UNIVERSIDADE ESTADUAL DE CAMPINAS
Instituto de Biologia

VANESSA VILLANOVA KUHNEN

“ECOLOGY OF THE MARSUPIALS *Didelphis aurita* AND *Metachirus nudicaudatus*”

“ECOLOGIA DOS MARSUPIAIS Didelphis aurita *E* Metachirus nudicaudatus*”*

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“ECOLOGIA DOS MARSUPIAIS Didelphis aurita E Metachirus nudicaudatus”

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> "A narrativa, em minha visão, é o registro de todas essas experiências para valorizar o outro que a nós tanto inspirou, e, em um ciclo virtuoso do compartilhar, inspirar a muitos outros motivados também a inspirar - e este é talvez, para mim, o sentido mais importante de uma produção acadêmica." A. Schroeder, 2013.

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ABSTRACT

The way to how species co-exist partly depends on how organisms utilize their environment and resources. If two sympatric species have similar ecological requirements, there is a niche overlap. Therefore, its coexistence may arise from shifts on its realized niche, for example, through partitioning resources along temporal, spatial and/or behavioral niche axes. Several factors can affect the co-existence and niche partitioning of two species, including dependent and independent density factors. If one of the two species has distinguish traits that make them a better competitor, such as generalist habits, larger size and/or aggressive behavior, it is expected that this will be the species that will drive shifts in the other species realized niche and/or its demographic parameters. *Didelphis aurita* and *Metachirus nudicaudatus* are two sympatric marsupials of the Atlantic Forest that have similar ecological requirements (i.e., solitary, nocturnal, omnivores). Although such similarities, individuals of *D. aurita* are about three times the size of *M. nudicaudatus*, are more aggressive, its diet is considered the most generalist among the Brazilian marsupials, and are the species is able to use all the forest strata. Because of such traits, *D. aurita* is considered a mesopredator. Therefore, taking into account the higher potential of *D. aurita* competitiveness and its similarity with *M. nudicaudatus* biology, it is expected that *D. aurita*'s population abundance will have a negative effect on *M. nudicaudatus* population. In this context, the general objective of this thesis was to investigate the interspecific relationships that mediate the co-occurrence of these two Neotropical marsupials. For this, we investigated if there is trophic or spatial niche partitioning among the two species. Subsequently, we investigated if the absence of top predators (e.g. large felids) changes the abundances and the diet overlap of *D. aurita* e *M. nudicaudatus.* Finally, we investigated if *D. aurita*'s abundance affects the demographic parameters of *M. nudicaudatus*. Our results demonstrated that the trophic niche of the two species is more similar than previously thought, and that *M. nudicaudatus* diet can be as generalist as *D. aurita*. We also found an evident spatial segregation in the area used by the two species, which indicates that spatial partitioning is the mechanism that enables the co-occurrence. According to our results, top predators extirpation increases the proportion of *D. aurita* by *M. nudicaudatus* population abundances and alters the species' realized trophic niche. Without top predators control, *D. aurita* expands its realized trophic niche, but retracts it when predators occurs. The opposite scenario was observed for *M. nudicaudatus*. Besides that, we found that all demographic parameters of *M. nudicaudatus* showed a negative relation to *D. aurita*'s abundance.

Indicating that the interspecific relationship with *D. aurita* seems to be more relevant to drive *M. nudicaudatus*' population than any other environmental covariate, at least in a short timescale and when *D. aurita* is the more abundant of the two species. The findings presented here innovate demonstrating that *D. aurita* negatively affects different aspects of *M. nudicaudatus* ecology and introduce a new perspective of the influence of this mesopredador on other species.

KEYWORDS: Didelphimorphia

RESUMO

A maneira como as espécies coexistem depende, em parte, de como os organismos utilizam o ambiente e seus recursos. Se duas espécies simpátricas possuem necessidades ecológicas similares, há uma sobreposição de nicho. Desta forma, a coexistência destas espécies será possível a partir de mudanças em seu nicho trófico realizado, como por exemplo, através de divisões de recursos ao longo do tempo e/ou do espaço. A forma como as espécies irão dividir seus nichos pode depender de fatores dependentes ou independentes de sua densidade. Se uma das duas espécies possuir características que fazem dela um melhor competidor, como por exemplo, hábitos generalistas, um tamanho corpóreo maior e comportamento agressivo, é esperado que será a abundância desta espécie que influenciará as mudanças nos parâmetros demográficos e/ou no nicho realizado da outra espécie. *Didelphis aurita* e *Metachirus nudicaudatus* são duas espécies de marsupiais que coocorrem em toda Mata Atlântica e possuem características semelhantes (i.e., são solitários, noturnos e onívoros). Apesar de algumas semelhanças, indivíduos de *D. aurita* tem cerca de três vezes o tamanho de *M. nudicaudatus*, possuem comportamento agressivo, sua dieta é considerada a mais generalista dentre todos os marsupiais brasileiros, e são capazes de explorar todos os estratos da floresta. Devido a estas características, *D. aurita* é considerado um mesopredador da Mata Atlântica. Desta forma, tendo em vista o potencial superior de competitividade de *D. aurita* e a similaridade com a biologia de *M. nudicaudatus*, é esperado que a abundância de *D. aurita* tenha efeito negativo sobre *M. nudicaudatus.* Neste contexto, o objetivo geral desta tese foi investigar as relações interespecíficas que mediam a coocorrência destas duas espécies. Para isto, investigamos se *D. aurita* e *M. nudicaudatus* dividem o uso do espaço e dos recursos alimentares. Posteriormente, investigamos se a ausência de predadores de topo (i.e., grandes felinos) altera as abundâncias e a sobreposição das dietas das duas espécies. Por fim, investigamos se a abundância de *D. aurita* influencia os parâmetros populacionais de *M. nudicaudatus*. Nossos resultados demonstraram que o nicho trófico destas espécies é mais similar do que previa a literatura, e que *M. nudicaudatus* pode ser tão generalista quanto *D. aurita*. Também descobrimos uma evidente segregação espacial, o que sugere que a divisão do nicho espacial é o mecanismo que permite a coocorrência das espécies na área estudada. De acordo com nossos resultados, a ausência de predadores de topo aumenta a proporção entre a abundância de *D. aurita* e de *M. nudicaudatus* e altera o nicho trófico realizado das duas espécies. Na ausência de predadores de topo, *D. aurita* expande seu nicho trófico realizado, retraindo-o na presença de predadores. Já para *M. nudicaudatus* ocorre o padrão inverso. Além disto, observamos que todos os parâmetros demográficos de *M. nudicaudatus* tiveram uma relação negativa com a abundância de *D. aurita*. Isto indica que em um cenário onde *D. aurita* é a mais abundante, e em uma curta escala de tempo, a relação interespecífica com *D. aurita* é mais relevante para a população de *M. nudicaudatus* do que qualquer outra co-variável ambiental. Os resultados aqui apresentados inovam ao demonstrar que *D. aurita* afeta negativamente diferentes aspectos da ecologia de *M. nudicaudatus*, lançando uma nova perspectiva da influência deste mesopredador sobre outras espécies.

PALAVRAS-CHAVE: Didelphimorphia

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INTRODUÇÃO GERAL

Em todos os biomas brasileiros existem marsupiais, sendo que o maior número de espécies ocorre na Mata Atlântica (Melo e Sponchiado 2012). Para a ocupação dos mais diferentes ambientes, as espécies de marsupiais apresentam variações ecomorfológicas. Por exemplo, as espécies escansoriais e arborícolas contam com cauda preênsil, as espécies semi-aquáticas possuem membranas interdigitais, e nas espécies de hábito predominantemente terrestre os membros posteriores são mais alongados (Vieira e Delciellos 2012). Além disto, as espécies brasileiras podem variar de algumas poucas gramas (ex. *Monodelphis* spp.), até mais de 3 quilos de massa corpórea (ex. *Didelphis* spp.) (Cáceres 2012). Considerando sua ampla distribuição, a grande diversidade de espécies, bem como sua variação morfológica, os marsupiais podem ser considerados bons modelos para o estudo de diferentes questões ecológicas (Johnson et al. 2007, Fernandez et al. 2012, Loyola et al. 2012).

Os marsupiais ocorrem em todos os estratos da floresta, solo, sub-bosque, sub-dossel e dossel. Porém, a maior parte das espécies ocorre principalmente no solo (Vieira e Camargo 2012). Estes marsupiais simpátricos, que compartilham necessidades ecológicas similares, podem utilizar diferentes estratégias para evitar a sobreposição de seus nichos, como por exemplo, a divisão no uso dos recursos ao longo do tempo e/ou do espaço (Schoener 1974, Benadi 2015). Porém, ainda existe uma grande lacuna de conhecimento sobre os mecanismos ecológicos que possibilitam a coocorrência destas espécies. A maior parte dos estudos já realizados limitou-se a descrever o uso dos diferentes estratos da floresta pelas espécies registradas (Vieira e Camargo 2012).

Além da similaridade no uso do espaço, parece haver também certo grau de sobreposição no nicho trófico dos marsupiais brasileiros. Grande parte das espécies brasieiras são onívoras em algum grau (Santori et al. 2012). Os principais itens consumidos costumam ser artrópodes (principalmente Hymenoptera, Isoptera e Coleoptera), pequenos vertebrados (roedores, aves e lagartos), e frutos (Santori et al. 2012). Para algumas espécies, como por exemplo *Gracilianus microtarsus* (Martins et al. 2006) e *Marmosops paulensis* (Leiner e Silva 2007), as variações sazonais na oferta de recursos parecem ser determinantes na constituição de suas dietas. Enquanto que para outras espécies, como por exemplo *Micoureus demerarae*, a dieta é constante ao longo do ano (Pinheiro et al. 2002, Lessa e Costa 2010).

O conhecimento sobre a dieta dos marsupiais brasileiros vem crescendo significativamente nas últimas décadas, porém, se considerarmos a diversidade de espécies que ocorrem no Brasil, a quantidade de trabalhos existentes ainda é pequena. Até 2010 a dieta de apenas 29% dos marsupiais brasileiros foram estudadas (Lessa e Geise 2010). Além do reduzido número de espécies estudadas, outro ponto relevante sobre os trabalhos já realizados é a metodologia adotada. A técnica mais adotada é a análise indireta através de amostras fecais (Lessa e Geise 2010). Este método detecta apenas os itens alimentares que perduram ao processo digestivo (exoesqueletos, sementes, ossos, etc.), omitindo itens da dieta que são totalmente digeridos (Dickman e Huang 1988). Além disto, a identificação taxonômica das partes encontradas é difícil, logo, os itens acabam sendo agrupados nas categorias taxonômicas mais abrangentes, como ordens ou famílias. Uma alternativa para a análise da dieta através de fezes seria a análise por isótopos estáveis (Peterson e Fry 1987, Kelly 2000, Bearhop et al. 2004), que possibilita a detecção de itens que dificilmente apareceriam nas fezes. Entretanto, até o presente momento nenhum trabalho foi publicado sobre dieta de marsupiais brasileiros com o uso desta metodologia e questões importantes sobre a ecologia trófica destas espécies permanecem em aberto.

Marsupiais são predadores, mas ao mesmo tempo também são presas. No Brasil, as principais espécies que predam marsupiais são os felinos, iraras e cachorros-do-mato (Emmons 1987, Gatti et al. 2006, Sollmann et al. 2006, Rocha-Mendes et al. 2010, Santos et al. 2012, Bianchi et al. 2014). Porém, com a fragmentação e perda de hábitat, muitos destes predadores de topo estão se extinguindo das florestas (Chiarello 1999, Prist et al. 2012). As drásticas conseqüências da ausência de predadores de topo já foram documentadas nos principais biomas do mundo (Estes et al. 2011). Quando as populações das espécies predadoras de topo são reduzidas ou extintas, diminui a pressão sobre predadores de menor porte (mesopredadores) que eram predados por estas espécies. Desta forma as populações de mesopredadores se tornam mais abundantes (um fenômeno conhecido como *mesopredator release*, Crooks e Soule 1999), e consequentemente as populações de suas presas são diretamente impactadas. Na Austrália, por exemplo, um de seus maiores predadores, o dingo (*Canis lupus dingo*), foi muito caçado por colonizadores europeus, especialmente em áreas tomadas para pastoreio de ovinos. Atualmente a espécie é rara e praticamente ausente em metade do continente. Com o declínio de suas populações a abundância de raposas e gatos aumentou, e consequentemente também a predação de marsupiais e outros pequenos mamíferos (Johnson et al. 2007).

No Brasil, as espécies do gênero *Didelphis* são mesopredadores, podem pesar até

1610g e alimentam-se de pequenos vertebrados (Eisenberg and Redford 1999). Tendo em vista que estas espécies são predadas pela maioria das espécies de carnívoros da Mata Atlântica (Emmons 1987, Gatti et al. 2006, Sollmann et al. 2006, Rocha-Mendes et al. 2010, Santos et al. 2012, Bianchi et al. 2014), suas populações tem potencial para aumentar em abundância na ausência destes predadores. Apesar de ainda não existirem estudos que avaliem a existência de um processo de liberação (*mesopredator release*) destas espécies, Fonseca e Robinson (1990) ao compararem fragmentos de Mata Atlântica de diferentes tamanhos, observaram que *Didelphis aurita* (Wied-Neuwied 1826) ocorria em maiores abundâncias nos fragmentos com baixa de diversidade de predadores. Neste mesmo estudo, os autores observaram que nos fragmentos onde a população de *D. aurita* era mais abundante, o marsupial *Metachirus nudicaudatus* (Desmarest 1817) ocorria em menor número. Porém, nos fragmentos mais preservados, onde a diversiade de predadores de topo ainda estava mantida, o inverso foi observado - as populações de *D. aurita* eram menores e a de *M. nudicaudatus* mais abundantes. Os resultados de outros levantamentos populacionais em áreas que *D. aurita* e *M. nudicaudatus* coocorrem, também indicam haver um padrão negativo entre a abundância destas duas espécies (Bergallo 1994, Santori et al. 1995, Cáceres 2004). Porém, apesar destes indícios, ainda não existem estudos demográficos que avaliem se há realmente uma relação densidade-dependente entre a dinâmica populacional destas duas espécies.

A biologia das espécies *Didelphis aurita* e *Metachirus nudicaudatus*

O gambá-de-orelha-preta, *Didelphis aurita* (Fig.1), é um dos maiores marsupiais brasileiros. Seu corpo tem em média 37 cm de comprimento, e sua cauda 33 cm (Vieira 1997, Salvador et al. 2009). A espécie pesa em média entre 1037 e 1523 g. (Vieira 1997, Cáceres e Monteiro-Filho 1999, Cunha e Vieira 2002), sendo que as fêmeas são menores e mais leves (Cáceres e Monteiro-Filho 1999, Salvador et al. 2009). Sua coloração é normalmente cinza ou preto, com uma camada de sobre-pêlos de pontas brancas. Em seu rosto ocorrem marcações na forma de três estrias escuras, uma ao longo de cada olho e uma ao longo da linha mediana do rosto. Apenas o décimo basal da cauda é coberta por pêlos (Nowak e Paradiso 1983). A distribuição da espécie está associada à Mata Atlântica, ocorrendo desde o nordeste do Brasil até o Paraguai e norte da Argentina (Gardner 1993).

Figura 1. Na parte superior: O gambá-de-orelha-preta, *Didelphis aurita*. Da esquerda para a direita: Fêmea com filhotes; Macho; Indivíduo em armadilha modelo Tomahawk. Na parte inferior: A cuíca-de-quatro-olhos marrom, *Metachirus nudicaudatus*. Da direita para a esquerda: Fêmea com filhotes; Macho jovem; Indivíduo em armadilha modelo Tomahawk. (Fotos arquivo pessoal)

A cuíca-de-quatro-olhos-marrom, *Metachirus nudicaudatus* (Fig.1), é o maior dos marsupiais neotropicais sem marsúpio (390 ± 120g.), além de ser a única espécie reconhecida para este gênero (Nowak e Paradiso 1983, Fonseca e Kierulff 1988, Cunha e Vieira 2002, Gardner e Dagosto 2007, Smith 2008, Crouzeilles et al. 2010). Todo seu corpo é de cor marrom claro, e apenas a parte basal de sua cauda possui pêlos (5-25mm iniciais) - daí o epíteto específico *nudicaudatus*. Já o nome popular cuíca-de-quarto-olhos-marrom, é por conta da macha branca presente acima de cada olho. Sua cauda é claramente não preênsil e bem longa (30 cm), quase 20% a mais do que o comprimento de seu corpo (Stallings 1988). *Metachirus nudicaudatus* ocorre desde o sul do México ao nordeste da Argentina e é dividida em cinco subespécies (Gardner e Dagosto 2007): *M. n. colombianus* (J.A. Allen 1900), *M. n. modestus* (Thomas 1923), *M. n. nudicaudatus* (É. Geoffroy 1803), *M. n. tschudii* (J.A. Allen 1900) e *M. n. myosuros* (Temmink 1824). A última é a subespécie que ocorre na Mata Atlântica brasileira. Além da Mata Atlância, *M. nudicaudatus* já foi registrado na Amazônia, Pantanal e Cerrado. Novos registros em regiões do nordeste vem sugerindo que sua distribuição da espécie pode ser mais ampla do que já se sabe (Oliveira et al. 2007, Miranda et al. 2009).

Metachirus nudicaudatus utiliza-se predominantemente do solo para deslocamento, sendo eventualmente registrado no sub-bosque (Miles et al. 1981, Fleck e

Harder 1995, Cunha e Vieira 2002, Grelle 2003, Santos et al. 2004, Astúa et al. 2006). O seu deslocamento pelo chão da floresta se dá por uma marcha habilidosa, sendo notável sua adaptação à vida terrestre (Miles et al. 1981). Para ser ágil e correr rapidamente, os indivíduos contam com pernas cerca de 10 cm mais alongadas do que os braços (Carvalho et al. 2000). Além disso, a sua coloração marrom dorsal se assemelha à coloração da serapilheira, apenas seu ventre é bem claro (Miles et al. 1981). Apesar de sua cauda não ser prênsil, *M. nudicaudatus* utiliza-a para carregar material da serapilheira para construção de seus ninhos (Delgado et al. 2014), que são normalmente feitos no chão ou em ocos de árvores caídas (Loretto et al 2005). O mesmo também foi observado para *Didelphis marsupialis*, este porém conta com seu marsúpio para carregar uma quantidade maior de material (Delgado et al. 2014). Uma característica típica da espécie é responder a perturbações batendo os dentes aceleradamente (Loretto et al. 2005, *obs. pess.*).

Ao contrário de *M. nudicaudatus*, *D. aurita* é capaz de utilizar todos os estratos da floresta (Vieira e Camargo 2012). A lonogevidade da espécie chegou a quatro anos em cativeiro (Weigl 2005). Aos cinco meses de idade indivíduos de *D. aurita* já são capazes de se reproduzir (Kajin et al. 2008). De modo geral, a espécie apresenta um padrão reprodutivo poliéstrico sazonal. Normalmente ocorrem duas proles consecutivas entre a metade da estação seca e o final da estação chuvosa (Hill 1918, Davis 1947, Gentille et al. 2000, Graipel e Santos-Filho 2006, Kajin et al. 2008). As fêmeas possuem em média nove mamilos, permanentemente protegidos por um marsúpio (Tyndale-Biscoe e Mackenzie 1976). Entretanto, o número médio de filhotes por ninhada varia entre 6,5 e 8,6 (Davis 1947, Fonseca e Kierulff 1988, Cerqueira et al. 1993, Bergallo 1994, Cherem et al. 1996, Cáceres e Monteiro-Filho 1997, Gentile et al. 2000, Graipel e Santos-Filho 2006, Graipel et al. 2006), podendo chegar a 12 filhotes (Graipel et al. 2006). Segundo Tyndale-Biscoe e Mackenzie (1976), os fatores que determinam o tamanho da ninhada no gênero *Didelphis* não são apenas a taxa de ovulação ou a disponibilidade de tetas. Os autores acreditam que pode haver um gradiente posteroanterior no desenvolvimento das glândulas mamárias, que limitaria o tamanho da ninhada de acordo com o estado e a capacidade nutricional da fêmea.

O padrão reprodutivo de *M. nudicaudatus* parece ser parecido com *D. aurita*, poliestrico sazonal (Fonseca e Krulff 1988, Crouzeilles et al. 2010), com fêmeas em condição reprodutiva também a partir dos 5 meses de idade (Diáz e Flores 2008). A longevidade máxima da espécie também se aproxima de *D. aurita*, sendo estimada em até quatros de vida (Hunsaker 1977). O número de filhotes por ninhada varia de um a nove (Eisenberg e Wilson 1981, Fonseca e Krulff 1988, Díaz e Flores 2008, Macedo et al. 2007). Em média as fêmeas possuem 9 mamas, mas já foram registradas fêmeas com apenas cinco, ou sete (Nowak e Paradiso 1983). Provavelmente, assim como *D. aurita*, deve haver algum mecanismo que regule o desenvolvimento das glândulas mamárias em *M nudicaudatus*.

Fêmeas de *D. aurita* costumam se movimentar menos do que machos, têm um território mais estável (Cáceres 2003, Cerboncini et al. 2011), e seus movimentos são influenciados pela disponibilidade de recursos (Loretto e Vieira 2005). Machos, porém, alteram seu padrão de deslocamento diário apenas durante o período de reprodução; percorrendo diariamente uma área maior nas estações reprodutivas do que percorrem em outras épocas do ano (Loretto e Vieira 2005). *Didelphis aurita* é uma espécie solitária que é capaz de utilizar todos os estratos da floresta, porém utiliza predominantemente o solo para seu deslocamento (Vieira e Monteiro-Filho 2003, Grelle 2003). A área de vida total de um indivíduo pode variar de 1,3 ha até 9,5 ha (Cáceres e Monteiro-Filho 2001, Cerboncini et al. 2011, Oliveira et al. 2014). Entretanto, o total utilizado em um único dia é bem menor, entre 0,5 e 2,7 ha (Loreto e Vieira 2005, Cerboncini et al. 2011). O tempo de permanência em uma área também é curto, cerca de 3 ou 4 meses (Gentile e Cerqueria 1995). Um indivíduo pode percorrer até 2,5 km em uma única noite (Miles et al. 1981). O período de maior atividade da espécie se concentra do pôr-do-sol até a meia noite, e não parece ser influenciado pela temperatura local (Cáceres e Monteiro-Filho 2001, Ferreira e Vieira 2014).

Estudos mostram que a área de vida de *M. nudicaudatus* pode ser tão grande quanto de *D. aurita*. Junior (2004) acompanhou por rádio-telemetria uma fêmea e calculou sua área de vida como sendo equivalente a 8,4 ha. Já a distância média percorrida pela espécie em uma noite costuma ser em torno de 500 m, mas varia muito entre as áreas estudadas (Miles et al. 1981, Gentille e Cerqueira 1995, Junior 2004). Os períodos em que *D. aurita* está ativo parece influenciar a atividade de *M. nudicaudatus*. Em um estudo na Mata Atlântica do Rio de Janeiro, Ferreira (2011) observou uma nítida segregação entre os horários de atividade das duas espécies. Nos horários da noite em que *D. aurita* estava mais ativo, praticamente não foi capturado nenhum indivíduo de *M. nudicaudatus*. Os picos de atividade da espécie ocorreram entre 20-22h e 4-6h justamente nos horários de menor atividade de *D. aurita*. O autor sugere que possivelmente *M. nudicaudatus* fica ativo em horários alternativos aos de *D. aurita* para evitar confrontos com este último.

Além de ser cerca de três vezes maior que *M. nudicaudatus*, *D. aurita* explora todos os estratos da floresta, e tem um comportamento mais agressivo. Estas características podem fazer desta espécie um melhor competidor, conferindo maiores vantagens à *D. aurita* para a captura de presas, além de ter acesso aos recursos restritos do dossel, como néctar de flores e frutos. De fato, na literatura *D. aurita* e *M. nudicaudatus* são classificados de forma distinta quanto à sua dieta - sendo *D. aurita* classificado como frugívoro/onívoro e *M. nudicaudatus* como insetívoro/onívoro (Santori et al. 2012). Apesar desta classificação, ao compilar os resultados obtidos em estudos feitos em diferentes regiões do Brasil, é possível observar que a espécie *M. nudicaudatus* consome uma ampla variedade de recursos, muito destes similares aos consumidos por *D. aurita* (Santori et al. 1995, Carvalho et al. 1999, Cáceres 2004, Lessa e Costa 2010). Porém, em função das metodologias utilizadas nestes estudos, ainda há uma lacuna de conhecimento sobre a contribuição proporcional dos diferentes tipos de recurso (e.g. frutos, artrópodes e pequenos vertebrados) para a dieta destas espécies. Desta forma, é possível que a sobreposição de seus nichos tróficos seja maior do que prevê a literatura.

Os marsupiais e o Parque Estadual da Serra do Mar

Criado em 30 de agosto de 1977, o Parque Estadual da Serra do Mar conta atualmente com 315.390 hectares de área protegida, sendo um dos maiores remanescentes de Mata Atlântica contínua do país (São Paulo 2006). Localizado no litoral do estado de São Paulo, o parque abrange 23 municípios e vai desde a divisa com o estado do Rio de Janeiro, até Pedro de Toledo no litoral sul de São Paulo. Sua importância ecológica não se restringe apenas à sua extensão, mas também pelo corredor ecológico que forma conectando o Parque Nacional da Serra da Bocaina, a Estação Ecológica de Juréia-Itatins, a APA Mananciais do Vale do Paraíba, a APA Capivari-Monos, e o Parque Estadual do Jurupará e a APA Federal Cananéia Iguape Peruíbe por meio da APA Serra do Mar (Lino e Albuquerque 2007). Atualmente é um dos poucos remanescentes de Mata Atlântica que ainda preserva a diversidade de formações vegetais das regiões costeiras; desde a restinga e os manguezais, passando pela floresta ombrófila densa, até a floresta montana (São Paulo 2006).

