseline an average producers sampled (fruits) and calculate the trophic position per individual and we consider ΔN=3.75‰.

2.2.3 Bayesian Mixing Models

To analyze the isotopic data, we used mix models to transform the bivariate isotope space (i.e. $\delta^{13}C$ and $\delta^{15}N$) into proportions of food items in the diet. For this analysis, we used the MIXSIAR Bayesian mixing model (Stock & Semmens 2016), which estimates the probability distributions of resource contributions to a mixture. This model considers uncertainties associated with the use of stable isotopes. These uncertainties may be related, for example, to the interindividual variation of the isotopic composition of the resource itself, to the presence of multiple sources and the different fractionation rates (Moore & Semmens 2008).

2.2.4 Individual isotope variation

To quantify the degree of interindividual variation in diet based on isotope variation between individuals, we used the method proposed by Araújo *et al.* (2007). This method uses the observed diet of the population, obtained by fecal analysis, to generate a large number of simulated populations with various degrees of interindividual variation (with IS index ranging from 0 to 1). The simulations establish a relationship between the isotopic variance ($Var\delta_i$) and the individual specialization (IS). Finally, we use this relationship to convert the empirical $Var\delta_i$ (empirical variance of the isotopic signatures of carbon or nitrogen of the individuals) into an IS estimate. For this analysis we use the proportions of diet established by average proportion calculated previously for the feces data.

Results

Interindividual variation in diet

Fecal sample analysis

From June 2015 to November 2016, 92 fecal samples were collected, of which 61 had materials that could be identified. The others consisted mainly of seedless fruit pulp. Eleven (18.03%) had insect remains and 53 (87%) had seeds of 9 genera. Twenty-six individuals (42.62%) had *Solanum* seeds (ranging from 1 to 42 seeds), 23 of *Piper* (37.70%, ranging from 1 to 300 seeds) and 2 of *Cecropia* (3.28%, 130 to 160 seeds), 6 morphotypes were present in feces of 8 individuals (ranging from 1 to 15 seeds). Most samples had only 1 type of item (87%), few with two items (11%) and only 1 with 3 items (2%). Averages of the proportion of individuals indicated that *Piper* corresponds to 44% of the diet of the population, followed by *Solanum* (36%), insects (17%) and

Cecropia (3%). We found no difference between males and females (F = 0.798, p = 0.6312).

Stable Isotopes

There was no difference between males and females in the carbon and nitrogen isotopic signal (F = 0.567 p = 0.6871). For Carbon the value of IS estimated by VarIso was 0.88 and for nitrogen 0.43, indicating that the individuals vary more with respect to the nitrogen source than with respect to the carbon source. The analysis of the trophic position indicated a great variation among the individuals (Fig. 1, mean = 2.15 sd = 0.36).

The analysis of the isotopes using the mixing models indicated that the population feeds more on *Solanum*, followed by insects and lastly *Cecropia* and *Piper* (Fig. 2 e 3). There is no difference in the order of preference between individuals, but we observed a difference in the proportion of the Solanum and Insects, with individuals whose diet is almost 100% *Solanum* and individuals that this represents 50% of the diet and insects approximately 40% (there are the mean values of the probability distribution estimated by MIXSIAR - supplementary material).

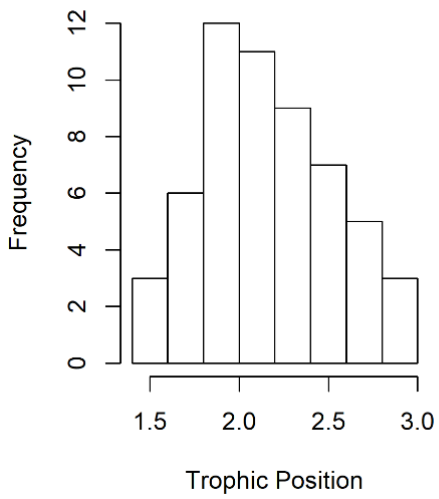

Figure 1: Histogram representing the frequency of the trophic position of the *Sturnira lilium* individuals studied.

Experiments in flight tent: optimal diet

Calorimeter bomb analysis indicated that *Solanum* fruits have 5763,926 calories (sd = 882.6), *Piper* have 4802.3 calories (sd 239.9 calories) and *Cecropia* have 5395.7 calories (sd = 805.5 calories) per gram of dried fruit. After correcting the values for fresh fruit and spats, we reach the value of energy ingested by individuals (see supplementary material for more details).

In flight tent experiments, we set the manipulation time and stablish the rank preference by each individual (Fig.4). Sixteen individuals had *Piper* as the most profitable fruit, 10 individuals had *Solanum* and 5 had *Cecropia*. Table 1 summarizes how many individuals had the 6 possible arrangements. We observed that individuals varied in relation to the order of the fruits (different preferences), and also individuals with the same optimal resource that differed in the alternative resource (competitive refuge).

Table 1: Number of *Sturnira lilium* individuals that have each of the 6 possible rank preferences, with 1st being the most profitable fruit, followed by the 2nd – second most profitable fruit, and the 3rd – third most profitable fruit. S indicates *Solanum,* P indicates *Piper* and C indicates *Cecropia*.

1st	**2nd**	**3rd**	**N**
S	P	C	**8**
S	C	P	**2**
P	S	C	**11**
P	C	S	**4**
C	S	P	**2**
C	P	S	**3**

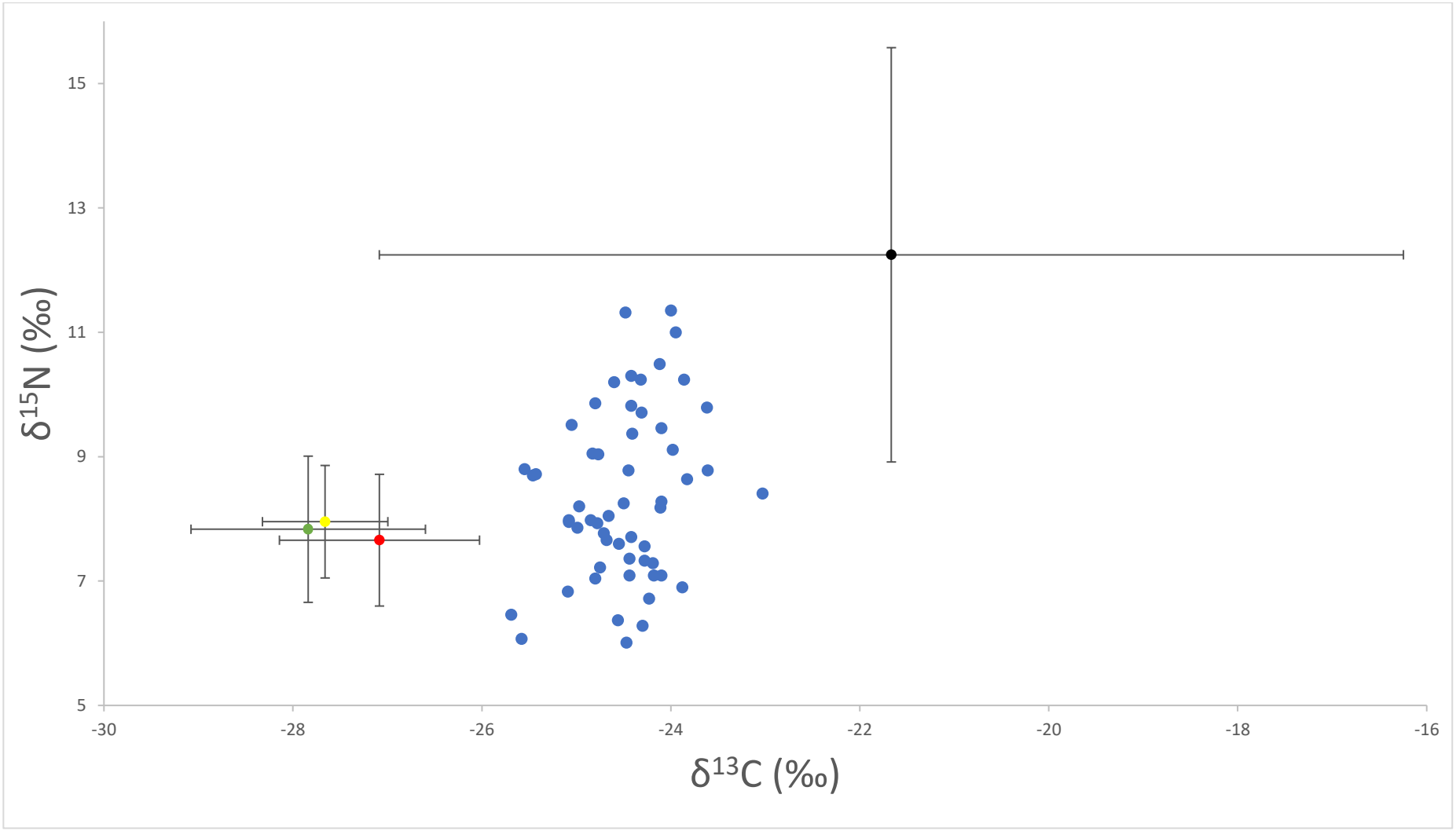

Figure 2: Position of individuals *Sturnira lilium* (blue dots) in dual $\delta^{13}C$ and $\delta^{15}N$ isotope space relative to the mean (+s.d.) isotope values of the resources: *Cecropia* (green), *Piper* (yellow), *Solanum* (red) and Insects (black).

