UNIVERSIDADE ESTADUAL DE CAMPINAS

ECOLOGIA ALIMENTAR E REPRODUTIVA DE *MARMOSOPS PAULENSIS* (DIDELPHIMORPHIA: DIDELPHIDAE) EM UMA ÁREA DE MATA ATLÂNTICA NO SUDESTE DE SÃO PAULO

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“Dig a hole

Forget the sun

And when at last

The work is done

Don’t sit down

It’s time to dig another one”

Breathe – Pink Floyd

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RESUMO

Marmosops paulensis [Tate, 1931] (Didelphimorphia: Didelphidae) é uma espécie de marsupial restrita a áreas de floresta atlântica com elevação acima de 800 metros. O objetivo do presente estudo foi avaliar a influência de variações na disponibilidade de recursos alimentares sobre a dieta, uso do espaço e padrões reprodutivos dos indivíduos desta espécie. O estudo foi realizado entre agosto de 2002 e julho de 2004 no Parque Estadual Intervales (24^{o}16'S, 48^{o}25'W), município de Ribeirão Grande, sudeste de São Paulo. Insetos, gastrópodes, aracnídeos, frutos e flores foram encontrados na dieta de *M. paulensis*. A maior parte dos frutos consumidos pertenceu a espécies pioneiras, sendo que piperáceas (*Piper gaudichaudianum* e *Piper* sp.1) foram os frutos mais abundantes na dieta da espécie. A freqüência de frutos na dieta de *M. paulensis* foi similar durante o ano todo, independente da abundância deste item no ambiente. Flores e artrópodes, entretanto, foram mais freqüentes durante o período de escassez de recursos. O tamanho diário da área de vida dos indivíduos (0,38 ± 0,18 ha), obtido artavés do método do carretel de rastreamento, não foi influenciado pelo sexo nem pela massa corporal. Porém, a abundância de frutos, especialmente de piperáceas, foi responsável por uma redução no tamanho diário da área de vida de *M. paulensis*. O período reprodutivo de *M. paulensis* foi altamente sincronizado entre os indivíduos, com a atividade reprodutiva concentrada entre setembro e março. Uma combinação de precipitação, fotoperíodo e disponibilidade de frutos parece regular o início da reprodução. Após o período reprodutivo, a mortalidade dos adultos foi muito alta, de maneira que cada indivíduo de *M. paulensis* participou de apenas um evento reprodutivo na população estudada. O consumo de frutos foi maior do que previamente esperado, sugerindo que *M. paulensis* supre parte de suas necessidades energéticas através de carbo-hidratos presentes nos frutos. Tanto a preferência por piperáceas quanto a redução no tamanho da área de vida diária em função da abundância das mesmas parece ocorrer devido a previsibilidade espacial e temporal destes frutos. Com relação à reprodução, *M. paulensis* exibe uma estratégia semélpara. A existência desta estratégia somada à alta sincronia reprodutiva dos indivíduos de *M. paulensis* sugere a atuação do fotoperíodo como peça-chave regulando a atividade reprodutiva.

ABSTRACT

Marmosops paulensis [Tate, 1931] (Didelphimorphia: Didelphidae) is a small marsupial occurring in montane forests above 800 m in the Brazilian Atlantic forest. The objective of the present study was to evaluate the influence of resource availability on the diet, space use and reproductive patterns of *M. paulensis*. This study was carried out from August 2002 to July 2004 at Parque Estadual Intervales (24°16'S, 48°25'W), an area located in Ribeirão Grande, southeastern Brazil. Insects, gastropods, arachnids, fruits and flowers were found in the diet of *M. paulensis*. Most fruits consumed by *M. paulensis* belonged to pioneer plants, and *Piper* (*Piper gaudichaudianum* and *Piper* sp.1) fruits were by far the most consumed. Fruits were regularly consumed year-round, while arthropods and flowers were highly consumed during the food shortage season. Daily home range size estimated using a spool and line device (0.38 ± 0.18 ha) was not influenced by body size or sex. However, fruit abundance, with especial regard to *Piper*, led to a reduction in the daily movements of *M. paulensis*. Reproductive activity was highly synchronized and markedly seasonal, occurring from September to March. A combination of rainfall, day length and fruit availability seemed to trigger the reproductive activity of *M. paulensis*. After the reproductive period, adults suffered a high mortality, in a way that each individual took part in only one reproductive event. *Marmosops paulensis* seems to rely more on fruits than previously thought and it is possible that they supply part of their energetic requirements through carbohydrates present in fruits. The preference for *Piper* fruits and their effect on home range size of *M. paulensis* may be due to the spatio-temporal predictability of these fruits. Regarding reproduction, *M. paulensis* exhibits a semelparous life-history. This strategy and the high synchrony in the reproductive activity of *M. paulensis,* suggests that day length acts as a major cue controlling reproduction, once this factor shows a high predictable variation in the study site.

INTRODUÇÃO GERAL

Uma gama de fatores abióticos e bióticos, como precipitação, temperatura e interações inter e intra-específicas influenciam a ecologia dos pequenos mamíferos (Bergallo & Magnusson 1999; Brown & Gibson 1983), entre eles os marsupiais (Julien-Laferrière & Atramentowicz 1990). Entre estes fatores, a disponibilidade de recursos alimentares desempenha um papel importante, tanto sobre a distribuição geográfica das espécies (Brown & Gibson 1983), como sobre aspectos da ecologia e o comportamento das mesmas (Julien-Laferrière 1995, Martins 2004). Em geral, os ambientes apresentam variações sazonais na quantidade de alimento, devido a padrões anuais de variação em temperatura e precipitação (Charles-Dominique *et al*. 1981, Wolda 1978). Desta forma, muitas vezes as estações do ano funcionam como bons indicadores da variação na disponibilidade de alimento, de maneira que na região tropical a estação úmida e quente corresponde ao período de alta abundância de alimento para os mamíferos (Bergallo & Magnusson 1999, Charles-Dominique *et al*. 1981), enquanto a estação seca e fria corresponde ao período de escassez de recursos. Diversos estudos já demonstraram que a variação sazonal na disponibilidade de recursos pode gerar, direta ou indiretamente, padrões sazonais na ecologia de espécies de marsupiais (Fleming 1973, Julien-Laferrière 1995, Julien-Laferrière & Atramentowicz 1990).

Com relação à composição da dieta os animais podem ser divididos em dois grupos, representando dois extremos de um contínuo: especialistas e generalistas. Entre os mamíferos generalistas, é comum observar alterações na composição da dieta de acordo com flutuações na disponibilidade de recursos (Alves-Costa *et al*. 2004, Hodges & Sinclair

2003, Mello *et al.* 2004, Sosa & Soriano 1996). Dessa forma, os estudos mencionados acima descrevem que alguns itens são mais consumidos enquanto são abundantes, porém deixam de ser consumidos quando são raros. Isso ocorre provavelmente devido aos altos custos de forrageamento associados ao consumo de itens escassos (Schoener 1971). Claramente, além da disponibilidade, outros fatores também são importantes na escolha dos itens, como o retorno energético, a facilidade de encontrar o alimento e a palatabilidade do item (Owen 1982).

Os marsupiais didelfídeos podem ser classificados como animais onívoros, uma vez que sua dieta é composta principalmente de insetos, frutos e ocasionalmente vertebrados (Santori & Ástua de Moraes 2004). Diversos estudos abordando espécies de marsupiais já descreveram variações sazonais na dieta. Cáceres (2002) e Julien-Laferrière & Atramentowicz (1990) encontraram maior freqüência de frutos na dieta de *Didelphis albiventris* e *Philander opossum*, respectivamente, durante a estação úmida. Esse resultado corrobora a hipótese de que marsupiais são frugívoros oportunistas (Atramentowicz 1988), uma vez que a estação úmida corresponde ao período de abundância de frutos nas áreas estudadas pelos autores. Vieira *et al.* (1991) observaram o consumo de flores por *Didelphis marsupialis* durante a estação seca, correspondente ao período de escassez de frutos e artrópodes no ambiente. Apesar das evidências de que a disponibilidade pode influenciar a composição da dieta, a maior parte dos estudos sobre dieta em marsupiais é descritiva (Fonseca & Kierulff 1989, Carvalho *et al.* 1999, Leite *et al.* 1996). Não obstante, os poucos estudos documentando variações na composição da dieta em função da disponibilidade de recursos (e.g; Pelegatti-Franco & Gnaspini 1996) se baseiam na premissa de que índices pluviométricos são indicadores de abundância de recursos e não quantificam a abundância relativa de cada um dos itens no ambiente (porém veja Julien-Laferrière & Atramentowicz 1990).

Visto que a composição da dieta de marsupiais pode ser afetada pelos custos da locomoção em busca de alimento, o uso do espaço também deve ser influenciado pela abundância dos itens alimentares no ambiente. Como uso do espaço entende-se a área de vida ocupada por um indivíduo e a organização espacial dos indivíduos, ou seja, o grau de sobreposição entre as áreas de vida. Burt (1943) definiu área de vida como a área percorrida por um animal em busca de alimento, abrigo e parceiros, sendo rotas exploratórias não consideradas como parte da sua área de vida. O tamanho da área de vida é bastante variável, podendo ser determinado por massa corporal, sexo, densidade e quantidade de alimento (Bergallo 1990). Diversos estudos já observaram uma relação entre o tamanho da área de vida e a produtividade do habitat (Lurz *et al*. 2000; McLoughlin *et al*. 2000). A hipótese proposta por esses autores acerca dessa relação é que espécies que vivem em ambientes mais produtivos, com maior disponibilidade de recursos, terão área de vida menor do que as espécies residentes em ambientes pouco produtivos. Estudos com carnívoros (Gehrt & Fritzell 1998) corroboram essa hipótese e a mesma hipótese também parece se aplicar a animais onívoros (Norbury *et al.* 1994, Tufto *et al.* 1996), como os marsupiais. Dessa forma, quando a produção dos recursos é maior, o tempo e a energia exigidos para encontrar o alimento são menores, diminuindo assim o caminho percorrido durante a busca de alimento e, conseqüentemente, a área de vida. Uma vez que a produtividade do habitat pode variar sazonalmente, estudos com marsupiais australianos (Fisher & Owens 2000) e neotropicais (Julien-Laferrière 1995, Martins 2004) já demonstraram que o tamanho da área de vida também pode variar sazonalmente, em função da quantidade de alimento. Porém, assim como os estudos com dieta, a maior parte das evidências acerca da variação sazonal no uso de espaço entre os marsupiais Neotropicais se restringe a estudos usando estações do ano como indicadores de disponibilidade de recursos.

Além da dieta e do uso do espaço, a atividade reprodutiva dos marsupiais também parece sofrer influência de variações na disponibilidade de recursos alimentares. Marsupiais, em geral, se reproduzem sazonalmente em períodos que se repetem anualmente. Os padrões reprodutivos variam entre espécies, com algumas apresentando monoestria, outras biestria ou até mesmo poliestria (Fleming 1973, O'Connell 1979). Diversos estudos encontraram uma alta correlação entre atividade reprodutiva de marsupiais e a estação chuvosa (Fleming 1973, O´Connell 1979, Quental *et al*. 1999), vista como um período de abundância de recursos. Como tanto gestação quanto lactação são eventos energeticamente dispendiosos em marsupiais (Harder *et al.* 1996, Krockenberger 2003), o ajuste do período reprodutivo ao período de abundância de alimentos é uma estratégia que pode propiciar maior sucesso reprodutivo às fêmeas. Mais além, Julien-Laferrière & Atramentowicz (1990) observaram que *Didelphis marsupialis* e *Philander opossum* interromperam a reprodução quando sujeitos a períodos de escassez de frutos. Dessa forma, a quantidade de energia adquirida através da dieta pode determinar a energia disponível para a reprodução, de maneira que variações na disponibilidade de recursos podem afetar as estratégias reprodutivas dos indivíduos (Braithwaite & Lee 1979). Diversos estudos com marsupiais australianos da família Dasyuridae (Mills & Bencini 2000, Oakwood *et al*. 2001, Wolfe *et al*. 2004) sugerem que limitações na quantidade de recursos podem restringir as chances de sobrevivência dos juvenis a apenas um determinado período do ano, favorecendo a existência de semelparidade neste grupo. A existência de estratégia semélpara também já foi documentada para espécies menores de marsupiais didelfídeos, como *Gracilinanus microtarsus* (Martins 2004), *Monodelphis dimidiata* (Pine *et al.* 1985) e *Marmosops incanus* (Lorini *et al.* 1994). Baseados nessa relação entre disponibilidade de alimento e reprodução, muitos autores sugeriram que o aumento dos recursos alimentares no ambiente pode funcionar como estímulo para o início do período reprodutivo de diferentes espécies de marsupiais (Fleming 1973, Quental *et al.* 1999). Porém, claramente outros fatores também participam da determinação da atividade reprodutiva das fêmeas de marsupiais, como fotoperíodo (Bergallo & Cerqueira 1994) e liberação de feromônios por machos (Perret & M'Barek 1991). Desta forma, parece que a interação de fatores climáticos, alimentares e sociais deve determinar direta e indiretamente a reprodução dos marsupiais neotropicais, sendo que o fotoperíodo deve agir fixando o início da estação reprodutiva enquanto o suprimento alimentar deve agir determinando a duração do período reprodutivo, tamanho de ninhada e sobrevivência de filhotes.

De acordo com a classificação de Wilson & Reeder (1993), atualmente a ordem Didelphimorphia compreende apenas uma família, denominada Didelphidae, que possui aproximadamente 70 espécies distribuídas ao longo do continente americano (Wilson & Reeder 1993). As espécies pertencentes aos gêneros *Gracilinanus, Thylamys, Marmosa, Marmosops* e *Micoureus* estão entre os mais diversificados representantes dos didelfídeos (Lee & Cockburn 1985, Eisenberg & Redford 1999), apresentando ampla distribuição pela região Neotropical (Eisenberg & Redford 1999). O gênero *Marmosops* é composto por seis espécies (Eisenberg & Redford 1999), com distribuição em localidades no Peru, Equador, Bolívia, Panamá, Colômbia, Venezuela, Trinidad, Suriname, Guiana e Brasil (Eisenberg & Redford 1999). No Brasil, há três espécies: *Marmosops noctivagus*, que ocorre na Amazônia brasileira (Emmons & Feer 1997), *M. incanus* e *M. paulensis* (Figura 1.1), que ocorrem em simpatria em muitas localidades do sudeste brasileiro (Mustrangi & Patton

1997). *Marmosops incanus* possui ampla distribuição no Brasil, ocorrendo desde São Paulo até o norte do Sergipe, geralmente abaixo dos 800 m de altitude (Mustrangi & Patton 1997), enquanto *Marmosops paulensis* é mais restrita em sua distribuição, ocorrendo desde o Rio de Janeiro até o Paraná, passando pelo sudeste de Minas Gerais e Espírito Santo (Figura 1.2), em geral em altitudes mais elevadas (Mustrangi & Patton 1997). Estudos sobre o gênero *Marmosops* estão restritos a *M. incanus* e, em sua maioria, fornecem informações sobre a história natural desta espécie. Estes estudos sugerem hábitos semi-terrestres (Cunha & Vieira 2002), atividade noturna, semelparidade (Lorini *et al.* 1994), presença de forte dimorfismo sexual de tamanho e dieta insetívora, composta ocasionalmente de frutos e alguns vertebrados (Fonseca & Kierulff 1989, Stallings 1989). Devido à proximidade filogenética entre *M. incanus* e *M. paulensis* (Mustrangi & Patton 1997), acredita-se que determinados aspectos da história natural de ambas as espécies sejam semelhantes.

OBJETIVOS

O objetivo central deste estudo foi avaliar de que forma a disponibilidade de recursos alimentares afeta três aspectos da ecologia de *Marmosops paulensis*: a dieta, o uso do espaço e a reprodução. Dessa forma, o primeiro capítulo analisa a dieta de *M. paulensis* e os efeitos da disponibilidade de alimento sobre a composição da mesma. O segundo capítulo aborda a relação entre disponibilidade de recursos alimentares e os padrões de uso do espaço de *M. paulensis*, analisando a influência dos recursos e do sexo na variação do tamanho diário da área de vida dos indivíduos. O terceiro capítulo descreve os padrões reprodutivos de *M. paulensis*, investigando os efeitos da disponibilidade de recursos, fatores climáticos e fotoperíodo na reprodução dessa espécie.