De acordo com o Plano de Manejo da unidade (São Paulo 2006), o Parque contribui para a conservação de 19% do total de espécies de vertebrados de todo o Brasil e 46% de toda a Mata Atlântica. Neste Parque ocorrem 53% das espécies de aves, 39% dos anfíbios, 40% dos mamíferos e 23% dos répteis registrados em todo o bioma. Além disto, das 704 espécies de vertebrados registradas no Parque, 70 (10%) estão compreendidas nas listas de espécies ameaçadas (internacional, nacional ou estadual). Durante os estudos para a elaboração do Plano de Manejo do Parque, foram registradas dez espécies de marsupiais, entre elas *D. aurita* e *M. nudicaudatus*.

Didelphis aurita e *M. nudicaudatus* coocorrem no núcleo Picinguaba do Parque

Estadual da Serra do Mar (município de Ubatuba/SP; Marques 2004, São Paulo 2006, Pinheiro e Geise 2008). Os limites do Núcleo Picinguaba têm a cota altimétrica ao nível do mar a partir da praia Brava do Cambuí, até a divisa com o Rio de Janeiro. Nesta região, as florestas situadas no sopé da encosta da Serra são florestas maduras, classificadas como Floresta Ombrófila Densa das Terras Baixas (Veloso et al. 1991), e cuja vegetação encontra-se bem preservada (Assis et al. 2011). A espécie arbórea mais abundante é o palmito (*Euterpe edulis*), seguido do bacupari (*Garcinia gardneriana*) e da laranjeira-do-mato (*Sloanea guianensis*) (Assis et al. 2011). O clima local é Tropical Úmido (Af ou Cfa, dependendo da intensidade do verão - segundo a classificação de Köppen 1948), sem estação seca, com uma temperatura média anual de 22 °C (Fig. 2) e precipitação média anual de 2.500 mm (Fig. 3) (CIIAGRO 2015).

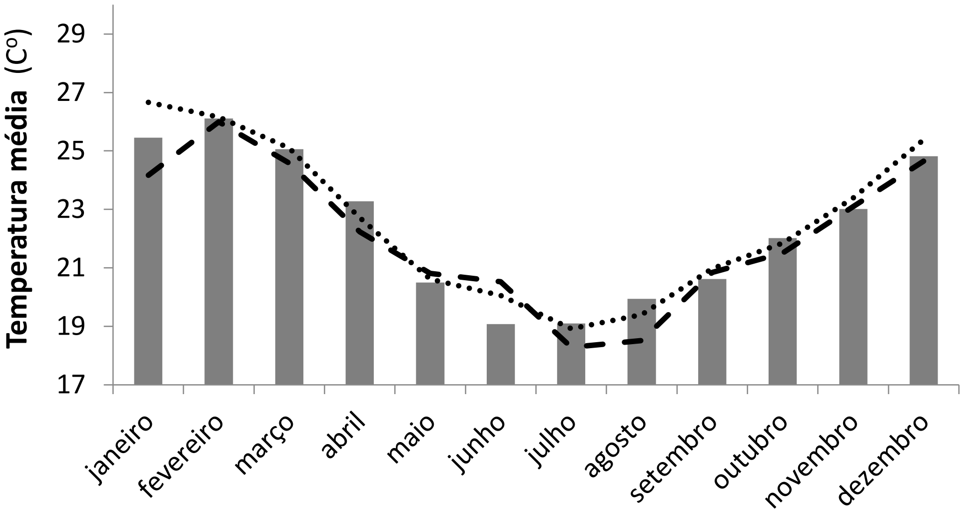

Figura 2. Temperatura média da região de Ubatuba (SP) na última década (barra cinza) em comparação aos dois anos que a região foi estudada (linha tracejada: médias do ano de 2013; linha pontilhada: médias do ano de 2014).

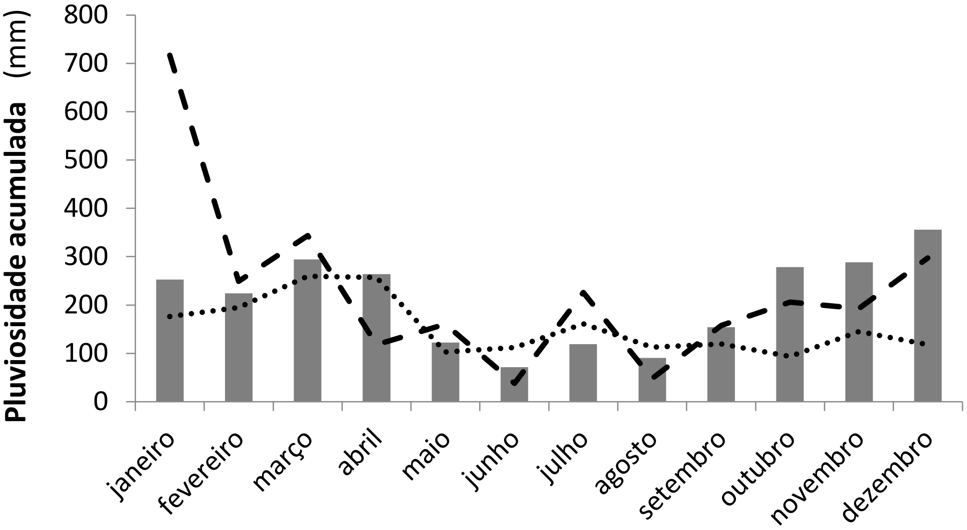

Figura 3. Média da pluviosidade acumulada na região de Ubatuba (SP) na última década (barra cinza) em comparação aos dois anos que a região foi estudada (linha tracejada: médias do ano de 2013; linha pontilhada: médias do ano de 2014).

Apesar de sua relevância ecológica, o Núcleo Picinguaba está em uma situação vulnerável de perda de área e de biodiversidade. Localizado em uma das regiões mais turísticas do estado, o Parque sofre as constantes pressões do desenvolvimento urbano, do turismo desordenado, e da especulação imobiliária (São Paulo 2006). Além destas ameaças, a caça ainda é presente na região (Marques 2004, *obs. pess.*). As primeiras comunidades tradicionais de caiçaras e quilombolas, já tinham em sua cultura o hábito da caça (Z. Pedro, *com. pess.*, 15 dezembro 2015). Infelizmente, a caça ainda faz parte da cultura dos moradores da cidade de Ubatuba, sendo um problema atual em toda região (Marques 2004). Como consequência, na região do Sertão da Fazenda (Casa da Farinha), por exemplo, mamíferos predadores são raramente registrados (*pers. obs.*).

Por seu contexto de defaunação, e pela biodiversidade florística ali presente (Assis et al. 2011), a região do Sertão da Fazenda se torna um ótimo modelo para o estudo das interações ecológicas entre *D. aurita* e *M. nudicaudatus*. Tendo em vista o potencial superior de competitividade de *D. aurita*, e a ausência de predadores de topo na região, é esperado que a abundância de *D. aurita* tenha efeitos negativos sobre a população de *M. nudicaudatus.* Neste contexto, o objetivo geral desta tese foi investigar as relações interespecíficas que mediam a coocorrência destas duas espécies.

Estrutura da tese:

Capítulo 1: Diet overlap and spatial partitioning between two Neotropical marsupials supported by multiple analytical approaches. O objetivo deste capítulo foi investigar se as populações de *D. aurita* e *M. nudicaudatus* do Sertão da Fazenda possuem similaridades no uso do espaço e em sua dieta. É esperado que caso a dieta seja similar, como estratégia de coexistência das duas espécies, o uso do espaço seja diferenciado. O capítulo foi escrito nas formatações exigidas pela revista Oikos.

Capítulo 2: Realized trophic niche driven by apparent competition: an example with marsupials. O objetivo deste capítulo foi verificar se a ausência de predadores de topo altera as abundâncias e a sobreposição das dietas de *D. aurita* e *M. nudicaudatus*. Para isto foi desenvolvido um modelo matemático que foi validado com dados da literatura e os dados de dieta obtidos no capítulo 1. É esperado que sem a pressão exercida pelos predadores de topo, a população de *D. aurita* aumente sua abundância, expanda seu nicho trófico realizado e como consquência do aumento da competição, a população de *M. nudicaudatus* diminua em abundância e tenha seu nicho trófico realizado reduzido. Enquanto que na presença de predadores de topo é esperado o cenário oposto. O capítulo foi escrito nas formatações exigidas pela revista Oikos.

Capítulo 3: Density-dependence relationship between two Neotropical marsupials. O objetivo deste capítulo foi investigar os possíveis fatores que poderiam influenciar a dinâmica populacional de *D. aurita* e *M. nudicaudatus*. Por conta da ausência de predadores na área, e das característica biológicas que conferem à *D. aurita* um potencial superior de competitividade Nossa hipótese é que, os parâmetros populacionais de *D. aurita* sejam influenciados por fatores independentes de densidade, enquanto que os parâmetros populacionais de *M. nudicaudatus* sejamsão influenciados pela abundância de *D. aurita*. Para isto, os indivíduos das duas populações do Sertão da Fazenda foram monitorados ao longo de dois anos. O capítulo foi escrito nas formatações exigidas pela revista Biotropica.

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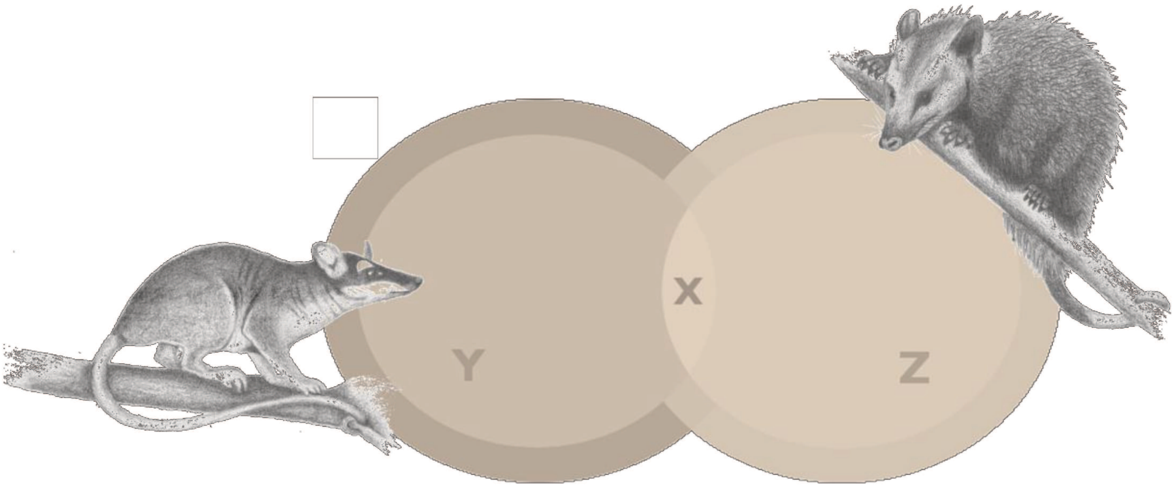
Capítulo 1

Diet overlap and spatial partitioning between two Neotropical marsupials supported by multiple analytical approaches



Diet overlap and spatial partitioning between two Neotropical marsupials supported by multiple analytical approaches

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Abstract

Species co-existence depends on how organisms utilize their environment and resources. When two sympatric species have similarity in some ecological requirements, its coexistence may arise from differences in resource use over time and/or space. Here we combine spatial niche measurements, individual-resource networks, and isotopic niche approach, to investigate the ecological strategies used by the marsupials *Didelphis aurita* and *Metachirus nudicaudatus* to co-occur in an area of Serra do Mar State Park (southeast of Brazil). Isotopic analyzes showed the species' trophic niche to be similar, with 52% of overlap, and no differences between the proportional contribution of each resource to their diets. Our individual-resource network analysis based on feces samples found no evidence of diet nestedness or segregation between both species. These results indicate that *D. aurita* and *M. nudicaudatus* trophic niche can be more similar than previously thought, highlighting the importance considering varying arrays of analytical approaches in the investigations of niche partitioning. We also found an evident spatial segregation in the area used by the two species over the time of the study, corroborating the idea that spatial partitioning can be used by species as an alternative strategy when there is a trophic niche overlap.

Introduction

The way to how species co-exist partly depends on how organisms utilize their environment and resources. All resources and conditions required by an organism to survive and reproduce are encompassed by the niche concept, which represents a n-dimensional hypervolume, where each dimension represents an ecological requirement (Hutchinson 1957). Hence, one way to analyze how species coexistence is possible is by measuring the niche parameters and comparing the niches among species (Krebs 1999, Jackson et al. 2011). When two sympatric species have similar ecological requirements, there is a niche overlap - that is the region of niche space shared by two or more continuous niches (Colwell and Futuyma 1971, Svendsen et al. 2015). However, if niche dimensions of two species are completely overlapped, one species will probably supplant the other, leading to its local extinction (i.e. Gause's competitive exclusion principle, Gause 1934). Therefore, coexistence may arise from niche shifts, for example, through partitioning resources along temporal, spatial and/or behavioral niche axes (Schoener 1974, Benadi 2015).

The most tractable and frequently studied component of niche space is trophic niche width, often evaluated using dietary diversity (Bearhop 2004). Sympatric species can segregate its trophic niche using different strategies, such as food type (Mohd-Azlan et al. 2014), foraging mode (Nakano et al. 1999), spatial segregation (Browning et al. 2014), or circadian activity pattern (Kronfeld-Schor and Dayan 1999). A species diet can also respond to resources seasonality, thus changes in food consumption across seasons can match fluctuations in food availability (Correa and Winemiller 2014). When resources are abundant, interspecific competition decreases and a higher trophic niche overlap is enabled (Reid et al. 2013). However, diet overlap can also be observed when the demand for resources exceeds supply, and species need to expand their trophic niche in order to make up their nutritional demands (Baldi et al. 2004). A high degree of niche overlap may lead to competitive interactions (Righetti et al. 2000, Harris and McDonald 2007), leading to species displacement (Remonti et al. 2012). Therefore, other mechanisms of niche partitioning (e.g., spatial segregation) could allow co-existence among species with similar ecological requirements (Macandza et al. 2012).

To describe the structure of trophic relationships there is a variety of different approaches, such as individual-resource networks (Araújo et al. 2010, Pires et al. 2011) and isotopic niche approaches (Crawford et al. 2008, Layman et al. 2007). Individual-resource networks are represented by two sets of nodes: one representing individuals of a population and the other food resource items or categories (*ca*. those found in fecal samples). The link between nodes represents the consumption of a given resource by an individual. Network structure can be detailed through several metrics that characterize the patterns of interactions observed (*see* Costa et al. 2007). There are some advantages associated to individual-resource networks based on fecal samples data, such as low costs and the possibility to collect data from recaptured animals. Despite all the applicability, there are some limitations and biases associated to fecal samples data. For example, some items have different rates of digestion (Putman 1984), thus, one sample may not contain traces from all items previously consumed. Besides that, the consumption of species without hard parts will probably not be tracked in the feces, biasing diet results. Food resource identification is not an accurate procedure, as specific parts of the digested animals' body are needed for reliable taxonomic identification. Many times those parts do not remain entire after digestive process, which may underrate diet composition. Alternatively, part of these limitations can be overcome by the use of stable isotope signatures to provide a quantitative description of diet (Crawford et al. 2008).

Stable isotope ratios can be used as diet descriptors because the values measured in consumer tissues are tightly linked to those in their diet (Jackson et al. 2011). For example, stable carbon isotope ratios ($\delta^{13}C$) vary mostly according to the photosynthetic metabolism of plants and can be very effective tracers of different carbon sources (Crawford et al. 2008). The stable isotope commonly utilized to trace protein sources is nitrogen ($\delta^{15}N$). The ratio of ^{15}N to ^{14}N generally exhibits an increase in the value of $\delta^{15}N$ at each trophic level, which allows identifying prey from different trophic levels (Bearhop et al. 2004). Thus, it is possible to quantify the proportional intake of various prey groups (Jackson et al. 2012). Another advantage of stable isotopes approach is the possibility to quantify prey items over varying temporal and spatial scales. Since different tissues integrate diet over different temporal scales, several distinct sources of information can be accessed from a single sampling event (Crawford et al. 2008). Potential drawbacks in using this approach are: the unknown rate with which isotopic values from a given resource is assimilated by the tissues of the consumer, making it difficult to compare different tissues; the impossibility of using tissue samples for isotopic analyses from recaptured animals, when lure is used; and, the difficulty of accessing the isotopic signature of each consumed species. Therefore, using stable isotopes and fecal samples in conjunction provides a more complete representation of a species dietary habit.

Here we combine spatial niche measurements, individual-resource networks analysis, and isotopic niche approach to investigate the ecological strategies of two Neotropical marsupials to co-occur: *Didelphis aurita* (Wied-Neuwied 1826) and *Metachirus nudicaudatus* (Desmarest 1817). Considering their similar food requirements (Santori et al.

1995, Cáceres 2004), we predict that for these species to co-exist, they will present low overlap in trophic niches or spatial segregation. We investigated trophic niche overlap using ^{13}C and ^{15}N isotopic approach (Jackson et al. 2012). Besides, we analyzed the individual-resource network structure. If *D. aurita* is a more generalist species, and *M. nudicaudatus* predominantly insectivorous, *M. nudicaudatus*'s diet would represent a subset of the broader diet of the generalist *D. aurita*. In this case, we would expect to arise a nestdness structure in the individual-resource network of the two species (Araújo et al. 2010, Pires et al. 2011). Alternatively, if individuals use distinct subsets of the available resources, we would expect a modular network structure, i.e. groups of individuals of the same species feeding in a subset of food items than those items used by the other species (Araújo et al. 2008, Pires et al. 2011).

Methodology

Study system

Didelphis aurita and *M. nudicaudatus* are sympatric species of the Atlantic Rainforest with similar habits: both are mainly terrestrial, nocturnal and solitary (Gardner 2007). *Didelphis aurita* is found in all forest strata, but uses preferentially the ground level (Passamani 2000, Cunha and Vieira 2002, Grelle 2003), whereas *M. nudicaudatus* has morphological adaptations to a cursorial behavior and is rarely captured on other strata than ground (Argot 2002, Astúa et al. 2006). *Didelphis aurita* is classified as a broad generalist species, and *M. nudicaudatus* to be an omnivore predominantly insectivore (Cáceres 2004, Vieira and Astúa 2006, Paglia 2012). However, a review of the literature provides evidence of potential overlap between the two species diet (Santori et al. 1995, Freitas et al. 1997, Carvalho et al. 1999, Cáceres e Monteiro-Filho 2001, Grelle 2003, Cáceres 2004, Ceotto et al. 2009, Lessa and Costa 2010, Lessa and Geise 2014).

Study area

The study was conducted in the Serra do Mar State Park, southeastern Brazil (São Paulo State coast). The Serra do Mar State Park comprises more than 300,000 ha of well preserved rainforest – it is the largest protected Atlantic Rainforest remnant in Brazil (Ribeiro et al. 2009). The studied area is located 35 km from the urban area of Ubatuba city, and 2 km from an isolated village (*Sertão da Fazenda*) (23°20'S and 44°50'W). The forest is characterized as lowland tropical evergreen, following Veloso et al. (1991). For a full description of the forest classification and structure, see Alves et al. (2010) and Eisenlohr et al. (2013). The altitudes range from 43 to 89 m above sea level (Eisenlohr et al. 2013). The regional climate is Tropical Humid, with no dry season and hot summers (Af/Cfa according to Köppen 1948). Average annual precipitation is 2,500 mm, and monthly average temperature is 22 ºC (CIIAGRO 2015).

Collection and preparation of samples

From May 2013 to April 2015, a trapping session of four consecutive nights was conducted every month. A hundred Tomahawk traps (45×16×16 cm) were used to capture the animals, baited with banana, peanut butter and bacon. Traps were placed along the river and besides a steep slope, 20 m apart from each other, compounding a rectangular grid of 3.4h (280 m x 120 m, Fig. A1). The spatial use of this grid, for each species, was analyzed by the percentage of spatial overlap, calculated through Morisita's Index of Overlap (Krebs 1999). The traps were placed on a hardboard platform, in order to minimize contamination of the feces with litter contents. After the second night of trapping, all baits were replaced for new ones. Individuals captured were marked in each ear with one 1-g monel ear tag (National Band and Tag Co.®), weighted, identified as to sex, age (Tyndale-Biscoe and MacKenzie 1976), and the sample station was recorded.

In the first capture of each adult captured (11 males and eight females of *D. aurita*, and seven females and seven males of *M. nudicaudatus*), we cut a nail sample of all fingers from the left-hind foot for analysis of stable isotope ratios of C ($\delta^{13}C$) and N ($\delta^{15}N$). Nails are keratin based and the turnover elements in such tissues are slower, therefore being considered metabolically inert tissues (Rubenstein and Hobson 2004). As stable isotopes are allocated into the keratin structure during growth, the information from the diet over the period during which the tissue was synthesized is preserved (Hobson 1999). However, the rate with which animals incorporate the isotopic values of the resources they consume can vary between individuals and tissue types (Caut et al. 2009). Since these rates are still unknown for Neotropical marsupials, we decided not to collect and analyze nails from recaptured individuals, thus minimizing bias from bait consumption. Given the close phylogenetic relationship of *Didelphis aurita* and *Metachirus nudicaudatus* (Jansa et al. 2014), we assumed that their nails integrate diet over similar amounts of time. With a stereoscope, nail samples were gently cleaned in a petri dish with water, then with alcohol 70%, and again with water. After cleaned, samples were oven dried at 60°C for 48 hours, and weighed up to ~1 mg into tin capsules for isotopic analyses.

We also collected samples of available diet sources for isotope analysis, based on literature about the species diet. Source samples were divided into six categories: small vertebrates (reptiles and rodents), fruits, and four different guilds of arthropods (herbivores, predators, omnivores and detritivores). Although we might miss some diet items that can be eventually consumed, those six categories encompass the main food resources used by *D. aurita* and *M. nudicaudatus* (Santori et al. 1995, Freitas et al. 1997, Carvalho et al. 1999, Cáceres e Monteiro-Filho 2001, Grelle 2003, Cáceres 2004, Ceotto et al. 2009, Lessa and Costa 2010, Lessa and Geise 2014). Fruits were collected opportunistically, and to collect small vertebrates and arthropods we used three lines with eight pitfalls each (pitfall volume of 60 liters). The source samples were oven dried at 60°C for 48 hours, and weighed out to ~1 mg into tin capsules for analysis for isotopic analyses.

Fecal samples were collected from the bottom of the trap, where the animal spent the night. The feces from recaptures during the same trapping season were not collected to avoid any influence of the bait on the samples. A total of 70 fecal samples were collected from nine females and nine males of *D. aurita*, and five females and ten males of *M. nudicaudatus*. Samples were frozen until analyzed. After thawing, they were dissolved in water, and then filtered through a 1 mm mesh screen sieve under running tap water. The material retained on the sieve was dried at environment temperature and analyzed with a stereoscope. The taxonomic identification of prey items was validated by specialists.

Isotopic analyses

All isotope analyses were conducted by the Stable Isotope Facility of the University of California, Davis, California, USA, using an online elemental analyzer (PDZ Europa ANCA-GSL, Sercon Ltd., Cheshire, UK) interfaced to a continuous flow isotope ratio mass spectrometer (PDZ Europa 20-20).

For the statistical analyses, we used the convex hull (TA) approach to represent the overall dispersion within isotope niche space of *D. aurita* and *M. nudicaudatus* (Layman et al. 2007). In order to analyze dietary similarity between the species, we compared the standard ellipse areas of the isotopic niches (SEA). SEA is estimated using Bayesian methods, which allows for robust statistical comparisons between populations with unequal sample sizes, and contains the mean core of the population isotopic niche (40% of 10000 replicas, Jackson et al. 2011). Due to the small sample size, we employed a corrected sample size version of the SEA (SEAc, Jackson et al. 2011). The overlap of SEAc was calculated as a measure of trophic niche overlap (Jackson et al. 2012). The relative contribution of each resource in *D. aurita* and *M. nudicaudatus* diets were estimated by the Bayesian mixing model SIAR (Parnell et al. 2010).

Intra-population variation in diets was analyzed using two quantitative metrics, developed originally by Layman et al. (2007) and then adapted for a Bayesian inference by Jackson et al. (2012): a) *Mean distance to centroid* (CD_b), infer the population trophic diversity; b) *Standard deviation of nearest neighbor distance* ($SDNND_b$), infer the population trophic evenness.

Metrics were calculated using the software package SIAR v4.2.2 (Parnell and Jackson 2013) in R programming environment (R Core Team 2015).