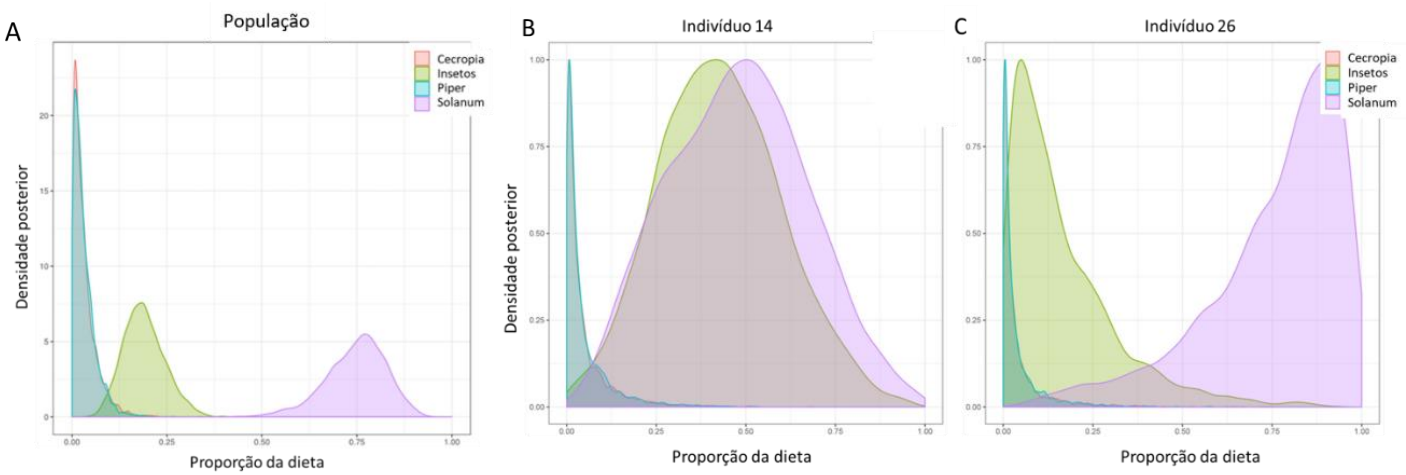

Figure 3: Posterior density generated by MIXSIAR indicating the proportion in the diet of each resource. (A) overall *S. lilium* diet – median diet proportions are 76% *Solanum*, 19% *Insect*, 2% *Cecropia* and 2% *Piper*, (B) example of the proportion in the diet of a more omnivorous individual – median diet proportions are 48% *Solanum*, 42% *Insect*, 2% *Cecropia* and 2.1% *Piper*, (C) example of the proportion of the diet of a more frugivorous individual – median diet proportions are 90% *Solanum*, 12% *Insect*, 1.4% *Cecropia* and 1.4% *Piper* (to check the charts of all individuals, see supplementary material).

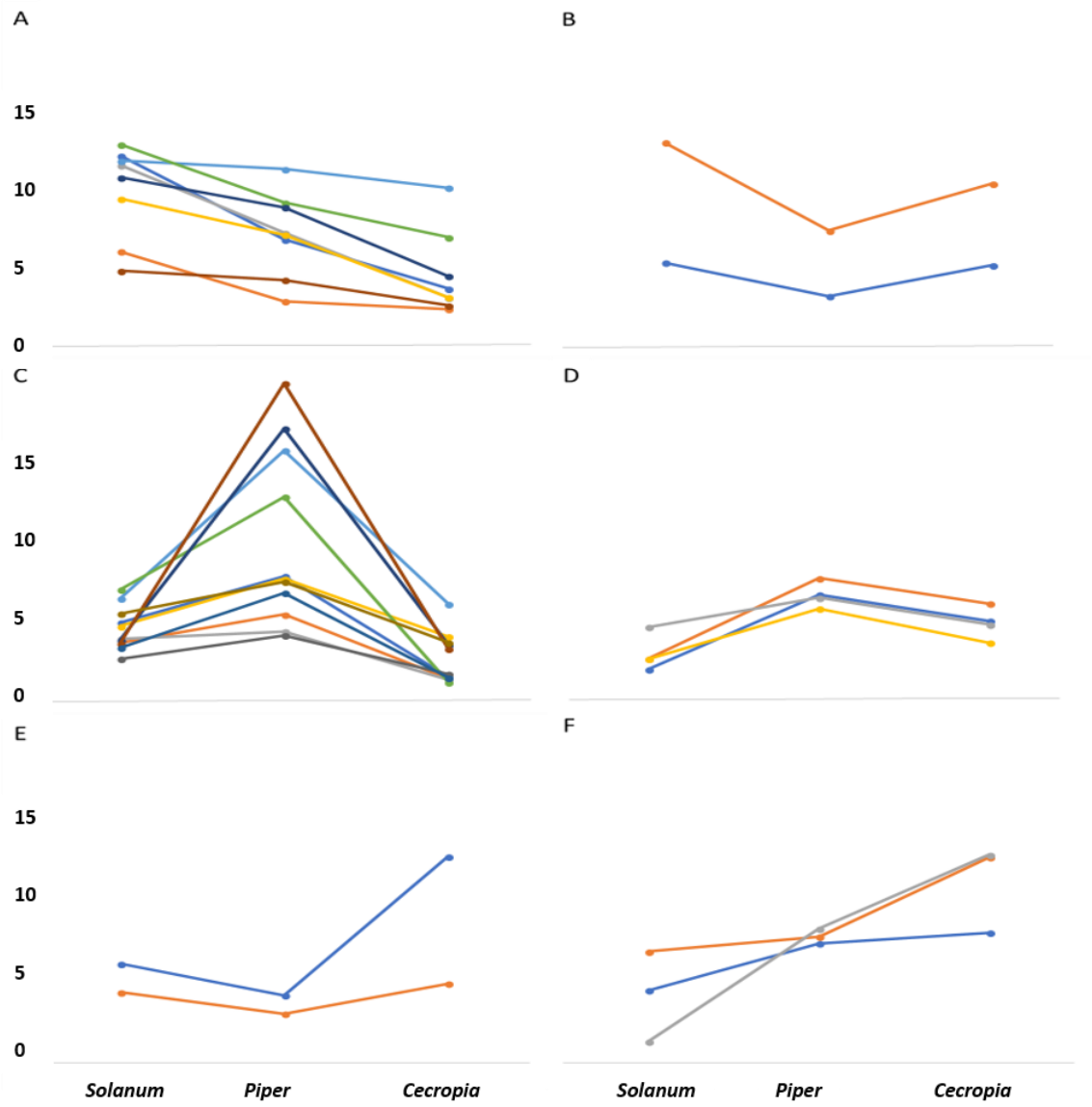

Figure 4: Fruit costing most profitable at least profitable according to the energy content / handling time of 30 individuals of *S. lilium* obtained in flight tent experiments. Each chart represents a ranking of the six possible ones and each row represents an individual. We can observe that the individuals between the graphs have different ordering (model of distinct preferences), between the graphs A and B, C and D, E and F, have the same most profitable resource, but vary in the second (competitive refuge model). Rank preference: (A) *Solanum* > *Piper* > *Cecropia*; (B) *Solanum* > *Cecropia* > *Piper*; (C) *Piper* > *Solanum* > *Cecropia*; (D) *Piper* > *Cecropia* > *Solanum*; (E) *Cecropia* > *Solanum* > *Piper*; (F) *Cecropia* > *Piper* > *Solanum*.

Discussion

We studied interindividual variation in the diet of *S. lilium* bats and a possible associated mechanism. Fecal sample data indicate that most individuals consumed *Solanum*, followed by *Piper*, insects and *Cecropia*, and that most of the samples had only one type of resource. But when we consider the averages of the proportion of individuals, *Piper* corresponds to almost half of the diet of the population. Isotopic analysis showed that individuals vary mainly in trophic position. Flight tent experiments revealed that individuals differ in their rank preferences for fruits due to differences in handling times.

The assessment of diets by fecal analysis reveals the items consumed for a short period of time. This explains why there was many individuals with only one type of resource in the feces. Although we found a large variation among individuals, this variation is subject to resource spatial aggregation and also to what were the resources surrounding the mist nets at the time of capture. In fact, since we aimed to capture only *S. lilium* and no other species of bats, we placed the nets in front of individuals in the Solanaceae and Piperaceae families, which may represent a bias in our fecal samples. Therefore, we also use stable isotopes to study the variation among individuals in this dimension of the niche.

Isotopic analysis revealed that the variation among individuals occurs mainly in the nitrogen isotopes. There is an idea that frugivorous bats supplement their high-carbohydrate diet with insects because fruits are relatively poor in protein (Thomas 1984). Some species of frugivorous bats, including *S. liium*, may reach their nitrogen requirements by feeding on fruits only (Fleming 1972, Herrera et al 2011), or have a seasonal variation in insect consumption (Herrera 2002). In fact, individuals with higher $\delta^{15}N$ values have higher trophic positions by consuming more insects. Our results

indicate that the propensity to include insects in the diet varies from individual to individual. We found a gradient of extremely frugivorous individuals and omnivorous individuals whose diets are divided equally between insects and fruits. It would be plausible to think that it could be result of a behavioral trade-off to capture and handle the prey, as we demonstrated that individuals have different ability to handle the fruits. It would be interesting in future studies to investigate whether there is interindividual variation in nitrogen requirement, which would also help to explain our results.

Our results indicate that the most profitable fruits are not exactly the most consumed fruits for most of the population and for a consolidated literature that indicates the strong relationship between *S. lilium* and the genus *Solanum*. We consider three factors that can help to understand our results. First, optimal foraging theory takes into consideration only energy and the requirement of essential nutrients may also be important (Belovsky 1984). Second, it is the result of intraspecific competition as predicted by the models proposed by Svanbäck and Bolnick (2005). And third it is the result of interspecific competition. We will address each of these factors in the following paragraphs.

We consider only the energy to determine the optimal diet of the individuals, as predicted in the models of Optimal Foraging Theory. However, in addition to energy, frugivorous bats choose their diet to obtain essential nutrients, such as proteins – the main resource of nitrogen for frugivorous bats (Jara-Servín, Saldaña-Vázquez & Schondube 2017). Bats of the genus *Sturnira* need to feed on fruits with high nutritional content to maintain a constant nutrient intake (36-50% soluble carbohydrates and 5-7% protein; Castaman Francener 2006; Saldaña-Vázquez & Schondube 2013), different from others frugivorous bats such as those of the genus *Artibeus* that are bats that feed on low-quality fruits (protein: 1-5%, carbohydrate: 10-23%, Saldaña-Vázquez *et al.*

2015). As *Piper* and *Solanum* are considered fruits with high nutritional content and *Cecropia* has an intermediate value (Estrada *et al.* 1984; Fleming 1986), we do not expect these fruits to differ in nitrogen content, which would not give us a different result than we did with energy.

Individuals presented two of the three models proposed by Svanback and Bolnick (2005): competitive refuge and distinct preferences. In the absence of competition, we would expect each individual to use its optimal resource. However, as we found that the diet performed by individuals is very similar, with *Solanum* being the primary resource used, then individuals that have *Piper* as the most profitable resource are using the alternative one. Which leads us to believe that *Piper* is the resource that is being disputed in the area of study. Svanbäck and Bolnick's (2005) models predict that the diet performed by individuals changes according to the density of co-specific competitors, a way to access intraspecific competition. However, interspecific competition may also be a determinant factor of the realized diet when species consuming the same optimal resource coexist (Araújo et al 2011).