ÁREA DE ESTUDO

O estudo foi realizado no Parque Estadual Intervales (PEI; 24°16'S, 48°25'W), Ribeirão Grande, sudeste de São Paulo (Figura 1.3). O PEI está localizado na Serra de Paranapiacaba e possui uma área de cerca de 49.000 ha, que, juntamente com outras três unidades de conservação contíguas (Parque Estadual Turístico do Alto Ribeira, Parque Estadual Carlos Botelho e a Estação Ecológica de Xitué), totaliza 120.000 ha contínuos de Mata Atlântica relativamente preservada. O relevo é do tipo "montanha com vales profundos", sustentado por rochas graníticas e calcáreas (Machado 1999). O clima é classificado como *Cfb* na classificação de Köppen, sendo que a temperatura média anual é de cerca de 22°C (Machado 1999) e a precipitação anual média varia entre 1600 e 1800 mm. De acordo com Rodrigues *et al.* (1994) existem duas estações do ano com relação à temperatura e precipitação. Há uma estação úmida e menos fria de outubro a março e uma estação menos chuvosa e fria de abril a setembro, denominada daqui para frente de estação seca.. A vegetação do PEI é bastante heterogênea, devido ao fato da existência de áreas em diferentes fases de desenvolvimento sucessional, ocorrendo então áreas de vegetação primária, secundária recente e secundária antiga (Machado 1999).

A área escolhida para a montagem da grade de capturas localiza-se na região da sede administrativa do Parque (Sede) e está localizada a aproximadamente 850 m de altitude. Nessa área, durante a estação seca a temperatura média é de 14,3°C (DP= 1,97 °C) e a precipitação média é de 44,4 mm (DP= 36,52 mm), enquanto durante a estação úmida a temperatura média é de 18,7°C (DP= 2,41 °C) e a precipitação média é de 196,1 mm (DP= 93,64 mm). A vegetação da Sede consiste basicamente de floresta secundária antiga, com grande abundância de plantas pioneiras, como piperáceas e solanáceas. Por outro lado, também é possível encontrar árvores atingindo mais de 30 m, como o manacá e o cedro. Bambus, em particular *Guadua angustifolia, Chusquea* spp. e *Merostachis* spp. também são muito comuns (Pizo, 1996).

Com relação aos marsupiais, a área da Sede se mostrou muito rica, apresentando oito espécies, incluindo *Marmosops paulensis*. Essas espécies foram: *Marmosa murina*, *Gracilinanus microtarsus*, *Monodelphis americana*, *M. scallops*, *Philander frenatus*, *Didelphis aurita* e *D. albiventris* (Figura 1.4).

METODOLOGIA GERAL

Os dados referentes à ecologia de *M. paulensis* foram coletados através do método de captura-marcação-recaptura. Oitenta armadilhas Sherman (modelo XLF15, 10,5 x 12 x 37,6 cm) foram dispostas em uma grade de 1,4 ha, contendo cinco trilhas paralelas de 140 m. Essas trilhas eram espaçadas por 50 m e, em cada uma foram demarcadas oito estações de captura distantes 20 m entre si (Figura 1.5). Em cada estação de captura foram colocadas duas armadilhas, uma no chão e outra na árvore a aproximadamente 2 m de altura. A isca utilizada para atrair os marsupiais foi uma mistura de banana, aveia, pasta de amendoim (Amendocrem®) e pedaços de bacon.

Mensalmente, de agosto de 2002 a agosto de 2004, durante cinco noites consecutivas as armadilhas foram colocadas na grade e as capturas realizadas. Todos os marsupiais capturados foram marcados individualmente com brincos numerados de latão, pesados com dinamômetros (Pesola®) de 100, 300 ou 1000 g (dependendo da espécie) e registrados sexo, ponto de captura, condição reprodutiva e estimativa de idade com base no padrão de erupção e substituição dos dentes (cf. Tyndale-Biscoe & Mackenzie 1976, Tribe 1990). Após a coleta dessas informações os animais foram soltos no mesmo local da captura.

No que se refere à condição reprodutiva, as fêmeas foram consideradas reprodutivas quando encontradas com filhotes ou com tetas inchadas e produzindo leite. A ausência de leite nas tetas foi considerada um indício de que a prole já havia sido amamentada, indicando um provável término da atividade reprodutiva. Dessa maneira, fêmeas encontradas com tetas ainda inchadas, porém sem leite, foram classificadas como não-reprodutivas. Com relação aos machos, foi registrada a posição do testículo. Porém, tal caráter não é útil na definição da atividade reprodutiva dos marsupiais, uma vez que os testículos destes animais descem quando eles atingem a maturidade sexual e permanecem nesta posição pelo resto da vida, em períodos reprodutivos e não-reprodutivos (Quental *et al*. 1999).

DISPONIBILIDADE DE RECURSOS

Estimativas de disponibilidade de recursos alimentares foram obtidas dentro da grade de captura simultaneamente às sessões de captura. Devido aos hábitos escansoriais de *M. paulensis* e a observações preliminares que demonstraram o consumo de frutos e artrópodos terrestres, a disponibilidade mensal de ambos os itens foi avaliada entre maio de 2003 e julho de 2004.

Para avaliar a disponibilidade de artrópodes foram usadas 40 armadilhas de queda (pitfall traps), uma em cada estação de captura (Figura 1.6). Essas armadilhas foram feitas com copos plásticos de 20 cm^3 enterrados com os bordos ao nível do solo. Cada armadilha continha uma solução de álcool 70% colocada no fundo do copo, de forma a preservar os artrópodes e evitar sua fuga após a captura. Tais armadilhas permaneceram expostas nas estações de captura por 72 h. Após esse período as armadilhas de queda foram retiradas da grade de capturas e os artrópodes coletados e identificados ao nível de ordem. O índice de disponibilidade foi obtido através do somatório dos números de indivíduos de todas as ordens de artrópodes capturadas.

O índice de disponibilidade de frutos foi obtido através do acompanhamento mensal de indivíduos pertencentes às famílias Piperaceae, Solanaceae, Melastomataceae e Rubiaceae (Figura 1.7). Estas famílias foram selecionadas devido à verificação anterior de seus frutos na dieta de outras espécies de marsupiais Neotropicais (Cáceres 2002, Pellegatti-Franco & Gnaspini 1996, Pinheiro *et al*. 2002). Além disso, devido aos hábitos semi-terrestres de *M. paulensis* (Leiner & Silva, dados não publicados), espécies de planta com altura superior a 5 m foram excluídas porque o consumo de seus frutos deve ocorrer apenas quando estes caem ocasionalmente no solo. Os indivíduos pertencentes às famílias mencionadas acima foram amostrados em transecções de 30 por 1,5 m, sendo quatro transecções por trilha de captura. Inicialmente, as plantas foram separadas em morfo-espécies e exsicatas foram trazidas para o Departamento de Botânica da Unicamp para identificação ao nível de espécie.

O número total de indivíduos de cada morfo-espécie por transecção e o número de indivíduos frutificando de cada morfo-espécie em cada transecção foram registrados simultaneamente nas sessões de captura. Assim, foi possível obter uma estimativa de porcentagem total de indivíduos frutificando no mês e a porcentagem de indivíduos de cada morfo-espécie frutificando no mês. Também foram obtidas estimativas mensais de número de frutos (verdes e maduros) produzidos por indivíduo de cada morfo-espécie por transecção e no geral.

DADOS METEOROLÓGICOS

Os dados meteorológicos referentes à precipitação foram obtidos na Estação Climatológica do PEI, distante aproximadamente 1 km da área de estudo. Foram utilizados os dados do período entre janeiro de 1992 e dezembro de 1997 somados aos dados do período do estudo (agosto de 2002 a julho de 2004; ver Figura 2.1) para obter uma curva de precipitação mensal média na área de estudo. Essa curva foi responsável pela determinação da duração da estação seca e da estação chuvosa. Os dados referentes à temperatura foram obtidos com a Fundação Florestal de São Paulo, responsável pela administração do PEI. Foram utilizados os dados do período entre janeiro de 1998 e julho de 2004 para a construção de uma curva de temperatura média mensal na área de estudo (ver Figura 2.1).

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FIGURAS

Figura 1.1: Macho adulto de *Marmosops paulensis* (Tate, 1931) capturado no Parque Estadual Intervales

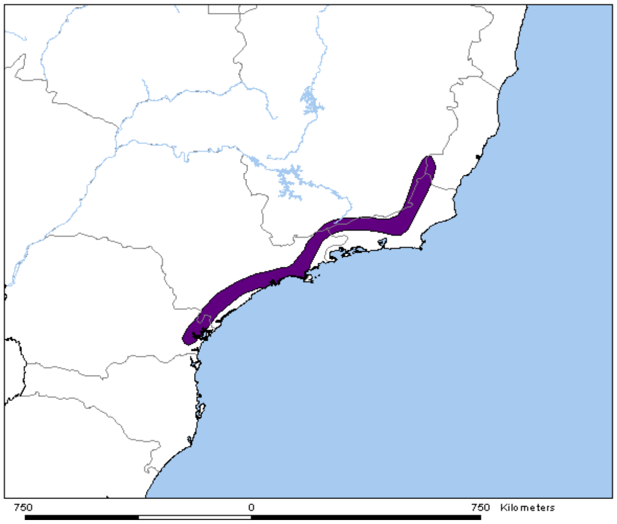

Figura 1.2: Recorte do mapa do Brasil mostrando um detalhe da região sudeste e em azul-marinho a distribuição geográfica de *Marmosops paulensis*.

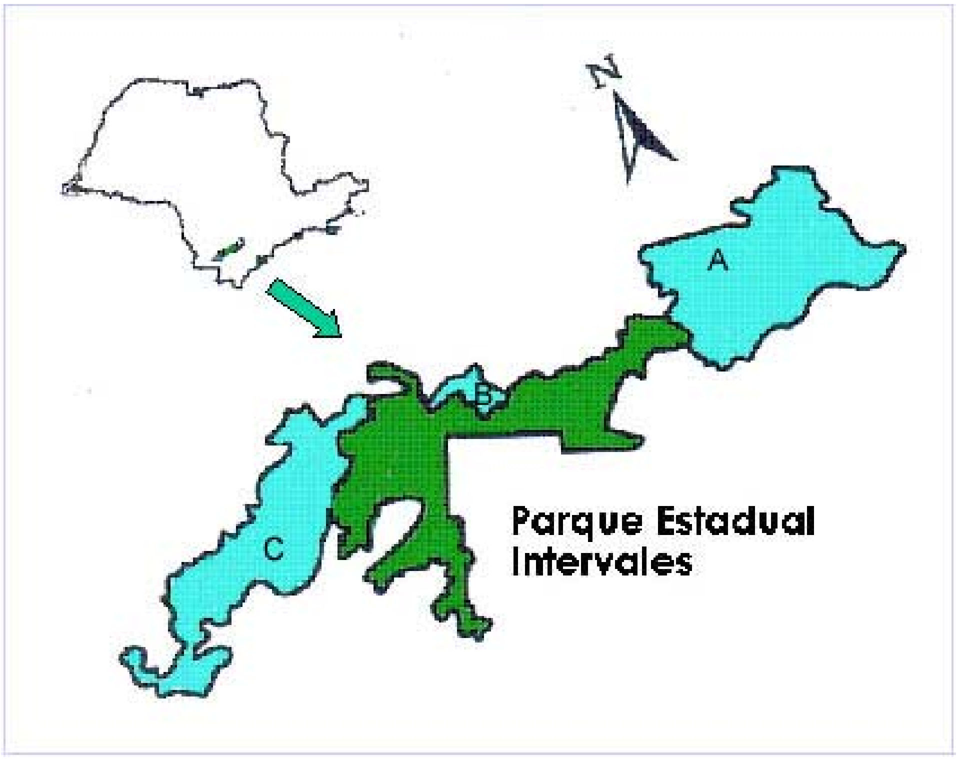

Figura 1.3: Localização do Parque Estadual Intervales no Estado de São Paulo. Em azul-claro as outras três Unidades de que fazem fronteira com o PEI. A: Parque Estadual Carlos Botelho; B: Estação Ecológica de Xitué e C: Parque Estadual Turístico do Alto Ribeiro – PETAR.

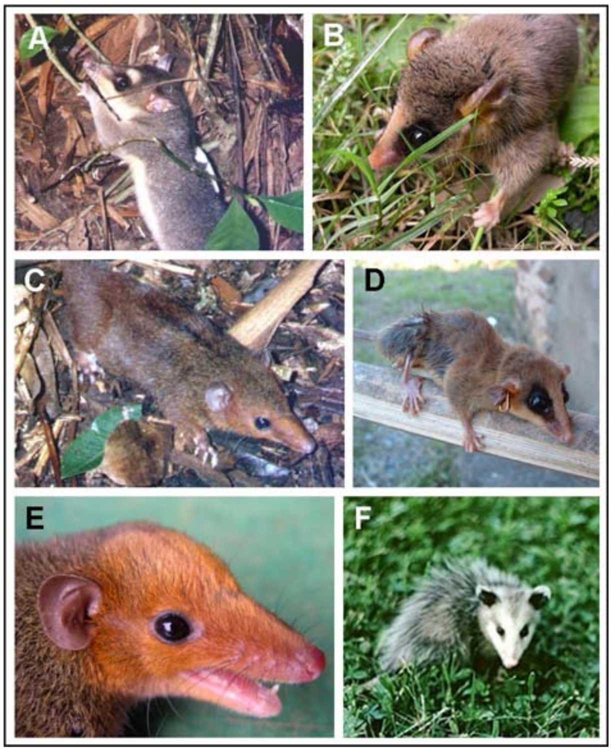

Figura 1.4: Membros da família Didelphidae encontrados na área da Sede, no Parque Estadual Intervales. A: *Philander frenatus* (foto: Marco A.R. Mello); B: *Marmosa murina* (foto: Marco A.R. Mello); C: *Monodelphis americana* (foto: Marco A.R. Mello); D: *Gracilinanus microtarsus* (foto: Marcelo O. Gonzaga); E: *Monodelphis scallops* (foto: Bruno Buzzato) e F: *Didelphis albiventris*.

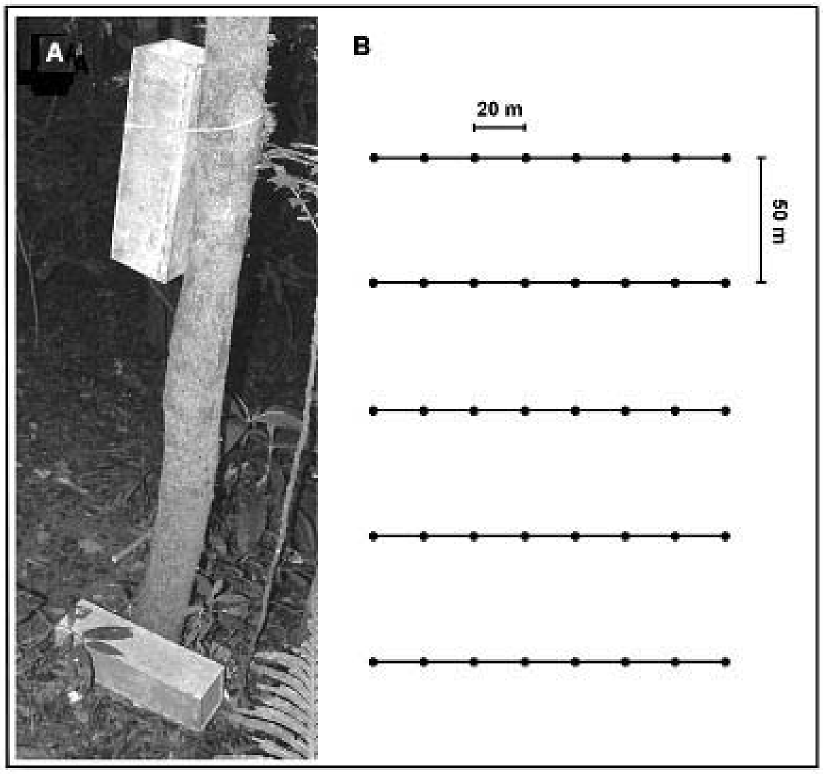

Figura 1.5A: Desenho esquemático da grade usada para a captura dos marsupiais. 1.5B: uma estação de captura, com duas armadilhas Sherman (modelo XLF15, 10,5 x 12 x 37,6 cm). Foto: Marcelo O. Gonzaga

Figura 1.6: Armadilha de queda usada para capturar artrópodes. Foto: Marcelo O. Gonzaga

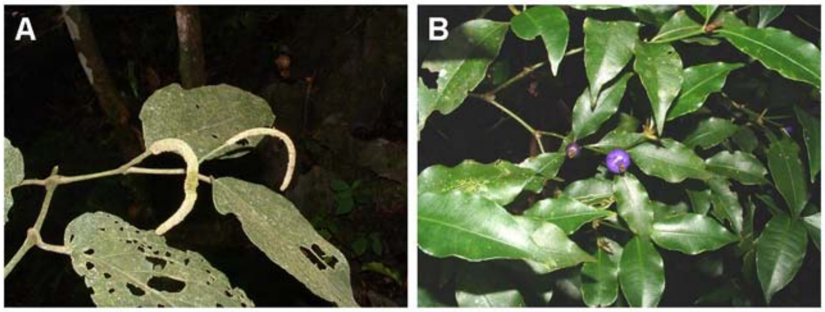

Figura 1.7: Duas das espécies mais abundantes na área de estudo (A: *Piper gaudichaudianum* e B: *Psychotria* sp.). Fotos: Marcelo O. Gonzaga.