Network analysis

We described the trophic interactions of *D. aurita* and *M. nudicaudatus* with their feeding items as a bipartite individual-resource network, consisting of two groups: captured individuals linked to each resource they consumed (Pires et al. 2011). For such, we defined an incidence matrix where rows (i) correspond to individuals, and columns (j) correspond to each food resource found in fecal samples. For the network analysis, food resources were not divided into categories but were considered all items found on feces, identified to the lowest taxon possible. Each element (a_{ij}) of the matrix corresponds to whether the consumption of a resource was recorded ($a_{ij} = 1$) or not ($a_{ij} = 0$). In order to account for potential biases caused by recaptures of the same individuals, we grouped into the same line the food items consumed by each individual within a season. To evaluate the impact of this choice on the network metrics, we also ran the models using the raw data without grouping recaptures and found the results to be very similar.

We searched for nestedness and modularity into this network to test whether individuals of some species uses a subset or resources used by individuals of another (nested network structure) or individuals of both species uses distinct subset or resources (modules should be detected). We used the nestedness metric based on overlap and decreasing fill for both lines and columns of the matrix (NODF; Almeida-Neto et al. 2008). To test this hypothesis, we used the modularity index (Q) with the optimization algorithm QuanBiMo - which find the partition of the individual–resource network that yields the largest degree of modularity (Dormann and Strauss 2014). Depite of *Q* was developed to explore quantitative networks (*see* Dormann and Strauss 2014), they are also suitable for binary networks (C. Dormann. pers. comm.). To access metric significances, we compared the observed NODF and *Q* values to those obtained by 1,000 and 100 null model randomization, respectively. The null model used was *shuffle.web*, which rearrange interactions randomly inside the matrix but keeps the dimensions of the observed matrix (Dormann et al. 2009). Due to large computational time required by the algorithm QuanBiMo, we used less randomizations for modularity. However, the values obtained with this metric can be slightly different among runs, due to the stochastic optimization technique associated to this algorithm (*i.e.* simullated annealing). Thus, for each network we chose the higher values from five independent runs set to 10^7 swaps (Dormann et al. 2009). As the algorithm aims to find the highest modularity, getting the higher values among runs is a suitable procedure, as done by previous in studies (e.g. Gonzalez et al. 2014). The same was done to the null models to which we chose the higher Q found among five runs to each of the 100 randomizations. Metrics were considered significant when the observed value fell outside the 95% confidence intervals expected by the null models (*i.e.* 1000 and 100 randomizations for NODF and *Q*, respectively). In order to evaluate if nestedness could be occurring only into a season, we subset the network in four seasons and re-analyzed the data. Also, we expect modules corresponding to seasons whether occurs shift in resource uses throughout the time. All analyses were run in R-package *bipartite* (Dorman et al. 2008).

Results

Arthropods were the main diet items found in scats of both mammal species (Fig. 1; Supplementary Material, Table A1). Coleoptera and Crustacea were the items most frequently found in *D. aurita* scats. For *M. nudicaudatus*, Hymenoptera and Coleoptera were the most frequently item found. Vertebrates were found more frequently in *D. aurita* scats than in *M. nudicaudatus*, which presented only reptiles traces. A wider diversity of seeds was found in *D. aurita* scats and in a higher frequency than in *M. nudicaudatus*. Inspite of those differences, isotopic analyzes showed that *D. aurita* and *M. nudicaudatus* feed in the same proportions of each food resource category. Mean values of $\delta^{15}N$ for *D. aurita* and *M. nudicaudatus* were 9.18 (±0.10 SE) and 9.32 (±0.16 SE), respectively; and, mean values of $\delta^{13}C$ were -23.58 (±0.10 SE) and -23.64 (±0.08 SE), for *D. aurita* and *M. nudicaudatus* respectively. Standard ellipse areas of isotopic niches of *D. aurita* (SEAc = 0.95) and *M. nudicaudatus* (SEAc = 0.56) were similar (p=0.34), and the two species showed 52% of trophic niche overlap (Fig. 2). Population-level metrics of trophic structure were also similar for both species (Table 1).

The SIAR dietary mixing model did not indicate any significant differences between the proportion that each resource group contributed to *D. aurita* and *M. nudicaudatus* diets (isotopic values for all resource samples is shown in Table A2). Both diets appear to be split in three main source groups (Fig. 3, Table A3): top food chain invertebrates (omnivores and predators), which are the main resources (~52.5%); vertebrates and detritivores, which showed a smaller, but also important, proportional contribution (~38%) - with vertebrates contributing more (~21.5%) than detritivores (~0.16%); and, sources from the base of the food chain (fruits and herbivores), which showed to be unimportant dietary components with a mode proportional contribution value of only 0.02%.

We found no evidence of diet nestedness or segregation between both species (Fig. 4), since there was no difference from the observed and expected by the null model neither for nestedness index (NODF = 44.74, 95%IC = 45.40-49.04) nor modularity (Q = 0.33, 95%IC = 0.31-0.33) for bipartite matrices. The absence of structured diet remained consistent among seasons, when both nestedness and modularity overlapped with the null models (Table A4).

Spatial analysis demonstrated that *D. aurita* and *M. nudicaudatus* showed 65% overlap in the use of the grid area (Fig. A1), during the 24 months sampled. However, when spatial use is analyzed separately for different seasons a spatial partitioning among the individuals becomes evident (Table 2). There was a complete spatial segregation among individuals during the two springs and in the winter of 2013. In the winter of 2014 and in the two autumns sampled, percentages of overlap ranged between 14% and 24%. Summer was the season when individuals of the two species had a higher overlap in the grid area used (36%). There was no evidence of relation between number of captures and spatial overlap. Winter of 2013 was the season with more captures of the two species, and there was no overlap on grid area used.

Discussion

The combination of isotopic analyses and individual-resource networks revealed that the trophic niches of *Didelphis aurita* and *Metachirus nudicaudatus* are more similar than previously described in literature. Our results indicate that both species have a high diet overlap, which provides a new perspective to *M. nudicaudatus* ecology. Besides that, although both species explored almost all grid area, over the period of two years there was a notable spatial segregation. Therefore, we believe that spatial partitioning is the main mechanism enabling the co-occurrence of *D. aurita* and *M. nudicaudatus* in the studied area.

Metachirus nudicaudatus diet has been considered in the literature to be predominantly insectivore (Cáceres 2004, Vieira and Astúa 2006, Paglia 2012). However, our results indicate that individuals of *M. nudicaudatus* can be as generalist as *D. aurita* individuals. Althought our isotopic analyzes can not differentiate diets in a refine taxonomic scale, the results of network analyzes also indicated that individuals of *M. nudicaudatus* feed on similar itens that *D. aurita*. The larger diversity of items found in *D. aurita* feces was not sufficient to support an statistical difference between the diets. This difference on prey diversity could be just a mothodological bias. In fecal analyses many parts can not be tracked or identified. Besides, *M. nudicaudatus* has longer molar series (Astúa et al. 2000), this trait can increase the crushing, cutting and grinding surface, which could decrease the probability to find resource parts on feces that allow proper identification. Moreover, the *M. nudicaudatus* rostrum is smaller and more elongated than *D. aurita* (Astúa et al. 2000), and may not eat large parts as *D. aurita* might be able, which could also make more difficult to find parts of the prey in the feces. On the other hand, those differences might have arised from the spatial segregation. Spatial segregation associated to trophic niche overlap has been described to other systems, such as Australian rodents (Maitz and Dickman 2001) and African grazers (Macandza et al. 2012). Our findings provides the first report showing this pattern to Neotropical marsupials.

Metachirus nudicaudatus and *D. aurita* has a high overlap of the grid area used over the two years of study. However, within a smaller temporal scale (within seasons), there is a dynamically spatial relationship of mutual exclusion. The period of higher spatial overlap was during summer likely because, normally, this is a period of high resource availability. Therefore, spatial segregation may be acting to promote coexistence and relax interspecific competition for food resources. Interference and avoidance might be the mechanism promoting spatial segregation. Direct interference can be a costly behavioral strategy, however, it may benefit larger species, such as *D. aurita* through prior access to food and shelters. On the other hand, it may be profitable to *M. nudicaudatus* to avoid *D. aurita* and reduce the chance of incurring injury in direct encounters. A strategy to avoid such encounters could be through recognition of signals in the environment. Other mammals, such as otters (McDonald and Mason 1980) and canids (Dietz 1984) use feces and urine as visual and olfactory signals. Cougars, for instance, leave scrapes along travel routes as interspecific signs (Logan and Sweanor 2010). *Didelphis aurita* and *M. nudicaudatu*s have paracloacal scent glands that confer a peculiar smell to individuals (Helder-José and Freymuller 1995, Munhoz and Merzel 1967), which are related to complex multifunctional behaviors (Thomson and Pears 1962, Helder-José 2012). It is possible that chemical substances secreted by these glands play a role in the interspecific recognition and spatial partition in these marsupials.

If spatial segregation is a consequence of *D. aurita* and *M. nudicaudatu*s competition, it is expected that the presence of one species alters the pattern to which the second species uses the available resources, affecting its population dynamics (MacNally 1983). Supporting this idea, it was recorded that in larger fragments of Atlantic Rain Forest, where top predators suppress *D. aurita*'s abundances, there is a larger population of *M. nudicaudatus*; on the other hand, in smaller fragments were top predators community is depauperated, the opposite occurs (Fonseca and Robinson 1990). The authors also found that when *D. aurita* was captured in a sample station there was a significant depression on the probability to capture an individual of *M. nudicaudatus* at the same sample station.

In conclusion, we suggest that the sympatric Neotropical marsupials *D. aurita* and *M. nudicaudatus* have extensive dietary overlap and similar use of the area, however, they partition the space over the time. These results are largely consistent with the idea that spatial partitioning can be a mechanism to reduce interspecific competition and be a major factor determining the species co-occurrence (Schoener 1974). This paper adds knowledge on the ecology of two Neotropical marsupials, *D. aurita* and *M. nudicaudatus*, and further studies on these species' behavior may provide a better understanding on how the interactions between individuals of these two species take place.

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Table 1. Population metrics of trophic structure for *Didelphis aurita* and *Metachirus nudicaudatus*. (CDb = mean distance to centroid; MNNDb = mean nearest neighbor distance; SDNNDb = standard deviation of MNNDb; SEAc = standard ellipse area; TA = total ellipse area)

	Didelphis aurita	***Metachirus nudicaudatus***
Sample size (n)	19	14
CDb	0.47	0.51
MNNDb	0.08	0.12
SDNNDb	0.12	0.14
SEAc	0.95	0.56
TA	2.28	1.27

Table 2. Percentage of spatial niche overlap between *Didelphis aurita* and *Metachirus nudicaudatus*. Percentage values were calculated based on Morisita’s index. The value in parenthesis represents the number of captures for each species (*D. aurita* / *M. nudicaudatus*). (n.s. means season not sampled)

	2013	**2014**	**2015**
Summer	n.s.	36% (32/16)	0% (59/0)
Autumn	20% (23/19)	24% (26/26)	20% (33/12)
Winter	0% (53/18)	14% (56/23)	n.s.
Spring	0% (22/11)	0% (30/2)	n.s.

Figure captions

Figure 1. Occurrence percentage of each food item found in *Didelphis aurita* and *Metachirus nudicaudatus* fecal samples.

Figure 2. Stable isotope bi-plot illustrating the isotopic niche of *Didelphis aurita* (black) and *Metachirus nudicaudatus* (red). Each point represents an individual; solid lines represent the mean core of the population isotopic niche (SEAc), and; dotted lines represent the overall isotopic niche of the population (convex hull).

Figure 3. Contributions of potential food sources to diets of *Didelphis aurita* (higher) and *Metachirus nudicaudatus* (lower). Boxes illustrate the relative proportions of each food source with 50%, 75% and 95% confidence intervals from dark to light grey.

Figure 4. Individual-resource network for *Didelphis aurita* and *Metachirus nudicaudatus.* Links represent the consumption of a resource (right column) by each individual (left column). Colors represent the species: black for *D. aurita* and red for *M. nudicaudatus*.

Fig. 1

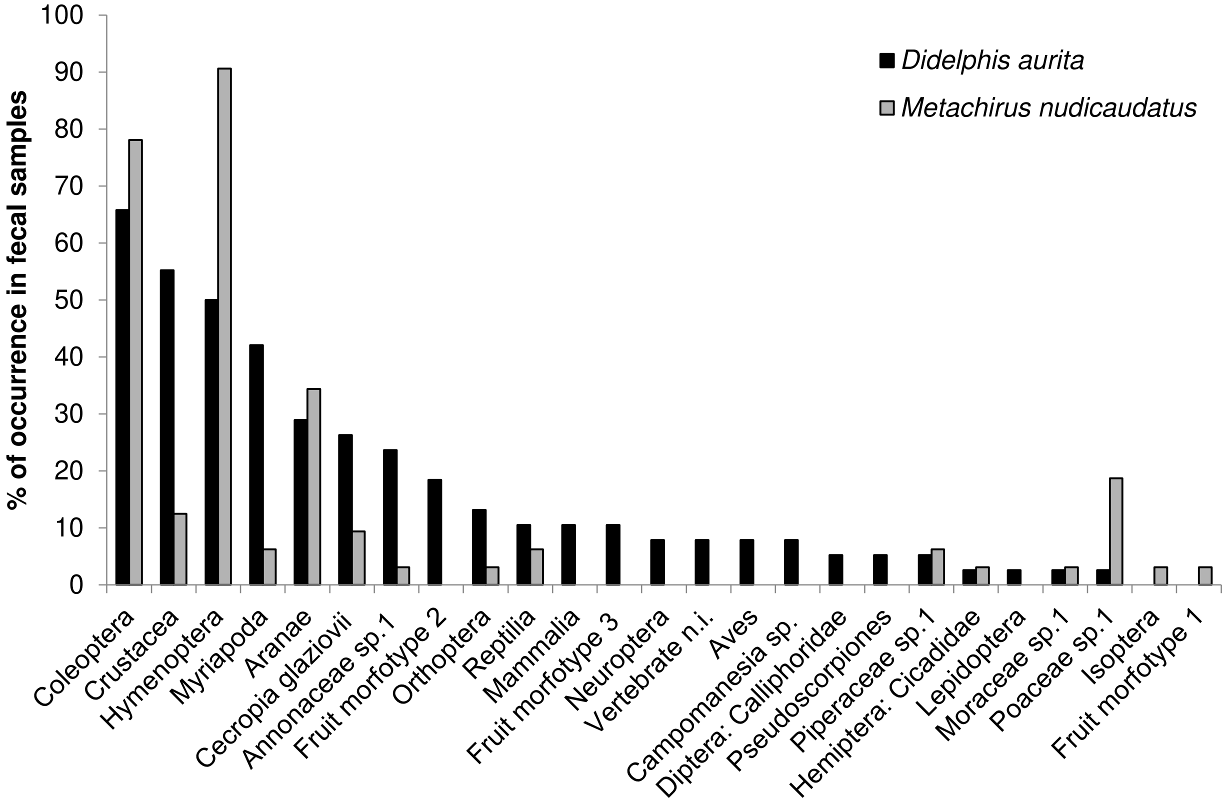

% of occurrence in fecal samples
0
10
20
30
40
50
60
70
80
90
100
■ Didelphis aurita
□ Metachirus nudicaudatus
Coleoptera
Crustacea
Hymenoptera
Myriapoda
Aranae
Cecropia glaziovii
Annonaceae sp.1
Fruit morfotype 2
Orthoptera
Reptilia
Mammalia
Fruit morfotype 3
Neuroptera
Vertebrate n.i.
Aves
Campomanesia sp.
Diptera: Calliphoridae
Pseudoscorpiones
Piperaceae sp.1
Hemiptera: Cicadidae
Lepidoptera
Moraceae sp.1
Poaceae sp.1
Isoptera
Fruit morfotype 1

Fig. 2

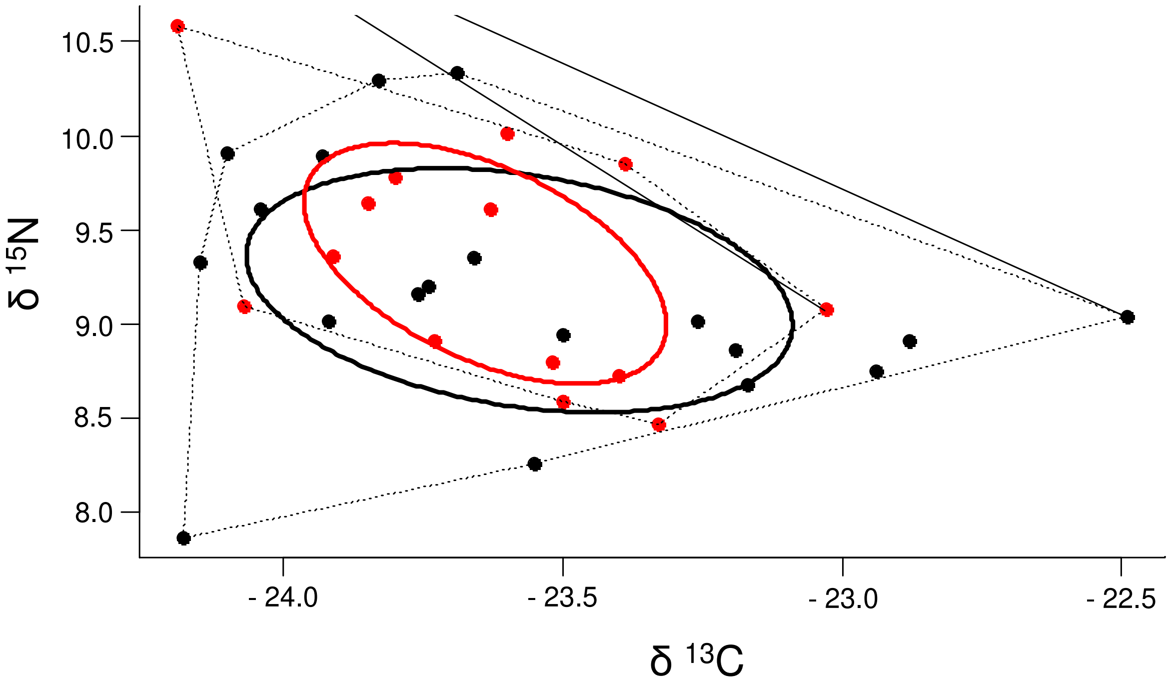


Fig. 3

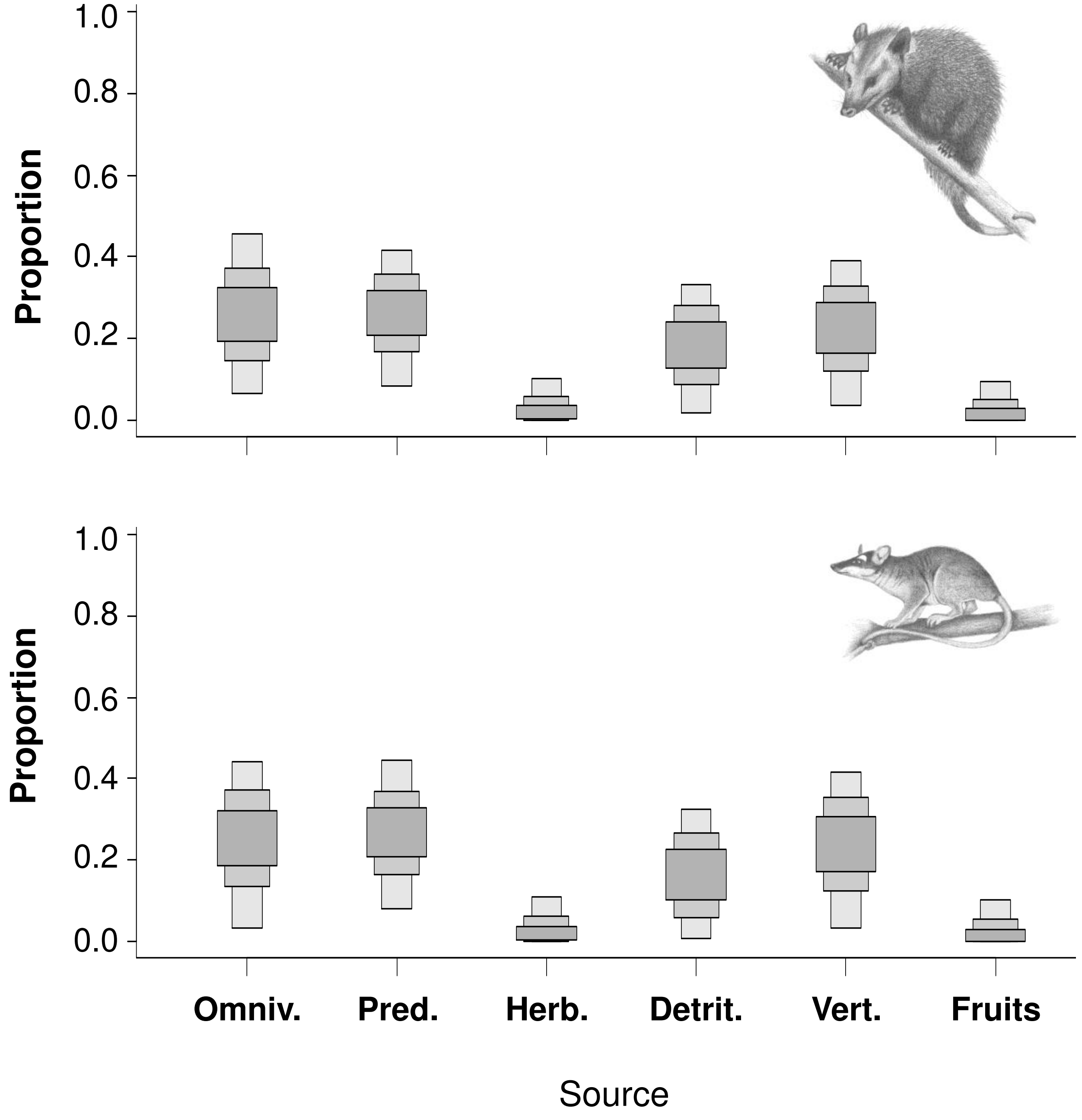
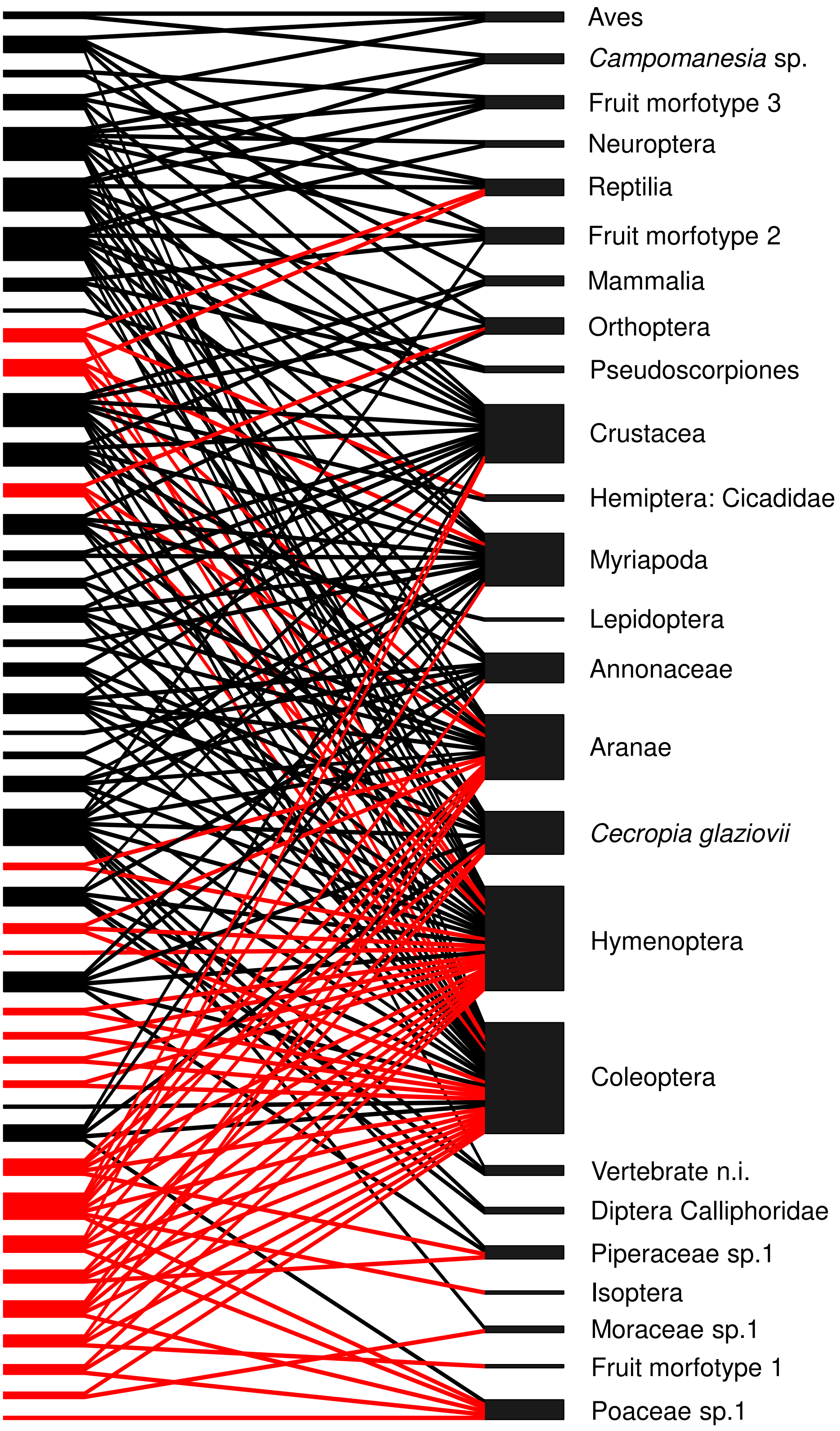

1.0
0.8
0.6
0.4
0.2
0.0
Proportion
1.0
0.8
0.6
0.4
0.2
0.0
Proportion
Omniv.
Pred.
Herb.
Detrit.
Vert.
Fruits
Source

Fig. 4


Aves
Campomanesia sp.
Fruit morfotype 3
Neuroptera
Reptilia
Fruit morfotype 2
Mammalia
Orthoptera
Pseudoscorpiones
Crustacea
Hemiptera: Cicadidae
Myriapoda
Lepidoptera
Annonaceae
Aranae
Cecropia glaziovii
Hymenoptera
Coleoptera
Vertebrate n.i.
Diptera Calliphoridae
Piperaceae sp.1
Isoptera
Moraceae sp.1
Fruit morfotype 1
Poaceae sp.1

Supplementary material:

Table A1. Frequencies of occurrence (in %) of food items found in *Didelphis aurita* and *Metachirus nudicaudatus* fecal samples. Sample sizes for each species in parenthesis (n.i. = not identified)

	Didelphis aurita (n=38)	***Metachirus nudicaudatus*** (n=32)
Arthropods		
Coleoptera	25 (65.8)	25 (78.1)
Crustacea	21 (55.3)	4 (12.5)
Hymenoptera	19 (50.0)	29 (90.6)
Myriapoda	16 (42.1)	2 (6.3)
Aranae	11 (28.9)	11 (34.4)
Orthoptera	5 (13.2)	1 (3.1)
Neuroptera	3 (7.9)	0 (0.0)
Diptera: Calliphoridae	2 (5.3)	0 (0.0)
Pseudoscorpiones	2 (5.3)	0 (0.0)
Hemiptera: Cicadidae	1 (2.6)	1 (3.1)
Lepidoptera	1 (2.6)	0 (0.0)
Isoptera	0 (0.0)	1 (3.1)
Vertebrates		
Reptilia	4 (10.5)	2 (6.3)
Mammalia	4 (10.5)	0 (0.0)
Aves	3 (7.9)	0 (0.0)
Vertebrate n.i.	3 (7.9)	0 (0.0)
Fruits		
Cecropia glaziovii	10 (26.3)	3 (9.4)
Annonaceae sp.1	9 (23.7)	1 (3.1)
Campomanesia sp.	3 (7.9)	0 (0.0)
Piperaceae sp.1	2 (5.3)	2 (6.3)
Moraceae sp.1	1 (2.6)	1 (3.1)
Poaceae sp.1	1 (2.6)	6 (18.8)
Morfotype 1	0 (0.0)	1 (3.1)
Morfotype 2	7 (18.4)	0 (0.0)
Morfotype 3	4 (10.5)	0 (0.0)

Table A2. $\delta^{13}C$ and $\delta^{15}N$ values for putative resources to the diet of *Didelphis aurita* and *Metachirus nudicaudatus*.