Interspecific competition may weaken interindividual variation (Araújo et al 2011). This can happen when part of the population has the same favorite resource as a competing species, so that these individuals begin to use the alternative resource. Little is known about the competition between fruit bats for resources. One idea is that there are enough fruits throughout the year to support a large assemblage of bats between specialized and opportunistic species, so they do not have to compete directly (Fleming 1986; Thies, Kalko & Schnitzler 2006; Sartore & Dos Reis 2016). However, fragmentation and habitat loss can influence food availability (Fahrig 2003; Jara-Servín *et al.* 2017). One hypothesis is that in a fragmented landscape, such as in our study, the amount of resources decreases throughout the year increasing competition among

frugivorous bat species, which leads to the weakening of individual specialization in diet. Some papers report that when abundance of *Piper* is large, *Piper* and *Solanum* together constitute the core diet of *S. lilium* (Saldaña-Vázquez *et al.* 2013; Sánchez & Giannini 2014), which supports our finding that some individuals prefer *Piper* and some individuals prefers *Solanum*.

In our study system, another understory frugivorous bat with a diet, body size and foraging behavior very similar to *S. lilium* is the species *Carollia perspicillata* (Heithaus, Fleming & Opler 1975; Marinho-Filho & Sazima 1989; Munin, Fischer & Gonçalves 2012). Much has been discussed that the partition of resources among these species occurs by means of genus-genus preferences: *Carollia-Piper* and *Sturnira-Solanum* (Fleming 1986; Marinho-Filho *et al.* 1991; Munin *et al.* 2012; Andrade *et al.* 2013; Sartore & Dos Reis 2016). Some characteristics about *C. perspicillata* lead us to assume its role as an interspecific competitor: first, aggressiveness has been reported to defend resources against conspecifics (the mating system is considered polygenic with defense of resource based on the quality of the territory, Fernandez *et al.* 2014), and this species does not have the biomechanical strength to feed on harder fruits such as *Solanum* and *Ficus* (Dumont 1999), which may make defending the main resource *Piper* vital for survival. A meta-analysis indicates that the consumption of *Piper* by *Carollia* does not vary with extrinsic factors such as latitude and altitude, different from what happens with *Solanum* consumption by *Sturnira*, which varied according to extrinsic factors and the availability of *Piper* (Saldaña-Vázquez *et al.* 2013).

We conclude that there is interindividual variation in the optimal diet of *S. lilium* bats and this variation is the result of cognitive trade-offs, in which individuals, when being very efficient when handling an item, are inefficient to manipulate others. However, there is no interindividual variation in the rank performed, especially in the

most consumed resource, which indicates that some individuals are consuming the sub-optimal resources. We believe that this occurs through an interaction between intra and interspecific competition intensified by a decrease in the abundance of resources in a highly fragmented landscape.

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Supplementary material

Interindividual variation in frugivorous bat: an optimal foraging theory approach

Patricia Kerches-Rogeri, Milton Cezar Ribeiro, Márcio Silva Araújo

Supplementary material

1. Tables

Table S1. – Number of seeds and insect fragments found in the feces samples of individuals of the species *Sturnira lilium* at the Vassununga State Park – Santa Rita do Passa Quatro – SP – Brazil.

Ind	*Solanum*	*Piper*	*Cecropia*	Insects	Morf1	Morf2	Morf3	Morf4	Morf5	Morf6
1	0	0	0	4	0	0	0	0	0	0
2	0	0	0	2	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	0	0
4	0	1	0	0	0	0	0	0	0	0
5	1	0	0	0	0	0	0	0	0	0
6	1	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	2
8	1	0	0	0	0	0	0	0	0	0
9	6	0	0	0	0	0	0	0	0	0
10	0	2	0	0	0	0	0	0	0	0
11	0	20	0	0	0	0	0	0	0	0
12	1	1	0	0	0	0	0	0	0	0
13	0	0	0	2	0	0	0	0	0	0
14	1	0	0	0	0	0	0	0	0	0
15	24	0	0	0	0	0	0	0	0	0
16	1	0	0	0	0	0	0	0	0	0
17	2	11	0	0	0	0	0	0	0	0
18	1	0	0	0	0	0	0	0	0	0
19	0	23	0	0	0	0	0	0	0	0
20	5	0	0	0	0	0	0	0	0	0
21	7	0	0	0	0	0	0	0	0	0
22	42	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	15	0
24	0	1	0	0	0	0	0	0	1	0
25	39	0	0	0	0	0	0	0	0	0
26	0	0	130	0	0	0	0	0	0	0
27	0	60	160	0	0	0	1	0	0	0
28	0	15	0	0	0	0	0	0	0	0
29	0	4	0	0	0	0	0	0	0	0
30	0	0	0	1	0	0	0	0	0	0
31	10	0	0	0	0	0	0	0	0	0

32	33	0	0	0	0	0	0	0	0	0
33	0	0	0	2	0	0	0	0	0	0
34	9	0	0	0	0	0	0	0	0	0
35	0	30	0	1	0	0	0	0	0	0
36	0	0	0	1	0	0	0	0	0	0
37	9	0	0	0	0	0	0	0	0	0
38	4	0	0	1	0	0	0	0	0	0
39	0	17	0	0	0	0	0	0	0	0
40	0	72	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	1	0	0
42	15	0	0	0	0	0	0	0	0	0
43	0	12	0	1	0	0	0	0	0	0
44	5	0	0	0	0	0	0	0	0	0
45	1	0	0	0	0	0	0	0	0	0
46	0	300	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	1	0	0	0
48	0	6	0	0	0	0	0	0	0	0
49	0	0	0	1	0	0	0	0	0	0
50	0	2	0	0	0	0	0	0	0	0
51	7	0	0	0	0	0	0	0	0	0
52	0	7	0	0	0	0	0	0	0	0
53	4	114	0	0	0	0	0	0	0	0
54	0	0	0	0	3	0	0	0	0	0
55	6	0	0	0	0	0	0	0	0	0
56	0	4	0	0	0	0	0	0	0	0
57	0	0	0	0	0	1	0	0	0	0
58	0	75	0	0	0	0	0	0	0	0
59	0	1	0	0	0	0	0	0	0	0
60	0	0	0	1	0	0	0	0	0	0
61	1	0	0	0	0	0	0	0	0	0
Sum	236	779	290	17	3	1	2	1	16	2
Proportion	0.175	0.578	0.215	0.013	0.002	0.001	0.001	0.001	0.012	0.001
Number of individuals	26	23	2	11	1	1	2	1	2	1

Table S2. – Number fruits and insects found in the feces samples of individuals of the species *Sturnira lilium* at the Vassununga State Park – Santa Rita do Passa Quatro – SP – Brazil.

INDIVIDUAL	**SEX**	***SOLANUM***	***PIPER***	***CECROPIA***	**INSECTS**	**SUM**
1	Male	0	0	0	1	1
2	Female	0	0	0	1	1
3	Male	0	1	0	0	1
4	Male	0	1	0	0	1
5	Male	1	0	0	0	1

6	Male	1	0	0	0	1
7	Female	0	0	0	0	0
8	Female	1	0	0	0	1
9	Male	1	0	0	0	1
10	Male	0	1	0	0	1
11	Female	0	1	0	0	1
12	Male	1	1	0	0	2
13	Female	0	0	0	1	1
14	Female	1	0	0	0	1
15	Female	1	0	0	0	1
16	Female	1	0	0	0	1
17	Female	1	1	0	0	2
18	Male	1	0	0	0	1
19	Female	0	1	0	0	1
20	Female	1	0	0	0	1
21	Female	1	0	0	0	1
22	Female	1	0	0	0	1
23	Male	0	0	0	0	0
24	Female	0	1	0	0	1
25	Female	1	0	0	0	1
26	Female	0	0	1	0	1
27	Female	0	1	1	0	2
28	Female	0	1	0	0	1
29	Female	0	1	0	0	1
30	Male	0	0	0	1	1
31	Male	1	0	0	0	1
32	Female	1	0	0	0	1
33	Male	0	0	0	1	1
34	Female	1	0	0	0	1
35	Female	0	1	0	1	2
36	Male	0	0	0	1	1
37	Female	1	0	0	0	1
38	Male	1	0	0	1	2
39	Female	0	1	0	0	1
40	Female	0	1	0	0	1
41	Female	0	0	0	0	0
42	Male	1	0	0	0	1
43	Male	0	1	0	1	2
44	Female	1	0	0	0	1
45	Male	1	0	0	0	1
46	Male	0	1	0	0	1
47	Male	0	0	0	0	0
48	Male	0	1	0	0	1
49	Male	0	0	0	1	1
50	Male	0	1	0	0	1
51	Male	1	0	0	0	1

52	Male	0	1	0	0	1
53	Male	1	1	0	0	2
54	Female	0	0	0	0	0
55	Female	1	0	0	0	1
56	Male	0	1	0	0	1
57	Male	0	0	0	0	0
58	Male	0	1	0	0	1
59	Male	0	1	0	0	1
60	Female	0	0	0	1	1
61	Male	1	0	0	0	1

Table S3. – Isotope signature of *S. lilium* individuals (SL), *Solanum* (SOL), *Piper* (PIP) and *Cecropia* (CEC) at the Vassununga State Park – Santa Rita do Passa Quatro – SP, Brazil.