CAPÍTULO 1

Seasonal variation in the diet of the mouse opossum *Marmosops paulensis* (Didelphimorphia: Didelphidae) in a Montane Atlantic Forest area in southeastern Brazil

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Key words: frugivory, omnivory, food availability, seed dispersal, mouse opossum, *Piper*

Running title: Variations in the diet of *Marmosops paulensis*

ABSTRACT

The diet of the mouse opossum, *Marmosops paulensis*, was determined through analysis of fecal samples collected in an area of Montane Atlantic forest in southeastern Brazil. *Marmosops paulensis* consumed insects, arachnids, gastropods, fruits, flower parts and vertebrates, characterizing an omnivorous diet. Preference for the Coleoptera, the Blattodea, the Opiliones, and *Piper* fruits was observed. One reason for the preference for *Piper* fruits could be its spatio-temporal predictability, whereas the preference for these arthropod orders could be due to overestimations of hard-bodied prey. Diet composition varied seasonally, with invertebrates and flower parts being more consumed during the dry season, probably due to their higher relative abundance when compared to fruits in this season. In this way, *M. paulensis* might have to eat additional or alternative food items during the food shortage period. Moreover, we suggest that *M. paulensis* can act as an important seed dispersal of pioneer plants, especially of *Piper* species.

INTRODUCTION

Diet is an important aspect of marsupial ecology and its knowledge is fundamental to understand and interpret life history data (Lee & Cockburn 1985), habitat use (Julien-Laferrière 1995) and community structure (Leite *et al.* 1996). In Australia marsupials present a wide variety of feeding habits, ranging from species feeding exclusively on nectar to carnivores, herbivores, frugivores, insectivores, and commonly omnivores (Lee & Cockburn 1985).

Differently from Australian species, Neotropical marsupials are predominantly omnivores (Santori & Àstua de Moraes 2004). Studies on diet composition of didelphids report a wide variety of food items, mainly invertebrates, fruits, small vertebrates and, occasionally, carrion, nectar, and other plant parts (Gribel 1988, Santori *et al.* 1995, 1997). Furthermore, numerous studies reported seasonal shifts among items consumed by opossums (Cáceres 2002, Julien-Laferrière 1999; Pelegatti-Franco & Gnaspini 1999), usually associating this seasonality to fluctuations in resource availability. Based on this argument, abundant items should be consumed more frequently, suggesting an opportunistic feeding strategy. However, most of those studies did not measure food availability directly in the field, and instead used rainfall patterns as an indirect index of food supply.

São Paulo's slender mouse opossum, *Marmosops paulensis* (Tate, 1931) is a nocturnal, small (20-70g) member of the Didelphidae family, which inhabits montane forests above 800 m in the Brazilian Atlantic forest (Mustrangi & Patton 1997). Reproduction occurs from September to March, and individuals take part in only one reproductive event, characterizing a semelparous reproductive strategy (Leiner *et al.*, in preparation). Data on the diet of other mouse opossums suggest a diet composed mainly by insects, but also fruits, and occasionally nectar and flowers (Carvalho *et al.* 1999, Charles-Dominique 1983, Martins & Bonato 2004, Vieira & Palma 1996, Vieira & Izar 1999). Therefore, Santori *et al.* (1995) suggested a trend towards insectivory in smaller opossums, whereas larger species tend towards omnivory. There is no current information on diet of the species *M. paulensis*, however, anecdotal data on the congeneric marsupial *M. incanus* suggest a diet constituted mainly by insects (Fonseca & Kierulff 1989, Stallings 1989).

The objective of the present study was two-fold. First, we described the diet of *M. paulensis* and the variations in its food supply (insects and fruits) in an area of Atlantic forest. Second, we evaluated if there was resource selection among food items, both within the invertebrate and fruit category.

STUDY SITE

This study took place in Parque Estadual Intervales (24^{o}16'S, 48^{o}25'W), an Atlantic Forest area situated in the southeast region of São Paulo state, in the municipality of Ribeirão Grande, Brazil. The park has approximately 49000 ha and it is connected to three other conservation units, totaling 120000 ha of protected Atlantic forest. Annual rainfall ranges from 1600 to 1800 mm and mean annual temperature is about 22^{o}C, with a wet season from October to February and a less-rainy and cold season, called hereafter as dry season, from March to September (Figure 2.1). The study grid was located in a region known as "Sede", covered with old secondary growth vegetation, at approximately 850 m of altitude.

METHODS

Data collection

We set 80 Sherman traps (XLF15, 10.5 x 12 x 37.6 cm) monthly in five 140 m parallel transects. Transects were 50 m apart from each other, and had eight trapping stations that were separated by 20 m. We placed two traps at each trapping point, one on the ground and the other on tree branches or vines at breast height (ca. 1.5 m). We baited all traps with a mixture of banana, peanut butter, oatmeal, and bacon. Traps were checked daily during five consecutive days, and baits were replaced when necessary. We marked the animals with individually numbered ear-tags, and recorded their sex, weight, reproductive condition (swollen nipples and presence of young for females). After recording those data, we collected fecal samples directly from each individual or inside the trap after releasing the animal. Feces were stored in small recipients and frozen to avoid deterioration. Then, fecal samples were dissolved in water, filtered using 0.1 mm mesh and analysed under a binocular microscope. Items were identified at the finest possible level, and separated in four categories: seeds, other plant parts, invertebrates and vertebrates. Consumption frequency of each food item was calculated as the proportion of samples that presented that item. Only one record per month for each individual was used to avoid pseudoreplication.

Arthropod and fruit availability were estimated from May 2003 to July 2004. We measured arthropod abundance using 40 pitfall traps, consisting of plastic recipients (20 cm^3), filled with 70% ethanol. We placed each pitfall trap in a trapping station, and removed them after three days of exposure. Trapped arthropods were identified at the level of order. Then, we counted the arthropods and used the sum of all orders, excluding those that were not consumed by *M. paulensis*, as an index of availability of this category.

We estimated fruit availability in 20 transects of 30 x 1.5 m, located inside the capture grid. In each transect we recorded monthly the number of fruits produced and the proportion of individuals bearing fruits of species belonging to four families: Piperaceae, Solanaceae, Melastomataceae, and Rubiaceae. We chose those families because earlier studies on Neotropical marsupial species recorded their seeds in the diet of these mammals (Cáceres 2002, Pellegatti-Franco & Gnaspini 1996, Pinheiro *et al*. 2002), and because those plants presented trees lower than 5 m. We excluded trees higher than 5 m assuming that *M. paulensis* would consume their fruits only if they occasionally fell on the ground, once *M. paulensis* has semi-terrestrial habits (Leiner & Silva, unpublished data). We used the total number of fruits produced in each month as the measure of fruit availability.

Data Analysis

First, we tested the relationship between abundance of both fruits and arthropods and rainfall patterns in the study site, using a Spearman rank correlation. To evaluate possible selection among the arthropod category we calculated the forage ratio (Krebs 1999) for each arthropod item, using the proportion of the item in the diet and the proportion available of the item in the environment. To test the null hypothesis that *M. paulensis* was selecting invertebrates at random we ran a modified G-test, following Krebs (1999). We ran the same procedure to evaluate selection among the fruit category.

We tested for seasonal variation in the diet of *M. paulensis* by comparing the number of occurrences of each food category between the dry and wet season, using a chi-square independence test with Yates correction (Zar 1999). Fruits (seeds), invertebrates (arthropods, arachnids and gastropods), vertebrates and flowers were used as food categories in the statistical analysis. We used only categories whose expected frequency was higher than five in chi-square calculations (Zar 1999). Therefore, we excluded vertebrates and flowers from the statistical analysis. We also calculated the diversity of items through the Shannon-Wiener index ($\log_2$) (Krebs 1999), and compared values of this index between seasons using a Hutcheson's t test (Zar 1999). All analyses were done using βιoεstat 3.0 (Ayres *et al*. 2003).

RESULTS

Patterns of resource availability

The abundance of fruits and arthropods fluctuated seasonally, and both were correlated with rainfall (fruits r_s= 0.68; p= 0.005; n= 15; arthropods r_s= 0.76; p= 0.0009; n= 15). Two periods were evident: a season of high fruit and arthropod availability from December to March, and a season of food shortage, with few plant species producing fruits and lower arthropod availability from May to September (Figure 2.2). Throughout the period of resource scarcity, which was associated to low temperatures and reduced rainfall, the only fruits available belonged to few individuals of *Ossaea amygdaloides* (Melastomataceae) (Figure 2.3). On the other hand, during the period of resource abundance, *Piper gaudichaudianum*, *Piper* sp.1 (Piperaceae), *Solanum* sp. (Solanaceae) and *Psychotria* sp. (Rubiaceae) were the most abundant fruiting plants in the study area (Figure 2.3).

Despite the high number of fruits produced by the large amount of *Piper* individuals (mean ± SD= 226 ± 145.3; N=60), only a few ripe fruits were available on a nightly basis (mean ± SD=15.3 ± 5.3). On the contrary, *Psychotria* sp. presented a high number of ripe fruits while fructifying (mean ± SD= 250.66 ± 205.42; N=63), what also occurred with Melastomataceae species, which produced more than 400 ripe fruits (N=5) during the wet season.

Food consumption

Seeds, arthropods, gastropods, flower parts, feathers, and bones were found in fecal samples (N=61) of *M. paulensis*. Feathers and bones were consumed in a very low frequency (4.9%) and we were unable to identify to whom they belonged, thus pooling them together in the vertebrate category. Regarding seeds and invertebrates, we recorded 18 different items: 11 fruit species, six arthropod orders, and one mollusk (Table 1). Insects (78.6%), fruits (54.1%), and also an unidentified spike-like inflorescence (39.3%) were the commonest items in the diet of *M. paulensis* (see Table 1).

Arthropod orders were not selected at random by *M. paulensis* (χ^2= 18.36; df= 5; p= 0.003). The Blattodea, the Coleoptera and the Opiliones were more frequent in the diet than expected due to their abundance in the environment (Figure 2.4). Random selection did not occur among fruits nor in the dry season (Figure 2.5) (χ^2=32.00; df= 2; p< 0.00001) neither in the wet one (Figure 2.6) (χ^2= 31.42; df= 2; p< 0.00001). *Piper* was by far the most consumed fruit, accounting for 95% of all fruits consumed by *M. paulensis*. During the wet season, which corresponded to the fruiting period of *Piper*, this fruit was found in 79% of the fecal samples On the other hand, fruits from the familiy Melastomataceae and the family Solanaceae were less consumed by *M. paulensis* than expected based on their availability.

Fruits and arthropods were consumed year-round, however their frequencies in the diet of *M. paulensis* changed seasonally. Invertebrates were more frequent during the dry season (χ^2= 6.4; df=1; p<0.05) while fruits were eaten at similar frequencies during both seasons (χ^2= 0.78; df= 1; p>0.05). Furthermore, during the dry season, the diet of *M. paulensis* was more diverse (H'_{wet}= 3.121; H'_{dry}= 3.498; t= -7.39; p<0.001). This result was due to the presence of new fruit species and the reduced contribution of *Piper* fruits in the diet of *M. paulensis* at this time of the year. Interestingly, this reduction in the frequency of *Piper* was followed by a rise in the frequency of a flower species in the diet of *M. paulensis*.

DISCUSSION

In this study *M. paulensis* consumed a wide variety of food items, such as insects, arachnids, mollusks, vertebrates, fruits, and even flowers, indicating a generalist diet. As the other mouse opossums studied so far (Pinheiro *et al*. 2002, Martins & Bonato 2004), the most abundant insect order found in the diet of *M. paulensis* was the Coleoptera, followed by the Hymenoptera. The high abundance of ants in the diet of *M. paulensis* does not necessarily imply a preference for this item, and instead may be due to its high abundance in our study site. On the other hand, the orders Coleoptera, Opiliones, and Blattodea were consumed in spite of their lower availability, suggesting that *M. paulensis* may prefer these items. However, this pattern could be due to an overestimation, since hard-bodied prey are easier to detect in the fecal samples (Dickman & Huang 1988). In fact, all the arthropods consumed by *M. paulensis* belonged to hard-bodied orders, while soft-bodied orders such as the Amphipoda and the Diptera, which were very abundant in the pitfall traps, were not found in the feces of *M. paulensis*. Moreover, the remains of Orthoptera were difficult to distinguish from Blattodea, and we may have assigned some of those remains to the latter, leading to a further overestimation of the Blattodea.

Regarding fruits, *M. paulensis* consumed mainly pioneer species. Pinheiro *et al*. (2002), working in an area of small fragments in the Brazilian Atlantic forest, also found only pioneer plants in the diet of *Micoureus demerarae*, especially *Cecropia pachystachya* (Cecropiaceae) and *Piper mollicomum* (Piperaceae). At our study site, *Cecropia* individuals were very rare, with only a few juveniles that did not produce fruits during the entire study period. Vieira & Izar (1999), also working at Parque Estadual Intervales, found a high frequency of seeds of epiphytic species of the family Araceae in the diet of *M. demerarae*, however, aroids were not observed in *M. paulensis* feces. This difference may be due to the more terrestrial habits of *M. paulensis*, which occasionally climbs trees (Leiner, unpublished data), when compared to *M. demerarae*, an arboreal species (Passamani 1995)

There seems to be a strong selection among fruits by *M. paulensis*, in both seasons. Four factors are important to determine food selection: availability, accessibility, palatability, and energetic value (Owen 1982). Despite the high abundance of *Psychotria* fruits, these were not consumed at all. On the other hand, *Piper* was by far the most consumed fruit, although other plant species produced a larger number of fruits (e.g., melastome shrubs), and even so they were less consumed. Phenological studies suggest that *Piper* is a "steady-state resource" (Fleming 1981), producing few fruits on a nightly basis during a long fructification period. Fleming (1981) and Mello *et al.* (2004) argued that the choice of Piperaceae plants by *Carollia* bats seems to be related to the high temporal and spatial predictability of these plants. This predictability could benefit *M. paulensis* by reducing its foraging costs, as was earlier proposed for fruit-eating bats (Fleming 1981, Thies & Kalko 2004).

Seasonal variation in food habits is a common pattern among generalist species and may be a consequence of fluctuations in resource availability (Julien-Laferrière 1999). Numerous studies on diet composition of opossums demonstrated a trend in which fruits and invertebrates were consumed in a higher frequency during the wet season, due to a higher abundance at this time of the year (Cáceres 2002, Charles-Dominique *et al*. 1981, Julien-Laferrière & Atramentowicz 1990). The diet of *M. paulensis* showed seasonal changes, such as the inclusion of new fruit species in the diet and the higher frequency of invertebrates and flowers during the dry season. Although invertebrate abundance dropped markedly at our study site during the dry season, its higher frequency in the diet of *M. paulensis* can be explained by its relative abundance when compared to fruits during this period. Alves-Costa *et al*. (2004) found a similar pattern among coatis (*Nasua nasua*), which consumed a higher frequency of fruits during the dry season due to their higher relative abundance compared to arthropods. Furthermore, several studies on the energetics of small mammals suggested that during periods of low availability and quality of resources, animals tend to increase their rate of food intake (Geluso & Hayes 1999).

Previous studies on *Caluromys derbianus*, *C. lanatus*, *Micoureus demerarae*, and *Didelphis marsupialis* have already described flower consumption by these species, especially during the dry season, when fruit abundance is low (Charles-Dominique 1983, Gribel 1988, Steiner 1981, Vieira *et al*. 1991). Unfortunately, we could not identify the flower species consumed by *M. paulensis*, and all we know is that it belongs to a species that produces erect, spike-like inflorescences. Generally, marsupials have been seen visiting chiropterophilous plants, such as species with nocturnal anthesis and strong odor (Steiner 1981). Since in our study flowers were more frequent in the diet during the period of resource scarcity, it is possible that *M. paulensis* may use nectar and pollen as an additional or alternative food source during this period, as was argued for *C. derbianus* in Panama (Steiner 1981) and for *D. marsupialis* in the southeastern Brazil (Vieira *et al.* 1991).

However, pollen grains were never recorded in the diet of *M. paulensis*, posing a question on whether flower consumption was incidental, while foraging for insects in the foliage. To answer this question, field observations on the foraging behavior of *M. paulensis* would be helpful.