Guild	Class	Order	Family / Sp.		δ15N	δ13C
Omnivores						
	Arachnida	Opiliones	-		7.71	-25.83
	Insecta	Orthoptera	Anostostomatidae		5.31	-27.14
	Insecta	Hymenoptera	Formicidae		4.81	-26.76
	Insecta	Hymenoptera	Formicidae		7.68	-26.87
				Mean	6.37	-26.65
				SD	± 1.53	± 0.57
Predators						
	Arachnida	Araneae	Lycosidae		7.38	-27.57
	Arachnida	Araneae	Lycosidae		8.25	-26.87
	Arachnida	Araneae	Lycosidae		5.07	-27.66
	Arachnida	Araneae	Theraphosidae		8.58	-26.83
	Arachnida	Scorpiones	-		8.57	-26.69
	Chilopoda	-	-		7.40	-27.91
	Insecta	Hymenoptera	Pompilidae		9.40	-26.84
	Insecta	Hymenoptera	Pompilidae		7.48	-27.03
	Insecta	Hymenoptera	Pompilidae		12.83	-25.43
	Insecta	Hymenoptera	Ponerinae		9.14	-26.24
	Insecta	Hymenoptera	Vespidae		6.65	-27.68
				Mean	8.25	-26.98
				SD	± 1.95	± 0.72
Herbivores						
	Insecta	Coleoptera	Cerambycidae		-1.30	-25.94
	Insecta	Coleoptera	Cerambycidae		-1.45	-26.24
	Insecta	Orthoptera	Tettigoniidae		5.28	-27.78
	Insecta	Orthoptera	Tettigoniidae		4.22	-27.97
	Insecta	Phasmatodea	-		0.37	-33.03
	Insecta	Phasmatodea	-		-0.22	-33.16
				Mean	1.15	-29.02
				SD	± 2.89	± 3.25
Detritivores						
	Diplopoda	-	-		6.78	-23.17
	Diplopoda	-	-		2.63	-26.22
	Insecta	Blattodea	-		3.16	-27.38
	Insecta	Blattodea	-		4.42	-26.37
	Insecta	Coleoptera	-		4.52	-28.20
	Insecta	Coleoptera	Passalidae		0.70	-27.36
	Insecta	Coleoptera	Scarabaeidae		4.88	-26.49
	Insecta	Coleoptera	Staphilinidae		6.93	-25.52
				Mean	4.25	-26.34

			SD	± 2.08	± 1.53
Vertebrates					
	Mammalia	Rodentia	*Euryoryzomys russatus*	6.33	-26.09
	Mammalia	Rodentia	*Euryoryzomys russatus*	6.48	-26.05
	Mammalia	Rodentia	*Juliomys pictipes*	4.76	-27.79
	Mammalia	Rodentia	*Oligoryzomys nigripes*	4.95	-31.30
	Mammalia	Rodentia	*Oxymycterus* sp.	10.26	-25.32
	Reptilia	Squamata	-	8.93	-23.61
			Mean	6.95	-26.69
			SD	± 2.20	± 2.62
Fruits					
			Morfotype 1	-0.06	-31.42
			Morfotype 2	1.15	-26.79
			Morfotype 3	5.78	-29.91
			Morfotype 4	4.74	-35.78
			Morfotype 5	-1.75	-28.10
			Morfotype 6	0.78	-29.59
			Morfotype 7	2.46	-28.02
			Morfotype 8	3.05	-33.11
			Morfotype 9	-1.09	-27.94
			Morfotype 10	1.16	-35.03
			Morfotype 11	0.42	-29.91
			Morfotype 12	0.05	-29.99
			Morfotype 13	2.80	-31.44
			Morfotype 14	1.37	-28.17
			Morfotype 15	2.21	-28.45
			Morfotype 16	0.02	-28.90
			Morfotype 17	0.21	-28.98
			Morfotype 18	2.01	-29.89
			Morfotype 19	-1.77	-29.84
			Morfotype 20	-2.11	-27.54
			Morfotype 21	-0.42	-29.23
			Morfotype 22	3.20	-25.85
			Morfotype 23	-2.36	-30.58
			Morfotype 24	0.95	-29.16
			Morfotype 25	3.26	-35.59
			Mean	1.04	-29.97
			SD	± 2.09	± 2.57

Table A3. Relative contribution of putative resources to the diet of *Didelphis aurita* and *Metachirus nudicaudatus*.

Species	Source category	Credible intervals		Mode	Mean
		Low 95%	High 95%		
Didelphis aurita					
	Omnivores	0.07	0.46	0.27	0.26
	Predators	0.08	0.41	0.26	0.26
	Herbivores	0.00	0.10	0.01	0.04
	Detritivores	0.02	0.33	0.19	0.18
	Vertebrates	0.04	0.39	0.21	0.22
	Fruits	0.00	0.09	0.01	0.03
	Nitrogen SD	0.00	0.77	0.07	0.30
	Carbon SD	1.41	3.66	2.26	2.47
Metachirus nudicaudatus					
	Omnivores	0.04	0.44	0.26	0.25
	Predators	0.08	0.44	0.26	0.27
	Herbivores	0.00	0.11	0.01	0.04
	Detritivores	0.01	0.33	0.14	0.17
	Vertebrates	0.03	0.41	0.22	0.23
	Fruits	0.00	0.10	0.01	0.04
	Nitrogen SD	0.00	0.95	0.10	0.38
	Carbon SD	1.17	3.88	2.29	2.45

Table A4. Nestedness (NODF) and Modularity (Q) values for *Didelphis aurita* and *Metachirus nudicaudatus* individual-resource networks. *Raw*: network analysis without grouping recaptures; *season*: network analysis grouping recaptures within seasons. *Spring, Summer, Autumn* and *Winter:* are network analysis for the respective season.

		Observed	**CI 95%**	
			Lower	Upper
NODF				
	raw	44.74	45.40	49.04
	season	48.37	47.83	52.90
	spring	63.02	59.65	66.68
	summer	63.99	60.57	65.76
	autumn	42.68	31.63	46.42
	winter	44.76	42.08	48.57
Q				
	raw	0.33	0.31	0.33
	season	0.30	0.28	0.31
	spring	0.24	0.23	0.26
	summer	0.29	0.27	0.31
	autumn	0.33	0.30	0.36
	winter	0.34	0.32	0.36

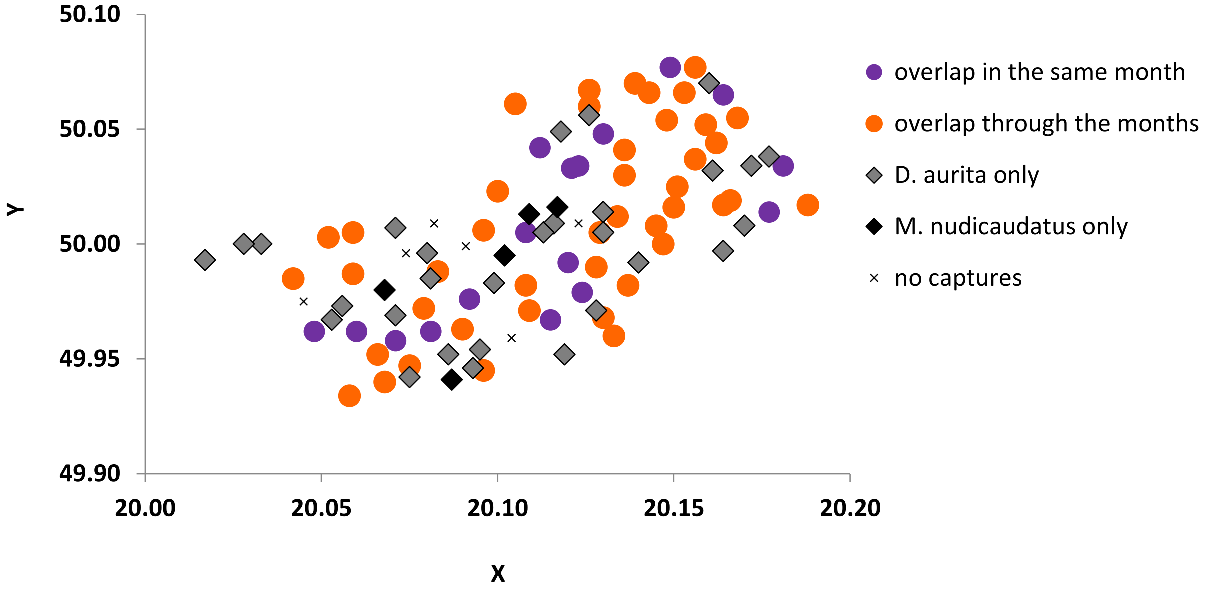
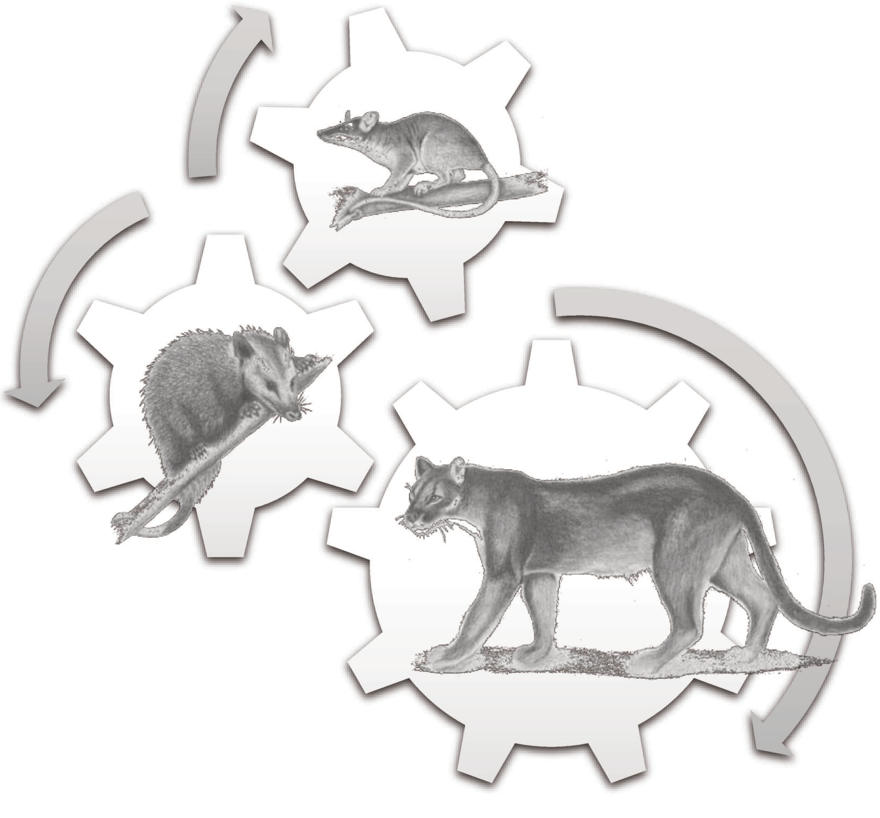


Figure A1. ***Didelphis aurita*** **and** ***Metachirus nudicaudatus*** **spatial use of the grid area over two years of study.** Each point in the graph represents the coordinates of a sample station: X axis represents minutes and seconds of South degree (23°S) and Y axis represents minutes and seconds of West degree (44°W). *D. aurita* n=334 and *M. nudicaudatus* n=127. Purple represents the sample stations that captured both *D. aurita* and *M. nudicaudatus* within trapping sessions. Orange represents the sample stations that captured *D. aurita* or *M. nudicaudatus* in different trapping sessions. Grey represents the sample stations that have captured only *D. aurita* and black represents the sample stations that have captured only *M. nudicaudatus*. Exes represents the sample stations that have never captured any individual.

Capítulo 2

Realized trophic niche driven by apparent competition: an example with marsupials



Realized trophic niche driven by apparent competition: an example with marsupials

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Abstract

According to apparent competition theory, the presence of two species that share the same predators affect each other's population growth and abundance. However, as a result of habitat loss and over-hunting, top predators are being made rare worldwide. Taking into account that apparent competitors share the same resources, we would expect the absence of top predators control to lead to changes on their respective realized trophic niches. To test our hypothesis, we developed a model to predict the abundance ratio of apparent competitor species based on changes in their realized trophic niches. We tested our model against field data on the marsupials *Didelphis aurita* and *Metachirus nudicaudatus*. It was evident that *D. aurita* and *M. nudicaudatus* are two species under apparent competition and that their realized trophic niche and diet overlap change according to the presence of top predators. The model was able to predict the actual relative abundances of *D. aurita* and *M. nudicaudatus* in the three empirical studies analyzed. Our study shows quantitative support to the apparent competition theory, however, the model's applications to other groups still need to be verified. In conclusion, our work shows that the lack of top predators has consequences not only on prey abundance, but also on their realized trophic niches. Therefore, it is becoming increasingly evident that conservation plans for top predator species are of great ecological importance.

Introduction

Hutchinson (1957) described niche as a *n*-dimensional hypervolume where each axis corresponds to a requirement for the species, with one of them corresponding to its resource requirements (i.e., trophic niche). According to Hutchinson's (1957) niche classification, the full range of resources that a species can explore, according to its morphology, physiology and behavior, constitutes its fundamental niche. However, constraints arising from interspecific competition force the individual to explore only a portion of its fundamental niche – that portion is its realized niche. Thus, the actual diet of a species is its realized trophic niche (Pekár and Addad 2011), and it can shift according to changes in ecological processes (Bearhop et al. 2004).

Top predators exert a controlling influence on species at the next lower level and so forth down the trophic ladder (Terborgh et al. 1999, Greenville et al. 2014). When two species share a common predator, the presence of either species can reduce the population density of the other species in equilibrium (i.e., apparent competition, Holt 1977). However, top predators are diminishing worldwide as a result of human activity. To our knowledge, little is known of the impacts on the realized trophic niche of two apparent competitors when top predators become extinct.

In Brazil, most top predators have not resisted the pressures of habitat loss and over-hunting, and are now absent in many mammal communities (Chiarello 1999, Prist et al. 2012). If the diversity and abundance of top predator species decreases, the remaining non-game species become more abundant. For example, in the Brazilian Atlantic Forest, the marsupial *Didelphis aurita* (Wied-Neuwied 1826, according to Cerqueira and Lemos 2000) is more abundant in areas where carnivore (i.e., members of the order Carnivora) predators are missing, suggesting that this species has the potential to increase dramatically in the absence of predators (Fonseca and Robinson 1990).

Didelphis aurita is the most common marsupial in Brazil, and co-occurs with many other marsupial species, like *Metachirus nudicaudatus* (Desmarest 1817). These two sympatric marsupials have similar habits: they are mainly terrestrial, nocturnal, solitary, and have similar diets (Santori et al. 1995, Grelle 2003, Cáceres 2004, Santori et al. 2012). However, *M. nudicaudatus* is around three times smaller than *D. aurita* (Eisenberg and Redford 1999). Probably given the difference in weight, large predators, like cougars, prefer to prey on *D. aurita* rather than *M. nudicaudatus* (Martins et al. 2008, Rocha-Mendes et al. 2010).

Although being sympatric species, different studies have shown that *D. aurita* and

M. nudicaudatus are not found in similar population levels. In areas where top predators were absent, the population level of *D. aurita* was higher than that of *M. nudicaudatus* (Fonseca and Robinson 1990, Santori et al. 1995), whereas in areas where the predator species were present, the opposite scenario of population levels was found (Fonseca and Robinson 1990, Bergallo 1994, Cáceres 2004). In this scenario, our hypothesis is that both species are in apparent competition and, therefore, the absence of predators has an effect on their realized trophic niches. To test our hypothesis, we developed a model to predict the proportional abundances of *D. aurita* and *M. nudicaudatus* based on changes in their realized trophic niches and examined it with field data. Our results demonstrate that top predators not only affect their prey's abundance, but also their resource use.

Material and methods

Our analysis was based on the Lotka-Volterra competition model (Lotka 1932, Volterra 1926). We built a model that considers a system where the two competing species, *Didelphis aurita* (D) and *Metachirus nudicaudatus* (M), co-exist and whose population growth rate is depressed by both intraspecific and interspecific competition. As in the Lotka-Volterra competition model, we assume there is no age or genetic structure to the populations, no migration, no time lags, limited supply of resources, constant competition coefficients and carrying capacities, and linear density dependence (Lotka 1932, Volterra 1926).

In this scenario, the population dynamics of the two species take the following forms (the parameters in the system are specified in Table 1):

$$\frac{dD}{dt} = r_D D\left[\frac{K-\left(D+\frac{a}{x}M\right)}{K}\right] \quad \text{(Equation 1)}$$

$$\frac{dM}{dt} = r_M M\left[\frac{xK-(M+bxD)}{xK}\right] \quad \text{(Equation 2)}$$

These equations represent the logistic growth of each species in the presence of the other and can be understood as follows: if M = 0, i.e., if *D* is the only species in the area, its population grows at rate rD and reaches the carrying capacity K. However, the presence of M decreases the resources that are available to D by the amount aM/x, where a is the proportion of *D. aurita* trophic niche that overlaps with that of *M. nudicaudatus* and x is the ratio of *D. aurita* to *M. nudicaudatus* body mass. Taking into consideration that *D. aurita* has about three times the body mass of *M. nudicaudatus* (Eisenberg and Redford 1999), we fixed x = 3. Therefore, it takes three *M. nudicaudatus* to consume the resources of one *D. aurita*.

The equation for M follows the same reasoning; however, the carrying capacity of the environment for *M. nudicaudatus* was also calculated considering the body mass ratio between the two species (x). We assumed that the environment supports x times more *M. nudicaudatus* individuals than *D. aurita*. Thus, if the carrying capacity of *D. aurita* is K*,* the carrying capacity for *M. nudicaudatus* is given by xK.

Trophic niche overlap was calculated using field data from three case studies (Santori et al. 1995, Cáceres 2004, Kuhnen *supplementar material*). The proportion of *D. aurita's* trophic niche overlapped by *M. nudicaudatus* (coefficient a) was calculated by dividing the number of items present in the diet of both *D. aurita* and *M. nudicaudatus*, by the total number of items in *D. aurita*'s diet. The proportion of *M. nudicaudatus*'s trophic niche overlapped by *D. aurita*'s (coefficient b) was calculated dividing the number of items present in the diet of both *D. aurita* and *M. nudicaudatus*, by the total number of items in *M. nudicaudatus* diet.

A key assumption of the model is that the constants a and b, that describe the niche overlaps between M and D, depend on the abundance of top predators. In areas where top predators are abundant, *D. aurita*'s abundance should decrease; therefore, the chances of a *M. nudicaudatus* individual to access that niche's food resource increases. Our prediction is that, in the absence of top predators control, the abundance of *D. aurita* will grow, increasing the chances of a *D. aurita* individual to access a food resource before a *M. nudicaudatus*. Thus, the proportion of *M. nudicaudatus*'s trophic niche overlapped by *D. aurita* (coefficient b) will increase with the decrease of the top predator's abundance (Fig. 1A). In an opposite scenario, where top predators are present, the proportion of *D. aurita*'s trophic niche overlapped by *M. nudicaudatus* (coefficient a) is going to increase, following the top predators' abundance (Fig. 1B).

Assuming that the populations of *D. aurita* and *M. nudicaudatus* were in equilibrium, we may set the time derivatives to zero in equations (1) and (2) and find the abundances of both species:

$$\mathrm{D} = \frac{\mathrm{K}}{\mathrm{x}^2} \quad \text{(Equation 3)}$$

$$\mathrm{M} = \left(\frac{1-\mathrm{b}}{1-\mathrm{a}}\right)\frac{\mathrm{K}}{\mathrm{x}} \quad \text{(Equation 4)}$$

In order to verify if the population abundances of *D. aurita* and *M. nudicaudatus* change depending on the presence of top predators, we calculated the proportion of each species population abundances based on equations 3 and 4, which becomes:

$$\frac{D}{M} = \frac{1}{x}\left(\frac{1-a}{1-b}\right) \quad \text{(Equation 5)}$$

To test if our model is able to predict the actual relative abundances, we used three case studies of *D. aurita* and *M. nudicaudatus* populations. The first study was conducted by Santori et al. (1995) at Barra de Maricá, Rio de Janeiro state, in southeast Brazil (22°57'S and 42°51'W). The main vegetation type is *Restinga*, a mosaic of plant communities that occupies the sandy plains formed by marine deposits (Cerqueira et al. 1993). Despite being preserved, the location is surrounded by urban areas and is therefore indirectly and directly affected by human activity. Thus, its mammalian community is depauperated, with most top predator species being absent.

The second study was conducted by Cáceres (2004) at Itapoá, Santa Catarina state, in southern Brazil (26°05'S and 48°50'W). The main vegetation type is lowland Atlantic Rain Forest. The area is well preserved and has a rich mammal community with most top predator species being present (Quadros and Cáceres 2001). The third study has intermediate top predator diversity. The study was conducted by Kuhnen (for methodology see Supplementary material Appendix - SM), carried out at Ubatuba, São Paulo state, in southeast Brazil (23°20’S and 44°49’W). The main vegetation type is lowland Atlantic Rain Forest. The area is preserved and has a diverse community of plants (Eisenlohr et al. 2013). However, it has a historical context of hunting by local people (Marques 2004). Therefore, the top predators *Panthera onca* (Linnaeus 1758) and *Puma concolor* (Linnaeus 1771) are missing. The ocelot *Leopardus pardalis* (Linné 1758) is registered in the area; however, other predators like small felids, tayras and crab-eating foxes, despite not being registered, may occur in low densities.

For the three case studies, we calculated coefficients a and b and estimated the proportion of each species’ population abundance in order to compare with the proportion found by the authors. It is relevant to bear in mind that diet determination through fecal analysis does not allow identification to species level. Therefore, subtle diet differences may have passed undetected and in cases where the values of a and b were equal, we adopted 0.99 instead of 1, thus rejecting full resource overlap.

Finally, we fixed the ratio of *D. aurita* to *M. nudicaudatus*’s body mass (x) at three and defined C equal to $^{D}/_{M}$. With these changes, we were able to transform the equation for the proportion of the species population abundances (Eq. 5) into a linear function, which becomes:

$$b = 1 - \frac{1}{3C} + \frac{a}{3C} \quad \text{(Equation 6)}$$

Through this equation it is possible to investigate the proportion of *D. aurita* and *M. nudicaudatus* population abundances according to the trophic niche's overlap parameters (a and b).