SAMPLE ID	δ13C	δ15N
SL01P	-24.12	10.49
SL02P	-23.95	11.00
SL03P	-24.18	7.09
SL05P	-24.77	9.04
SL07P	-24.10	9.46
SL08P	-23.86	10.24
SL08VP	-24.32	10.24
SL09P	-24.11	8.18
SL10P	-23.62	9.79
SL11P	-24.10	7.09
SL13P	-25.09	6.83
SL14P	-24.10	8.28
SL16P	-24.80	9.86
SL17P	-24.00	11.35
SL18P	-23.61	8.78
SL19P	-24.42	10.30
SL20P	-24.31	9.71
SL21P	-24.97	8.20
SL22P	-24.28	7.56
SL23P	-24.42	7.71
SL24P	-24.50	8.25
SL25P	-24.30	6.28
SL26P	-24.44	7.36
SL27P	-25.58	6.07
SL28P	-24.19	7.29
SL28VP	-24.23	6.72
SL29P	-24.68	7.66
SL30P	-24.41	9.37
SL42TP	-24.99	7.86
SL42TVP	-25.08	7.95
SL43TP	-23.83	8.64
SL44TP	-24.48	11.32
SL45TP	-24.47	6.01
SL48TP	-24.83	9.05
SL49TP	-24.60	10.20

SL50TP	-25.43	8.72
SL51TP	-24.80	7.04
SL52TP	-24.44	7.09
SL53TP	-23.88	6.90
SL54TP	-24.55	7.60
SL55TP	-25.46	8.70
SL56TP	-23.03	8.41
SL57TP	-24.42	9.82
SL58TP	-24.66	8.05
SL59TP	-24.28	7.33
SL60TP	-23.98	9.11
SL61TP	-24.56	6.37
SL62TP	-25.08	7.98
SL63TP	-24.45	8.78
SL65TP	-24.75	7.22
SL66TP	-24.78	7.93
SL67TP	-24.85	7.98
SL70TP	-25.05	9.51
SL72TP	-25.55	8.80
SL74TP	-25.69	6.46
SL75TP	-24.71	7.77
SOL01POL	-27.87	5.54
SOL02POL	-27.45	6.32
SOL03POL	-27.99	3.62
SOL04POL	-28.92	2.92
SOL05POL	-27.64	4.74
SOL06POL	-32.39	2.10
SOL07POL	-28.63	3.93
SOL08POL	-29.40	3.94
SOL09POL	-27.46	5.09
SOL10POL	-27.33	4.17
SOL11POL	-29.03	2.75
SOL12POL	-29.48	2.38
SOL13POL	-28.93	4.17
SOL14POL	-28.43	4.05
SOL15POL	-29.85	4.96
SOL16POL	-28.86	3.79
SOL17POL	-27.58	3.55
SOL18POL	-28.27	3.83
SOL19POL	-28.23	3.02
SOL20POL	-28.57	2.24
SOL21POL	-29.37	2.36
SOL22POL	-28.85	5.18
SOL23POL	-28.92	2.66
SOL24POL	-28.21	4.27
SOL25POL	-28.46	5.64
SOL26POL	-30.65	4.19
SOL27POL	-27.47	3.96
SOL28POL	-27.65	4.00
SOL29POL	-28.79	3.93
SOL30POL	-28.37	3.49
CEC01POL	-28.89	5.11
CEC02POL	-28.96	4.91
CEC03POL	-29.54	4.86

CEC04POL	-30.38	4.12
CEC05POL	-28.26	4.14
CEC06POL	-29.68	3.40
CEC07POL	-28.93	2.79
CEC08POL	-28.99	3.63
CEC09POL	-29.07	4.54
CEC10POL	-28.86	5.00
CEC11POL	-28.87	3.88
CEC12POL	-28.87	4.38
CEC13POL	-29.01	4.91
CEC14POL	-28.74	4.05
CEC15POL	-28.49	4.74
CEC16POL	-28.87	3.95
CEC17POL	-28.40	1.78
CEC18POL	-28.46	3.61
CEC19POL	-30.50	5.22
CEC20POL	-30.46	4.25
CEC21POL	-29.38	4.50
CEC22POL	-28.90	3.90
CEC23POL	-29.50	4.33
CEC24POL	-29.34	5.64
CEC25POL	-29.19	3.89
CEC26POL	-31.11	5.23
CEC27POL	-29.13	5.32
CEC28POL	-29.42	3.42
CEC29POL	-29.12	2.41
CEC30POL	-29.71	2.98
PIP01POL	-32.45	3.89
PIP02POL	-28.62	3.14
PIP03POL	-28.62	2.86
PIP04POL	-29.95	4.52
PIP05POL	-27.45	3.17
PIP06POL	-28.24	2.32
PIP07POL	-30.07	5.15
PIP08POL	-29.97	3.41
PIP09POL	-29.23	4.40
PIP10POL	-29.68	3.62
PIP11POL	-30.42	3.27
PIP12POL	-29.98	6.08
PIP13POL	-29.14	3.34
PIP14POL	-30.69	4.49
PIP15POL	-30.81	4.44
PIP16POL	-29.28	6.40
PIP17POL	-27.62	5.66
PIP18POL	-29.75	6.77
PIP19POL	-31.06	5.25
PIP20POL	-31.89	5.20
PIP21POL	-28.07	2.67
PIP22POL	-27.84	5.01
PIP23POL	-29.19	2.74
PIP24POL	-27.77	2.78
PIP25POL	-29.09	3.18
PIP26POL	-29.79	3.65
PIP27POL	-29.33	3.07

PIP28POL	-28.24	3.83
PIP29POL	-28.29	4.08
PIP30POL	-28.56	4.28

Table S4. – Values used to calcule the Interindividual Isotopic Variance (VarIso).

MEAN	***SOLANUM***	***PIPER***	***CECROPIA***	**INSECTS**	**VARIANCE BATS**	**IS**
$\delta^{15}N$	3.9	4.2	4.08	8.49	1.93	0.43
$\delta^{13}C$	-28.64	-29.21	-29.39	-23.22	0.27	0.87
DIET PROPORTION	0.44	0.36	0.03	0.17		

Table S5. – Values used to calcule the individual trophic position and the trophic position (discriminant factor = 3.75).

IND	**δN(IND)**	**δN(BASELINE)**	**TROPHIC LEVEL BASE LINE**	**TROPHIC POSITION (DISC=3.75)**
SL01P	10.49	4.05	1.00	2.72
SL02P	11.00	4.05	1.00	2.85
SL03P	7.09	4.05	1.00	1.81
SL05P	9.04	4.05	1.00	2.33
SL07P	9.46	4.05	1.00	2.44
SL08P	10.24	4.05	1.00	2.65
SL08VP	10.24	4.05	1.00	2.65
SL09P	8.18	4.05	1.00	2.10
SL10P	9.79	4.05	1.00	2.53
SL11P	7.09	4.05	1.00	1.81
SL13P	6.83	4.05	1.00	1.74
SL14P	8.28	4.05	1.00	2.13
SL16P	9.86	4.05	1.00	2.55
SL17P	11.35	4.05	1.00	2.95
SL18P	8.78	4.05	1.00	2.26
SL19P	10.30	4.05	1.00	2.67
SL20P	9.71	4.05	1.00	2.51
SL21P	8.20	4.05	1.00	2.11
SL22P	7.56	4.05	1.00	1.94
SL23P	7.71	4.05	1.00	1.98
SL24P	8.25	4.05	1.00	2.12
SL25P	6.28	4.05	1.00	1.59
SL26P	7.36	4.05	1.00	1.88
SL27P	6.07	4.05	1.00	1.54
SL28P	7.29	4.05	1.00	1.86
SL28VP	6.72	4.05	1.00	1.71
SL29P	7.66	4.05	1.00	1.96
SL30P	9.37	4.05	1.00	2.42

SL42TP	7.86	4.05	1.00	2.02
SL42TVP	7.95	4.05	1.00	2.04
SL43TP	8.64	4.05	1.00	2.22
SL44TP	11.32	4.05	1.00	2.94
SL45TP	6.01	4.05	1.00	1.52
SL48TP	9.05	4.05	1.00	2.33
SL49TP	10.20	4.05	1.00	2.64
SL50TP	8.72	4.05	1.00	2.25
SL51TP	7.04	4.05	1.00	1.80
SL52TP	7.09	4.05	1.00	1.81
SL53TP	6.90	4.05	1.00	1.76
SL54TP	7.60	4.05	1.00	1.95
SL55TP	8.70	4.05	1.00	2.24
SL56TP	8.41	4.05	1.00	2.16
SL57TP	9.82	4.05	1.00	2.54
SL58TP	8.05	4.05	1.00	2.07
SL59TP	7.33	4.05	1.00	1.87
SL60TP	9.11	4.05	1.00	2.35
SL61TP	6.37	4.05	1.00	1.62
SL62TP	7.98	4.05	1.00	2.05
SL63TP	8.78	4.05	1.00	2.26
SL65TP	7.22	4.05	1.00	1.85
SL66TP	7.93	4.05	1.00	2.04
SL67TP	7.98	4.05	1.00	2.05
SL70TP	9.51	4.05	1.00	2.46
SL72TP	8.80	4.05	1.00	2.27
SL74TP	6.46	4.05	1.00	1.64
SL75TP	7.77	4.05	1.00	1.99
MEAN	8.37	4.05	1.00	2.15
VARIANCE	1.86			0.13

2. Figures

Correlation dry fruit X fresh fruit

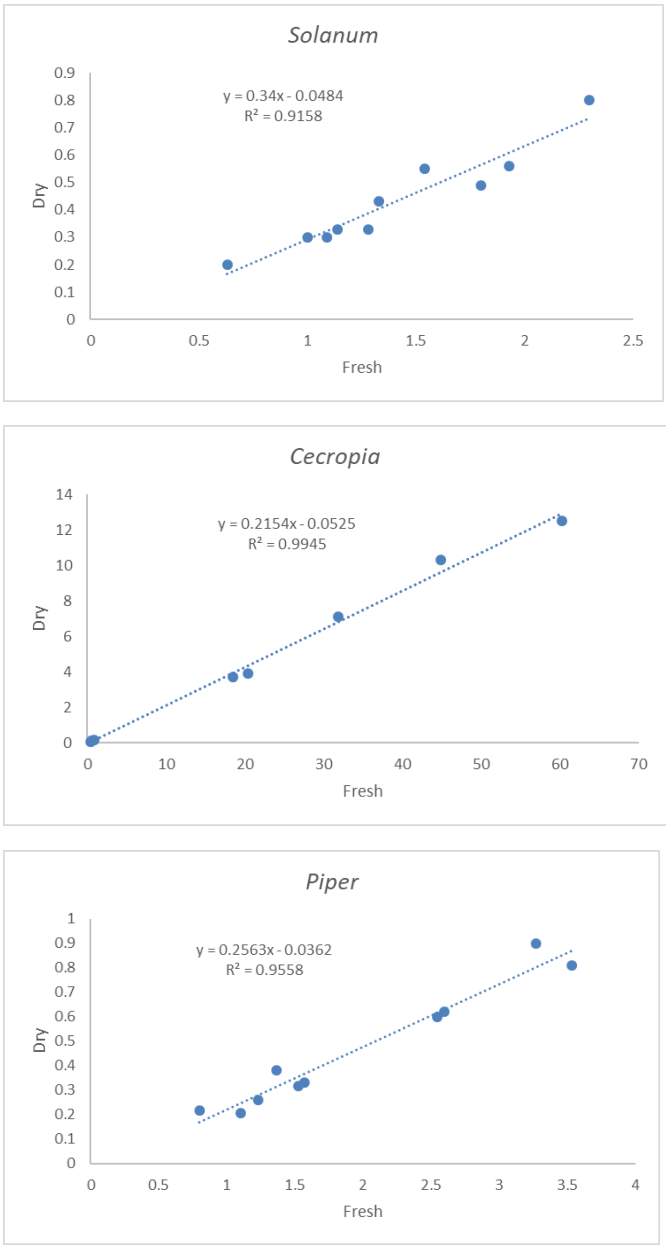

Figure S3: Correlation between dry fruit mass and fresh fruit mass of *Solanum*, *Piper* and *Cecropia*.