Usually, opossums are viewed as opportunistic fruit eaters (Atramentowicz 1988) and mouse opossums are described as highly insectivore species (see revision in Santori *et al*. 1995). However, in our records the diet of *M. paulensis* presented a larger amount of plant parts (fruits and flowers) than in other studies on congeneric species, which found arthropods in 100% of the fecal samples, and only few seeds and other plant parts (Palma 1996, Stallings 1989). Our findings are in agreement with Astúa de Moraes *et al*. (2003). These authors revealed that mouse opossums rely more on fruits than previously thought and may meet most of their energetic requirements by eating fruits. As discussed by Santori & Astúa de Moraes (2004), the earlier classification of mouse opossum as insectivores species could be due to the underestimation of seeds in fecal analysis, once fruit pulp is rarely recognizable in the feces and larger seeds are not ingested (Charles-Dominique *et al*. 1981) or even spitted (Santori, personal communication). Moreover, our results suggest that when fruits were not available, more precisely *Piper* fruits, *M. paulensis* increases the consumption of other items. This pattern of diet seems to be in accordance with the theory of optimal diet, as proposed by Schoener (1971), however further tests are required to test this hypothesis.

In spite of our findings regarding a higher fruit consumption than expected, we consider it improper to place *M. paulensis* in a strict feeding category (like frugivore-omnivore), since it may overlook subtle important differences in its natural diet. However, our results allow considerations on the role of *M. paulensis* on forest regeneration through seed dispersal, since this marsupial consumes large amounts of fruits, mainly from pioneer plants. Furthermore, several studies discussed that didelphids can act as important dispersal agents in Neotropical forests (Cáceres *et al*. 1999, Cáceres 2002, Medellín 1994), even accelerating germination rate of seeds (Grelle & Garcia 1999). Although we did not run germination experiments, most seeds were found intact in fecal samples of *M. paulensis*. Data on *M. paulensis* movements indicates that this marsupial can act as an efficient disperser through a reduction on seed mortality near the parent plant (Janzen 1970). Since *Piper* presents clonal growth, *M. paulensis* may enhance not only the establishment of new individuals but also the genetic diversity of this plant population. In this way, we suggest that *M. paulensis* may play an important role in the seed dispersal of *Piper* fruits.

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FIGURES

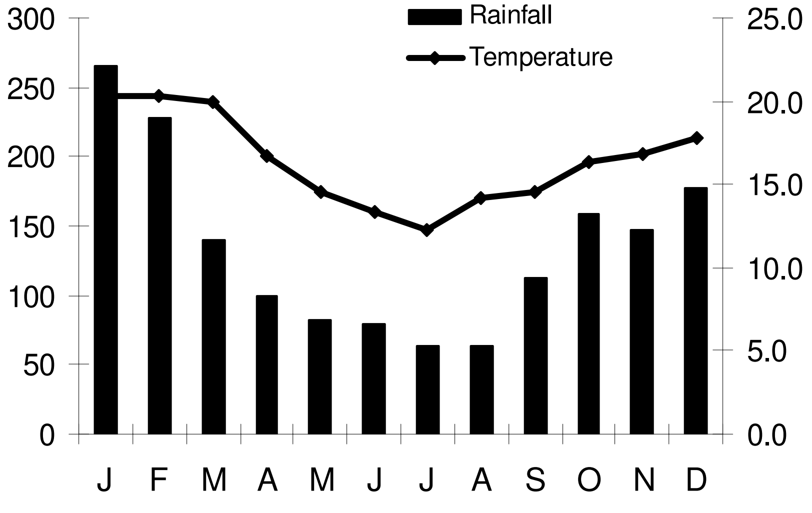

Figure 2.1: Monthly averages of rainfall (black bars) and daily temperature (solid line) at Parque Estadual Intervales from 1992 to 2004.

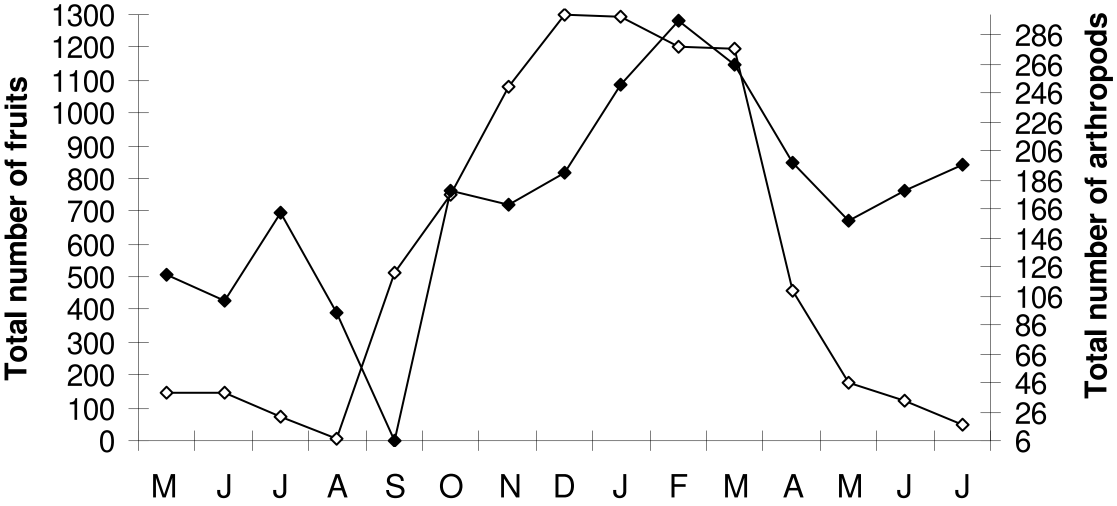

Figure 2.2 Monthly variation in arthropod (black dots) and fruit (white dots) availabilities at Parque Estadual Intervales from May 2003 to July 2004.

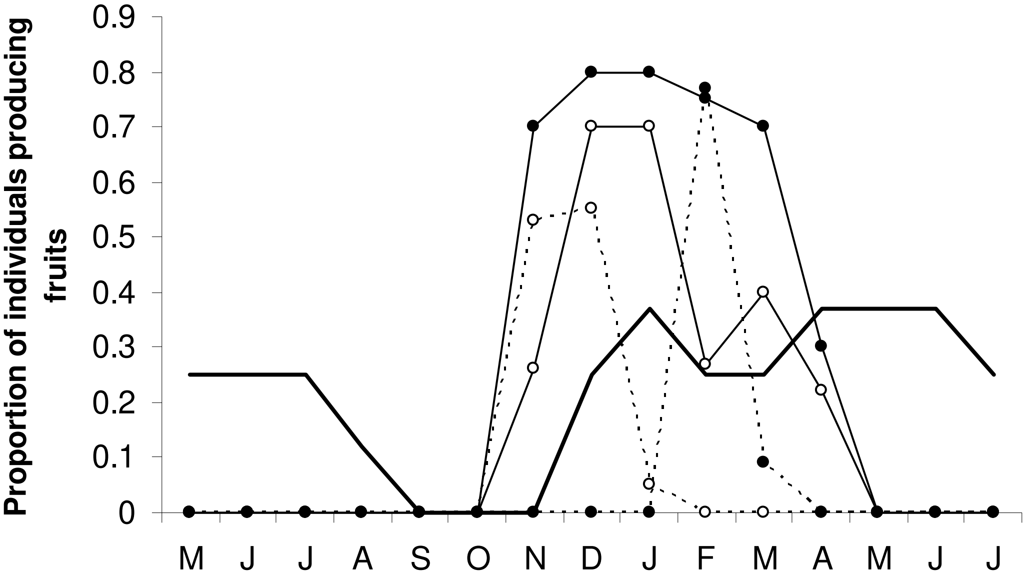

Figure 2.3: Seasonality of fruit production by the commonest plant species found in the sampled transects from May 2003 to July 2004. *Ossaea amygdaloides* (solid line – December to August), *Solanum* sp. (solid line and black dot – November to August), *Psychotria* sp. (solid line and white dot – November to April), *Piper gaudichaudianum* (dashed line and white dot – November to January) and *Piper* sp. 1 (dashed line and black dot – February to March).

Table 1: Consumption frequency and availability of the food items consumed *by M. paulensis* in dry and wet seasons at PEI .

Food item	Dry season		Wet season	
	Eaten (N=37)	Available	Eaten (N=24)	Available
PIPERACEAE				
Piper gaudichaudianum	1 (2.70 %)	0	16 (66.67 %)	591 (21.39 %)
Piper sp. 1	3 (8.11 %)	7 (0.49 %)	3 (12.5 %)	145 (5.25 %)
Piper sp. 2	7 (18.91 %)	___________	0	___________
SOLANACEAE				
Solanum sp.	4 (10.81 %)	72 (5.08 %)	1 (4.16 %)	700 (25.33 %)
MELASTOMATACEAE				
Leandra dasytricha	1 (2.70 %)	___________	0	___________
Ossaea amygdaloides	1 (2.70 %)	1337 (94.42 %)	1 (4.16 %)	1327 (48.03 %)
MYRTACEAE				
Psidium cattleyanum	1 (2.70 %)	___________	0	___________
Campomanesia sp.	1 (2.70 %)	___________	0	___________
ROSACEAE				
Rubus rosaefolius	2 (5.41 %)	___________	0	___________
UNIDENTIFIED SEEDS	4 (10.8 %)	___________	0	___________
FLOWER PARTS				
Spike-like flower	19 (51.35 %)	___________	5 (20.83 %)	___________
ARTHROPODS				
Coleoptera	16 (43.24 %)	252 (17.25 %)	11 (45.83 %)	277 (26.95 %)
Orthoptera	7 (18.91 %)	468 (32.04 %)	7 (29.16 %)	129 (12.55 %)
Hymenoptera (Formicidae)	18 (48.65 %)	555 (37.99 %)	7 (29.16 %)	524 (50.97 %)
Blattodea	10 (27.03 %)	128 (8.76 %)	8 (33.34 %)	44 (4.28 %)
Araneae	1 (2.70 %)	24 (1.64 %)	0	21 (2.04 %)
Opiliones	7 (18.91 %)	34 (2.33 %)	5 (20.83 %)	33 (3.21 %)
MOLLUSCA				
Pulmonata (Gastropod)	3 (8.11 %)	___________	4 (16.6 %)	___________
VERTEBRATE	1 (2.70 %)	___________	2 (8.3 %)	___________

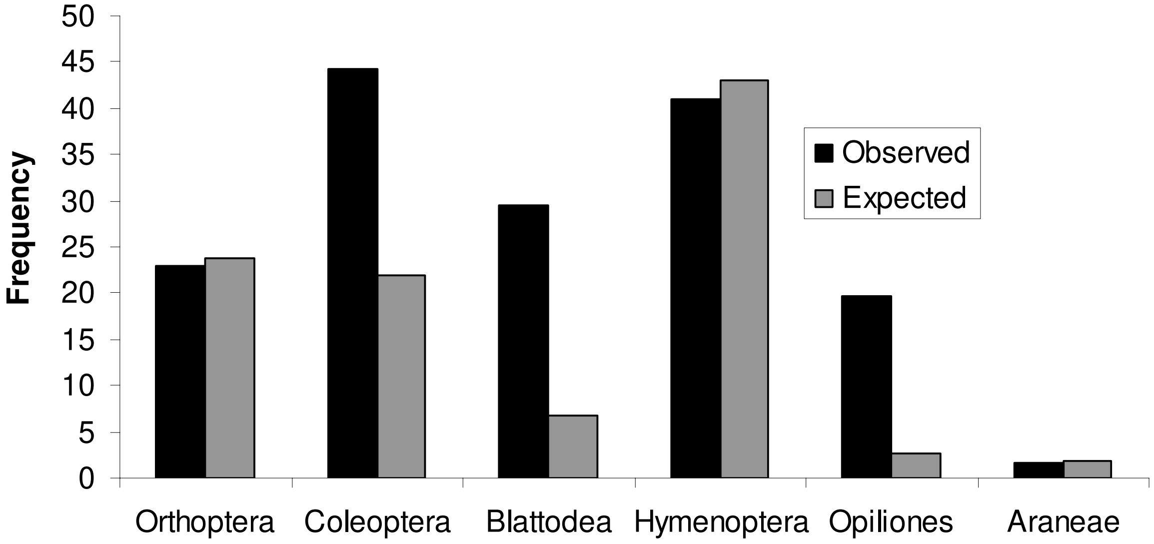

Figure 2.4: Consumption of arthropod items by *M. paulensis* (black columns) and availability of arthropod items in the environment (gray columns).

χ^2= 19.71; df= 5; p= 0.0015.

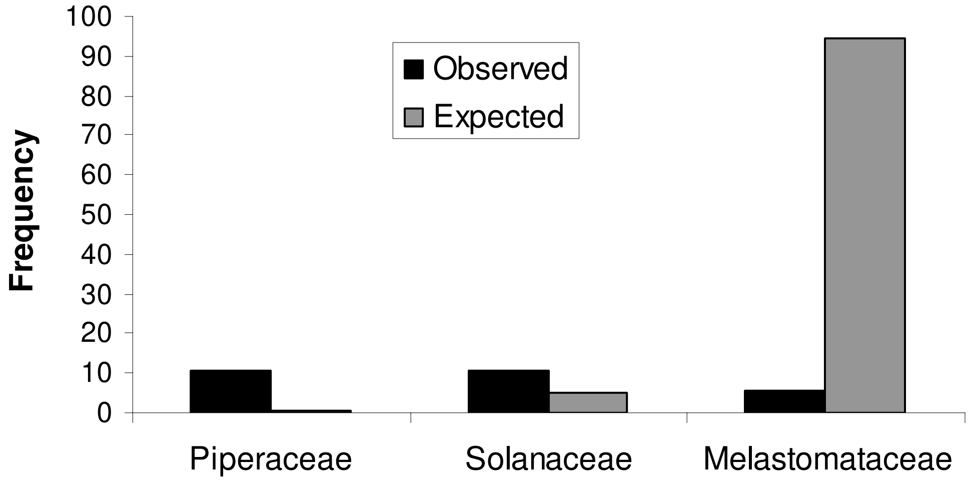

Figure 2.5: Consumption frequency of fruit items by *M. paulensis* (black columns) and availability of fruit items in the environment (gray columns) during the dry season.

χ^2=32.03; df= 2; p< 0.0001.

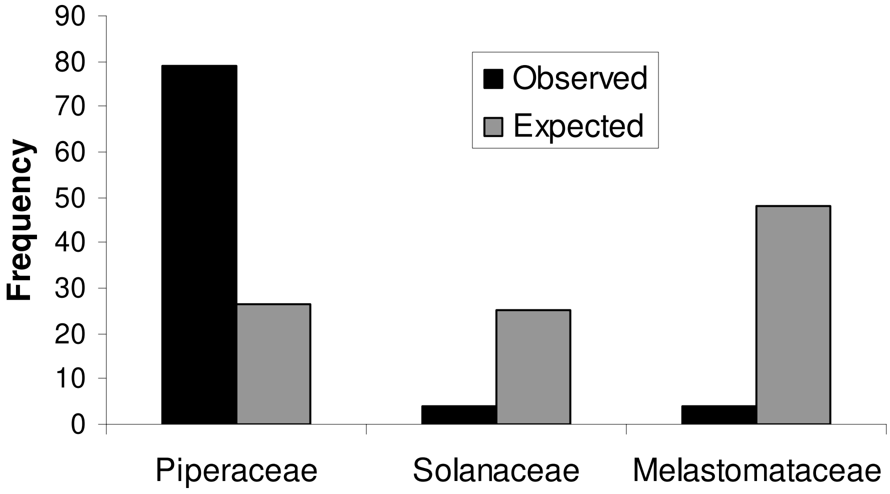

Figure 2.6: Consumption of fruit items by *M. paulensis* (black columns) and availability of fruit items in the environment (gray columns) during the wet season.

χ^2= 31.42; df= 2; p< 0.00001.

CAPÍTULO 2

Effects of resource availability on the use of space by the mouse opossum *Marmosops paulensis* (Didelphimorphia: Didelphidae) in a Montane Atlantic forest area in southeastern Brazil.

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Key words: daily home range, marsupials, food availability, resource predictability, Piperaceae, spool and line device.

Running title: Resource availability and use of space by *Marmosops paulensis*.

ABSTRACT

In the present study we analyze data on the influence of sex and food supply on the variation of daily home range size movement areas in the mouse opossum *Marmosops paulensis* (Tate, 1931). *Marmosops paulensis* is a member of the Didelphidae family, occurring in areas of high altitude in the Brazilian Atlantic Forest. Mean daily home range size of *M. paulensis* estimated through spool and line device was about 0.40 ha and it was not different between body sizes and sexes, although females had a much wider range of variation than males. As we expected, there was an inverse relationship between daily home range size and food supply. This relationship was due only to the effect of fruit abundance on the space use patterns of *M. paulensis*. Moreover, abundance of *Piper* fruits alone led to a reduction on daily home range size of *M. paulensis*. The relative aggregated distribution of fruits when compared to the sparser distribution of arthropods could explain why daily home range size was determined exclusively by fruits, with especial regard to *Piper*, a species known by its temporal and spatial predictability.