Results

The coefficient values for trophic niche overlap (a and b) for Santori et al. (1995), Cáceres (2004) and Kuhnen (SM) were 0.526/0.900, 0.769/0.666 and 0.600/0.923, respectively. The proportions of the species' population abundances found by the authors in all three case studies were very similar to the values predicted by the model (Table 2). In Cáceres (2004), where top predators were present, the proportion of *D. aurita* in relation to *M. nudicaudatus* was very low if compared to Santori (1995), where top predators were absent. In Kuhnen (SM) the values found for the coefficients of competition and proportion of abundances were very similar to Santori et al. (1995).

Exploring equation 6 with different proportions of population abundances (C), it was possible to observe that there are different values of trophic niche overlap (a and b) that lead to the same value for the proportion of *D. aurita* and *M. nudicaudatus* population abundances ($^{D}/_{M}$). Figure 2 shows how the same value of $^{D}/_{M}$ (represented by a line) is obtained from different values of trophic niche overlap parameters (a and b). However, any change in the proportion of *M. nudicaudatus* trophic niche overlapped by *D. aurita* (b) is followed by changes in $^{D}/_{M}$ with a positive correlation: when b decreases $^{D}/_{M}$ also decreases, with the opposite also being true. This relationship can be analyzed with two different perspectives: the proportion of *M. nudicaudatus* trophic niche overlapped by *D. aurita* (b) is the critical parameter to define $^{D}/_{M}$; or, the proportion of *D. aurita* and *M. nudicaudatus* population abundances ($^{D}/_{M}$) is what affects the *M. nudicaudatus* trophic niche overlapped by *D. aurita* (b). In our point of view, the last perspective is more reasonable as it is in accordance with the theory of apparent competition.

Discussion

Our model was able to predict the same *Didelphis aurita* and *Metachirus nudicaudatus* relative abundances as found in the three empirical studies analyzed. Besides, according to our model, changes in *D. aurita* abundance have a direct impact on trophic niche overlap with *M. nudicaudatus*. Therefore, this shows that the two species are apparent competitors and that top predators' abundances have an extreme influence on driving their ecological interactions.

The first model of apparent competition was built in the late 70's (Holt 1977). It demonstrated that predators can mimic the effect of exploitative interspecific competition by reducing the abundance of species sharing a predator. Since then, apparent competition continues on evidence (e.g. Abrams and Chen 2002, Serrouya et al. 2015) and several models have been built for the most different systems (e.g. Thomas et al. 1997, Yamamura 2007). With our model we could support the notion, theoretically and empirically, that top predators have an effect on the population abundances of their prey and also on their realized trophic niches. A key feature of our approach is that our model was based on parameters easily obtained in the field: prey species' abundance and diet.

The dominance of *D. aurita* in areas without top predators is consistent with the mesopredator release theory: the decline of top predators would result in the ecological release of mesopredators (smaller carnivores), that are the main predators of small vertebrates (Crooks and Soulé 1999, Letnic et al. 2011). Our results support the idea that top predators would be responsible for limiting populations of *D. aurita*, which could otherwise become overabundant. However, even when a top predator species is present in a certain area, if the predator community is depleted, *D. aurita* dominance will not be controlled. Fonseca and Robinson (1990) found *D. aurita* to be relative more abundant in areas with low diversity of predators; and in Kuhnen's area (SM), where the ocelot was the only carnivore registered, the proportion of *D. aurita* and *M. nudicaudatus* abundances and trophic niche overlap had the same pattern as that of Santori et al. (1995), a defaunated area. As in Aristotle's (1893) quote, "one swallow does not make a summer", the sole presence of ocelots may not be able to sustain the equilibrium of the ecosystem.

Besides the influence of top predators on prey abundances, their influence on the prey trophic niches remains poorly understood. According to competitive release theory, a consumer can expand its niche in the absence of a larger competitor; therefore, we would expect that changes in prey abundance would reflect on its realized trophic niche (Brown and Wilson 1956, Moreno et al. 2006, Morlon et al. 2014). Dickman's (1986) experiment with marsupials demonstrated that the breadth of resources used by non-dominant species generally increased when numbers of the dominant species reduced, and decreased when the numbers increased. This result could support the idea of how top predators can affect their prey's realized trophic niche if we compare this artificial reduction to predation by top predators. Our results support this idea: an increase in *D. aurita* abundance has a greater influence on its trophic relationship with *M. nudicaudatus* when the ratio of their population abundances ($^{D}/_{M}$) is greater than one. Therefore, when this proportion is larger than one, a small increase in *D. aurita*'s abundance has a higher effect on the proportion of *M. nudicaudatus*'s trophic niche overlap with *D. aurita* (b) than when it is smaller than one. Besides that, when the proportion is smaller than one and *D. aurita* abundance increases, it generates a higher impact on *D. aurita* trophic niche overlap with *M. nudicaudatus* (a).This highlights how ecologically important are top predators in controlling the abundances of *D. aurita* and other mesopredators.

Although top predator effects, mesopredator release, and food web connections are all related, it is very difficult to conduct field experiments with mammals that cover all of these levels. These experiments face certain challenges, such as the spatial scale of such systems, less tractable organisms, and societal concerns for animal welfare (Garrott et al. 2008). These challenges faced by mammal researchers are probably the reason why it was so hard to find more studies on *D. aurita* and *M. nudicaudatus* with data on the local carnivore predator community, local prey abundance and prey diet - even though both species are relatively common in Brazil. Most studies on apparent competition of mammals are mainly focused on the effects of predator-mediated change on the prey's population density (Harrington et al. 1999, Robinson et al. 2002, Wittmer et al. 2005, DeCesare et al. 2010). That is probably a consequence of the challenge in quantifying interactions among intra and inter-trophic species and the variety of parameters required for theoretical models, such as: carrying capacity, attack rate of focal species and intrinsic rates of resource (*e.g.* Holt 1977, Chesson and Kuang 2008). Thus, models should be as simple as possible and take into account the difficulties in obtaining field data. Models can be very useful, but if parameters cannot be obtained, they are nothing more than assumptions.

In conclusion, our work finds evidence to support the idea that top predators play an important role in structuring the abundances of their prey. For now, our model was tested only for *D. aurita* and *M. nudicaudatus* populations while its application to other groups still needs to be verified. Our study also shows that top predator absence directly impacts the realized trophic niche of its prey. However, the model still needs improvements in order to understand other consequences caused on different ecological processes by the lack of top predators. Besides, it is becoming increasingly evident that conservation plans for top predator species are of great ecological importance.

Acknowledgements

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Table 1. Parameter definitions in the dynamical equations (1) and (2).

Parameter	Definition
D	population abundance of *Didelphis aurita*
M	population abundance of *Metachirus nudicaudatus*
r_D	intrinsic growth rate of *D. aurita*
r_M	the intrinsic growth rate of *M. nudicaudatus*
a	proportion of *D. aurita* trophic niche overlapped by *M. nudicaudatus*
b	proportion of *M. nudicaudatus* trophic niche overlapped by *D. aurita*
x	ratio of *D. aurita* to *M. nudicaudatus* bodies mass
K	carrying capacity for *D. aurita*
xK	carrying capacity for *M. nudicaudatus*
x/a	effect of *M. nudicaudatus* on the growth of *D. aurita*
bx	effect of *D. aurita* on the growth of *M. nudicaudatus*

Table 2. Proportion of *Didelphis aurita* (D) and *Metachirus nudicaudatus* (M) population abundances predicted by the model and found in three case studies conducted in different scenarios of top predator presence.

Top predator presence	**Proportion of abundances ($^D/_M$)**		**Case study**
	predicted by the model	found by the authors	
Absent	1.58	1.82	Santori 1995
Present	0.23	0.21	Cáceres 2004
Low densities	1.73	1.84	Kuhnen (SM)

Figure captions

Figure 1. Diagram showing apparent competition effects between *Didelphis aurita* and *Metachirus nudicaudatus* under presence (A) and absence (B) of top predators. Letter b represents the proportion of *D. aurita* trophic niche overlapped by *M. nudicaudatus* and a represents the proportion of *M. nudicaudatus* trophic niche overlapped by *D. aurita*. The arrows' width represents the overlap's extent. Original artwork: Marcos Almir Polettini.

Figure 2. The proportion of *Didelphis aurita* and *Metachirus nudicaudatus* population abundances ($^{D}/_{M}$) in function of trophic niche overlap parameters. Letter a represents the proportion of *D. aurita* trophic niche overlapped by *M. nudicaudatus* and b represents the proportion of *M. nudicaudatus* trophic niche overlapped by *D. aurita.* The number on each line represents the $^{D}/_{M}$ value. Circle represents a and b values for Santori (1995) data; square for Cáceres (2004) data, and triangle for Kuhnen (SM) data.

Fig. 1

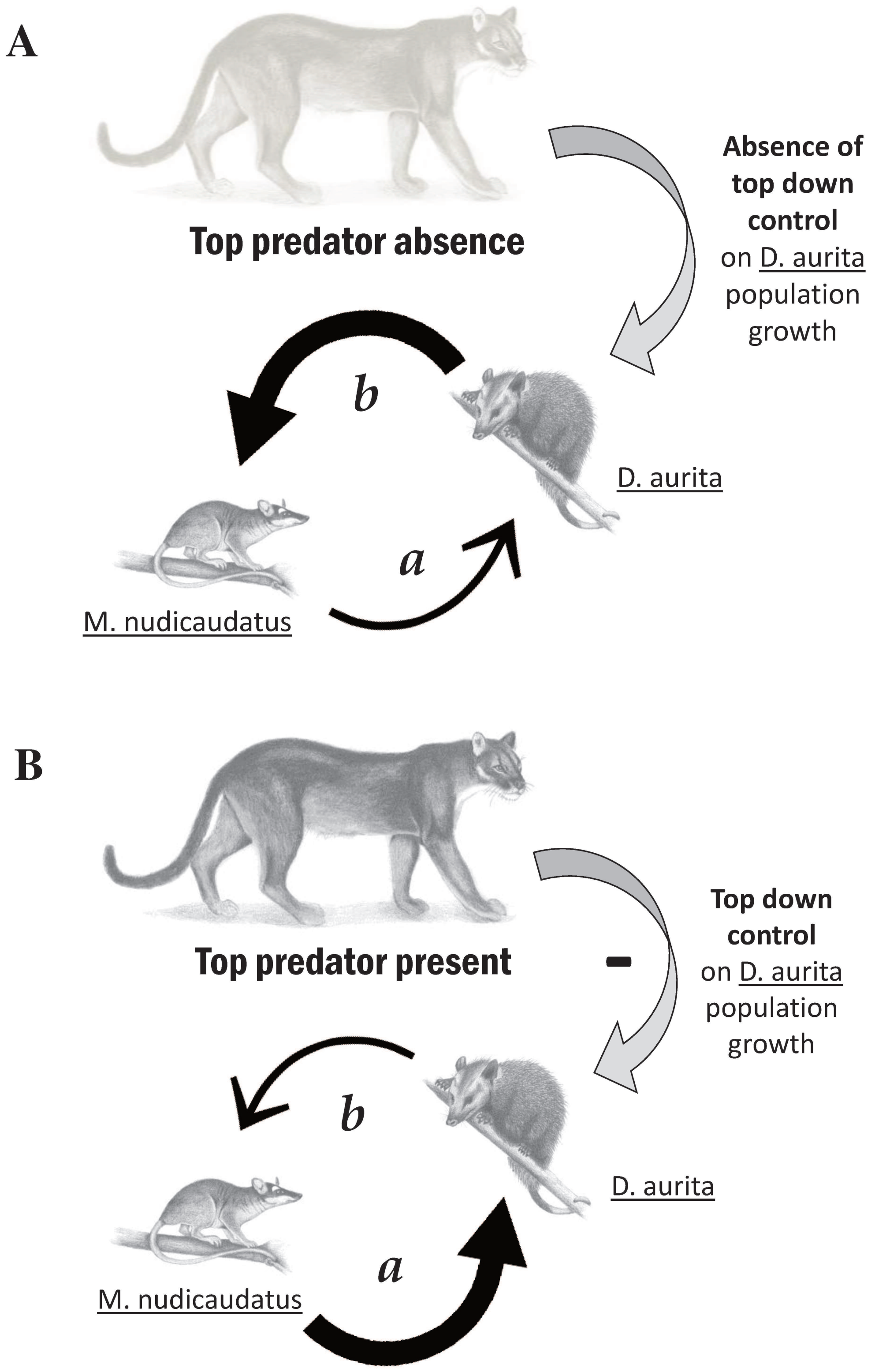
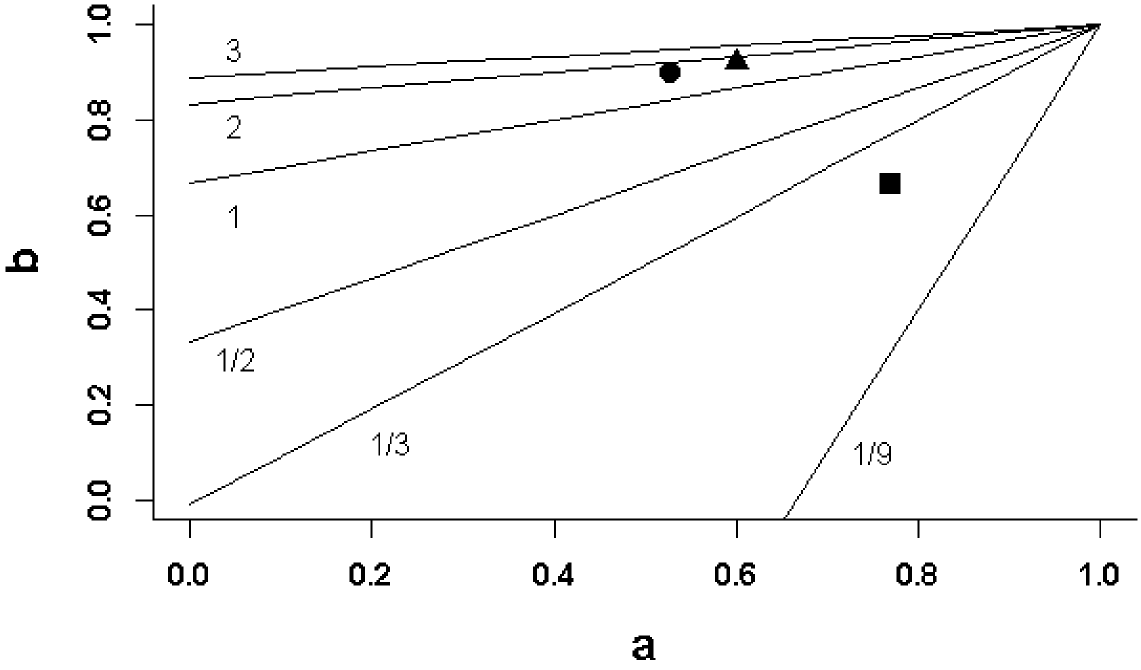

A
Top predator absence
Absence of top down control on D. aurita population growth
b
D. aurita
a
M. nudicaudatus
B
Top predator present
-
Top down control on D. aurita population growth
b
D. aurita
a
M. nudicaudatus

Fig. 2



Supplementary Material Appendix

The study was conducted in an Atlantic Rainforest area, in the Serra do Mar State Park (23°20’S and 44°50’W), southeast of Brazil (São Paulo State coast), at altitudes between 43 and 89m asl (Eisenlohr et al. 2013). A trapping session of four consecutive nights was conducted monthly from October 2013 to November 2014. In order to capture the animals we used one hundred Tomahawk traps (45×16×16 cm) on the ground, baited with banana, peanut butter, and bacon. The traps were 20 m apart from each other, forming a 3.4 ha grid (280m x120m).

Individuals captured were marked in each ear with one 1-g monel ear tag (National Band and Tag Co.®), weighted, and identified by sex and age (Tyndale-Biscoe and MacKenzie 1976). Samples of scats were collected from adults only. Scats were collected from the bottom of the trap where the animal spent the night. The traps were placed on a platform of hardboard in order to isolate the scats from litter. Feces samples were dissolved in water and then filtered through a 1mm mesh screen sieve under running tap water. Then the material retained on the sieve was dried at ambient temperature. This undigested material was analyzed with a stereoscope and the taxonomic classification of the prey items found was done by specialists.

During three months of the study (from July to September 2014) four camera traps (Tigrinus®) were placed in the grid to survey the location’s potential marsupial predators. The cameras monitored each site for 24 continuous hours for 30 days, after which they were moved to a new site within a minimal distance of 50 meters. Two of the four sites were randomly selected to receive Bobcat lure (Carman®).

After one year of trapping sessions (48 nights of trapping, 4800 trap-nights) we recorded 35 individuals of *Didelphis aurita* and 19 individuals of *Metachirus nudicaudatus.* Thirty-two fecal samples were collected from 15 adults of *M. nudicaudatus*, and 38 fecal samples were collected from 18 adults of *D. aurita*. Their diet items are described in table A1. The only predator registered by the camera traps was the Ocelot (*Leopardus pardalis*, Linnaeus, 1758) and only in two of the 12 sites. Other species registered were the Azara’s agouti (*Dasyprocta azarae*, Lichtenstein 1823), the Southern tamandua (*Tamandua tetradactyla*, Linnaeus, 1758), and the Armadillo (*Dasypus novemcinctus*, Linnaeus, 1758).

Table A1. Occurrence of food items (1 = present, 0 = absent) found in *Didelphis aurita* and *Metachirus nudicaudatus* fecal samples. (n.i. = not identified)

	Didelphis aurita	***Metachirus nudicaudatus***
Vertebrates		
Mammalia	1	0
Aves	1	0
Reptilia	1	1
Vertebrate n.i.	1	0
Invertebrates		
Araneae	1	1
Pseudoscorpiones	1	0
Crustacea	1	1
Myriapoda	1	1
Coleoptera	1	1
Hymenoptera	1	1
Calliphoridae	1	0
Orthoptera	1	1
Lepidoptera	1	0
Isoptera	0	1
Cicadidae	1	1
Neuroptera	1	0
Fruits		
Annonaceae	1	1
Piperaceae	1	1
Poaceae	1	1
Campomanesia sp.	1	0
Fruit n.i.	1	1

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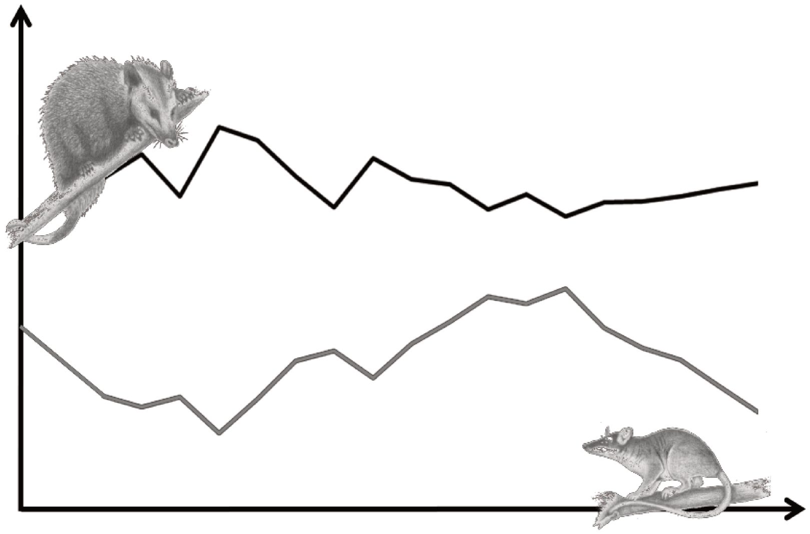
Capítulo 3

Density-dependence relationship between two Neotropical marsupials



LRH: Kuhnen, Wedekin, Setz

RRH: Marsupials Density-Dependence Relationship

Density-dependence relationship between two Neotropical marsupials

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Abstract

Didelphis aurita and *Metachirus nudicaudatus* are two sympatric Neotropical marsupials with very similar ecological requirements. Both have similar diets, are solitary, nocturnal, and terrestrial. *Didelphis aurita* is about three times the size of *M. nudicaudatus*, and is a mesopredator of Brazilian Atlantic Forest. Considering that and its similarity with *M. nudicaudatus*'s ecological requirements, our hypothesis is that the abundance of *D. aurita* may negatively affect *M. nudicaudatus*'s population. To test this hypothesis we conducted a two year capture-mark-recapture study with populations of these species in an area were top predators community is depauperated, in the Southeast of Brazil. Supported models indicated that *D. aurita* demographic parameters showed subtle oscillations over the study period. Apparent survival probability was the only parameter that fluctuated, and could be affected either by temperature or litterfall. The temporal fluctuation of *D. aurita*'s abundance was the only covariate that fitted to all *M. nudicaudatus* demographic parameters. Rainfall was the only environmental covariate that fitted *M. nudicaudatus*' time series, but only to apparent survival in two of the eight models selected. Thus, we suggest that, at least in a small time scale, the interspecific relationship with *D. aurita* seems to be more relevant to drive *M. nudicaudatus*' population than any other environmental covariate. In conclusion, we suggest that *M. nudicaudatus* has a close density-dependence relationship to *D. aurita*. Our findings have important implications for a better understanding of interspecific interactions and were consistent with the hypothesis that mesopredator release will affect its competitors' dynamics.

Key words: apparent competition; Brazil; *Didelphis aurita*; interference; *Metachirus nudicaudatus*; POPAN; population dynamic; tropical rain forest.

Resumo

Didelphis aurita e *Metachirus nudicaudatus* são dois simpátricos marsupiais Neotropicais, com exigências ecológicas muito semelhantes. A dieta de ambos é semelhante, são solitários, noturnos, e terrestres. *Didelphis aurita* é considerado um dos mesopredadores da Mata Atlântica brasileira. Considerando isso, e sua semelhança com *M. nudicaudatus*, nossa hipótese é que a abundância de *D. aurita* afete negativamente a população de *M. nudicaudatus*. Para testar esta hipótese foi realizado um estudo de captura-marcação-recaptura durante dois anos em uma área no sudeste do Brasil, onde a comunidade de predadores de topo é empobrecida. Os modelos selecionados indicaram que os parâmetros demográficos de *D. aurita* oscilaram sutilmente ao longo do tempo. A sobrevivência aparente foi o único parâmetro que flutuou, podendo ser relacionada tanto à temperatura quanto à serrapilheira. A flutuação da abundância de *D. aurita* foi a única co-variável selecionada para todos os parâmetros demográficos de *M. nudicaudatus*. A precipitação foi a única covariável ambiental selecionada, mas apenas para a sobrevivência aparente e em dois dos oito modelos seleccionados. Assim, sugerimos que, pelo menos em uma curta escala de tempo, a relação interespecífica com *D. aurita* parece ser mais relevante para a população de *M. nudicaudatus* do que qualquer outra co-variável ambiental. Em conclusão, sugerimos que *M. nudicaudatus* tem uma estreita relação de densidade-dependência com *D. aurita*. Nossos resultados têm implicações importantes para a compreensão das interações interespecíficas e é consistente com a hipótese de que a overabundância de mesopredadores afeta diretamente a dinâmica populacional de seus competidores.

POPULATION DYNAMICS IS A CENTRAL GOAL OF POPULATION ECOLOGY AND IT IS RELATED TO HOW populations oscillates (Turchin 2003). These dynamics encompass different parameters that interact to generate complex patterns of animal abundance over time and space. Some of those parameters are: population structure (*e.g.*, age distribution), movements, survival, recruitment and fecundity (Begon *et al.* 1996). Understanding the dynamics of populations over time is invaluable to solve many ecological problems (Hastings 2010), such as: the consequences of shifts in global climate patterns (Sillett *et al.* 2000, Bromaghin *et al.* 2015), development of population management programs (López-Parra *et al.* 2012), evaluation of impacts of non-native species introduction on local populations (Chantrey *et al.* 2014), and habitat fragmentation (Riley *et al.* 2014).

Several factors affect fluctuation of population parameters through time, which are divided into two kinds: I) Density-independent or environmental factors, for instance: seasonality, weather, climate (Lima *et al.* 2001), resource availability (Lobo & Millar 2013), and environmental disturbance; II) Density-dependent factors (Intra and interspecific interactions), such as: diseases (Strauss *et al.* 2012), bottom–up and top–down mechanisms (Sinclair & Krebs 2002), and also by intra or interspecific competition. Competition occurs when one individual prevents another from exploiting the resources within a portion of the habitat (*interference*); or when they do not interact directly, but each individual is affected by the amount of resource that remains after that resource has been exploited by others (*exploitation*) (Birch 1957). Here, we investigated the factors that may be affecting fluctuation on population dynamics of two sympatric marsupial species from the Atlantic Rain Forest, *Didelphis aurita* (Wied-Neuwied 1826) and *Metachirus nudicaudatus* (Desmarest 1817).