3. Equations for calculating the value of e (energy content)

Solanum: Y= 0.34x – 0.0484

Piper: Y=0.2563x – 0.0362

Cecropia: Y=0.2049x – 0.1495

Y is MSI (dry mass ingested) and x is the MFI (fresh mass ingested)

$MFI = w_f – (r + z)$ (1)

w_f: initial fresh mass offered during the experimente

r: remains

z: spat mass (fiber material chewed by the individual)

Fruit energy content

$$CEF = CET – (P_{SPAT}*E_{SPAT}) \quad (2)$$

CEF: Fruit energy content

CET: Energy stablished in the calorimeter

P_{SPAT}: Spat proportion

$E_{SPAT:}$ Spat energy

Ingested energy

$$CEI = MSI*CEF \quad (3)$$

CEI: Ingested energy

MSI: Dry mass ingested

CEF: Fruit energy content

Capítulo 3 – Movement syndromes of a Neotropical frugivorous bat inhabiting a heterogeneous landscape in Brazil

Patricia Kerches-Rogeri[1,*], Jukka Siren[2,3], Beatriz de Oliveira Teles[1], Rafael Souza C. Alves[1], Camila de Fátima Priante Bernardo[1], Milton Cezar Ribeiro[1], Márcio Silva Araújo[1], Otso Ovaskainen[2,4]

1 Departamento de Ecologia, Universidade Estadual Paulista 'Julio de Mesquita Filho', Avenida 24 A,1515, Rio Claro, São Paulo, Brazil

2 Faculty of Biological and Environmental Sciences, P.O. Box 65, Viikinkaari 1, 00014 University of Helsinki, Finland

3 Department of Computer Science, Aalto University, Espoo, Finland

4 Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology. N-7491 Trondheim, Norway

* corresponding author: parogeri@gmail.com

Abstract

1. There is growing evidence that individuals within populations can vary in habitat use and movement behavior, but it is still not clear what are the mechanisms that explain this variation. Here, we analyzed movement patterns of individual bats in a population of *Stunira lilium* in a landscape composed of open areas and forest fragments.

2. The aim of this study was to test if individuals of *S. lilium* have different preferences for landscape features and how such preferences are associated with variation in movement activity.

3. We collected data on movements of 27 individuals using radiotelemetry and fitted a heterogeneous-space diffusion model to the movement data in order to evaluate signals of movement variation among individuals.

4. *S. lilium* individuals generally preferred open habitats with *Solanum* fruits, regularly switched between forest and open areas, and showed high site fidelity. Movement variation among individuals could be summarized in five movement syndromes: (1) specialization in forest habitat with *Piper* fruits, (2) specialization in forest edge with *Solanum* and *Cecropia* fruits, (3) specialization in open areas and low movement activity, (4) habitat generalists with high movement activity, and (5) explorative individuals that cover large areas.

5. An important implication of our findings is that bat individuals vary in their quality as fruit dispersers, as well as in their responses habitat loss and fragmentation. Consequently, conservation and restoration efforts are likely to benefit from the understanding of within-species variation of the causes and consequences of movement behavior.

Key-words: behavior, diffusion model, individual specialization, habitat fragmentation, frugivory, Phyllostomidae, seed dispersal, space use.

Introduction

Movement is defined as the change in the spatial location of an organism over time, and it has a crucial role in determining the fate and trajectories of individuals, and consequently the structure and dynamics of populations, communities and ecosystems (Nathan *et al.* 2008). Habitat fragmentation and climate change are pervasive anthropogenic impacts on ecosystems (Turner 1996) which can have severe consequences on animal movement. For example, a survey of a GPS-tracking database

of 803 individuals across 57 mammals species found that movement activity in areas with high anthropogenic impact was on average less than half of that areas with low anthropogenic impact (Tucker *et al.* 2018). To better predict how animals are likely to respond to environmental change, it is therefore important to characterize movement patterns and in particular to infer the underlying mechanisms driving those patterns.

A growing number of studies in the last few years have shown that individuals differ substantially in resource use (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011) and movement patterns (Austin, Bowen & McMillan 2004; Ciuti *et al.* 2012; Farwell *et al.* 2014; Bonnot *et al.* 2015; Spiegel *et al.* 2015) in many kinds of taxa. For example, in gray and schoolmaster snapper populations inhabiting Bahamian coastal wetlands (locally known as tidal creeks), individuals vary in their preferred location in the creek, the size of the area they move within, an consequently in the resource pools they utilize (Hammerschlag-Peyer & Layman 2010). Although many studies have demonstrated that individuals vary in movement patterns and habitat use, it has remained less clear what mechanisms explain this variation.

In heterogeneous landscapes, where animals move around to seek shelter and resources needed for their reproduction and survival, the structure of the landscape directly affects the realized movement patterns (Van Moorter *et al.* 2016). For example, in a patchy landscapes, individuals typically move fast and in a directed manner when moving among the patches, whereas their movements are slow and tortuous when moving within the patches (Morales *et al.* 2004). More generally, in heterogeneous landscapes, individual preferences for resource and habitat types interact with landscape features to generate complex movement patterns (Leclerc *et al.* 2016). Inferring the underlying mechanisms behind such interactions can be challenging, as it requires an appropriate combination of relevant data and analytical tools (Spiegel *et al.* 2017).

The frugivorous bats in the family Phyllostomidae are very abundant in the Neotropics and play an important role as seed dispersers, pollinators and insectivores (Voigt & Kingston 2015). The frugivore species *Sturnira lilium* is one of the most abundant and widespread bats in the Atlantic Forest (Muylaert *et al.* 2017), exhibiting a strong preference for fruits of the genus *Solanum*, followed by *Piper* and to a smaller degree *Cecropia*, *Ficus* and *Vismia* (Mello, Kalko & Silva 2008; Andrade *et al.* 2013). In a previous study on a population of *S. lilium* inhabiting a fragmented landscape of Brazilian savanah (Cerrado), we found profound variation among the individuals in their foraging areas (Rogeri 2011). The mechanism behind this variation is still unknown, but the fact that the foraging areas differed greatly in the availability of *Solanum*, *Piper* and *Cecropia* suggests that one driver is individual variation in food preferences. Landscape features might also affect bat movement, as suggested by several studies linking landscape structure to the richness and abundance of frugivorous bats (e.g. Gorresen, Willig & Strauss 2014; Muylaert, Stevens & Ribeiro 2016; Ferreira *et al.* 2017), and the strong relation between species mobility and sensitivity to habitat fragmentation (Meyer *et al.* 2008).

Here, we investigated how the movement patterns of *S. lilium* individuals inhabiting a heterogeneous landscape respond to landscape features. We hypothesized that (i) the use of space by the frugivorous bat *S. lilium* is influenced by landscape features; (ii) there are individual differences in the use of landscape features; (iii) there are individual differences in movement activity; and that (iv) variation in habitat use and movement activity are correlated and can thus be summarized as low-dimensional behavioral syndromes. To test these hypotheses we used radiotelemetry data obtained on fixed dataloggers to a mark-recapture data, and then fitted the heterogenous-space diffusion model introduced by Ovaskainen (2004).

Material and Methods

Study Area

The Vassununga State Park (Parque Estadual de Vassununga - PEV) is a state conservation unit c.a. 2070 ha, divided into six disjoint fragments, all of which are located in the city of Santa Rita do Passa Quatro, state of São Paulo (21º 42' 37" S, 47º 28' 41" W). The main vegetation types of the PEV is semideciduous forest (Atlantic Forest; 858.5 ha) and cerrado (1.212.92 ha) –Brazilian savanna – surrounded by 2776.28 ha of sugar cane and 1959.61 ha of natural vegetation composed mainly by different physiognomy of Cerrado and riparian forest (Fig. 1).

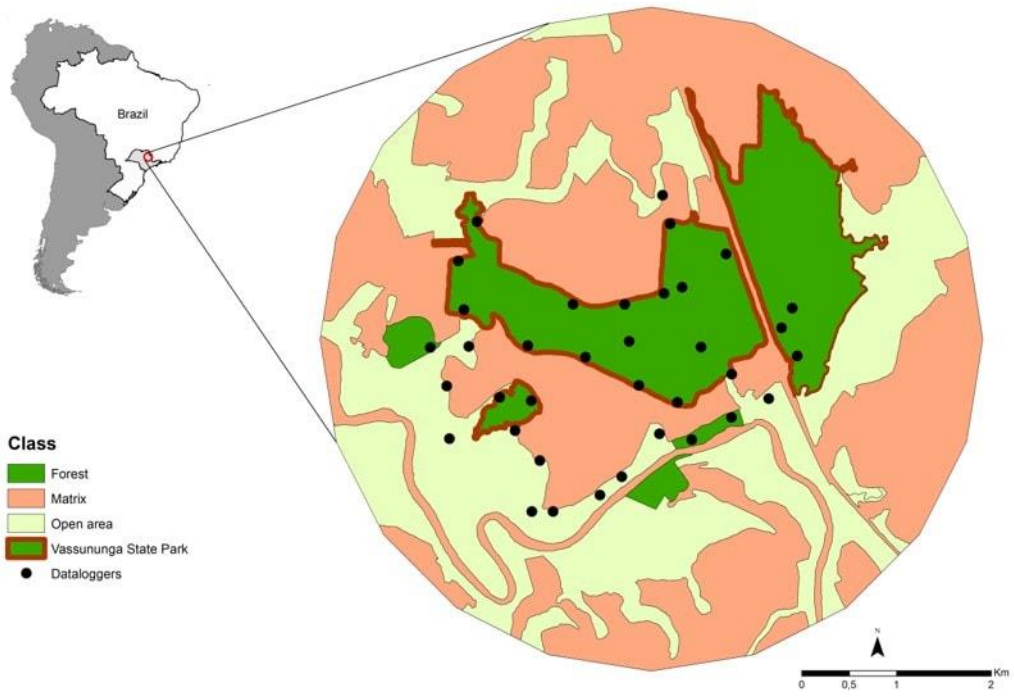

Figure 1 – Study site: Vassununga State Park and its surroundings.