INTRODUCTION

Since the work of McNab (1963), interspecific variation in home range size has been viewed as an allometric function of body size. Several other studies with mammals (e.g., Harestad & Bunnell 1979, Harvey & Clutton-Brock 1981, Gittleman & Harvey 1982) suggested that this allometric relationship occurs because there is a positive correlation between energetic requirements and body size. However, when the effects of body size are controlled, a considerable variation in home range size still remains (Harestad & Bunnell

1979). Hence, other factors account for this residual variation, such as diet, habitat productivity and interspecific competition (Harestad & Bunnell 1979, Harvey & Clutton-Brock 1981). Intraspecific variation in mammal home range size is less understood, however factors associated with energetic demands of individuals should also play an important role. Previous studies recorded the influence of several factors on home range size variation, such as population density (Abramsky & Tracy 1980), food distribution (Joshi *et al*. 1995), food abundance (Mares *et al*. 1982, McLoughlin *et al.* 2000), sex (Attuquaeyfio *et al.* 1986), predation risk (Longland & Price 1991), and reproductive condition (Julien-Laferrière 1995).

Assuming that each individual uses the minimum area that can allow it to meet its energetic requirements, when the resources are abundant or distributed in an aggregated way, the foraging area (and consequently the home range size) can be reduced (Lurz *et al*. 2000). On the other hand, when resources are regularly distributed or are scarce, individuals have to enlarge their home range as a way of gathering enough food to meet their energetic demands. Indeed, an inverse relationship between home range size and food abundance has been found in several mammalian species, such as the roe deer, *Capreolus capreolus* (Tufto *et al*. 1996); the brown bear, *Ursus arctos* (McLoughlin *et al.* 2000); the raccoon, *Procyon lotor* (Gehrt & Fritzell 1998), and the wood mouse, *Apodemus sylvaticus* (Attuquayefio *et al.* 1986).

Since female reproductive success is generally limited by food supply, and male reproductive success is determined by the number of mates achieved (Trivers 1972), Clutton-Brock (1989) argued that there should be a difference on factors affecting the use of space on both sexes. In this way, in species presenting a polygynous/promiscuous mating system, variations on food supply should affect only female movements (Gaulin &

Fitzgerald 1988), whereas male movements are attuned to their reproductive condition. Despite the huge literature discussing the negative effects of abundance and food distribution on space use patterns in eutherians (see references herein), there are few studies on this topic for marsupials (but see Norbury *et al*. 1994, Fisher & Owens 2000). Moreover, apart from Australian marsupials, most studies on didelphids are mainly descriptive (but see Julien-Laferrière 1995, Martins 2004).

São Paulo's slender mouse opossum, *Marmosops paulensis* (Tate, 1931), a small (20-70g) member of the Didelphidae family, is a nocturnal species, with semi-terrestrial habits (Leiner & Silva, unpublished data). It is endemic to the southeastern Brazilian Atlantic Forest, and it is restricted to montane forests above 800 m (Mustrangi & Patton 1997). Fruits, especially of Piperaceae, and insects are the most frequent items in the diet of this species (Leiner & Silva, in preparation). In the study area, *M. paulensis* reproduces from September to March and exhibits semelparity (Leiner *et al*., in preparation)

The objective of the present study was to characterize the space use patterns of *M. paulensis*, estimating its daily home range size and evaluating the influence of sex and body weight on its variation. We also tested the hypothesis that there was an inverse relationship between daily movement area and food abundance, measured as arthropod and fruit availability. Since fruits of the genus *Piper* were the most consumed food item by *M. paulensis* (Leiner & Silva, in preparation), we also tested whether there was a negative relationship between the abundance of *Piper* fruits and home range size of *M. paulensis*.

STUDY SITE

This study took place in Parque Estadual Intervales (24^o16'S, 48^o25'W), an Atlantic Forest area situated in the southeast region of São Paulo state, in the municipality of Ribeirão Grande, Brazil. The park has approximately 49000 ha and it is connected to three other conservation units, totaling 120000 ha of protected Atlantic forest. Annual rainfall ranges from 1600 to 1800 mm and mean annual temperature is about 22^oC, with a wet season from October to February and a less-rainy and cold season, called hereafter as dry season, from March to September. The study grid was located in a region known as "Sede", covered with old secondary growth vegetation, at approximately 850 m of altitude.

METHODS

Data collection

We set 80 Sherman traps (XLF15, 10.5 x 12 x 37.6 cm) monthly in five 140 m parallel transects. Transects were 50 m apart from each other, and had eight trapping stations that were separated by 20 m. We placed two traps at each trapping point, one on the ground and the other on tree branches or vines at breast height (ca. 1.5 m). We baited all traps with a mixture of banana, peanut butter, oatmeal, and bacon. Traps were checked daily during five consecutive days, and baits were replaced when necessary. We marked the animals with individually numbered ear-tags, and recorded the following data from them: sex, weight, reproductive condition and age, which was estimated based on teeth eruption pattern (cf. Tribe 1990). Females were considered reproductive if they had swollen nipples or were carrying young. Once the male's testes become scrotal when they reach sexual maturiy and stay in this position permanently (Quental *et al*. 2001), we could classify the males as potentially reproductive when they had scrotal testes and were captured during the reproductive period.

After recording the data mentioned above, we equipped some individuals with a spool-and-line device based on Boonstra & Craine (1996). Quilting cocoons of nylon thread weighing approximately 1.7 g (175 m of thread) were used. Following Cunha & Vieira (2002) procedure, we covered the cocoons with PVC plastic film and wrapped them with masked-tape to form the spool. The spool was attached between the shoulders of the animals with Superbonder®, an ester-cyanocrylate based glue. After attaching the spool, we released the animal in the station it was trapped, and tied the free end of the line in the vegetation close to the trap. We always tracked individuals on the following day, to allow a full night of activity. During animal tracking, we mapped the points of trajectory change along the thread released, and measured the distance and the azimuth to the next point. We transformed these measures into Cartesian coordinates (x,y), in order to map individual paths and to calculate their daily home range based on the area of the minimum convex polygon that encompassed all points of the trajectory. We used the program CALHOME (Kie *et al*. 1996) for calculations. To avoid pseudo-replication (*sensu* Hurlbert 1984), each individual was tracked only one time per season.

We measured arthropod abundance using 40 pitfall traps, consisting of plastic recipients (20 cm^3), containing 70% ethanol. We placed each pitfall trap in a trapping station, and removed them after three days of exposure. Trapped arthropods were identified at the level of order. Then, we counted the arthropods and used the sum of all orders, excluding those that were not consumed by *M. paulensis*, as an index of availability of this category.

We estimated fruit availability in 20 transects of 30 x 1.5 m, located inside the capture grid. In each transect we recorded monthly the number of fruits produced and the proportion of individuals bearing fruits of species belonging to four families: Piperaceae, Solanaceae, Melastomataceae, and Rubiaceae. We chose those families because earlier studies on Neotropical marsupial species recorded their seeds in the diet of these mammals (Cáceres 2002, Pellegatti-Franco & Gnaspini 1996, Pinheiro *et al*. 2002), and because those plants presented trees lower than 5 m. We excluded trees higher than 5 m assuming that *M. paulensis* would consume their fruits only if they occasionally fell on the ground, once *M. paulensis* has semi-terrestrial habits (Leiner & Silva, unpublished data). We used the total number of fruits produced in each month as the measure of total fruit availability and the proportion of *Piper* individuals producing fruits as a measure of *Piper* availability, since the removal rate of *Piper* fruits is usually very high (Fleming 1981).

Data Analysis

To evaluate the influence of body weight on daily home range size of *M. paulensis* we ran a simple linear regression, using body size as the independent variable and daily home range size as the dependent one. We ran a *t* test to check for differences between the daily home range sizes of males and females and a Mann-Whitney *U* test to analyze differences in home range sizes between seasons. We performed a multiple linear regression to evaluate the effect of fruit and arthropod availabilities on the variation of daily home range size of *M. paulensis.* For this, the fruit and arthropod availabilities were used as independent variables, and daily home range size as the dependent variable. Based on the assumption that movements of males are determined by females, rather than by the availability of food, we used only data from females and males captured out of the reproductive season. In order to evaluate the role of *Piper* fruits on the variation in home range size we used a simple linear regression. To perform this analysis we arcsine transformed the proportion of individuals of *Piper* producing fruits on each month. All analyses were done using the software Statistica 6.0.

RESULTS

We analyzed nineteen tracks (12 females and 7 males) mapped from August 2002 to July 2004. We recovered 115.4 m (SD= 41.4) of thread for males and 127.1 (SD= 41.0) of thread for females during the dry season. During the wet season, we recovered 125.3 m (SD= 45.7) of thread for females and 161 m of thread for a single male tracked in this period. Individual daily home range size based on the spool and line device ranged from 0.17 to 0.75 ha (n= 19), with a mean value of 0.38 ha (SD= 0.18). Daily home range size was not determined by the amount of thread tracked (Figure 3.1) (R^2= -0.01; p= 0.37; n= 20) or by body weight of *M. paulensis* (Figure 3.2) (R^2= -0.04; p= 0.61; n= 22). There was no significant difference (t= 0.91; DF= 17; p= 0.37) between daily home range size of males ($\overline{X}$= 0.43 ± 0.12, n=7) and females ($\overline{X}$= 0.35 ± 0.23, n= 12). However, daily home range size of males varied within a narrow range (from 0.30 to 0.63) when compared to daily home range size of females (from 0.17 to 0.75).

Individuals of *M. paulensis* presented larger daily home ranges during the dry season ($\overline{X}$=0.47 ± 0.15 ha), and smaller ones during the wet season ($\overline{X}$=0.19 ± 0.05 ha)

(Mann-Whitney U test: U= 3.37; p= 0.0005; n_{dry}=12 and n_{wet}=7). Moreover, daily home range size was determined by food supply, since an increase in resource abundance led to a reduction on the space used by *M. paulensis* (R^2= 0.62; n= 12; p= 0.005). However, only fruit abundance (Figure 3.3) (b= -0.83; p= 0.001) had a significant effect on daily home range size of *M. paulensis*, while arthropod abundance was not related to daily home range size variation (Figure 3.4) (b= -0.20; p= 0.54). Finally, the abundance of fruits from the genus *Piper* was also strongly related to daily home range size of *M. paulensis* (Figure 3.5) (R^2= 0.44; n= 16; p= 0.003). During the period of higher availability of *Piper* fruits, daily home range size of *M. paulensis* was reduced, corroborating the inverse relationship between food supply and the space used by *M. paulensis*.

DISCUSSION

Our study is the first to present data on the use of space by *Marmosops paulensis*. The results presented here differ from those obtained for other species of mouse opossums. Pires & Fernandez (1999) found home range sizes ranging from 0.10 to 2.45 ha for *Micoureus demerarae*, while Martins (2004) found mean values of 0.09 ha for *Gracilinanus microtarsus*. Part of those differences could be due to methodological differences in home range estimates and grid sizes among studies. Indeed, the larger estimates recorded *for M. demearae* when compared to *M. paulensis* could be explained by the fact that in our study we presented a measure of daily home range size. Furthermore, the differences in body weight among the three species could also play a role. Large opossums, such as *Caluromys philander* (Julien-Laferrière 1995) and *Didelphis aurita* (Cáceres &

Monteiro-Filho 2001), had even larger home range sizes than *M. paulensis* and the other mouse opossums studied so far (Table 3.1). Although interspecific differences in home range size of opossums seem to be explained by body weight variation, the intraspecific variation in home range size of *M. paulensis* was not related to body weight in the present study. Martins (2004) also did not found this relationship in *Gracilinanus microtarsus*. In fact, the narrow body weight range within *M. paulensis* and *G. microtarsus* seems to preclude the occurrence of this relationship.

A common pattern among didelphids is that sexually dimorphic species usually present significant differences on home range size between the sexes (e.g., Cáceres & Monteiro-Filho 2001, Martins 2004, Sunquist *et al.* 1987). This pattern could be due to the relationship between home range size and body size (McNab 1963, Fonseca & Kierulff 1989), or due to the fact that use of space is determined by different factors in males and females (Clutton-Brock 1989, Ostfeld 1990). Nevertheless, in our study daily home range size of males and females was not different. This lack of difference might be due to the fact that we captured and tracked only one potentially reproductive male. Once males tend to expand their home range during the reproductive period, as a way to find more mates, we may have missed the variability in male home range size. Gaulin & Fitzgerald (1988) demonstrated that non-reproductive meadow voles do not present home range expansion. They suggested that this occurred because males cannot profit by exposure to additional females during the non-reproductive period, and so should avoid energetic risk factors associated to high mobility.

Home range size of *M. paulensis* had larger values during the dry season when compared to the values found during the wet season. Previous studies with *Micoureus demerarae* (Pires & Fernandez 1999) and *Caluromys philander* (Julien-Laferrière 1995) found the same yearly pattern of variation on home range size that we found in *M. paulensis*. Seasonal fluctuations in resource availability seem to be responsible for this pattern, however other factors can also play a role. Pires & Fernandez (1999) argued that population density was the factor responsible for the temporal variability on home range size of *Micoureus demerarae*, evocating the inverse relationship between density and home range size already documented for mammals (Abramsky & Tracy 1980). However, this relationship does not apply to *M. paulensis*, because the reduction in daily home range size occured when the population density was reduced (Leiner, unpublished data). As argued for *Caluromys philander* (Julien-Laferrière 1995), the reproductive condition of females could contribute to a decrease in home range size. It is possible that females *M. paulensis* restricted their movements during the wet season due to the presence of young at the nest. Furthermore, the age of the individuals could also influence the variations in daily home range size of *M. paulensis*. During the dry season, all the captured individuals of *M. paulensis* belonged to the juvenile and subadult age classes (Leiner *et al.* in preparation). These individuals could present larger daily home range sizes if they were establishing new areas or if they were being forced into suboptimal habitats, as was discussed by Harestad & Bunnell (1979). Future studies are needed to disentangle the role of each factor and understand the interactions among them.

Our observation that the reduction in home range size was explained by high resource availability supports the inverse relationship between daily home range size and food supply. Several other studies have already documented this relationship among eutherian mammals (Mares *et al.* 1982, McLoughlin *et al.* 2000). Fisher & Owens (2000) also found the same pattern in marsupials from the Macropodidae family (e.g. kangaroos). However, unlike the pattern in eutherians, climate was more strongly associated to home range size than was body weight (Fisher & Owens 2000). An interesting point of our data is that only fruit abundance was significantly related to the variation of home range size in *M. paulensis*, whereas arthropod abundance was not. When the reduction of home range size occurred, *Piper* fruits were one of the most consumed items in *M. paulensis* diet (Leiner & Silva, in preparation), and we found a strong negative relationship between availability of *Piper* fruits and daily home range of this marsupial. In this way, we suggest that *M. paulensis* may be searching actively for *Piper* fruits during their foraging bouts, in a way that *Piper* fruits play a key role on the patterns of use of space by *M. paulensis*.

Fruits, especially from the *Piper* genera (Fleming 1981), present a high spatio-temporal predictability when compared to arthropods, which show a more scattered distribution. We suggest that this different predictability of fruits and arthropods can be the reason why the home range size of *M. paulensis* was solely determined by *Piper* fruits. Earlier studies have already argued that food abundance and distribution are important factors influencing use of space by mammals, such as didelphid marsupials (Charles-Dominique 1983, Sunquist *et al.* 1987), and that more predictable food items lead to smaller home range sizes (Lurz *et al.* 2000). This relationship is clearly determined by the energetic requirements of each species, since by using this strategy animals can combine enough resource acquisition to obtain their energetic needs and economy of foraging costs.

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FIGURES

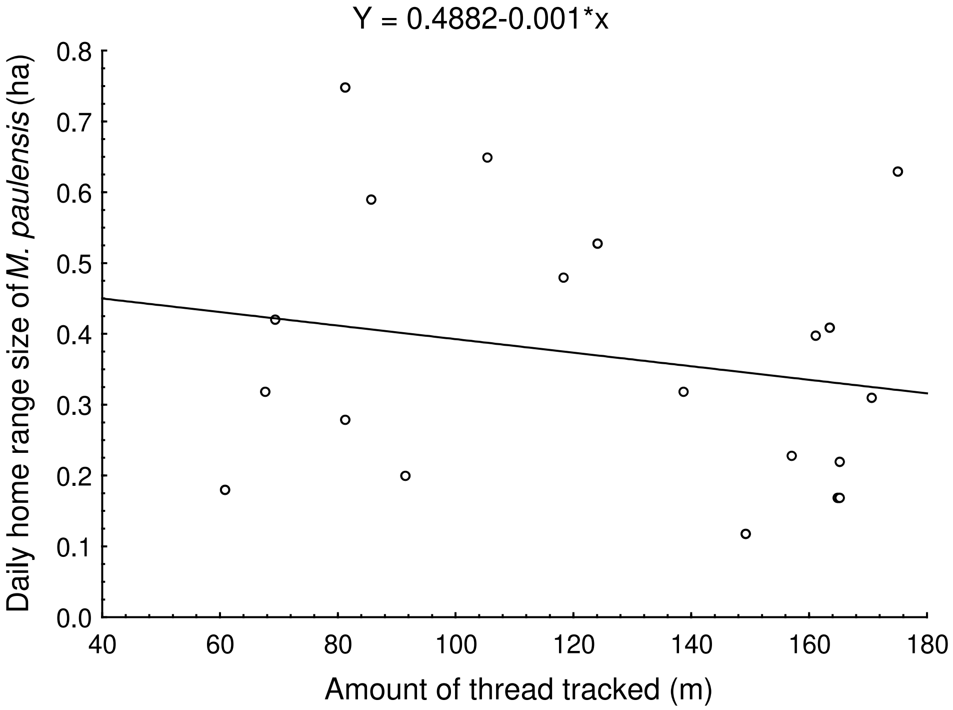

Figure 3.1: Relationship between the amount of thread tracked (m) and daily home range size (ha) of *M. paulensis*.