Didelphis aurita is one of the largest marsupials of the neotropical region (Salvador *et al.* 2009). The species distribution is associated to the Atlantic Rain Forest domain, with records from northeastern Brazil to Paraguay and northern Argentina (Gardner & Dagosto 2007). Marsupials from *Didelphis* genus have the most generalist diet within the Neotropical marsupials (Santori *et al.* 2012). *Didelphis aurita* preys on small vertebrates, invertebrates and also consume fruits (Cáceres & Monteiro-Filho 2001, Casella 2011). Its diet is similar to the marsupial *M. nudicaudatus* that co-occurs in the Atlantic Rain Forest (Santori *et al.* 1995, Carvalho *et al.* 1999, Cáceres 2004, Lessa & Costa 2010). Both species are solitary, nocturnal and terrestrial. *Metachirus nudicaudatus* is considered exclusiely terrestrial, whereas *D. aurita* could either use all forest strata or be predominantly terrestrial, depending on the habitat (Grelle 2003, Vieira and Monteiro-Filho 2003, Vieira and Camargo 2012). *Metachirus nudicaudatus* is the largest Neotropical marsupial without pouch, nonetheless, it is around three times smaller than *D. aurita* (Eisenberg & Redford 1999). Probably because of the difference in weight, large predators, like cougars, seem to prefer preying on *D. aurita* rather than *M. nudicaudatus* (Martins *et al.* 2008, Rocha-Mendes *et al.* 2010). Consequently, in areas where top predators are absent, *D. aurita* is abundant (Fonseca & Robinson 1990, Santori *et al.* 1995). In addition, in areas where the predator species are present, the population level of *D. aurita* was lower than *M. nudicaudatus* (Fonseca & Robinson 1990, Bergallo 1994, Cáceres 2004).

Considering *D. aurita* a mesopredator and its similarity with *M. nudicaudatus*'s ecological requirements, our hypothesis is that, the overabundance of *D. aurita* may negatively affect *M. nudicaudatus*'s population. Thus, we investigated the population parameters of both species in an area with a depauperated carnivores' (i.e., members of the order Carnivora) community. Specifically, we tested if the oscillations of *M. nudicaudatus*'s parameters over time are determined by *D. aurita*'s abundance, rather than other covariates.

METHODS

STUDY AREA. —The study was conducted in the Atlantic Rainforest, in Serra do Mar State Park (23°20'S and 44°50'W), southeastern Brazil (São Paulo State coast). The Park is the largest protected Atlantic Rainforest remnant in Brazil, comprising more than 300,000 ha of well preserved rainforest (Ribeiro *et al.* 2009). The studied area is located 35 km away from the urban area of Ubatuba city, and 2 km from a small village (*Sertão da Fazenda*) (23°20' S, 44°50' W). There are approximately fifty families living in the village and the main economical activity is ecotourism.

The site is characterized as lowland tropical evergreen forest, following Veloso *et al.* (1991). For a full description of the forest classification and structure see Alves *et al.* (2010) and Eisenlohr *et al.* (2013). The altitude ranges from 43 to 89 m asl (Eisenlohr *et al.* 2013). The regional climate is Tropical Humid, with no dry season and hot summers (Af/Cfa according to Köppen 1948). Average annual precipitation is 2,500 mm, and monthly average temperature is 22°C (CIIAGRO 2015).

TRAPPING DESIGN. —A trapping session of four consecutive nights was conducted monthly from May 2013 to April 2015. The animals were captured using one hundred Tomahawk traps (45×16×16 cm), all baited with banana, peanut butter and bacon. The traps were 20 m apart from each other, forming a 3.4-ha grid (280 × 120 m). Every morning the traps were checked, individuals captured were marked in each ear with one 1-g monel ear tag (National Band and Tag Co.®), weighted, and their sex and age were recorded. After marking, we released the individual at the same place it was captured. Traps were permanently kept in the field and were closed when not in use.

MODELING DEMOGRAPHIC PARAMETERS. —Demographic parameters were estimated by POPAN formulation for the Jolly–Seber model of open populations (Schwarz & Arnason 1996). POPAN parameterization approach is based on the existence of a super-population (*N*). This super-population is the 'total number of animals ever in the sampled area between the first and last occasion of the study' (Nichols 2005). The four demographic parameters estimated by POPAN are: the size of the super-population (*N*); the probabilities of capture (*p*) and apparent survival (ϕ) of marked and unmarked animals, and the probability that an animal from the super-population would enter the population between two occasions (*pent*). The model also derives the number of births (*B*) and the population abundance (*n*) for each occasion.

In order to determine if demographic patterns were species dependent, we modeled each parameter to be constant over time, or as function of time, species, and the interaction between time and species. The parameter N was modeled only as a function of species. After, we ran a model selection for each species separately. At this point each parameter was modeled as constant over time, or as a function of specific covariates (Table 1). According to our hypothesis, demographic parameters could be affected by:

(1) Climatic changes (represented by temperature, *t*; rainfall, *r*; and last year's rainfall, *rb*): temperature and rainfall are known to be climatic covariates that interfere on different parameters of environment, like photosynthesis and productivity. Changes on these covariates may directly affect food resources of *D. aurita* and *M. nudicaudatus*, which would indirectly affect survival probability. Population emigration patterns would also be driven by indirect changes on food resources, interfering on the probability of super-population animals entering the sampled population (*pent*). Besides that, it has been shown that *D. aurita* and *M. nudicaudatus* population structure are influenced by last year's rainfall (Mendel *et al.* 2008, Ferreira 2011). Therefore, we included this climatic covariate. Temperature and precipitation data were obtained from CIIAGRO data base (available at http://www.ciiagro.sp.gov.br/ciiagroonline/MenuMonClim.htm);

(2) Food resource abundance (represented by litterfall covariate, *l*): the main food resource for *M. nudicaudatus* and *D. aurita* (Santori *et al.* 2012) are arthropods. The

abundance of arthropods increases linearly with net primary production (Meehan 2006) and its density is correlated to litterfall (Palacios-Vargas *et al.* 2007). Therefore, we adopt litterfall as a proxy of invertebrate's availability. Litterfall data were obtained by seventeen 0.22 m^2 litterfall traps, deployed at randomized points in the grid and at 0.5 m above ground. Samples were collected every fifteen days, kept in paper bags, labeled, and dried at 60ºC (~3-4 days). After drying, samples were weighed and the mean value of all traps was used;

(3) Seasonality (represented by seasons of the year, *s*): seasons drive many different ecological processes and marsupial's ecology may also be driven by seasonality. For example, *D. aurita* and *M. nudicaudatus*, like many other marsupial species, begin its reproduction in dry periods and lasts until the end of the rainy periods (Gentile *et al.* 2012). The seasonality of reproduction may be correlated with photoperiod, which would explain how all the mature females synchronize their reproduction (Cerqueira & Bergallo 1993). In some cases, males appear in the area mainly during the reproductive season (Cáceres 2003), which result in larger population sizes at the end, and after, rainy periods (Gentile *et al.* 2000). Therefore, it is expected that demographic parameters fluctuations follow the seasons. Although the differences between each season of the year are not evident in the area, we deaded that four seasons would be the best approach to our data. To evaluate the impact of this choice on the analysis, we also ran the model selection dividing data into only dry and wet season and found the results to be very similar;

(4) Sex differences on behavior (represented by 'males' vs. 'females', *sex*); Females and males of marsupials tend to have different behaviors. For example, males' home range can be two times larger than females' (Cáceres & Monteiro-Filho 2001, Cáceres 2003). Therefore, many captured males are not residents and may pass through the study area (Cáceres 2003). On the other hand, females move less than males and can defend territories (Cáceres 2003, Cerboncini *et al.* 2011). Besides that, movements of males and females are determined by different factors, such as resource availability and reproductive season, respectively (Loretto & Vieira 2005). Taking into account the larger home range and movement patterns of males, we would expect that: a) they are exposed to more predation risk, thus having a lower survival probability than females, b) the probability that males entered the population would be higher, c) the probabilities of capture of a male would be lower, since they do not have nutritional demands from pregnancy, or are transients in the study area;

(5) Interspecific interactions (represented by *D. aurita* estimated abundances): Considering that *D. aurita* and *M. nudicaudatus* have very similar ecological requirements,

we believe that they may interact by interference competition for food and space resources. *Didelphis aurita* is larger size and aggressiveness (Moura *et al.* 2009) probably makes him a superior competitor. If our hypothesis is correct, we would observe a negative influence of *D. aurita* abundances on *M. nudicaudatus* demographic parameters. To address this hypothesis, we used *D. aurita* abundances, estimated by POPAN models, as a covariate for *M. nudicaudatus* parameters. For *pent* and ϕ covariates we used *D. aurita* abundances from the previous month.

MODEL SELECTION. —In order to build our model set, we used the all-combination approach. In this model construction strategy, the number of models built is defined as being conditional on all possible combinations of a set of predictor variables, and a single analysis is used to identify the most favorable model (Whittingham *et al.* 2006, Murtaugh 2009, Doherty *et al.* 2012). Models were constructed using the following link functions: logit (for ϕ and p), Mlogit1 (for Pent), and log (for N) (Cooch & White 2015). POPAN formulation makes specific assumptions such as: capture probabilities are the same for all individuals (homogeneity); and all identifiable individuals have the same probability of survival between sampling; catchablity is the same for all animals (marked na unmarked); tags are read properly and the animals retain their tags throughout the experiment. For a correctly specified model, the deviance divided by the degrees of freedom, should be approximately equal to one (Cooch & White 2015). When their values are much larger than one, there is variation in excess according to the multinomial distribution and the data is said to exhibit over dispersion.

To estimate the demographic parameters of each model we used the maximum-likelihood method (Burnham & Anderson 2002), assuming a multinomial distribution over all the observed capture histories (Lebreton *et al.* 1992). The small sample size bias-corrected version of the Akaike Information Criterion (AICc) was then used to rank all models (Burnham & Anderson 2002). AICc weighs the deviance (quality of fit) and the precision (by number of estimable parameters) to select a model that best describes the data. Thus, the model with the lowest AICc value has the best fit using the fewest parameters to describe the data (Lebreton *et al.* 1992). The best-fit model has ΔAICc equal to zero, and whenever the difference of AICc between the best and other model is larger than 2 (ΔAICc > 2), we may discard the other model as a plausible explanation of the data (Burnham & Anderson 2002). However, all models with ΔAICc < 2 are considered plausible and inferred to have similar support from the data. When several models showed some support, we applied a modelaveraging procedure in which the parameters were estimated from the models with some support, proportional to their AICc weights (Burnham and Anderson 2002). We run, built, fit, and selected models using the package 'RMark' (Laake 2013) in R software, version 3.2.2 (R Development Core Team 2015).

TOP PREDATORS SURVEY. —During three months of the capture-mark-recapture study (from July to September 2014) four camera traps (Tigrinus®) were placed in the grid to survey potential marsupial predators. The cameras monitored each site for 24 continuous hours for 30 days, after which they were moved to a new site within a minimal distance of 50 meters. Two of the four sites were randomly selected to receive Bobcat lure (RussCarman®).

RESULTS

CAPTURES. — The sampled area has a depauperated mammalian community and top predators species were rare or absent. The only predator registered by the camera traps was the Ocelot (*Leopardus pardalis*, Linnaeus, 1758) and only in two of the 12 sites stations. Other mammal species registered were the Azara's-agouti (*Dasyprocta azarae*, Lichtenstein 1823), the Southern-tamandua (*Tamandua tetradactyla*, Linnaeus, 1758), the Armadillo (*Dasypus novemcinctus*, Linnaeus, 1758), and *Didelphis aurita,* which was the most photographed species.

After 9600 trap-nights, we captured 68 individuals of *Didelphis aurita* (42 males and 26 females) and 34 individuals of *Metachirus nudicaudatus* (20 males and 14 females). There was not sufficient evidence from the data to state that the sex ratios of both species was different from 1:1 (*D. aurita* – Exact binomial test, p = 0.07; *M. nudicaudatus* – Exact binomial test, p = 0.39). Overall, there was a total of 334 captures of *D. aurita*, and 127 captures of *M. nudicaudatus*.

The species ratio varied monthly but was skewed towards *D. aurita*, in general the ratio was 1.93 individuals of *D. aurita* for each individual of *M. nudicaudatus*. An average of 5.8 (range, one to 10) individuals of *D. aurita* and 2.5 (range, zero to eight) of *M. nudicaudatus* were captured each month, and mean estimated densities were 1.71 and 0.74 individuals per hectare, respectively. In both species, males were heavier than females and were also recaptured more frequently. The mean body weight for *D. aurita* was 1188 g. (± 266) for males and 994 g. (± 216) for females. Individuals of *D. aurita* were about 2.91 times heavier than of *M. nudicaudatus*. The mean body weight for *M. nudicaudatus* was 400 g. (± 87) for males and 296 g. (± 54) for females.

AURITA X META. —Model selection process for *M. nudicaudatus* and *D. aurita* combined data indicated that all demographic parameters were function of the interaction between species and time, and the super population parameter was selected as a function of species (Table S1). These results demonstrate that demographic parameters are different between the species and fluctuate distinctly in time according to the species, supporting separated analysis for each species.

DIDELPHIS AURITA DEMOGRAPHIC PARAMETERS. —Model selection process for *D. aurita* is summarized in Table 2. Due to the model uncertainty, we model-averaged the results over all models with support (ΔAICc <2). Population size fluctuated during the study period, however there was no evidence of a specific pattern in this fluctuation (Fig. 1). The model-averaged estimate for *D. aurita* super-population size was 31 females (95% CI: 29 to 33), and 53 males (95% CI: 49 to 57). Although the population's sex ratio estimation was skewed towards males, females showed to have a higher capture probability (100%) than males (75%). Supported models indicated that *D. aurita*'s survival probability showed a low variation through time (from 0.55 to 0.6), with males having a lower probability than females (Fig. 2). Model selection indicated that this parameter could be affected either by temperature, litterfall, or even to be constant. The higher probabilities of survival were observed during the wet seasons (Fig. 3). There was no evidence of any covariates affecting the probability that an individual from the super-population would enter the population between two occasions (pent). This parameter was only dependent of sex, with males being more likely (0.04 ± SE 0.001) than females (0.03 ± SE 0.004).

METACHIRUS NUDICAUDATUS DEMOGRAPHIC PARAMETERS. —Model selection process for *M. nudicaudatus* is summarized in Table 2. Due to the model uncertainty, we model-averaged the results over all models with support (ΔAICc < 2). Population size fluctuated during the study period, with peaks in abundance during the dry seasons (Fig. 1). The model-averaged estimate for *M. nudicaudatus* super-population size was 19 females (95% CI: 15 to 23), and 27 males (95% CI: 22 to 32). *Metachirus nudicaudatus*' survival probability varied according to sex, with males having a lower survival probability than females. The survival probability of *M. nudicaudatus* was lower than *D. aurita*'s and fluctuated more over time (from 0.3 to 0.6; Fig. 2). Best descriptors for this parameter were the covariates litterfall, rainfall and *D. aurita*'s abundance (Fig. 4). *Metachirus nudicaudatus*' capture probability was similar or varied according to sex, being higher to males (0.84, 95% CI: 0.56 to 0.96) than to females (0.81, 95% CI: 0.54 to 0.94). Supported models indicated that this parameter could be constant over time or be determined by *D. aurita*'s abundance. Although *M. nudicaudatus*' capture probability was significantly associated to *D. aurita*'s abundance in the respective month (Fig. 5a), when *M. nudicaudatus*' capture probability is plotted against *D. aurita*'s abundance of the earlier month, becomes evident that *D. aurita*'s abundance causes a density-dependence response on *M. nudicaudatus*' capture probability on the next month (Fig. 5b). Besides that, all supported models indicated *D. aurita*'s abundance to be the only covariate to affect the probability that an individual from the super-population would enter the population between two occasions (Fig. 6).

DISCUSSION

The studied area has an impoverished mammal community, with all large predators and most medium sized predators absent. Therefore, *Didelphis aurita* is probably one of the most important mesopredator. Probably because of the absence of top-down control, *D. aurita* is abundant in the area. Besides that, *D. aurita* demographic parameters oscillated over the two years of study, and *Metachirus nudicaudatus*'s population parameters were sensitive to this oscillation, suggesting that populations of the marsupials are coupled.

Didelphis aurita was the most frequent mammal species recorded by both camera and Toamhawk traps in our study area. High abundance of *D. aurita* was also registered in other areas with human disturbance (Gentile *et al.* 2000, Graipel & Santos-Filho 2006, Mendel *et al.* 2008), which may be an indication that the populations of *D. aurita* releases when top predators are extirpated. This process is known as *mesopredator release*, which predicts that in the absence of predators and therefore a top-down control, mid-sized predators become over abundant (Crooks & Soulé 1999, Johnson *et al.* 2007).

Sex was the covariate that influenced all demographic parameters of *D. aurita*. Although not statistically significant, the observed biased sex ratio towards males is consistent with the idea that in continuous forest areas, marsupials tend to have unequal sex ratio as a consequence of sub-adult males' dispersion (Graipel *et al.* 2006). While in small islands or in isolated forest fragments, where dispersion is unlikely, there is a balanced proportion between males and females (Cherem *et al.* 1996, Cáceres & Monteiro-Filho 1998).

Apparent survival probability was the only parameter of *D. aurita* that fluctuated through time. The higher survival probabilities observed in wet seasons, followed by litterfall and temperature covariates, was expected because resources are normally more abundant during this season. However, it is worth noting that this increase in survival probability in wet seasons could be apparent and be only a result from increased residence of individuals in the area, due to resource supply and also for being the reproductive period (Gentile *et al.* 2000, Kajin *et al.* 2008). This may also be due to an increased probability of emigrating during periods of food scarcity or outside the reproductive season. On the other hand, seasonality did not affect any other parameters. Overall, the species populations did not present a clear fluctuation pattern and this result may be due to the small time scale. Other studies with similar duration also did not find any population trend (Graipel & Santos-Filho 2006, Graipel *et al*. 2006). *Didelphis aurita* may be a species with pluriannual patterns of population fluctuation that would probably become evident only by long-term studies; or seasonal differences in climatic factors are not strong enough to induce marked patterns (Cerqueira *et al*. 1993). The uniformity observed for the probability that an individual from the super-population would enter the population is an evidence for the stability of *D. aurita*'s population.

In contrast to *D. aurita*, demographic parameters of *M nudicaudatus* presented specific patterns of fluctuation through time. Ferreira (2011) analyzed a *M. nudicaudatus* population during a long time series of 13 years and found a regular pattern of fluctuation. Her findings demonstrated that the dominant mechanism in *M. nudicaudatus* was endogenous, that is, the per-capita rate of population growth depends only on the population size (first-order negative feedback), suggesting that the population was regulated by intraspecific competition. The only climate factor observed influencing the per-capita growth rate was local rainfall with a time-lag of one year. Although *D. aurita* co-occur in the area, it was not considered by the authors as a covariate in no parameter of the population. In our analyses, *D. aurita*'s abundance was the only covariate that consistently influenced all *M. nudicaudatus*' demographic parameters according to our model selection criteria. Rainfall was the only environmental covariate that was included in the best models of *M. nudicaudatus*', but only to apparent survival (two of the eight models selected). Thus, we suggest that, at least on a short time scale, the interspecific relationship with *D. aurita* seems to be more relevant to drive *M. nudicaudatus*' population than any other environmental covariate. Different factors of perturbed areas could affect population growth of the generalist species *D. aurita*, such as: few competitors, great food availabity and abscense of predators. Fonseca and Robinson (1990) demonstrated that in larger fragments of Atlantic Rain Forest, where top predators are present, *D. aurita*'s abundances is suppressed and there is a larger population of *M. nudicaudatus*. On the other hand, in smaller fragments were top predators community is depauperated, the opposite occurs. Our results support the idea that *D. aurita*'s *mesopredator release* process might have an impact on the population dynamics of smaller predators, such as *M. nudicaudatus*, owing to interspecific competition.

The density-dependence relationship between *D. aurita* and *M. nudicaudatus* could be based on exploitation and/or interference competitions. The two species have very similar ecological requirements: both are terrestrial, nocturnal, therefore might compete for shelters; besides, their diet is similar (Kuhnen *in prep.*) which may lead to competiton for food resources. Agonistic interactions can also occurr between the species, such as direct conflicts and avoidance. It may be profitable for *M. nudicaudatus* to avoid *D. aurita* and reduce the chance of incurring injury in direct encounters. Chemical substances secreted by scent glands present in both species (Helder-José and Freymuller 1995, Munhoz and Merzel 1967) could be one of the mechanisms promoting interspecific recognition and avoidance. We consider that future studies should focus on these species' behavior, to provide a better understanding on the role of interference on *D. aurita* and *M. nudicaudatus* coexistence.

In conclusion, our data show that *M. nudicaudatus* has a close density-dependence relationship to *D. aurita*. Our findings have important implications for a better understanding of interspecific interactions and are consistent with the hypothesis that when top-predators are extirpated there is a release in mesopredator abundance, which will direct affect its competitors.

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Table 1. Covariates for each demographic parameter according to biological hypothesis.

Demographic parameter	Covariates	Biological hypothesis
Probability that an animal enter the population (*pent*) and **Survival probability (ϕ)**		
	temperature (t) rainfall (r) year before rainfall (rb)	Climatic changes
	litterfall (l)	Food resource abundance
	season (s)	Seasonality
	sex (sx)	sex differences on behavior
	D. aurita's abundance* (Da)	Interspecific interactions
	(.)	Constant over time
Probabilities of capture (p)		
	sex (sx)	sex differences on behavior
	season (s)	Seasonality
	D. aurita's abundance* (Da)	Interspecific interactions
	(.)	Constant over time

*It was used to estimate population parameters for *Metachirus nudicaudatus* species only.

Table 2. Highest ranking of POPAN's models selected for demographic parameters of *Didelphis aurita* and *Metachirus nudicaudatus* merged data.

model	**ϕ**	***p***	***pent***	**N**	**npar**	**AICc**	**ΔAICc**	***w***	**Deviance**
43	sp*t	sp*t	sp*t	sp	142	-1461.1	0	1	-223.2
13	.	t	.	sp	28	347.4	1808.5	0	-138.1
49	t	.	.	sp	27	350.3	1811.4	0	-131.9

Covariates considered in the analysis were species (sp), time (t) and its interaction (*). The notation ϕ means apparent survival; *p*, capture probability; pent, probability of new animal entrance; *w*, weight; and npar, the number of parameters.

Table 3. Highest ranking POPAN's models selected for demographic parameters of *Didelphis aurita* and *Metachirus nudicaudatus*.

Sp.	**Model**	**ϕ**	***p***	***pent***	**npar**	**AICc**	**ΔAICc**	***w***	**Deviance**
Didelphis aurita									
	62	.	sx	sx	6	371.6	0	0.205	-75.9
	104	l	sx	sx	7	373.1	1.57	0.093	-76.5
	146	t	sx	sx	7	373.5	1.90	0.079	-76.2
	125	sx	sx	sx	7	373.5	1.95	0.077	-76.2
	41	r	sx	sx	7	373.7	2.12	0.071	-76.0
Metachirus nudicaudatus									
	100	Da	.	Da	6	213.4	0	0.081	30.4
	36	r	.	Da	6	214.0	0.67	0.058	31.1
	68	.	.	Da	5	214.4	0.93	0.051	33.8
	196	sx	.	Da	6	214.6	1.15	0.045	31.6
	108	Da	Da	Da	7	214.7	1.31	0.042	29.1
	124	Da	sx	Da	7	215.2	1.75	0.034	29.6
	220	sx	sx	Da	7	215.2	1.82	0.033	29.6
	60	r	sx	Da	7	215.3	1.93	0.031	29.8
	44	r	Da	Da	7	215.4	2.02	0.029	29.9

Models are ranked according the differences to the model's Akaike Information Criterion Corrected for small samples (ΔAICc). Complete model set is shown in Table S2 for *D. aurita*, and Table S3 for *M. nudicaudatus*. For covariates considered in the analysis and its abbreviation see Table 1. (The notation ϕ means apparent survival; *p*, capture probability; pent, probability of new animal entrance; *w*, weight; and npar, the number of parameters)

FIGURE 1. Model-averaged abundance estimates for *Didelphis aurita* (solid line) and *Metachirus nudicaudatus* (dashed line) per survey occasion.

FIGURE 2. Apparent survival probability for *Didelphis aurita* (solid lines) and *Metachirus nudicaudatus* (dotted lines) over the study period. (male's probability is represented in grey and female's probability is represented in black)

FIGURE 3. *Didelphis aurita*'s apparent survival probability (solid line), litter (dotted line) and mean temperature (dashed line) over the period of study. Vertical grey bars represent wet season. (values represents the mean value of males and females)

FIGURE 4. *Metachirus nudicaudatus*' apparent survival probability (solid black line), abundance estimates for *Didelphis aurita* (solid grey line) and square root of mean rainfall (dotted line) over the period of study.