Bat sampling

Bats were caught using mist nets. For each captured bat, a routine procedure was conducted, measuring its forearm with a caliper (precision 0.01 mm) and its weight with portable dynamometer (0.1 g precision) to help in species identification in the field. Captured bats were identified by a combination of taxonomic keys (Vizotto &

Taddei 1973; Gardner 2008). Twenty seven adult (observing the degree of ossification of the epiphyses of the phalanges of the wings, *cf.* Kunz & Fenton 2003) individuals of *S. lilium* were selected for radiotelemetry. We selected only adult individuals to avoid ontogenetic effects (Powers, Kandarian & Kunz 1991), and used both males and females to be able to ask if there is a systematic variation between them. In order to capture possible variability of habitat preference within the population, we sampled individuals both inside the forest and in the open areas (Fig. 1).

Radiotelemetry

We used the *Axabixo* equipment developed by *Trapa-camera* ®. The *Axabixo* device is a terrestrial radio telemetry system with digital encoding that operates both in the VHF frequency of 173,225 MHz and the UHF frequency of 433,920 MHz (http://www.trapacamera.com.br/indexbixo.htm). The datalogger (i.e., the receiver) is based on an omnidirectional antenna, with range about 300 meters in open area, and it can identify the bat individual through a transmitter-specific digital code. We utilized thirty-six dataloggers (Fig. 1) that continuously recorded transmitter signals, storing information on date, time, transmitter identity and signal strength. Radio transmitters were attached to the back of the bats using veterinary glue (Vetbond). The weight of the transmitter represented a maximum of 5% of the weight of each individual.

Landscape analysis

We mapped the landscape within a 4.5km radius buffer (in our previous unpublished study on *S. lilium* we recorded a maximum distance flight of 6km) around the captures sites. The mapping was made by manual digitalization and visual interpretation using high resolution satellite images (Open Layers Plugin Google Satellite at Quantum Gis 1.8) at the 1:5,000 scale. The following cover classes were

included: semidecidous forest (PEV), natural vegetation, sugar cane, agriculture, forestry, pasture, rural facilities and water. For the diffusion model, we reclassified the landscape into classes that we expected to be relevant for modelling bat movements: forest (18%; consisting of PEV), open area (31%; consisting of regeneration areas and natural open physiognomies such as gramineous-woody savanna; with a predominance of pioneer plants and shrubs) and matrix (51%; mainly sugarcane, water and highways).

We computed a set of eight landscape attributes for each location of dataloggers: Forest cover (FC), open-area (OA) and matrix (MA) in a circular buffer with 200 meters radius, the spatial heterogeneity (HE) of the buffer calculated by the Shannon's landscape diversity index; distance of the datalogger to the nearest forest fragment (NN), and estimated numbers of ripe fruits of trees in the genera *Piper* (PI), *Solanum* (SO) and *Cecropia* (CE). These trees provide the main resources consumed by S. *lilium* (Mello *et al.* 2008; Andrade *et al.* 2013). The landscape was mapped using Quantum Gis 1.8 (QGIS Development Team) and ArcGis 10.5. The landscape features were calculated on the extension V-Late.

Fitting the diffusion model

We fitted to the bat detection data the heterogenous-space diffusion model introduced by Ovaskainen (2004), using the software Disperse (Ovaskainen *et al.* 2008). Prior to the analyses, we triangulated the landscape classified to the three habitat types of forests, open areas, and matrix, using the software Mapper (Ovaskainen *et al.* 2008). The model contained seven parameters to be estimated: a) three habitat-specific movement rates (the diffusion parameters for each habitat type); b) two habitat preference parameters (relative preference, normalized to one for forests); c) mortality parameter (assumed to be the same for all habitat types) and d) detection probability.

We note that in the present study the mortality parameters more likely to represent the death of the battery of the tracking equipment rather the death of the bat individual.

The data are in continuous-time, but the implementation of the diffusion model requires one to define discrete time intervals at which the detections are attempted. To examine the robustness of the results against the choice of the time-step, we analyzed the data at both 1 hr and at 12 hr intervals. The detection probability measures the probability of observing the individual by a datalogger conditional on the individual being in the vicinity of it. We defined for each datalogger a detection area based on a field experiment where we examined from which locations the datalogger was able to detect the tracking equipment. We then doubled the sizes of these areas to account for small-scale bat movements that may bring the individual to the detection area during one-time step when the individual is nearby it.

We fitted the diffusion model to the data in the Bayesian framework following Ovaskainen et al. (2008). We run the Monte Carlo Markov Chain (MCMC) algorithm first for 1000 iterations during which we adapted the proposal distributions to achieve optimal mixing, and then sampled the posterior by running the MCMC algorithm further by 6000 iterations.

Deriving ecological inference from the diffusion model

To assess model fit and to examine for signals for variation among individuals, we used the fitted diffusion model to generate simulated movement tracks, from which we generated detection data based on the estimated detection probability. To make real and simulated as comparable as possible, we "released" each virtual bat in the location where a real bat was first observed, and we assumed the same distribution of dataloggers as was used in the actual field study. We compared 1000 replicates of

simulated data to observed data file with sixteen statistics (S1-S16) that we considered relevant indicators of movement behavior. The statistics S1-S8 are the mean values of the eight landscape indices describe above (FC, OA, MA, HE, NN, PI, SO and CE), averaged over the locations where the individual was observed. The remaining statistics are the fraction of observations in forest (S9) and open habitats (S10), the proportion of consecutive observations in which the bat changed from one habitat type to another habitat type (S11), the mean distance between consecutive observations (S12), the distance between the first and the last observation (S13), the number of distinct receivers in which the bat was observed (S14), the proportion of observations in the receiver from which there were most observations (S15), and the proportion of time-steps from first to last observation in which the bat was observed (S16).

To validate the structural assumptions of the diffusion model, we averaged the statistics S1-S16 over the individuals and compared the statistics for real data to posterior mean and 95% credibility interval [CI] derived from the simulations. To assess for signals for variation among individuals, we further compared the statistics S1-S16 between the data and simulations separately for each individual. We classified each bat in terms of each statistic into three categories, depending on whether the observed statistic was (a) above, (b) below, or (c) within the 95% CI. For example, an individual for which the observed statistic S9 is above (respectively, below) its 95% CI shows evidence of a higher (respectively, lower) preference to forests than predicted by the fitted model. As another example, an individual for which the observed statistic S15 is above (respectively, below) its 95% CI shows evidence of being more (respectively, less) confined to a particular location in the landscape than predicted by the fitted model.

We assessed the presence of characteristic movement syndromes by examining if the variation among bats showed correlated patterns among the statistics S1-S16. To do so, we computed for each bat residual statistics, defined as the observed minus predicted value of each of the S1-S16. To make statistics with different units comparable, we normalized them to zero mean and variance one over the individuals. We then computed the correlations (among individuals) for all pairs of residual statistics as well as their significances. We the performed a cluster analysis on the correlation matrix using the hclust function in R.

Results

Parameter estimates

The posterior means and 95% CI of the diffusion model parameters are shown in Table 1. Both models (data discretized to 1 hr or 12 hr intervals) indicate that the habitat preference order of the bats was open areas > forest > matrix, and that movement rates were related to habitat preferences so that the movement was the slowest in the most preferred habitat. The mean lifetime of bats (or batteries), which can be computed as the reciprocal of the mortality rate, was ca. 7 days in the 1 hr model and ca. 11 days in the 12 hr model. In both models, the estimated detection probability was very close to one, indicating that bats that were close to the vicinity of the datalogger were very likely to be observed by the equipment.

Structural model validation

The simulated data and the real data matched well in terms of the statistics S1-S5 and S9-S10 describing the distribution of the bats with respect to habitat types (Table 2). This is to be expected, as the diffusion model accounted explicitly for the habitat composition of the landscape. However, the simulated data underestimated the amount

of fruits in the locations where the bats visited (S6-S8), in particular for *Solanum*, meaning that the bats preferred locations with high availability of fruits. In the 12 hr model the bats changed between habitat types more often than proposed by the simulated data (S11), indicating that they alternate between forest and open habitats. The movement distances (S12-S13) matched otherwise between simulated and real data except that in the 1 hr data the model overestimated the distance from first to last observation. Simulated data generated by the 1 hr model (but not the 12 hr model) underestimated the proportion of time the bats were found from their favorite data logger. Both of these results suggest a pattern of site fidelity, as the real bats were confined into a smaller area than the virtual bats that followed the diffusion (random walk) model. For both models, the simulated data matched with real data in terms of the number of distinct receivers in which the bats were observed (S14). Simulated data generated by the 12 hr model (but not the 1 hr model) underestimated the proportion of times the bat was seen, suggesting the delineated detection area was too small for modelling the detection process of bats at this time scale.

Individual variation in movement behavior

At the level of a particular individual, there was not much statistical power to differentiate characteristics of real data from simulated data, as reflected by the low numbers of individuals that showed significant residual statistics S1-S16 (Table 3). Reflecting the population level result, some individuals showed a preference for fruiting trees (S6-S8), and one individual changed between habitat types more often than expected (S11). Additionally, a few individuals showed preferences with respect to habitat type composition that differed from the population average (S1-S5).

We identified consistent movement syndromes in the cluster analysis (Table 4, Fig. 2). The two main behavioral syndromes correspond to habitat generalists (A) and open area specialists (B). These are further split into five subclasses that characterize individuals that have high movement activity and utilize many habitat types (A1), individuals that are specialized in forests with *Piper* fruits (A2), individuals that are specialized in open areas and that show high site fidelity (B1), individuals that are specialized in edges with *Solanum* and *Cecropia* fruits (B2), and individuals that are explorative and thus cover a large area (B3).