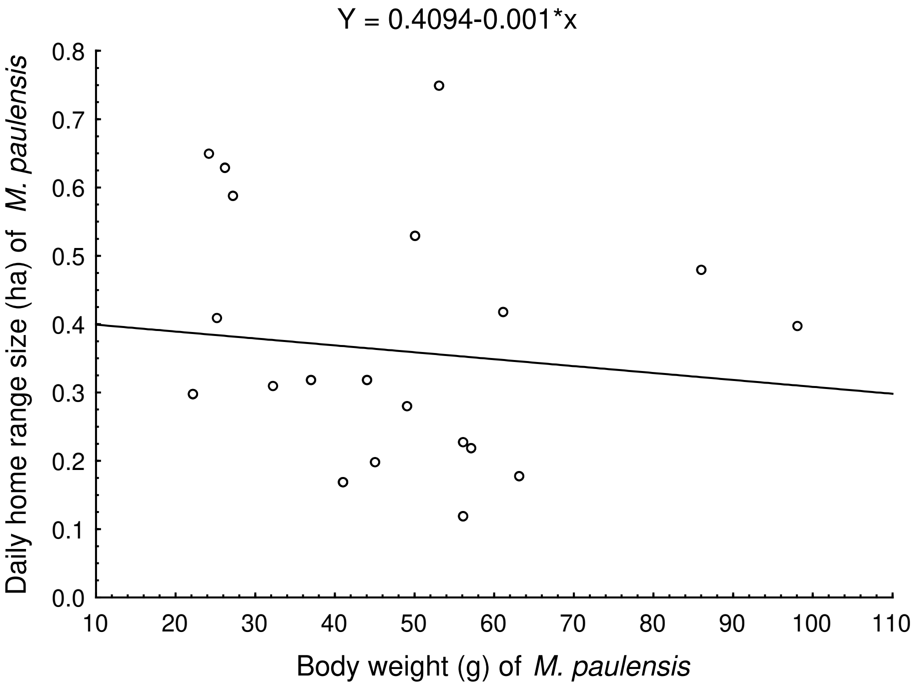

Figure 3.2: Simple linear regression between body weight (g) and daily home range size (ha) of *Marmosops paulensis*. Black dots: males and white dots: females.

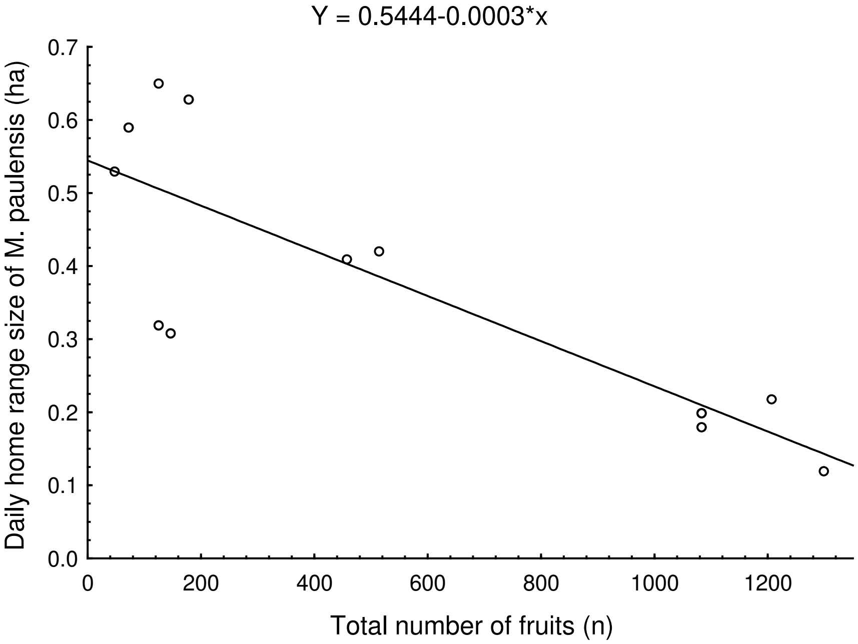

Figure 3.3: Relationship between total fruit availability (N) and daily home range size (ha) of *Marmosops paulensis*.

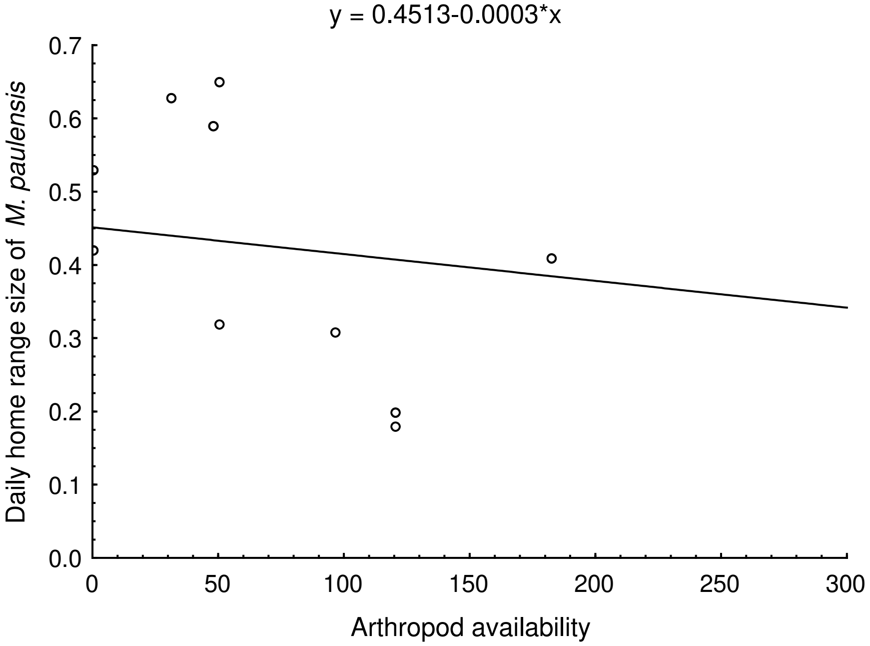

Figure 3.4: Relationship between arthropod availability and daily home range size (ha) of *M. paulensis*.

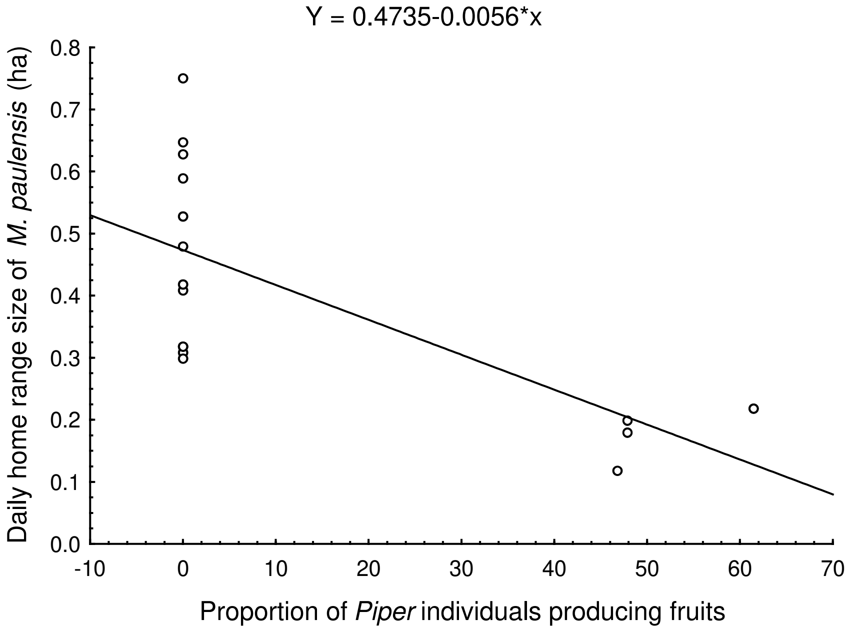

Figure 3.5: Relationship between *Piper* availability (%) and daily home range size (ha) of *Marmosops paulensis*.

Table 3.1: Body weight (g) (see Emmons & Feer 1997, Eisenberg & Redford 1999) and home range estimates in didelphid marsupials.

Species	Body weight	Mean home range size (ha)	Variation (ha)
Marmosops paulensis [1A]	20-70	0.38 (SD= 0.18)	0.17 to 0.75
Gracilinanus microtarsus [2B]	19-40g	0.08 (SD= 0.08)	0.005 to 0.24
Micoureus demerarae [3B]	80-152 g	0.59 (SD= 0.51)	0.10 to 2.45
Caluromys philander [4C]	140-270 g	1.1 (SD= 0.3)	1.3 to 8.9
Didelphis aurita [5B]	565-1610 g	-	0.2 to 3
Didelphis marsupialis [6C]	565- 2450 g	40 (SD= 56.5)	5.3 to 165

1: present study; 2: Martins 2004; 3: Pires & Fernandez 1999; 4: Julien-Laferrière 1995; 5: Cáceres 2002, and 6: Sunquist *et al*. 1987. A: Spool and line device; B: Captures, and C: Radiotracking.

CAPÍTULO 3

Semelparity and the role of photoperiod on the reproduction of the mouse opossum *Marmosops paulensis* (Didelphimorphia: Didelphidae) in a Montane Atlantic forest area

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Key words: resource availability , reproductive timing, onset of reproduction, seasonality, population ecology.

Running title: Reproductive patterns of *Marmosops paulensis*.

ABSTRACT

Data on the reproductive patterns of *Marmosops paulensis* (Tate, 1931) were collected in an area of Montane Atlantic Forest, southeastern Brazil. Reproduction was highly synchronized, occurring from September to March on both studied years. A combination of factors seemed to trigger the breeding season of *M. paulensis*, such as a prolonged dry period, increasing day length, and an increase in fruit availability. After the reproductive period, adult mortality was very high. Thus, no individual took part in more than one breeding event. This strategy characterizes a semelparous life-history, which was already described in other small didelphids and dasyurids. Seasonality of food resources, which can determine the survival of juveniles, might play an important role on the existence of semelparity in this species. Moreover, we suggest that an increase in day length is the key-factor controlling the onset of reproduction of *M. paulensis.*

INTRODUCTION

In most mammals, reproduction is usually associated to favorable periods of the year, in order to maximize reproductive success (Flowerdew 1987). In this way, many mammals reproduce opportunistically, such as cricetid rodents that reproduce whenever rainfall reaches a threshold in the Brazilian Caatinga (Cerqueira & Lara 1991). Other mammals show seasonally marked reproductive periods, such as marsupials, which generally start to reproduce when environmental conditions are still unfavorable (Bronson 1989). In this case, both endogenous and exogenous factors are responsible for the onset and duration of reproduction (Bronson 1989). The presence of males can act as trigger leading females to oestrous due to pheromonal cues (Fadem 1985), assuring synchronization of reproduction (Perret & Ben M'Barek 1991, Scott 1986). Among exogenous factors, reliable cues such as photoperiod and rainfall seems to play a role on reproduction regulation (Renfree 1981), whereas the availability of resources can work determining the amount of energy invested in reproduction, hence, the duration of the reproductive period (Julien-Laferrière & Atramentowicz 1990).

There are several studies describing the reproductive patterns of Australian marsupials, including carnivorous dasyurids, which are considered distantly related to the Neotropical didelphid species (Cockburn 1997). Among dasyurids, mating occurs during a highly synchronized and short breeding season (Bradley 1997, Lee & Cockburn 1985, Oakwood *et al.* 20001), which is triggered by photoperiodic cues, such as the rate of change of photoperiod per day and critical day length (Renfree 1981, McAllan & Dickman 1986). Moreover, males die after mating due to stress-related pathologies (Bradley *et al.* 1980, Oakwood *et al.* 2001), whereas females survive to breed a second time, with each generation separated in age by one year. Although females can breed a second time, they are subject to exaggerated senescence (see revision in Cockburn 1997). These events characterize a semelparous reproductive strategy.

Reproductive patterns of the Neotropical marsupials, including the didelphids, are poorly understood. Numerous studies suggest that rainfall should play a role on the onset of didelphid reproduction (Charles-Dominique 1983, Fleming 1973, Julien-Laferrière & Atramentowicz 1990), leading to a pattern in which lactation and/or weaning periods are usually correlated to periods of high fruit and insect abundance. Bergallo & Cerqueira (1994), on the other hand, demonstrated that photoperiod and not rainfall control the reproductive activity of *Monodelphis domestica*, similarly to Australian marsupials. Moreover, similar to some dasyurids species, *Marmosops incanus*, *Gracilinanus* *microtarsus* and *Monodelphis dimidiata* present a higher male mortality after the reproductive period (Lorini *al.* 1994, Martins 2004, Pine *et al.* 1985). Notwithstanding, females that breed a second time also have a decline in fecundity, resembling dasyurids. In this way, the presence of a semelparous reproductive strategy seems to be also common in didelphids, especially among smaller species.

São Paulo's slender mouse opossum, *Marmosops paulensis* (Tate, 1931), is a small (20-70g), nocturnal marsupial occurring in the southeastern part of the Brazilian Atlantic forest, restricted to montane forests above 800 m (Mustrangi & Patton 1997). Insects and fruits, especially from the genus *Piper*, are the major food items of this species (Leiner & Silva, in preparation). There are no data on the reproductive patterns of *M. paulensis*, but Lorini *et al*. (1994) presented data on the reproduction of *Marmosops incanus*, a closely related species that has previously been mistaken with *M. paulensis*. These authors suggested that the reproductive activity of *M. incanus* occurs between October and December and that each individual participate in only one reproductive season, characterizing a semelparous life-history. Moreover, since data used in the mentioned study came from museum specimens collected over five Brazilian states, semelparity seems to be a rather widespread phenomenon in *M. incanus*. The objectives of the present study were to describe the reproductive patterns of *M. paulensis,* and to analyze factors involved in the onset of its reproductive activity.

STUDY SITE

This study took place in Parque Estadual Intervales (24°16'S, 48°25'W), an Atlantic Forest area situated in the southeast region of São Paulo state, in the municipality of

Ribeirão Grande, Brazil. The park has approximately 49000 ha and it is connected to three other conservation units, totaling 120000 ha of protected Atlantic forest. Annual rainfall ranges from 1600 to 1800 mm and mean annual temperature is about 22°C, with a wet season from October to February and a less-rainy and cold season, called hereafter as dry season, from March to September (Figure 2.1). The study grid was located in a region known as "Sede", covered with old secondary growth vegetation, at approximately 850 m of altitude.

METHODS

Data collection

We set 80 Sherman traps (XLF15, 10.5 x 12 x 37.6 cm) monthly in five 140 m parallel transects. Transects were 50 m apart from each other, and had eight trapping stations that were separated by 20 m. We placed two traps at each trapping point, one on the ground and the other on tree branches or vines at breast height (ca. 1.5 m). We baited all traps with a mixture of banana, peanut butter, oatmeal, and bacon. Traps were checked daily during five consecutive days, and baits were replaced when necessary. We marked the animals with individually numbered ear-tags, and recorded the following data from them: sex, weight, reproductive condition and age class, which was estimated based on teeth eruption pattern (cf. Tribe 1990).

Females were considered reproductive if they had swollen nipples or if they were carrying young. Nipples were checked for the presence of milk, since we assumed that swollen nipples without milk belonged to females that had already weaned their young, and are not receptive to further mates. Males were not used in the analysis of reproductive activity, once the male's testes become scrotal when they reach sexual maturity, and stay in this position permanently (Quental *et al.* 2001).

We gathered precipitation and temperature data at the park's meteorological station, approximately 1 km from the study area, and photoperiod data at the Brazilian's National Observatory homepage. We measured arthropod abundance using 40 pitfall traps, consisting of plastic recipients (20 cm^3) filled with 70% ethanol and detergent. We placed each pitfall trap in a trapping station, and removed them after three days of exposure. Trapped arthropods were identified at the level of order. Then, we counted the arthropods and used the sum of all orders, excluding those that were not consumed by *M. paulensis*, as an index of availability of this category.