FIGURE 5. Recapture probability for *Metachirus nudicaudatus* per survey occasion (grey) and *Didelphis aurita*'s abundance (black). a) *M. nudicaudatus*' capture probability is plotted against *D. aurita*'s abundance in the respective month; b) *M. nudicaudatus*' capture probability is plotted against *D. aurita*'s abundance of the earlier month. (values represents the mean value of males and females)

FIGURE 6. Negative relationship between *Metachirus nudicaudatus*' pent probability and abundance estimates for *Didelphis aurita*. (Pent is the probability that an individual from the super-population would enter the population between two occasions)

Fig. 1

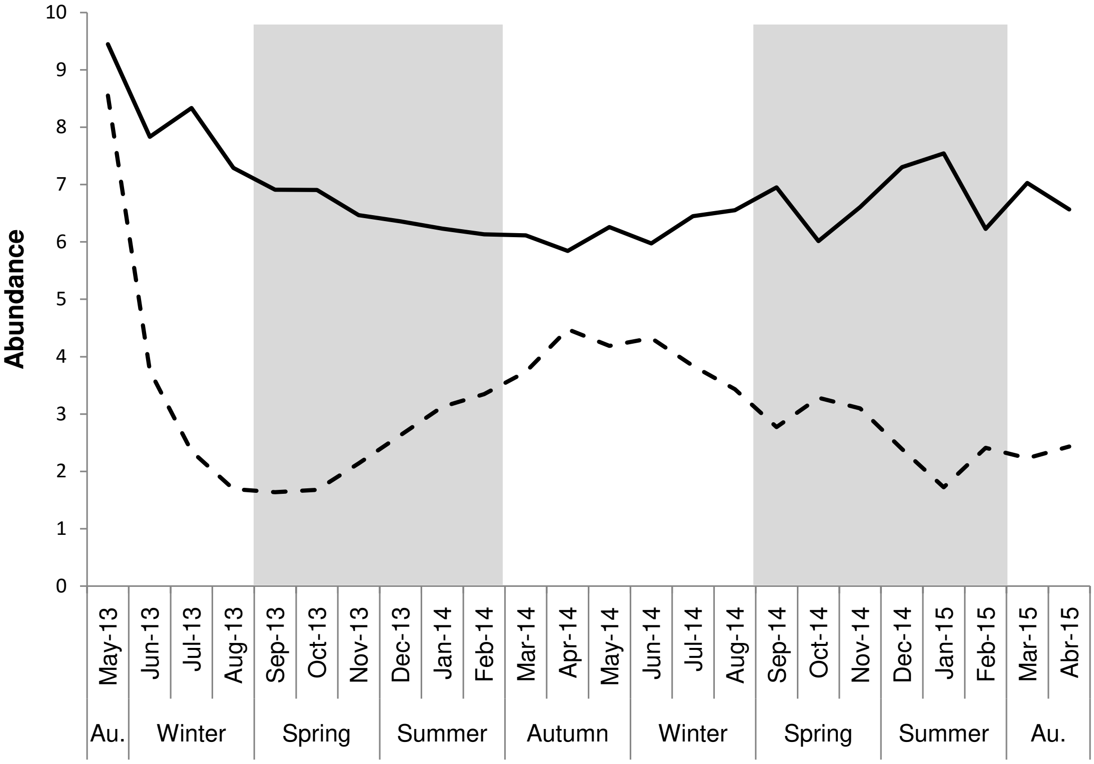

Abundance
10
9
8
7
6
5
4
3
2
1
0
May-13
Jun-13
Jul-13
Aug-13
Sep-13
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Jun-14
Jul-14
Aug-14
Sep-14
Oct-14
Nov-14
Dec-14
Jan-15
Feb-15
Mar-15
Abr-15
Au.
Winter
Spring
Summer
Autumn
Winter
Spring
Summer
Au.

Fig. 2

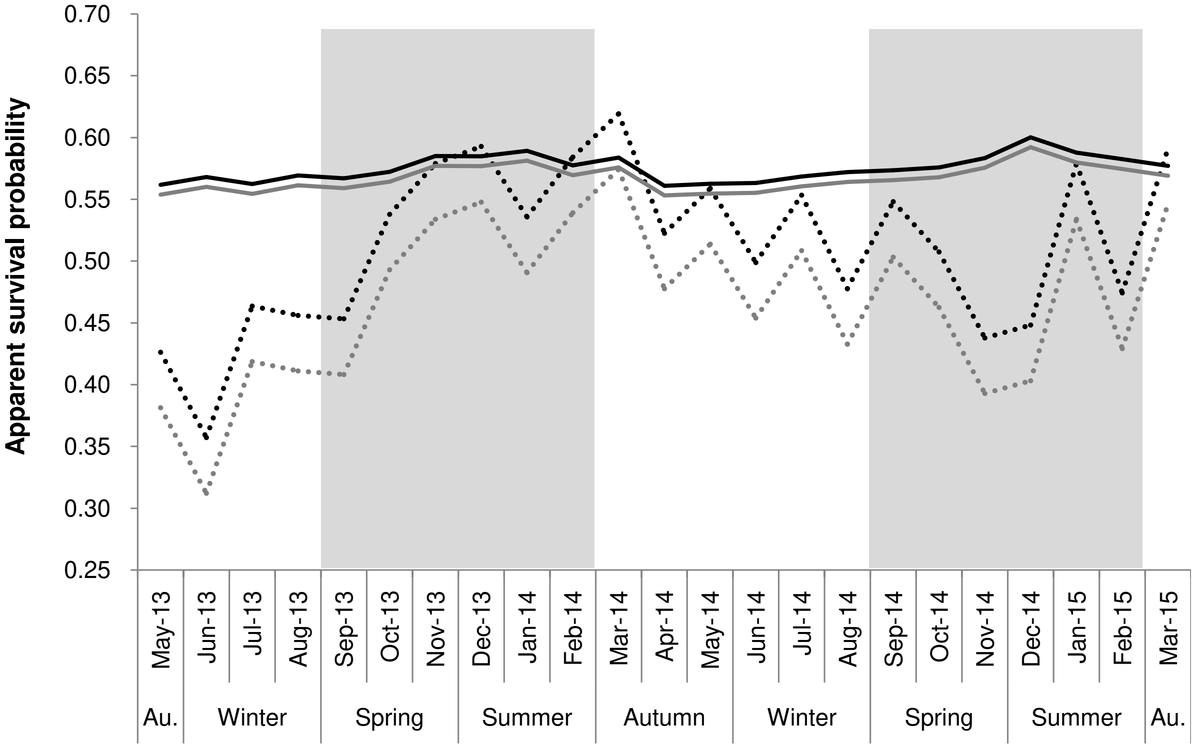

Apparent survival probability
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
May-13
Jun-13
Jul-13
Aug-13
Sep-13
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Jun-14
Jul-14
Aug-14
Sep-14
Oct-14
Nov-14
Dec-14
Jan-15
Feb-15
Mar-15
Au.
Winter
Spring
Summer
Autumn
Winter
Spring
Summer
Au.

Fig. 3

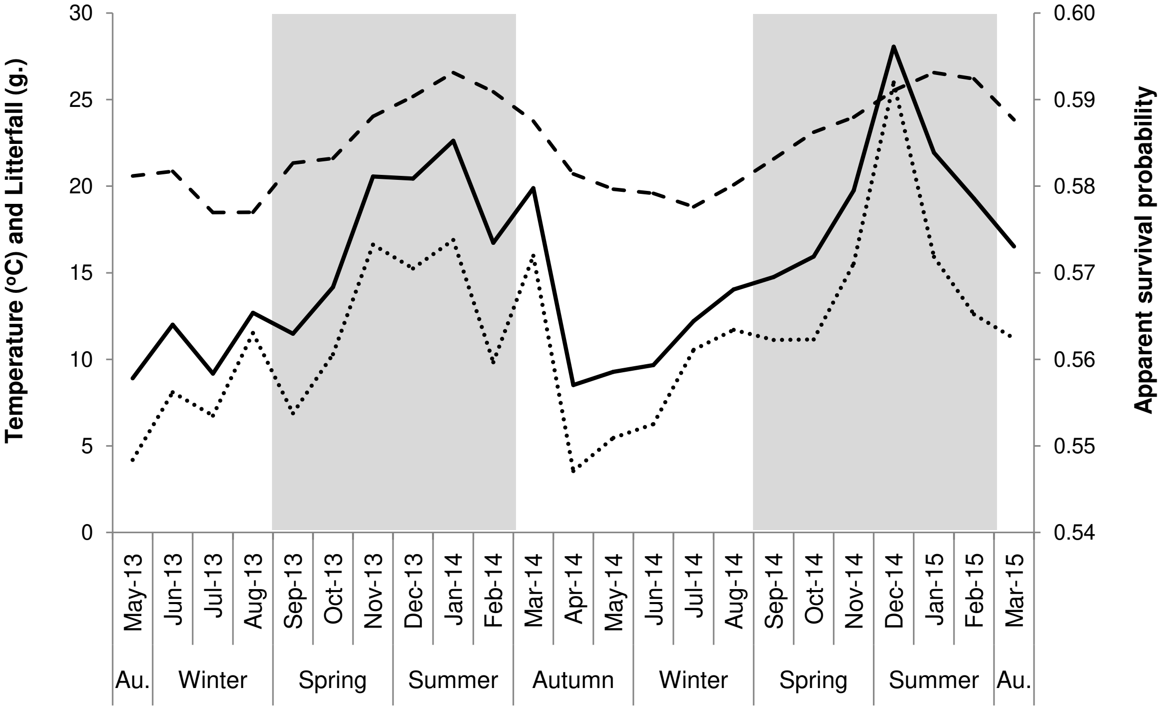

Temperature (ºC) and Litterfall (g.)
30
25
20
15
10
5
0
Apparent survival probability
0.60
0.59
0.58
0.57
0.56
0.55
0.54
May-13
Jun-13
Jul-13
Aug-13
Sep-13
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Jun-14
Jul-14
Aug-14
Sep-14
Oct-14
Nov-14
Dec-14
Jan-15
Feb-15
Mar-15
Au.
Winter
Spring
Summer
Autumn
Winter
Spring
Summer
Au.

Fig. 4

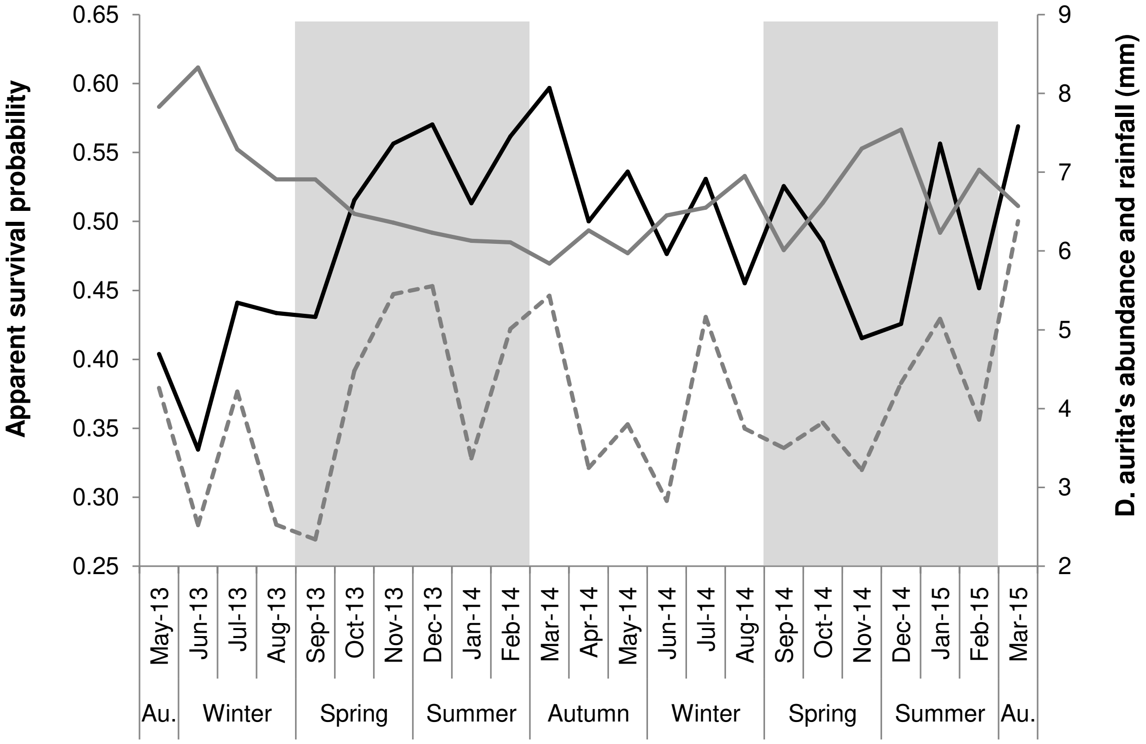

Apparent survival probability
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
D. aurita's abundance and rainfall (mm)
9
8
7
6
5
4
3
2
May-13
Jun-13
Jul-13
Aug-13
Sep-13
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Jun-14
Jul-14
Aug-14
Sep-14
Oct-14
Nov-14
Dec-14
Jan-15
Feb-15
Mar-15
Au.
Winter
Spring
Summer
Autumn
Winter
Spring
Summer
Au.

Fig. 5

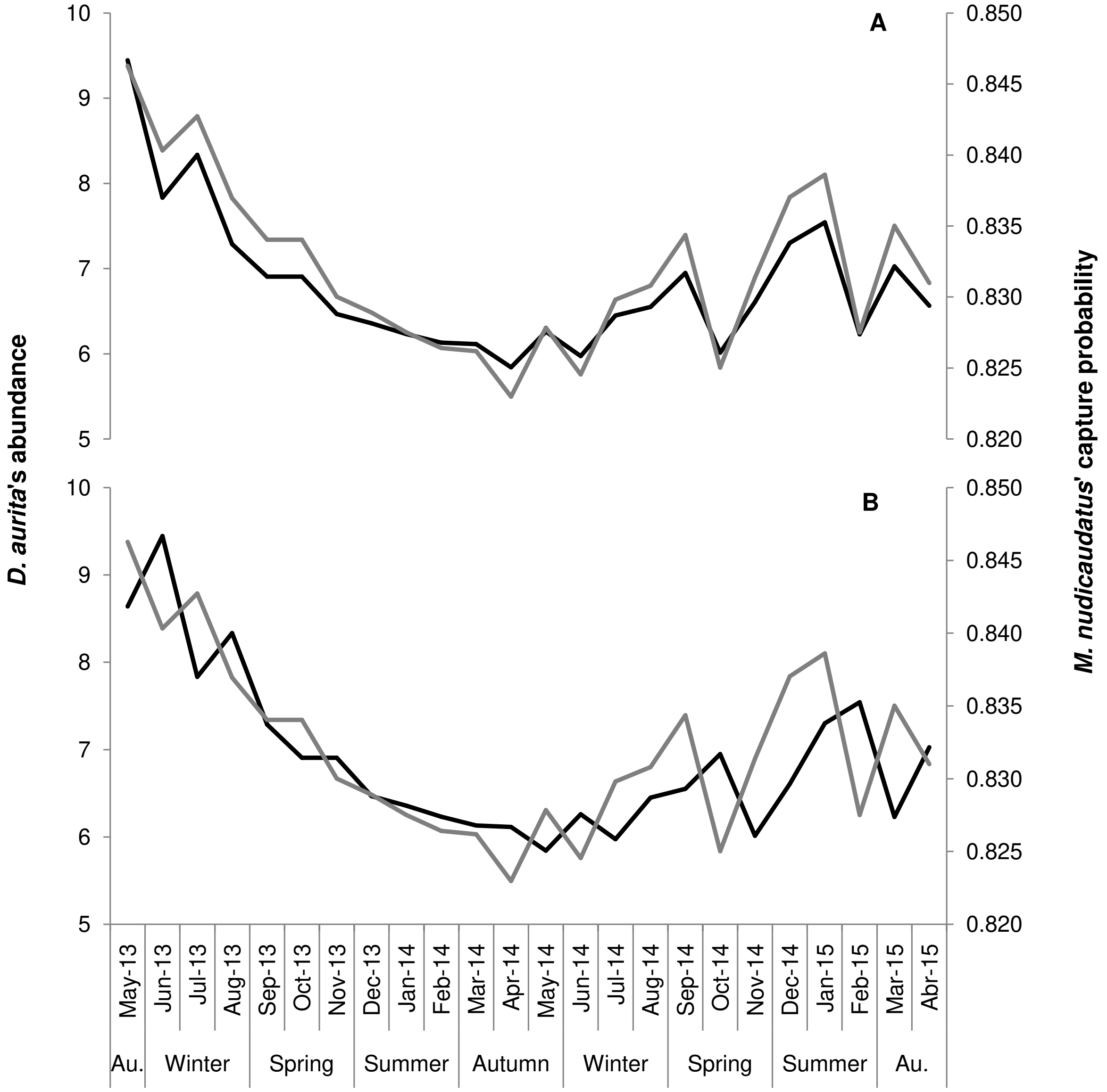
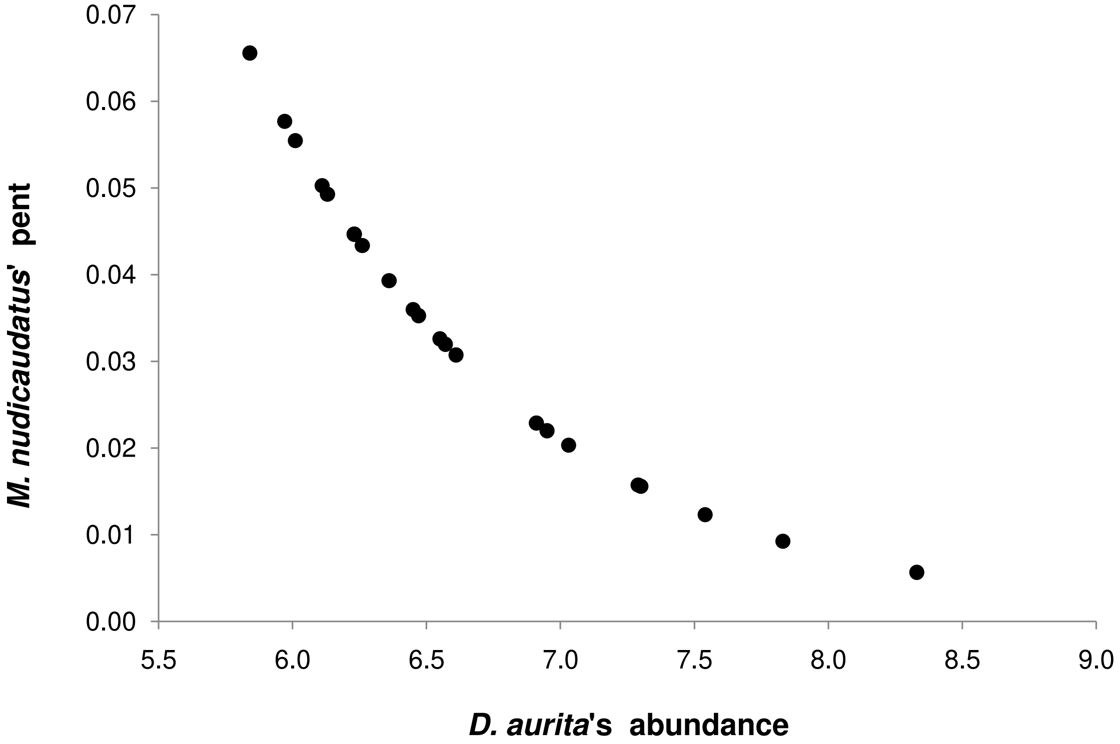

A
B
D. aurita's abundance
M. nudicaudatus' capture probability
10
9
8
7
6
5
0.850
0.845
0.840
0.835
0.830
0.825
0.820
May-13
Jun-13
Jul-13
Aug-13
Sep-13
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Jun-14
Jul-14
Aug-14
Sep-14
Oct-14
Nov-14
Dec-14
Jan-15
Feb-15
Mar-15
Abr-15
Au.
Winter
Spring
Summer
Autumn
Winter
Spring
Summer
Au.

Fig. 6


0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
M. nudicaudatus' pent
D. aurita's abundance

Supporting Information

Table S1. Model selection results for POPAN models to estimate apparent survival (ϕ), capture probability (p), probability of new animal entrance (pent) and the super-population size (N) of *Didelphis aurita* and *Metachirus nudicaudatus* merged.

Model	npar	AICc	ΔAICc	*w*	Deviance
Φ(sp *t)p(sp *t)pent(sp *t)N(sp)	142	-1461.1	0.0	1	-223.2
Φ(.)p(t)pent(.)N(sp)	28	347.4	1808.5	0	-138.1
Φ(t)p(.)pent(.)N(sp)	27	350.3	1811.4	0	-131.9
Φ(sp)p(t)pent(.)N(sp)	29	350.8	1812.0	0	-138.1
Φ(.)p(t)pent(sp)N(sp)	29	350.9	1812.0	0	-138.1
Φ(t)p(.)pent(sp)N(sp)	28	353.6	1814.7	0	-131.9
Φ(t)p(sp)pent(.)N(sp)	28	353.6	1814.7	0	-131.9
Φ(sp)p(t)pent(sp)N(sp)	30	354.4	1815.5	0	-138.1
Φ(t)p(sp)pent(sp)N(sp)	29	357.1	1818.2	0	-131.9
Φ(.)p(.)pent(t)N(sp)	27	359.9	1821.0	0	-122.2
Φ(.)p(sp)pent(t)N(sp)	28	363.3	1824.4	0	-122.2
Φ(sp)p(.)pent(t)N(sp)	28	363.3	1824.4	0	-122.2
Φ(.)p(.)pent(.)N(sp)	5	366.0	1827.2	0	-56.5
Φ(sp)p(sp)pent(t)N(sp)	29	366.7	1827.9	0	-122.2
Φ(.)p(.)pent(sp)N(sp)	6	368.3	1829.4	0	-56.5
Φ(.)p(sp)pent(.)N(sp)	6	368.3	1829.4	0	-56.5
Φ(sp)p(.)pent(.)N(sp)	6	368.3	1829.4	0	-56.5
Φ(.)p(sp)pent(sp)N(sp)	7	370.5	1831.6	0	-56.5
Φ(sp)p(.)pent(sp)N(sp)	7	370.5	1831.6	0	-56.5
Φ(sp)p(sp)pent(.)N(sp)	7	370.5	1831.6	0	-56.5
Φ(sp)p(sp)pent(sp)N(sp)	8	372.8	1833.9	0	-56.5
Φ(t)p(.)pent(t)N(sp)	49	381.8	1842.9	0	-196.3
Φ(t)p(sp)pent(t)N(sp)	50	387.6	1848.7	0	-196.3
Φ(t)p(t)pent(.)N(sp)	50	394.7	1855.8	0	-189.2
Φ(t)p(t)pent(sp)N(sp)	51	400.6	1861.7	0	-189.2
Φ(.)p(t)pent(t)N(sp)	50	409.9	1871.0	0	-173.9
Φ(sp)p(t)pent(t)N(sp)	51	415.9	1877.0	0	-173.9
Φ(sp*t)p(.)pent(.)N(sp)	50	452.0	1913.1	0	-131.9
Φ(.)p(sp*t)pent(.)N(sp)	52	457.8	1918.9	0	-138.1
Φ(sp*t)p(.)pent(sp)N(sp)	51	457.9	1919.1	0	-131.9
Φ(sp*t)p(sp)pent(.)N(sp)	51	457.9	1919.1	0	-131.9
Φ(.)p(.)pent(sp*t)N(sp)	50	461.7	1922.8	0	-122.2
Φ(sp*t)p(sp)pent(sp)N(sp)	52	464.1	1925.2	0	-131.9
Φ(sp)p(sp*t)pent(.)N(sp)	53	464.1	1925.2	0	-138.1
Φ(.)p(sp*t)pent(sp)N(sp)	53	464.1	1925.2	0	-138.1
Φ(sp)p(.)pent(sp*t)N(sp)	51	467.6	1928.7	0	-122.2

Φ(.)p(sp)pent(sp*t)N(sp)	51	467.6	1928.7	0	-122.2
Φ(sp)p(sp*t)pent(sp)N(sp)	54	470.6	1931.7	0	-138.1
Φ(sp)p(sp)pent(sp*t)N(sp)	52	473.7	1934.8	0	-122.2
Φ(t)p(t)pent(t)N(sp)	72	547.3	2008.4	0	-223.2
Φ(sp*t)p(.)pent(t)N(sp)	72	574.3	2035.4	0	-196.3
Φ(t)p(.)pent(sp*t)N(sp)	72	574.3	2035.4	0	-196.3
Φ(sp*t)p(sp)pent(t)N(sp)	73	586.8	2047.9	0	-196.3
Φ(t)p(sp)pent(sp*t)N(sp)	73	586.8	2047.9	0	-196.3
Φ(sp*t)p(t)pent(.)N(sp)	73	593.9	2055.1	0	-189.2
Φ(t)p(sp*t)pent(.)N(sp)	74	607.0	2068.1	0	-189.2
Φ(sp*t)p(t)pent(sp)N(sp)	74	607.0	2068.1	0	-189.2
Φ(.)p(t)pent(sp*t)N(sp)	73	609.2	2070.3	0	-173.9
Φ(t)p(sp*t)pent(sp)N(sp)	75	620.7	2081.8	0	-189.2
Φ(.)p(sp*t)pent(t)N(sp)	74	622.3	2083.4	0	-173.9
Φ(sp)p(t)pent(sp*t)N(sp)	74	622.3	2083.4	0	-173.9
Φ(sp)p(sp*t)pent(t)N(sp)	75	635.9	2097.0	0	-173.9
Φ(sp*t)p(t)pent(t)N(sp)	95	1080.3	2541.4	0	-223.2
Φ(t)p(t)pent(sp*t)N(sp)	95	1080.3	2541.4	0	-223.2
Φ(sp*t)p(.)pent(sp*t)N(sp)	95	1107.3	2568.4	0	-196.3
Φ(t)p(sp*t)pent(t)N(sp)	96	1125.8	2586.9	0	-223.2
Φ(sp*t)p(sp)pent(sp*t)N(sp)	96	1152.7	2613.8	0	-196.3
Φ(sp*t)p(sp*t)pent(.)N(sp)	97	1209.0	2670.1	0	-189.2
Φ(.)p(sp*t)pent(sp*t)N(sp)	97	1224.3	2685.4	0	-173.9
Φ(sp*t)p(sp*t)pent(sp)N(sp)	98	1262.5	2723.6	0	-189.2
Φ(sp)p(sp*t)pent(sp*t)N(sp)	98	1277.7	2738.8	0	-173.9
Φ(sp*t)p(t)pent(sp*t)N(sp)	118	9786.1	11247.2	0	-223.2
Φ(t)p(sp*t)pent(sp*t)N(sp)	119	14706.8	16167.9	0	-223.2
Φ(sp*t)p(sp*t)pent(t)N(sp)	119	14706.8	16167.9	0	-223.2

Models are ranked according the differences to the model's Akaike Information Criterion Corrected for small samples (ΔAICc) (*w* means weight and npar the number of parameters). Covariates considered in the analysis were: *sp*, species effect; *t*, time effect; *dot*, constant over time; *asterisks*, represents the interactive effect between covariates.