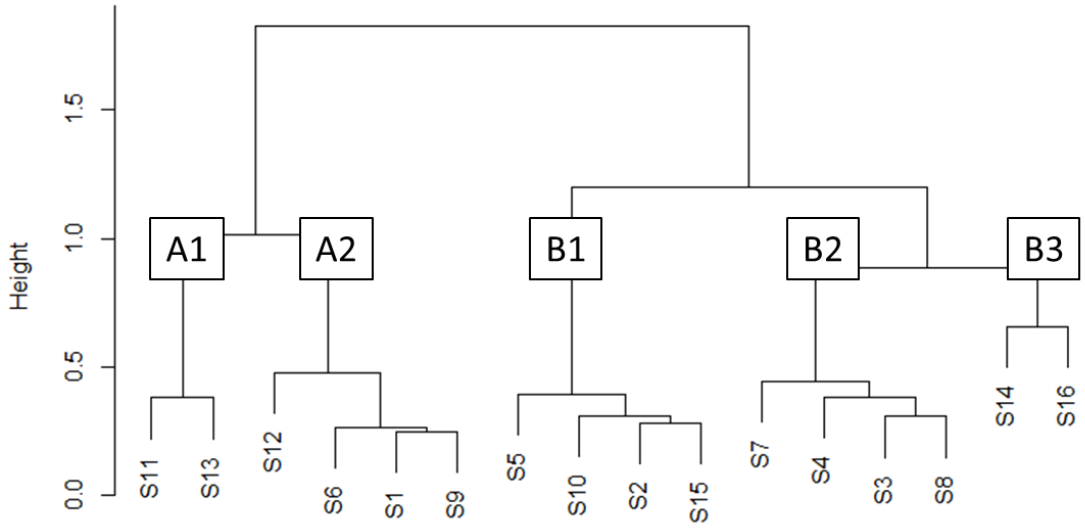

Figure 2. Results of a cluster analysis aimed for detecting behavioral syndromes of *S. lilium*. The movement statistics S1-S16 are defined in Table 2, and the syndromes A1-A2 and B1-B3 are described in the main text. The rationale behind the interpretation of the syndromes is given in the Supporting Information.

Discussion

Our results indicate that individuals in a population of a common frugivorous bat species vary in how their movement depends on landscape elements. Importantly, we show that variation in different aspects of movement behavior can be summarized in terms of consistent behavioral movement syndromes.

At a proximate level, movement syndromes might potentially be related morphology (e.g., wing morphology; Kalcounis & Brigham 1995; Adams 2007), have a behavioral basis, or a combination of both. Assuming they have a behavioral basis (Fortin *et al.* 2005; Patterson *et al.* 2008) it is unclear at this point if syndromes are learned (e.g., matrilineal cultural transmition; Estes *et al.* 2003) or have a genetic basis. Personality traits such as shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness may be heritable, and may have important consequences for several ecological and evolutionary processes at the population (e.g. individual movement, gene flow) and community levels (Réale *et al.* 2007). Therefore, more research should be done on the mechanisms that underline this variation, and in particular if the variation is heritable.

One of the main consequences of the presence of movement syndromes is the fact that individuals should be subject to different interactions within each habitat type. For example, during sampling in forest areas we captured five individuals of the carnivore bat species *Chrotopterus auritus*, a natural predator of smaller bat species. These bats are more prevalent in denser forest areas (Fenton *et al.* 1992; Gorresen & Willig 2004), suggesting the possibility that individuals of *S. lilium* using preferentially forest habitats are more prone to predation by this carnivore bat. The abundance of the food resources consumed by *S. lilium* in the area varies substantially between habitats, for example *Cecropia* is more abundant in open areas and *Piper* in forest areas.

Assuming that *Piper* has more nutritional value than *Cecropia* (Saldaña-Vázquez *et al.* 2015) this could create a trade-off between food quality and predation risk that could partly explain the observed syndromes (Werner & Hall 1988; Darimont, Paquet & Reimchen 2007).

Because *S. lilium* is an important seed disperser for many plant species in the Neotropics, the presence of movement syndromes may have implications for this ecological service. Individuals with different syndromes should interact with different plant species and disperse seeds to different areas with different efficiencies, so that they might vary in their quality as dispersers (Pollux 2017; Zwolak 2017). For example, individuals using forest areas should disperse *Piper* seeds more efficiently, whereas individuals in open areas should be better dispersers of *Solanum*. Understanding how interindividual variation in movement patterns in *S. lilium* affects seed dispersal and the plants they disperse should be addressed in future research.

On a conservation level, the presence of movement syndromes suggests that individuals should respond differently to habitat change. For example, individuals specialized in open habitats might benefit from forest fragmentation, whereas those specialized in forest habitats should be negatively impacted. By the same token, restoration programs aiming at recovering only dense forest habitats may be advantageous for only a subset of the population. Therefore, conservation efforts may benefit from considering how changes in habitat may impact individuals differently in a population.

Some studies indicate that *S. lilium* is preferentially associated with secondary forest (e.g. Castro-Luna, Sosa & Castillo-Campos 2007), whereas other studies indicate an association with more mature forests (e.g. Gorresen & Willig 2004). Our results add a new level of complexity to these descriptions, by showing that one single population

may contain individuals with preferences for different habitat types. Because the degree of interindividual variation may vary among populations (Bolnick et al. 2003), the presence of syndromes may be population-specific rather than universal, since each population faces different environments and conditions, e.g. resource availability and predation pressure (Nilsson *et al.* 2014). It is possible that some populations are behaviorally monomorphic (either specializing on open or forest habitats) and others (e.g., the population studied here) are polymorphic, which would help to explain these apparent conflicting findings.

In conclusion, our results indicate that individuals may vary consistently in their movement patterns, which can be considered movement syndromes. Individual preferences for elements of the landscape highlight the importance of incorporating explicitly the landscape to descriptions of animal movement. An important step in future research is to incorporate movement syndromes into the study of seed dispersal and the consequences of habitat fragmentation, as well as conservation efforts in general.

Acknowledgements

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Authors' contributions

PKR, MCR and MSA conceived the ideas and designed methodology; PKR, BOT, RSCA and CFPB collected the data; PKR, JS and OO analyzed the data; PKR, MSA and OO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supporting Information

Appendix S1. The rationale behind the interpretation of the syndromes

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Table 1: The posterior means and 95% credibility intervals of the diffusion model parameters.

Parameter	Mean (1h)	0.025 (1h)	0.975 (1h)	Mean (12h)	0.025 (12h)	0.975 (12h)
Density in forests (k1)	1.00	1.00	1.00	1.00	1.00	1.00
Density in matrix (k2)	0.05	0.02	0.16	0.12	0.03	0.42
Density in open areas (k3)	14.83	10.38	20.90	8.77	4.69	16.59
Diffusion in forest (d1)	5.25	5.32	5.77	5.61	5.31	5.97
Diffusion in matrix (d2)	6.81	6.36	7.35	6.58	6.06	7.20
Diffusion in open areas (d3)	3.46	3.35	3.61	3.57	3.32	3.94
Mortality	0.01	0.00	0.01	0.05	0.02	0.08
Capture probability	1.00	0.99	1.00	0.99	0.96	1.00

Table 2: A comparison of movement statistics between real and simulated data. The values of the each of the 16 movement statistics S1-S16 are average values over individuals. For the simulated data, the posterior mean and 95% credibility interval is shown.

	1HOUR RESOLUTION				**12 HOURS RESOLUTION**			
Statistic	Data	Mean simulated	0.025 simulated	0.975 simulated	Data	Mean simulated	0.025 simulated	0.975 simulated
S1 mean buffer forest	0.23	0.20	0.13	0.29	0.24	0.26	0.19	0.32
S2 mean buffer open	0.42	0.45	0.38	0.52	0.42	0.40	0.35	0.46
S3 mean buffer matrix	0.35	0.34	0.29	0.39	0.34	0.34	0.30	0.39
S4 mean heterogeneity	0.54	0.57	0.51	0.62	0.54	0.59	0.53	0.64
S5 mean distance to nearest forest	240.22	255.81	210.73	304.21	232.63	229.81	188.60	275.10
S6 mean P*iper*	152.70	119.76	65.63	188.89	154.31	133.14	79.95	188.29
S7 mean S*olanum*	338.18	233.67	172.78	300.69	337.86	268.45	207.28	327.75
S8 mean *Cecropia*	63.97	51.74	29.84	76.37	64.26	47.31	30.83	66.27
S9 proportion forest	0.27	0.27	0.17	0.38	0.30	0.33	0.23	0.42
S10 proportion open	0.73	0.73	0.62	0.82	0.70	0.67	0.58	0.77
S11 proportion changed habitat	0.21	0.16	0.09	0.24	0.27	0.15	0.05	0.27
S12 mean distance between observations	446.36	433.00	299.80	613.57	589.74	418.91	224.90	650.47
S13 distance from first to last	937.33	1317.76	941.88	1690.74	947.04	767.99	427.81	1147.15
S14 number of distinct receivers	3.37	4.53	3.26	6.33	2.63	2.25	1.67	3.00
S15 proportion in favorite receiver	0.70	0.57	0.47	0.67	0.67	0.72	0.60	0.82
S16 proportion of times with observation	0.18	0.19	0.11	0.28	0.45	0.24	0.13	0.35

Table 3: Individual-level evidence on movement behavior differing from that predicted by a population-level heterogeneous space diffusion model. The numbers in the table show the number of individuals (out of the total of 27 individuals) for which the particular movement statistic was below (lower) or above (higher) than the 95% credibility interval predicted by the population-level model.

	1 Hour		**12 hours**	
Statistic	Lower	Higher	Lower	Higher
S1 mean buffer forest	1	2	0	2
S2 mean buffer open	1	1	1	1
S3 mean buffer matrix	2	1	1	0
S4 mean heterogeneity	3	3	2	2
S5 mean distance to nearest forest	2	0	1	0
S6 mean P*iper*	0	2	1	3
S7 mean S*olanum*	0	3	0	2
S8 mean C*ecropia*	0	1	0	1
S9 proportion forest	0	0	0	0
S10 proportion open	0	0	0	0
S11 proportion changed habitat	0	1	0	1
S12 mean distance between observations	0	2	0	1
S13 distance from first to last	0	0	0	0
S14 number of distinct receivers	0	0	0	0
S15 proportion in favorite receiver	0	0	0	0
S16 proportion of times with observation	0	0	0	0

Table 4: Correlation matrix between the statistics that characterize the use of space and movement of the frugivore bat *Sturnira lilium* that based the movement syndromes.