We estimated fruit availability in 20 transects of 30 x 1.5 m, located inside the capture grid. In each transect we recorded monthly the number of fruits produced and the proportion of individuals bearing fruits of species belonging to four families: Piperaceae, Solanaceae, Melastomataceae, and Rubiaceae. We chose those families because earlier studies on Neotropical marsupial species recorded their seeds in the diet of these mammals (Cáceres 2002, Pellegatti-Franco & Gnaspini 1996, Pinheiro *et al.* 2002), and because those plants presented trees lower than 5 m. We excluded trees higher than 5 m assuming that *M. paulensis* would consume their fruits only if they occasionally fell on the ground, once *M. paulensis* has semi-terrestrial habits (Leiner & Silva, unpublished data). We used the total number of fruits produced in each month as the a measure of total fruit availability.

Data Analysis

To evaluate the influence of abiotic factors on the onset of *M. paulensis* reproduction we performed four logistic regressions. The dependent variable used in all the regressions was the reproductive activity of *M. paulensis* females, codified as reproductive (1) or not reproductive (0). Then, we used the following factors as independent variables in each logistic regression: monthly average rainfall, monthly average day length expressed in minutes, abundance of arthropods and abundance of fruits. All analyses were done using the software STATISTICA 6.0.

RESULTS

We captured 42 individuals of *Marmosops paulensis*, 22 females and 20 males, during more than 10,000 trap-nights. On both years, females presenting swollen nipples were first captured in mid October, which is probably the beginning of the lactation period. Once gestation in marsupials lasts approximately 15 to 30 days (Lee & Cockburn 1985), mating seems to occur on early September, followed by pregnancy. Female reproductive activity lasts until March, and during this period all trapped females presented swollen nipples, indicating a high synchrony among females in the population (Figure 4.1). However, on March females were no longer producing milk, indicating that at this time they already weaned their young. In fact, the first juveniles were trapped in March, and at this month we found (by using the spool and line device) a female’s nest, which had four young. This behavior of leaving the young in a nest seems to be common in *M. paulensis*, since we never captured a single female carrying her young. Moreover, the number of nipples indicates that litter size is approximately nine, with a maximum of 11 and a minimum of seven (personal observation).

The beginning of the reproductive season coincided with an increase in day length (Figure 4.2A) and with the end of the dry season (Figure 4.2B). Moreover, an increase in food supply, both of fruits and arthropods, was also observed when *M. paulensis* began its reproductive activity (Figures 4.3A and 4.3B). Therefore, all analyzed factors, except arthropod availability, influenced significantly the onset of reproduction in *M. paulensis* (Figures 4.4-4.7). Although day length presented a small annual variation (677 to 816 minutes), it presented the better adjustment with *M. paulensis* reproduction, followed by fruit production.

All males disappeared from the population after January in the first year, while in the second year the same phenomenon occurred after December (Figure 4.8). Thus, no adult males were trapped from January to July despite the effort of 2,400 trap-nights per year during this period. The only males present during these months were juveniles followed by sub-adults. This disappearance of males could be caused by dispersion to another area, although the lack of immigration of foreign adult males argues against this hypothesis. Hence, this result points out to a high male mortality following the breeding season, in a way that each male can take part in only one reproductive event. Females did not exhibit the striking mortality pattern present in males. However, on both years, all females captured after April were juveniles. Appearance of adults from both sexes occurred only in August, near the beginning of the reproductive season. In this way, individuals of both sexes reproduce once in a lifetime, and each generation is discrete and separated in age by approximately one year.

DISCUSSION

The reproductive activity of *Marmosops paulensis* was markedly seasonal, occurring from September to March on both years. Several studies found seasonal patterns of reproductive activity in didelphids (Fleming 1973, Julien-Laferrière & Atramentowicz 1990, Lorini *et al.* 1994, Martins 2004, Quental *et al.* 2001). Moreover, although the beginning of the reproductive period of *M. paulensis* occurred in the end of the dry season, most lactant females were present during periods of high food abundance, which corresponded to the rainy season at our study site. By adjusting lactation to food abundance periods, females of *M. paulensis* can maintain their investment in reproduction (e.g., milk production), and increase survival probabilities of the young. In this way, Cothran *et al.* (1985) suggested that larger females of *Monodelphis domestica* produced and weaned larger litters and heavier neonates, which was translated into a higher reproductive success, when compared to smaller females with a poorer body condition. Data on other didelphids also found a correspondence between lactation and high food supply (Fleming 1973, Julien-Laferrière & Atramentowicz 1990, Lorini *et al.* 1994, Martins 2004, Quental *et al.* 2001).

The use of seasonal predictors to trigger reproductive activity is widely known among marsupials (Bronson 1989). *Marmosops paulensis* seems to use rainfall, day length and fruit availability as cues to the onset of its reproduction. Regarding rainfall, Julien-Lafferière & Atramentowicz (1990) stated that a more or less long dry period is needed for opossums to initiate reproduction, while a decrease in rainfall ceases their reproductive activity. This statement is corroborated by results of several studies (Fleming 1973, O'Connell 1979, Tyndale-Biscoe & Mackenzie 1976), including ours, and also reinforces the notion that most part of the reproductive period is coincident with the rainy season. Considering photoperiod, there seems to be a critical day length or a critical rate of change of photoperiod that determines the beginning of the reproductive season, as was early described in *Antechinus* marsupials (McAllan & Dickman 1986).

In the population studied, each *M. paulensis* individual participated in a single reproductive event, thus presenting semelparity. Semelparity was first defined by Cole (1954) as “multiplying once in a lifetime”, while Braithwaite & Lee (1979) have used this word to describe the situation where males participate in one breeding season and females are iteroparous. Although semelparity is unusual among eutherian mammals, it evolved at least six different times among members of the families Dasyuridae and Didelphidae (Cockburn 1997). Among the dasyurids, males die just after the mating season, while some females are able to survive for a second breeding season (Braithwaite & Lee 1979). On the other hand, there is a high adult mortality after the reproductive period among didelphids, with males surviving longer than in dasyurids and only some females breeding a second time (Pine *et al*. 1985; Lorini *et al*. 1994). Interestingly, besides the post-reproductive mortality of males, females show a strong senescence on both groups. Cockburn (1997) argued that there might be a phylogenetic predisposition in the species belonging to both clades (Dasyuridae and Didelphidae) towards post-reproductive senescence, leading to male die-off in one extreme. Martins (2004), in a study with a population of *Gracilinanus microtarsus*, found that although the mortality was high after the reproductive period, few males and females were able to survive until the next breeding season, characterizing functional semelparity, a concept conceived for insects by Tallamy & Brown (1999). In our study, adults of both sexes did not survive to reproduce a second time on both years, although females could have occasionally reached another breeding event, since the gap between generations was shorter, as Lorini *et a*l. (1994) supposed for *M. incanus*.

Usually, semelparity occurs in species coping with major fluctuations in adult or juvenile survival (Promislow & Harvey 1990). In this way, assuming that juvenile survival is consistently higher during one season of the year, selection should result in an intense, synchronized reproductive period during this season (Braithwaite & Lee 1979). Intuitively, this high reproductive effort of males and females should lead to a decrease in longevity. Data on Australian marsupials, especially *Antechinus*, found a link between semelparous life-history and predictable seasonal environments. Moreover, Mills & Bencini (2001) and Wolfe *et al.* (2004) found that semelparity can be facultative, depending on environmental characteristics, in a way that different populations of *Parantechinus apicalis* presented semelparity when coping with variations in food supply, and presented iteroparity when coping with a more constant food supply. Notwithstanding, a single population of *M. incanus* inhabiting an area of low latitude and a high level of rainfall also presented iteroparity (Lorini *et al*. 1994).

At Parque Estadual Intervales, *Marmosops paulensis* faced seasonal variations in food supply, and its reproductive activity was restricted to the period of higher food abundance, when juvenile survival could be enhanced. Due to the small size of *M. paulensis*, the period between conception and weaning is prolonged, reducing the probability of raising a second litter in the same season. These patterns argue in favor of the role of seasonality on semelparity. However, none of the semelparous didelphids found to date, including *M. paulensis*, inhabits predictable, strongly seasonal environments as those inhabited by the Australian semelparous species (Braithwaite & Lee 1979, Dickman & Braithwaite 1992, Oakwood *et al*. 2001). *Marmosops paulensis* and *M. incanus* are found in the Atlantic forest, known by high levels of rainfall and relatively constant temperature, although at Parque Estadual Intervales temperatures are highly variable. Comparisons among populations of *M. paulensis* living in contrasting environments regarding resource availability, and experiments using additional food supply should help to elucidate the role of seasonality in the existence of semelparity in this species, and in other didelphids.

Moreover, future studies should take the phylogeny of the marsupials into account, since the evolution of semelparity could be due to phylogenetic constraints, while seasonality of resource act as a selective force maintaining this trait.

Fruits can be an important food resource for the reproduction of marsupials (Julien-Laferrière & Atramentowicz 1990). These authors demonstrated that *Didelphis marsupialis* and *Philander opossum* interrupted reproduction when coping with fruit scarcity. Based on Astúa de Moraes *et al*. (2003) results, which showed that mouse opossums are more frugivorous than the two species mentioned above, it is reasonable to expect a tight relationship between reproduction and fruit production in *M. paulensis*. Hence, it may be possible that the seasonality in fruit production plays a role on the existence of the semelparous strategy found in *M. paulensis*.

As already mentioned, the reproduction of *M. paulensis* was highly synchronized, and individuals presumably experienced strongly selection to produce young when food was abundant. In this way, it is reasonable to expect that a high predictable cue controlled *M. paulensis* reproduction, especially because both sexes invested all their energy in a single reproductive event. Although annual variations in day length were small, they were highly predictable. Nevertheless, rainfall presented a less predictable annual variation; while food supply varied accordingly to rainfall patterns. Hence, we suggest that photoperiod was the key-factor acting on the onset of the reproduction of *M. paulensis*. A similar trend was previously suggested for *Antechinus stuartii* (Scott 1986), and it is possible that the same pattern extends to all species presenting semelparity. Future studies in the laboratory manipulating the factors involved in the onset of reproduction would be helpful to understand the role of each factor and interactions among them.

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FIGURES

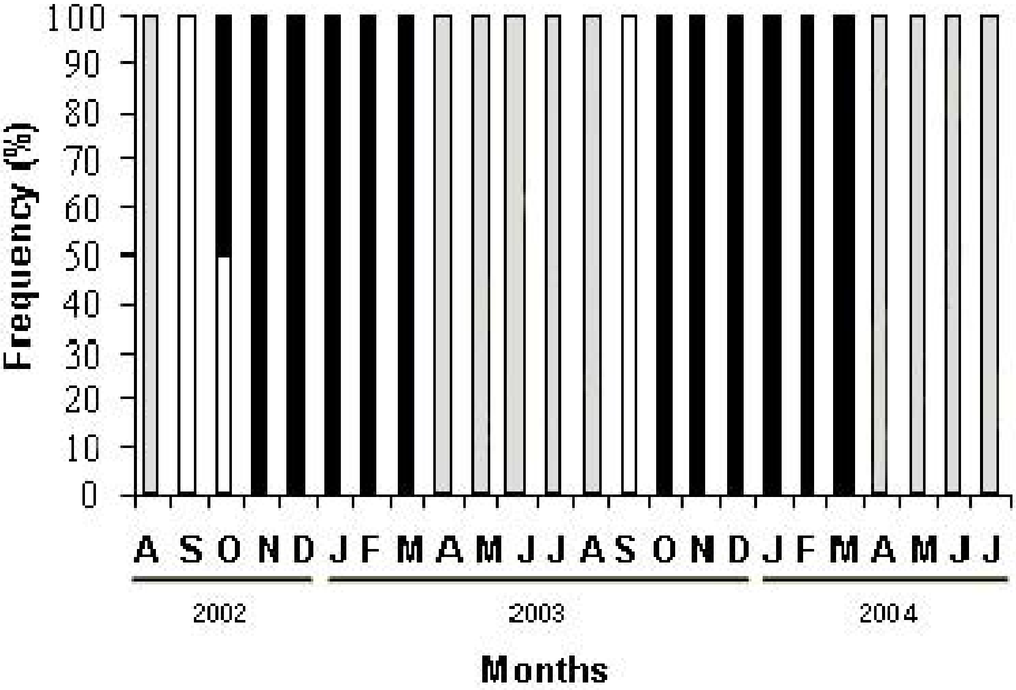

Figure 4.1: Reproductive patterns of *M. paulensis* females at Parque Estadual Intervales. Black bars: lactant females; white bars: pregnant females and gray bars: non-reproductive females.

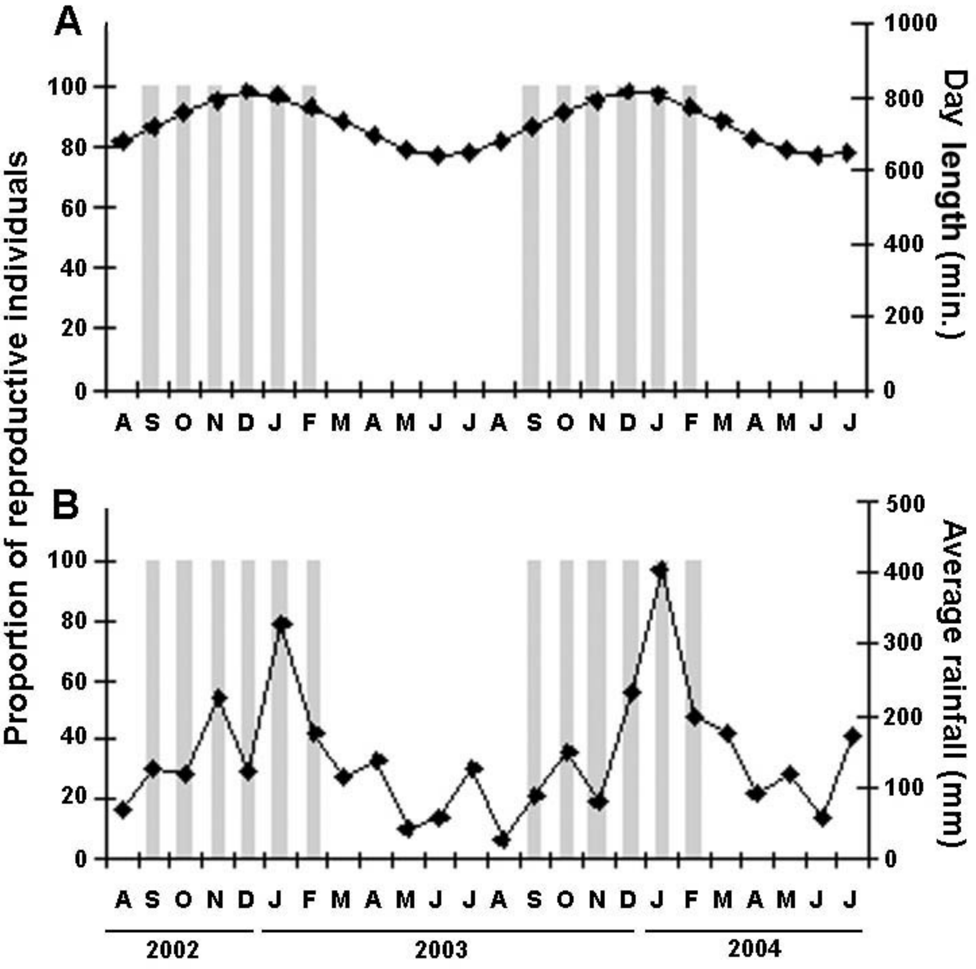

Figure 4.2: Relationship between reproductive activity of *Marmosops paulensis* and climatic factors.

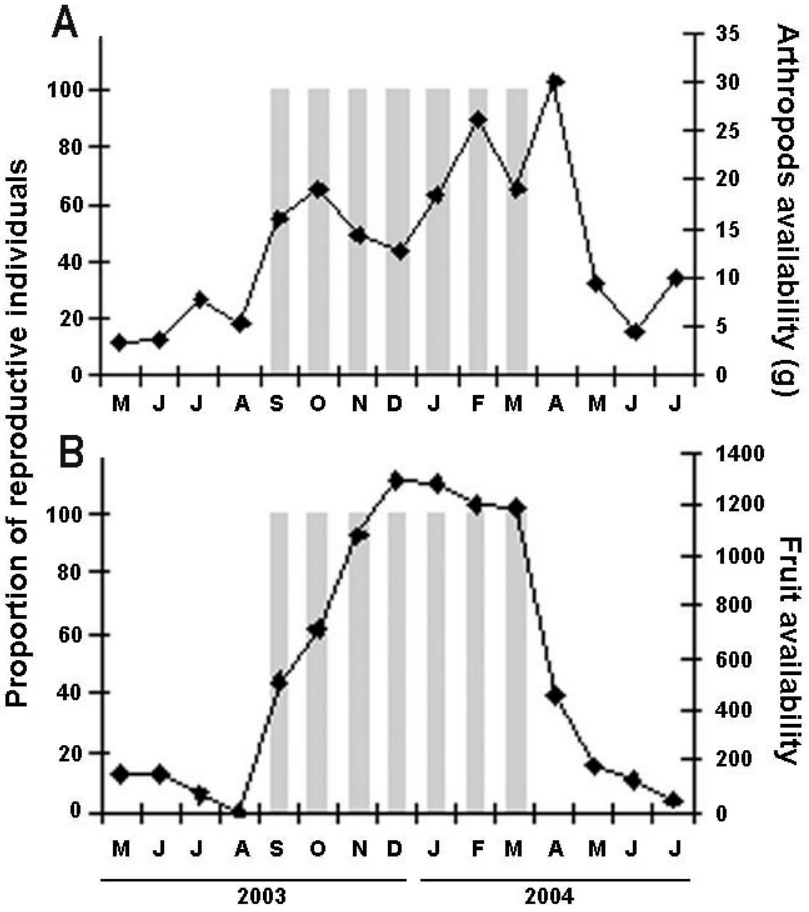

Figure 4.3: Relationship between reproductive activity of *Marmosops paulensis* and resource availability.

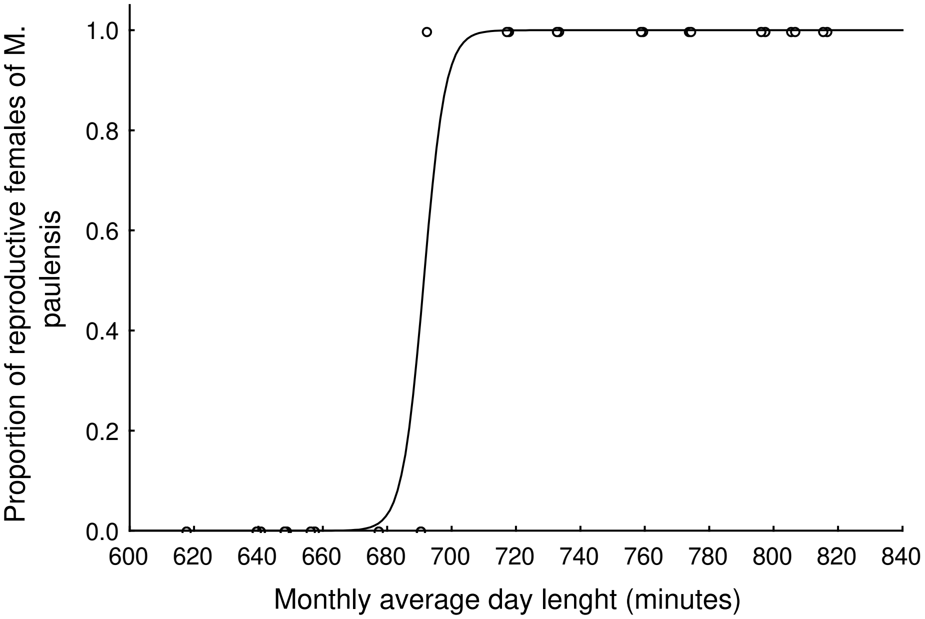

Figure 4.4: Logistic regression between monthly average day length (minutes) and reproductive activity of *Marmosops paulensis* (χ^2 =29.54; p=0.0000001). y=exp(-206.74+(.299032)*x)/(1+exp(-206.74+(.299032)*x)).

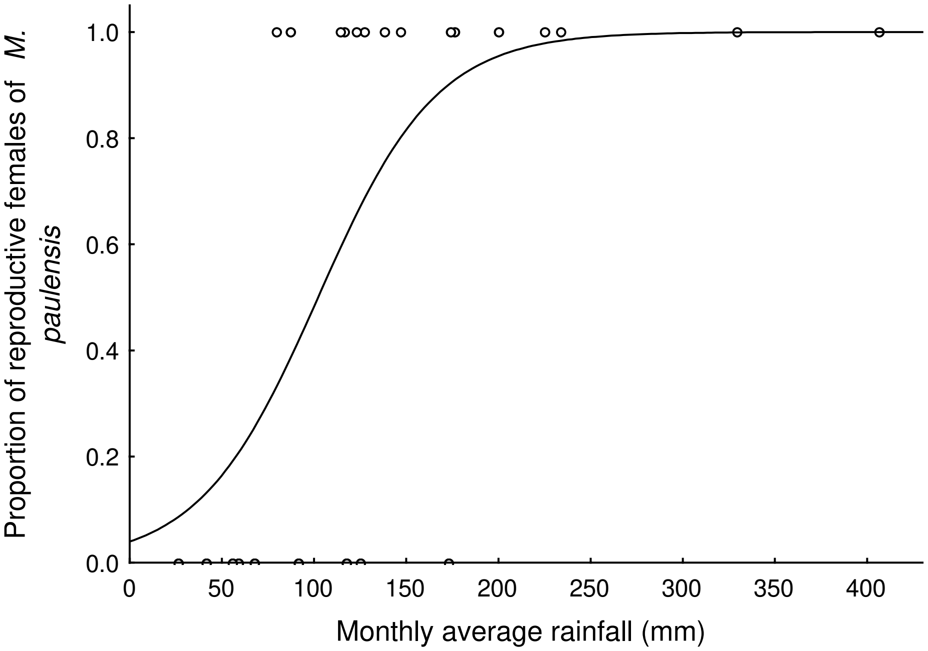

Figure 4.5: Logistic regression between monthly average rainfall (mm) and reproductive activity of *M. paulensis* ($\chi^2 = 10.68$; p=0.01).

y=exp(-3.1792+(.031119)*x)/(1+exp(-3.1792+(.031119)*x)).

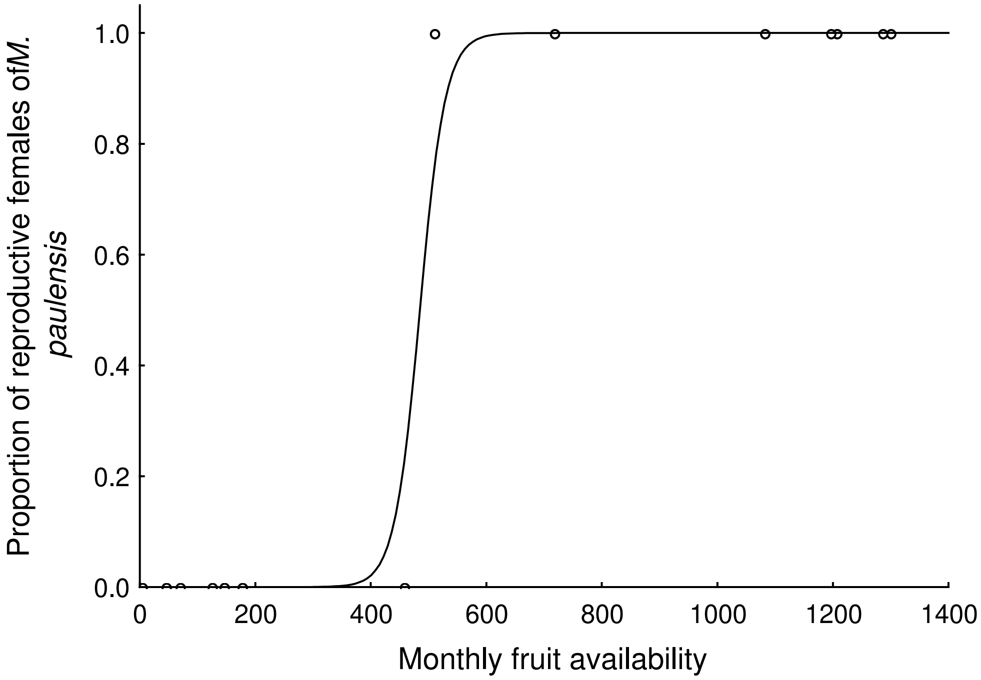

Figure 4.6: Logistic regression between monthly fruit availability and reproductive activity of *M. paulensis* (χ^2 =19.71; p=0.000009).

y=exp(-21.942+(.045241)*x)/(1+exp(-21.942+(.045241)*x)).

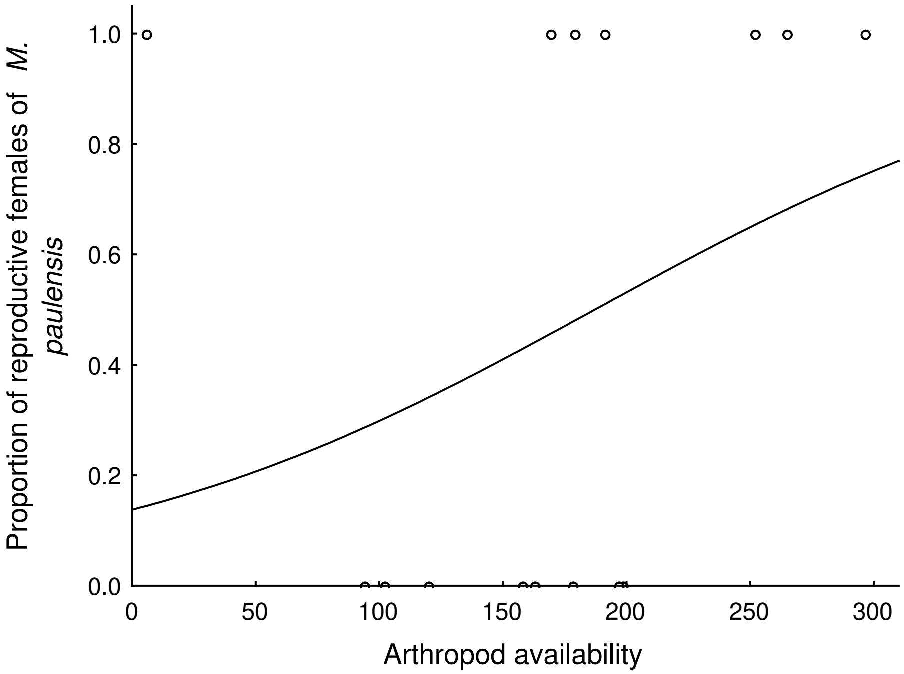

Figure 4.7: Logistic regression between monthly arthropod availability and reproductive activity of *M. paulensis* ($\chi^2 = 1.47$; p= 0.22).

$y=\exp(-1.8334+(.009799)*x)/(1+\exp(-1.8334+(.009799)*x))$.

Figure 4.8: Minimum numbers of *Marmosops paulensis* known to be alive at Parque Estadual Intervales. Numbers of females are shown in the lower, black-shaded part of the figure; number of males in the upper, gray-shaded part. The top of the curve indicates the total number of both sexes known to be alive in each month.

DISCUSSÃO GERAL

Insetos e frutos foram encontrados na dieta de *M. paulensis*, como já havia sido observado em estudos com outras espécies de marsupiais da tribo Marmosini (Martins & Bonato 2004, Pinheiro *et al*. 2002, Vieira & Izar 1999). Ao contrário de resultados anteriores e sugestões de que marsupiais menores possuem uma tendência para insetivoria (Santori *et al*. 1995), *M. paulensis* apresentou uma dieta mais frugívora do que previamente esperado, corroborando os resultados encontrados por Astúa de Moraes *et al.* (2003). Em um experimento de preferência alimentar, esses autores demonstraram que após *Caluromys philander*, as espécies menores (*Gracilinanus agilis*, *Micoureus demerarae* e *Marmosops incanus*) foram as mais frugívoras, consumindo altas proporções de carbo-hidratos e fibras provenientes da polpa de frutos.

Os frutos dominantes na dieta de *M. paulensis* durante a estação úmida pertenciam à família Piperaceae (*Piper gaudichaudianum* e *Piper* sp.1). Essa dominância somada à inclusão de novos itens alimentares em períodos de escassez destes frutos, sugere que piperáceas podem funcionar como item ótimo (*sensu* Schoener 1971) na dieta de *M. paulensis*. Diversos estudos com morcegos do gênero *Carollia* também descreveram uma forte relação entre esses animais e frutos do gênero *Piper* (Fleming 1988, Thies & Kalko 2004). Mello *et al.* (2004) inclusive sugeriram que *Piper* funciona como item ótimo na dieta de *Carollia perspicillata*, com base em dados semelhantes aos nossos. A previsibilidade espacial e temporal de frutos do gênero *Piper* (Fleming 1981, Thies & Kalko 2004) somado ao seu conteúdo protéico (Herbst 1986) parecem explicar a preferência por esses frutos, tanto na dieta de morcegos do gênero *Carollia* quanto na dieta de *M. paulensis*.

Durante a estação seca, *M. paulensis* consumiu uma maior proporção de artrópodes e de flores. O consumo desses itens parece estar relacionado a maior abundância relativa dessas categorias alimentares quando comparadas com frutos. É possível que flores funcionem como fonte alternativa de carbo-hidrato para *M. paulensis* em períodos de escassez de recurso, assim como já foi sugerido para outras espécies de marsupiais (Gribel 1988, Steiner 1981).

O uso do espaço de *M. paulensis* foi diretamente influenciado pelas flutuações da disponibilidade de recursos alimentares, de maneira que houve uma relação inversa entre o tamanho diário da área de vida e abundância dos recursos alimentares no ambiente. Essa relação já foi encontrada anteriormente em estudos com diversos grupos de eutérios (McNab 1963, Harvey & Clutton-Brock 1981) e espécies de marsupiais Neotropicais (Julien-Laferrière 1995, Martins 2004). Visto que o tamanho da área de vida está relacionado com as necessidades energéticas do indivíduo (McNab 1963, Harestad & Bunnell 1979), em épocas de grande oferta alimentar é possível suprir as necessidades energéticas com menor gasto energético, alterando as táticas de forrageamento ao diminuir o tamanho da área de vida. Neste estudo, a redução da área de vida de *M. paulensis* ocorreu em função da abundância de frutos, enquanto não houve relação com disponibilidade de artrópodes. É possível que a distribuição mais previsível dos frutos no espaço, quando comparada aos artrópodes, seja responsável por esse padrão. A abundância de piperáceas também foi inversamente relacionada com o uso de espaço de *M. paulensis*, o que pode ter ocorrido em função da alta previsibilidade espacial destes frutos. A previsibilidade espacial dos recursos geralmente permite uma redução na rota de forrageamento (Lurz *et al*. 2000), o que reduz os custos dessa atividade.

Os indivíduos de *M. paulensis* apresentaram uma estratégia reprodutiva semélpara. A ocorrência dessa estratégia geralmente está relacionada com espécies que enfrentam flutuações sazonais na disponibilidade de recursos, de forma que a sobrevivência dos juvenis é muito maior durante um determinado período do ano (Braithwaite & Lee 1979, Promislow & Harvey 1990). É possível que a disponibilidade de frutos desempenhe um papel importante na ocorrência de semelparidade em *M. paulensis*, uma vez que houve uma alta sincronia entre o período reprodutivo e a disponibilidade de frutos. Além disso, marsupiais menos frugívoros do que *M. paulensis*, como é o caso de *Didelphis marsupialis* e *Philander frenatus* (veja Astúa de Moraes *et al.*2003) interrompem a reprodução quando a disponibilidade de frutos diminui (Julien-Laferrière & Atramentowicz 1990). A filogenia também pode desempenhar um papel importante na existência de semelparidade em *M. paulensis*. Outro membro do gênero *Marmosops, M. incanus*, também exibe uma estratégia semélpara (Lorini *et al.* 1994), indicando que talvez esta história de vida tenha surgido dentro deste clado e esteja presente em todos os membros do gênero. Porém, pouco se sabe sobre as outras espécies de *Marmosops*, de forma que mais informações sobre o grupo são necessárias para testar esta sugestão. *Gracilinanus microtarsus* também apresenta uma história de vida semélpara (Martins 2004), e diversos estudos sobre a filogenia dos didelfídeos encontraram espécies de *Gracilinanus* e *Marmosops* próximas filogeneticamente (Jansa & Voss 2000, Kirsch & Palma 1995).

De acordo com Astúa de Moraes *et al.* (2003), marsupiais menores (“mouse opossums”) suprem boa parte de suas necessidades energéticas através do consumo de carbo-hidratos encontrados em polpa de frutos. A forte relação encontrada entre os frutos e a ecologia de *M. paulensis* sugere que a espécie estudada segue este padrão. Mais além, com base nos dados apresentados é possível especular sobre o papel de *Marmosops* *paulensis* como dispersor de piperáceas, uma vez que as sementes foram encontradas intactas nas amostras fecais. A dominância de piperáceas na dieta durante a estação úmida sugere que há uma alta taxa de visitação de *M. paulensis* a indivíduos de *Piper* e os dados sobre padrões de uso de espaço mostram que *M. paulensis* pode estar depositando as sementes de *Piper* longe da planta-mãe, aumentando as chances de estabelecimento das sementes e plântulas (Janzen 1970). Além de piperáceas, sementes de outras espécies pioneiras, como *Solanum*, também foram encontradas intactas nas amostras analisadas. Estes fatos sugerem que *M. paulensis* pode contribuir para a regeneração natural da floresta Atlântica, através da dispersão de sementes destas espécies.

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