	S1	***S2***	***S3***	***S4***	***S5***	***S6***	***S7***	***S8***	***S9***	***S10***	***S11***	***S12***	***S13***	***S14***	***S15***	***S16***
S1	0.00	-0.68	-0.56	-0.32	-0.50	0.74	-0.37	-0.18	0.95	-0.95	0.06	0.38	-0.02	-0.06	-0.39	-0.25
S2	-0.68	0.00	-0.23	-0.22	0.67	-0.54	0.06	0.18	-0.69	0.69	-0.24	-0.41	-0.17	-0.03	0.42	0.02
S3	-0.56	-0.23	0.00	0.67	-0.09	-0.37	0.42	0.03	-0.48	0.48	0.18	-0.04	0.23	0.11	0.05	0.30
S4	-0.32	-0.22	0.67	0.00	-0.31	-0.57	0.36	0.12	-0.23	0.23	0.23	0.04	0.26	0.14	0.06	0.16
S5	-0.50	0.67	-0.09	-0.31	0.00	-0.26	-0.32	-0.35	-0.48	0.48	-0.23	-0.35	-0.25	-0.18	0.38	-0.05
S6	0.74	-0.54	-0.37	-0.57	-0.26	0.00	-0.25	-0.26	0.66	-0.66	-0.19	0.04	-0.24	0.04	-0.36	-0.13
S7	-0.37	0.06	0.42	0.36	-0.32	-0.25	0.00	0.43	-0.30	0.30	0.14	-0.06	-0.19	-0.13	0.12	-0.11
S8	-0.18	0.18	0.03	0.12	-0.35	-0.26	0.43	0.00	-0.22	0.22	0.18	-0.01	0.06	0.07	-0.01	0.02
S9	0.95	-0.69	-0.48	-0.23	-0.48	0.66	-0.30	-0.22	0.00	-1.00	0.16	0.47	-0.04	-0.09	-0.38	-0.31
S10	-0.95	0.69	0.48	0.23	0.48	-0.66	0.30	0.22	-1.00	0.00	-0.16	-0.47	0.04	0.09	0.38	0.31
S11	0.06	-0.24	0.18	0.23	-0.23	-0.19	0.14	0.18	0.16	-0.16	0.00	0.89	0.52	0.00	-0.40	-0.15
S12	0.38	-0.41	-0.04	0.04	-0.35	0.04	-0.06	-0.01	0.47	-0.47	0.89	0.00	0.49	-0.02	-0.48	-0.18
S13	-0.02	-0.17	0.23	0.26	-0.25	-0.24	-0.19	0.06	-0.04	0.04	0.52	0.49	0.00	0.13	-0.24	-0.04
S14	-0.06	-0.03	0.11	0.14	-0.18	0.04	-0.13	0.07	-0.09	0.09	0.00	-0.02	0.13	0.00	-0.55	0.50
S15	-0.39	0.42	0.05	0.06	0.38	-0.36	0.12	-0.01	-0.38	0.38	-0.40	-0.48	-0.24	-0.55	0.00	-0.19
S16	-0.25	0.02	0.30	0.16	-0.05	-0.13	-0.11	0.02	-0.31	0.31	-0.15	-0.18	-0.04	0.50	-0.19	0.00

Appendix S1. The rationale behind the interpretation of the syndromes

Appendix S1

The rationale behind the interpretation of the syndromes

1. Syndrome A - habitat generalists (A)

We consider individuals as habitat generalists, individuals for whom there is a strong correlation among the proportion of consecutive observations in which the bat changed from one habitat type to another habitat type (S11), the distance between the first and the last observation (S13), the mean distance between consecutive observations (S12), estimated numbers of ripe fruits of trees in the genera *Piper* (S6), Forest cover (S1) and fraction of observations in forest (S9). This strong correlation means that these individuals change habitat type constantly, exhibit high activity and speed, use habitat with high availability of *Piper* and, though they constantly change habitat, they spend most of the time in forests.

2. Syndrome B - open area specialists (B)

We consider individuals as open area specialists, individuals for whom there is a strong correlation among the distance of the datalogger to the nearest forest fragment (S5), fractions of observations in open habitats (S10), open-area (S2), the proportion of observations in the receiver from which there were most observations (S15), estimated numbers of ripe fruits of trees in the genera *Solanum* (S7), spatial heterogeneity (S4), matrix (S3), estimated numbers of ripe fruits of trees in the genera *Cecropia* (S8), the number of distinct receivers in which the bat was observed (S14) and the proportion of time-steps from first to last observation in which the bat was observed (S16). It means that these individuals spend most of the time in open areas (which have more Solanum and Cecropia fruits), they show strong habitat fidelity (once they concentrate their activity in the preferred receiver), though they can use larger areas inside the forest and close to edges (associated with spatial heterogeneity).

These two general movement syndromes can be split into five more specific syndromes:

3. Syndrome A1 - high movement activity and utilize many habitat types (A1)

We consider individuals with high movement activity and that utilize many habitats types the individuals for whom there is a high correlation between the proportion of consecutive observations in which the bat changed from one habitat type to another habitat type (S11) and the distance between the first and the last observation (S13). An individual with high S11 change constantly from one habitat type to another, and an individual with high S13 have large distance between the first and the last observation, which means it has high movement activity.

4. Syndrome A2 - specialized in forests with *Piper* fruits (A2)

We consider individuals as specialized in forest with Piper fruits, the individuals that have high correlation among forest cover (S1), fraction of observations in forest (S9), estimated numbers of ripe fruits of trees in the genera *Piper* (S6) and the mean distance between consecutive observations (S12). It means that one individual has higher proportion of records in forest and in places with more ripe fruits of the genera Piper. Besides, these individuals have higher distance between consecutive observations, which can indicate high speed.

5. B1 - specialized in open areas and that show high site fidelity (B1)

We consider specialized in open areas and that show high site fidelity, individuals that have high correlation among open-area (S2), distance of the datalogger to the nearest forest fragment (S5), fractions of observations in open habitats (S10), the proportion of observations in the receiver from which there were most observations (S15). An individual with high S2 and S10 is specialized in open-areas, individuals with high S5 is more frequently away from forest and an individual with high S15 has a high proportion of observations in one receiver, indicating the intense use of a certain site.

6. B2 - specialized in edges with *Solanum* and *Cecropia* fruits (B2)

We consider an individual as being specialized in edges with *Solanum* and *Cecropia* fruits, an individual with positive correlation among matrix (S3), spatial heterogeneity (S4), estimated numbers of ripe fruits of trees in the genera *Solanum* (S7)

and estimated numbers of ripe fruits in trees of the genera *Cecropia* (S8). It means individuals with more frequent observations in matrix, in areas with high diversity of habitats, which indicates high activity in edges, where there is a high proportion of *Solanum* and *Cecropia* fruits.

7. B3 - explorative and thus cover a large area (B3)

We consider individuals as explorative and thus cover a large area, individuals that have high proportion of time-steps from the first to last observations in which the bat was observed (S16) and has high number of distinct receivers in which the bat was observed (S14). It means that the individuals exhibit more tortuous trajectories, indicating explorative behavior, and the more dataloggers it has observations, the larger is the area it uses, because the dataloggers were spread in the landscape.

Considerações finais

O presente estudo teve como objetivo estudar a variação interindividual com relação a dieta, uso do espaço e movimento na espécie de morcego frugívoro *Sturnira lilium*. Para isso, utilizamos dados de fezes e isótopos para determinar a dieta realizada, experimentos em tenda de voo para determinar a dieta ótima e receptores fixos para monitorar o uso do espaço e movimento dos indivíduos. Encontramos que os indivíduos variam na forma como utilizam os elementos da paisagem e também em características de movimento. Além disso, essa variação pode ser descrita em síndromes de movimento, uma vez que encontramos forte correlação entre diferentes parâmetros. As duas principais síndromes de movimento foram indivíduos que são generalistas de habitat e indivíduos que são especialistas em áreas abertas.

Para verificar a especialização individual na dieta, utilizamos dados de fezes e isótopos estáveis. Além disso, investigamos um possível mecanismo para essa especialização individual na dieta por meio de experimentos em tenda de voo. O objetivo desses experimentos foi determinar a ordem de preferência de recurso de cada indivíduo de acordo com a rentabilidade (medido pela razão entre conteúdo energético e tempo de manipulação). Encontramos que os indivíduos variam principalmente no consumo de insetos, com indivíduos muito frugívoros e indivíduos onívoros. A análise de isótopos estáveis indicou que o fruto mais consumido pelos indivíduos foi *Solanum*. No entanto, segundo os experimentos em tenda de voo, muitos indivíduos estudados não possuem *Solanum* como o fruto mais rentável. Para esses indivíduos, o fruto mais rentável foi *Piper*. Discutimos nos capítulos anteriores que essa diferença entre recurso preferido e "recurso realizado" pode ser resultado de competição interespecífica, uma vez que existem outras espécies que podem competir por *Piper* na área de estudo.

As duas principais síndromes foram generalistas de habitat e especialistas em área aberta e os dados de dieta mostram que existem indivíduos para os quais o fruto mais rentável é *Solanum* e indivíduos para os quais o fruto mais rentável é *Piper*, presentes principalmente em áreas abertas e florestas, respectivamente. Possivelmente os indivíduos que possuem preferência por *Solanum* são os especialistas em áreas abertas, enquanto os que preferem *Piper* são na verdade especialistas em floresta, que precisam forragear também em áreas abertas por incorporarem o recurso alternativo para eles, ou seja *Solanum*, devido a competição interespecífica por *Piper*, provavelmente com a espécie *Carollia perspicillata*, tornando-se generalistas de habitats. Nossos resultados sugerem que na ausência do competidor, a especialização

individual na dieta e no uso do espaço seria alta, uma vez que parte da população consumiria *Piper* e seria especialista em floresta, e a outra parte consumiria *Solanum* e seria especialista em áreas abertas.

Esses resultados são importantes por evidenciar que a variação no uso do recurso está presente em mais de um aspecto do nicho ecológico e comportamental na população estudada. Além disso, esses aspectos do nicho interagem entre si gerando padrões complexos de movimento e uso do espaço, que por sua vez podem influenciar em outros processos ecológicos, como dispersão de sementes.

Assim, nossos resultados sugerem que a diferença na ordem de preferência dos recursos, somada à competição interespecífica e características comportamentais parecem ser os mecanismos por trás dos padrões de movimento e uso do espaço observados em uma população do morcego frugívoro *S. lilium* em uma paisagem fragmentada. Mais estudos são necessários para confirmar essa relação, por exemplo, para testar se a competição interespecífica realmente diminui a especialização individual na dieta. Sugerimos também mais estudos para uma maior compreensão das implicações ecológicas e evolutivas da presença dos padrões encontrados e se os mesmos ocorrem em outras populações de *S. lilium* e de outras espécies.