Table S2. Model selection results for POPAN models to estimate apparent survival (ϕ), capture probability (p), probability of new animal entrance (pent) and the super-population size (N) of *Didelphis aurita* population. Models are ranked according the differences to the model's Akaike Information Criterion Corrected for small samples (ΔAICc) (*w* means weight and npar the number of parameters). For covariates considered in the analysis and its abbreviation see Table 1.

Model	npar	AICc	ΔAICc	*w*	Deviance
Φ(.)p(sx)pent(sx)N(.)	6	371.6	0.0	0.2	-75.9
Φ(l)p(sx)pent(sx)N(.)	7	373.1	1.6	0.1	-76.6
Φ(t)p(sx)pent(sx)N(.)	7	373.5	1.9	0.1	-76.2
Φ(sx)p(sx)pent(sx)N(.)	7	373.5	2.0	0.1	-76.2
Φ(r)p(sx)pent(sx)N(.)	7	373.7	2.1	0.1	-76.0
Φ(rb)p(sx)pent(sx)N(.)	7	373.7	2.2	0.1	-76.0
Φ(.)p(sx)pent(.)N(.)	5	374.7	3.1	<0.1	-70.6
Φ(.)p(sx)pent(rb)N(.)	6	375.1	3.5	<0.1	-72.4
Φ(l)p(sx)pent(.)N(.)	6	376.3	4.7	<0.1	-71.2
Φ(t)p(sx)pent(.)N(.)	6	376.5	5.0	<0.1	-70.9
Φ(.)p(sx)pent(r)N(.)	6	376.5	5.0	<0.1	-70.9
Φ(.)p(sx)pent(t)N(.)	6	376.7	5.1	<0.1	-70.8
Φ(sx)p(sx)pent(.)N(.)	6	376.7	5.1	<0.1	-70.8
Φ(r)p(sx)pent(.)N(.)	6	376.7	5.2	<0.1	-70.7
Φ(l)p(sx)pent(rb)N(.)	7	376.8	5.2	<0.1	-72.9
Φ(rb)p(sx)pent(.)N(.)	6	376.8	5.2	<0.1	-70.7
Φ(.)p(sx)pent(l)N(.)	6	376.8	5.2	<0.1	-70.7
Φ(t)p(sx)pent(rb)N(.)	7	377.0	5.4	<0.1	-72.7
Φ(sx)p(sx)pent(rb)N(.)	7	377.1	5.5	<0.1	-72.6
Φ(r)p(sx)pent(rb)N(.)	7	377.2	5.6	<0.1	-72.5
Φ(rb)p(sx)pent(rb)N(.)	7	377.2	5.7	<0.1	-72.5
Φ(s)p(sx)pent(sx)N(.)	9	377.5	6.0	<0.1	-76.7
Φ(l)p(sx)pent(r)N(.)	7	378.2	6.7	<0.1	-71.4
Φ(l)p(sx)pent(t)N(.)	7	378.4	6.8	<0.1	-71.3
Φ(t)p(sx)pent(r)N(.)	7	378.5	6.9	<0.1	-71.2
Φ(l)p(sx)pent(l)N(.)	7	378.5	6.9	<0.1	-71.2
Φ(t)p(sx)pent(t)N(.)	7	378.6	7.0	<0.1	-71.1

Φ(sx)p(sx)pent(r)N(.)	7	378.6	7.0	<0.1	-71.1
Φ(r)p(sx)pent(r)N(.)	7	378.7	7.1	<0.1	-71.0
Φ(rb)p(sx)pent(r)N(.)	7	378.7	7.1	<0.1	-71.0
Φ(sx)p(sx)pent(t)N(.)	7	378.7	7.2	<0.1	-71.0
Φ(t)p(sx)pent(l)N(.)	7	378.7	7.2	<0.1	-71.0
Φ(r)p(sx)pent(t)N(.)	7	378.8	7.2	<0.1	-70.9
Φ(rb)p(sx)pent(t)N(.)	7	378.8	7.3	<0.1	-70.9
Φ(sx)p(sx)pent(l)N(.)	7	378.9	7.3	<0.1	-70.8
Φ(r)p(sx)pent(l)N(.)	7	378.9	7.4	<0.1	-70.8
Φ(rb)p(sx)pent(l)N(.)	7	379.0	7.4	<0.1	-70.7
Φ(.)p(.)pent(sx)N(.)	5	379.8	8.2	<0.1	-65.5
Φ(.)p(sx)pent(s)N(.)	8	380.2	8.7	<0.1	-71.7
Φ(s)p(sx)pent(.)N(.)	8	380.5	8.9	<0.1	-71.5
Φ(sx)p(.)pent(sx)N(.)	6	380.5	9.0	<0.1	-66.9
Φ(s)p(sx)pent(rb)N(.)	9	381.0	9.4	<0.1	-73.3
Φ(l)p(.)pent(sx)N(.)	6	381.2	9.7	<0.1	-66.2
Φ(t)p(.)pent(sx)N(.)	6	381.7	10.1	<0.1	-65.8
Φ(r)p(.)pent(sx)N(.)	6	381.8	10.2	<0.1	-65.7
Φ(rb)p(.)pent(sx)N(.)	6	381.9	10.4	<0.1	-65.5
Φ(l)p(sx)pent(s)N(.)	9	382.0	10.5	<0.1	-72.2
Φ(t)p(sx)pent(s)N(.)	9	382.3	10.7	<0.1	-72.0
Φ(sx)p(sx)pent(s)N(.)	9	382.4	10.8	<0.1	-71.9
Φ(r)p(sx)pent(s)N(.)	9	382.5	10.9	<0.1	-71.8
Φ(rb)p(sx)pent(s)N(.)	9	382.5	10.9	<0.1	-71.7
Φ(s)p(sx)pent(r)N(.)	9	382.5	10.9	<0.1	-71.7
Φ(s)p(sx)pent(t)N(.)	9	382.6	11.0	<0.1	-71.6
Φ(s)p(sx)pent(l)N(.)	9	382.7	11.2	<0.1	-71.5
Φ(.)p(.)pent(.)N(.)	4	384.0	12.4	<0.1	-59.2
Φ(.)p(s)pent(sx)N(.)	8	384.4	12.8	<0.1	-67.5
Φ(.)p(.)pent(rb)N(.)	5	384.5	12.9	<0.1	-60.8
Φ(sx)p(.)pent(.)N(.)	5	384.8	13.3	<0.1	-60.4
Φ(sx)p(s)pent(sx)N(.)	9	385.3	13.7	<0.1	-68.9
Φ(sx)p(.)pent(rb)N(.)	6	385.4	13.8	<0.1	-62.1
Φ(l)p(.)pent(.)N(.)	5	385.5	13.9	<0.1	-59.8
Φ(l)p(s)pent(sx)N(.)	9	385.6	14.0	<0.1	-68.6
Φ(s)p(.)pent(sx)N(.)	8	385.7	14.2	<0.1	-66.2
Φ(.)p(.)pent(r)N(.)	5	385.8	14.3	<0.1	-59.5

Φ(.)p(.)pent(t)N(.)	5	385.9	14.3	<0.1	-59.4
Φ(t)p(.)pent(.)N(.)	5	385.9	14.3	<0.1	-59.4
Φ(r)p(.)pent(.)N(.)	5	386.0	14.4	<0.1	-59.3
Φ(.)p(.)pent(l)N(.)	5	386.0	14.4	<0.1	-59.3
Φ(t)p(s)pent(sx)N(.)	9	386.0	14.5	<0.1	-68.2
Φ(l)p(.)pent(rb)N(.)	6	386.0	14.5	<0.1	-61.4
Φ(rb)p(.)pent(.)N(.)	5	386.1	14.6	<0.1	-59.2
Φ(t)p(.)pent(rb)N(.)	6	386.4	14.9	<0.1	-61.1
Φ(s)p(sx)pent(s)N(.)	11	386.5	14.9	<0.1	-72.4
Φ(r)p(.)pent(rb)N(.)	6	386.5	15.0	<0.1	-60.9
Φ(r)p(s)pent(sx)N(.)	9	386.6	15.0	<0.1	-67.6
Φ(rb)p(s)pent(sx)N(.)	9	386.7	15.1	<0.1	-67.6
Φ(rb)p(.)pent(rb)N(.)	6	386.7	15.1	<0.1	-60.8
Φ(sx)p(.)pent(r)N(.)	6	386.7	15.2	<0.1	-60.7
Φ(sx)p(.)pent(t)N(.)	6	386.8	15.2	<0.1	-60.7
Φ(sx)p(.)pent(l)N(.)	6	386.9	15.4	<0.1	-60.5
Φ(l)p(.)pent(r)N(.)	6	387.4	15.9	<0.1	-60.1
Φ(l)p(.)pent(t)N(.)	6	387.5	15.9	<0.1	-60.0
Φ(l)p(.)pent(l)N(.)	6	387.6	16.1	<0.1	-59.9
Φ(t)p(.)pent(r)N(.)	6	387.8	16.2	<0.1	-59.7
Φ(t)p(.)pent(t)N(.)	6	387.8	16.3	<0.1	-59.6
Φ(r)p(.)pent(r)N(.)	6	387.9	16.3	<0.1	-59.6
Φ(r)p(.)pent(t)N(.)	6	387.9	16.4	<0.1	-59.5
Φ(t)p(.)pent(l)N(.)	6	388.0	16.4	<0.1	-59.5
Φ(rb)p(.)pent(r)N(.)	6	388.0	16.4	<0.1	-59.5
Φ(rb)p(.)pent(t)N(.)	6	388.0	16.5	<0.1	-59.4
Φ(r)p(.)pent(l)N(.)	6	388.1	16.5	<0.1	-59.4
Φ(rb)p(.)pent(l)N(.)	6	388.2	16.6	<0.1	-59.3
Φ(.)p(s)pent(.)N(.)	7	388.4	16.9	<0.1	-61.2
Φ(.)p(s)pent(rb)N(.)	8	389.1	17.5	<0.1	-62.9
Φ(sx)p(s)pent(.)N(.)	8	389.4	17.9	<0.1	-62.5
Φ(.)p(.)pent(s)N(.)	7	389.6	18.0	<0.1	-60.1
Φ(l)p(s)pent(.)N(.)	8	389.7	18.2	<0.1	-62.2
Φ(s)p(.)pent(.)N(.)	7	389.8	18.2	<0.1	-59.9
Φ(t)p(s)pent(.)N(.)	8	390.0	18.5	<0.1	-61.9
Φ(sx)p(s)pent(rb)N(.)	9	390.0	18.5	<0.1	-64.2
Φ(.)p(s)pent(t)N(.)	8	390.1	18.6	<0.1	-61.8

Φ(.)p(s)pent(r)N(.)	8	390.2	18.7	<0.1	-61.7
Φ(.)p(s)pent(l)N(.)	8	390.3	18.8	<0.1	-61.6
Φ(s)p(.)pent(rb)N(.)	8	390.4	18.8	<0.1	-61.5
Φ(l)p(s)pent(rb)N(.)	9	390.4	18.8	<0.1	-63.8
Φ(sx)p(.)pent(s)N(.)	8	390.5	19.0	<0.1	-61.4
Φ(r)p(s)pent(.)N(.)	8	390.6	19.0	<0.1	-61.4
Φ(rb)p(s)pent(.)N(.)	8	390.7	19.1	<0.1	-61.3
Φ(t)p(s)pent(rb)N(.)	9	390.8	19.2	<0.1	-63.4
Φ(s)p(s)pent(sx)N(.)	11	390.8	19.2	<0.1	-68.1
Φ(sx)p(s)pent(t)N(.)	9	391.2	19.6	<0.1	-63.0
Φ(l)p(.)pent(s)N(.)	8	391.2	19.6	<0.1	-60.7
Φ(r)p(s)pent(rb)N(.)	9	391.3	19.7	<0.1	-63.0
Φ(sx)p(s)pent(r)N(.)	9	391.3	19.7	<0.1	-62.9
Φ(rb)p(s)pent(rb)N(.)	9	391.3	19.8	<0.1	-62.9
Φ(sx)p(s)pent(l)N(.)	9	391.4	19.8	<0.1	-62.9
Φ(l)p(s)pent(t)N(.)	9	391.5	19.9	<0.1	-62.8
Φ(l)p(s)pent(r)N(.)	9	391.6	20.0	<0.1	-62.7
Φ(t)p(.)pent(s)N(.)	8	391.6	20.0	<0.1	-60.3
Φ(t)p(s)pent(t)N(.)	9	391.7	20.1	<0.1	-62.6
Φ(l)p(s)pent(l)N(.)	9	391.7	20.1	<0.1	-62.5
Φ(r)p(.)pent(s)N(.)	8	391.7	20.2	<0.1	-60.2
Φ(s)p(.)pent(r)N(.)	8	391.8	20.2	<0.1	-60.2
Φ(t)p(s)pent(r)N(.)	9	391.8	20.2	<0.1	-62.4
Φ(s)p(.)pent(t)N(.)	8	391.8	20.2	<0.1	-60.2
Φ(rb)p(.)pent(s)N(.)	8	391.8	20.3	<0.1	-60.1
Φ(t)p(s)pent(l)N(.)	9	391.9	20.3	<0.1	-62.3
Φ(s)p(.)pent(l)N(.)	8	391.9	20.4	<0.1	-60.0
Φ(r)p(s)pent(t)N(.)	9	392.3	20.7	<0.1	-61.9
Φ(rb)p(s)pent(t)N(.)	9	392.4	20.8	<0.1	-61.9
Φ(r)p(s)pent(r)N(.)	9	392.4	20.9	<0.1	-61.8
Φ(rb)p(s)pent(r)N(.)	9	392.5	20.9	<0.1	-61.7
Φ(r)p(s)pent(l)N(.)	9	392.5	20.9	<0.1	-61.7
Φ(rb)p(s)pent(l)N(.)	9	392.6	21.0	<0.1	-61.7
Φ(.)p(s)pent(s)N(.)	10	394.6	23.1	<0.1	-61.9
Φ(s)p(s)pent(.)N(.)	10	394.7	23.1	<0.1	-61.8
Φ(s)p(s)pent(rb)N(.)	11	395.5	24.0	<0.1	-63.4
Φ(sx)p(s)pent(s)N(.)	11	395.7	24.2	<0.1	-63.2

Φ(s)p(.)pent(s)N(.)	10	395.8	24.2	<0.1	-60.7
Φ(l)p(s)pent(s)N(.)	11	396.0	24.5	<0.1	-62.9
Φ(t)p(s)pent(s)N(.)	11	396.3	24.7	<0.1	-62.6
Φ(s)p(s)pent(t)N(.)	11	396.4	24.9	<0.1	-62.5
Φ(s)p(s)pent(r)N(.)	11	396.5	25.0	<0.1	-62.4
Φ(s)p(s)pent(l)N(.)	11	396.6	25.1	<0.1	-62.3
Φ(r)p(s)pent(s)N(.)	11	396.9	25.3	<0.1	-62.0
Φ(rb)p(s)pent(s)N(.)	11	396.9	25.4	<0.1	-62.0
Φ(s)p(s)pent(s)N(.)	13	401.2	29.7	<0.1	-62.5

Table S3. Model selection results for POPAN models to estimate apparent survival (ϕ), capture probability (p), probability of new animal entrance (pent) and the super-population size (N) of *Metachirus nudicaudatus* population.

Model	npar	AICc	ΔAICc	*w*	Deviance
Φ(Da)p(.)pent(Da)N(.)	6	213.4	0.0	0.08	30.4
Φ(r)p(.)pent(Da)N(.)	6	214.1	0.7	0.06	31.1
Φ(.)p(.)pent(Da)N(.)	5	214.4	0.9	0.05	33.8
Φ(sx)p(.)pent(Da)N(.)	6	214.6	1.2	0.05	31.6
Φ(Da)p(Da)pent(Da)N(.)	7	214.7	1.3	0.04	29.2
Φ(Da)p(sx)pent(Da)N(.)	7	215.2	1.8	0.03	29.6
Φ(sx)p(sx)pent(Da)N(.)	7	215.2	1.8	0.03	29.7
Φ(r)p(sx)pent(Da)N(.)	7	215.3	1.9	0.03	29.8
Φ(r)p(Da)pent(Da)N(.)	7	215.4	2.0	0.03	29.9
Φ(.)p(Da)pent(Da)N(.)	6	215.7	2.3	0.03	32.7
Φ(.)p(sx)pent(Da)N(.)	6	215.9	2.5	0.02	32.9
Φ(sx)p(Da)pent(Da)N(.)	7	216.0	2.6	0.02	30.4
Φ(t)p(.)pent(Da)N(.)	6	216.1	2.7	0.02	33.1
Φ(l)p(.)pent(Da)N(.)	6	216.6	3.2	0.02	33.6
Φ(Da)p(.)pent(.)N(.)	5	216.7	3.2	0.02	36.1
Φ(rb)p(.)pent(Da)N(.)	6	216.7	3.2	0.02	33.7
Φ(t)p(Da)pent(Da)N(.)	7	217.5	4.1	0.01	31.9
Φ(r)p(.)pent(.)N(.)	5	217.6	4.2	0.01	37.1
Φ(t)p(sx)pent(Da)N(.)	7	217.7	4.2	0.01	32.1
Φ(Da)p(.)pent(rb)N(.)	6	217.7	4.2	0.01	34.7
Φ(Da)p(.)pent(l)N(.)	6	217.7	4.3	0.01	34.7
Φ(.)p(s)pent(Da)N(.)	8	217.9	4.5	0.01	29.7
Φ(Da)p(.)pent(sx)N(.)	6	218.0	4.6	0.01	35.0
Φ(.)p(.)pent(.)N(.)	4	218.0	4.6	0.01	39.9
Φ(Da)p(s)pent(Da)N(.)	9	218.1	4.6	0.01	27.1
Φ(l)p(Da)pent(Da)N(.)	7	218.1	4.7	0.01	32.5
Φ(rb)p(Da)pent(Da)N(.)	7	218.1	4.7	0.01	32.6

Φ(l)p(sx)pent(Da)N(.)	7	218.3	4.8	0.01	32.7
Φ(sx)p(.)pent(.)N(.)	5	218.3	4.8	0.01	37.7
Φ(rb)p(sx)pent(Da)N(.)	7	218.4	5.0	0.01	32.8
Φ(r)p(.)pent(rb)N(.)	6	218.4	5.0	0.01	35.4
Φ(r)p(s)pent(Da)N(.)	9	218.5	5.1	0.01	27.5
Φ(Da)p(Da)pent(.)N(.)	6	218.5	5.1	0.01	35.5
Φ(s)p(.)pent(Da)N(.)	8	218.5	5.1	0.01	30.3
Φ(Da)p(sx)pent(.)N(.)	6	218.6	5.1	0.01	35.6
Φ(r)p(.)pent(l)N(.)	6	218.6	5.2	0.01	35.6
Φ(sx)p(s)pent(Da)N(.)	9	218.8	5.4	0.01	27.8
Φ(r)p(.)pent(sx)N(.)	6	218.9	5.5	0.01	35.9
Φ(.)p(.)pent(rb)N(.)	5	218.9	5.5	0.01	38.4
Φ(r)p(sx)pent(.)N(.)	6	219.0	5.6	<0.01	36.0
Φ(Da)p(.)pent(t)N(.)	6	219.1	5.7	<0.01	36.1
Φ(.)p(.)pent(l)N(.)	5	219.1	5.7	<0.01	38.5
Φ(sx)p(sx)pent(.)N(.)	6	219.1	5.7	<0.01	36.1
Φ(Da)p(.)pent(r)N(.)	6	219.1	5.7	<0.01	36.1
Φ(.)p(.)pent(sx)N(.)	5	219.2	5.8	<0.01	38.7
Φ(sx)p(.)pent(rb)N(.)	6	219.2	5.8	<0.01	36.2
Φ(sx)p(.)pent(l)N(.)	6	219.4	6.0	<0.01	36.4
Φ(Da)p(.)pent(s)N(.)	8	219.4	6.0	<0.01	31.2
Φ(r)p(Da)pent(.)N(.)	6	219.5	6.0	<0.01	36.4
Φ(Da)p(s)pent(rb)N(.)	9	219.5	6.1	<0.01	28.5
Φ(sx)p(.)pent(sx)N(.)	6	219.5	6.1	<0.01	36.5
Φ(Da)p(sx)pent(rb)N(.)	7	219.7	6.3	<0.01	34.1
Φ(Da)p(Da)pent(rb)N(.)	7	219.7	6.3	<0.01	34.1
Φ(Da)p(Da)pent(l)N(.)	7	219.7	6.3	<0.01	34.1
Φ(Da)p(sx)pent(l)N(.)	7	219.7	6.3	<0.01	34.1
Φ(.)p(sx)pent(.)N(.)	5	219.7	6.3	<0.01	39.2
Φ(t)p(.)pent(.)N(.)	5	219.7	6.3	<0.01	39.2
Φ(.)p(Da)pent(.)N(.)	5	219.8	6.4	<0.01	39.3
Φ(Da)p(Da)pent(sx)N(.)	7	219.9	6.4	<0.01	34.3
Φ(.)p(s)pent(rb)N(.)	8	219.9	6.4	<0.01	31.6

Φ(s)p(Da)pent(Da)N(.)	9	219.9	6.5	<0.01	28.9
Φ(Da)p(sx)pent(sx)N(.)	7	220.0	6.5	<0.01	34.4
Φ(r)p(sx)pent(rb)N(.)	7	220.0	6.6	<0.01	34.4
Φ(r)p(.)pent(t)N(.)	6	220.0	6.6	<0.01	37.0
Φ(r)p(.)pent(r)N(.)	6	220.1	6.6	<0.01	37.0
Φ(r)p(sx)pent(l)N(.)	7	220.1	6.6	<0.01	34.5
Φ(sx)p(Da)pent(.)N(.)	6	220.1	6.7	<0.01	37.1
Φ(r)p(s)pent(rb)N(.)	9	220.2	6.8	<0.01	29.2
Φ(t)p(s)pent(Da)N(.)	9	220.2	6.8	<0.01	29.2
Φ(sx)p(sx)pent(rb)N(.)	7	220.2	6.8	<0.01	34.7
Φ(l)p(.)pent(.)N(.)	5	220.2	6.8	<0.01	39.7
Φ(r)p(.)pent(s)N(.)	8	220.2	6.8	<0.01	32.0
Φ(rb)p(.)pent(.)N(.)	5	220.2	6.8	<0.01	39.7
Φ(rb)p(s)pent(Da)N(.)	9	220.3	6.9	<0.01	29.4
Φ(sx)p(sx)pent(l)N(.)	7	220.3	6.9	<0.01	34.8
Φ(.)p(.)pent(t)N(.)	5	220.4	6.9	<0.01	39.8
Φ(r)p(sx)pent(sx)N(.)	7	220.4	7.0	<0.01	34.8
Φ(.)p(.)pent(s)N(.)	7	220.4	7.0	<0.01	34.8
Φ(s)p(sx)pent(Da)N(.)	9	220.4	7.0	<0.01	29.4
Φ(.)p(.)pent(r)N(.)	5	220.4	7.0	<0.01	39.9
Φ(r)p(Da)pent(rb)N(.)	7	220.4	7.0	<0.01	34.9
Φ(Da)p(s)pent(.)N(.)	8	220.5	7.0	<0.01	32.2
Φ(sx)p(sx)pent(sx)N(.)	7	220.5	7.1	<0.01	34.9
Φ(l)p(s)pent(Da)N(.)	9	220.5	7.1	<0.01	29.5
Φ(r)p(Da)pent(l)N(.)	7	220.6	7.1	<0.01	35.0
Φ(t)p(.)pent(rb)N(.)	6	220.6	7.2	<0.01	37.6
Φ(sx)p(.)pent(t)N(.)	6	220.7	7.3	<0.01	37.7
Φ(.)p(sx)pent(rb)N(.)	6	220.7	7.3	<0.01	37.7
Φ(sx)p(.)pent(r)N(.)	6	220.7	7.3	<0.01	37.7
Φ(.)p(s)pent(.)N(.)	7	220.8	7.3	<0.01	35.2
Φ(r)p(Da)pent(sx)N(.)	7	220.8	7.4	<0.01	35.2
Φ(t)p(.)pent(l)N(.)	6	220.8	7.4	<0.01	37.8
Φ(.)p(Da)pent(rb)N(.)	6	220.8	7.4	<0.01	37.8

Φ(.)p(sx)pent(l)N(.)	6	220.9	7.4	<0.01	37.9
Φ(sx)p(.)pent(s)N(.)	8	220.9	7.5	<0.01	32.7
Φ(.)p(Da)pent(l)N(.)	6	221.0	7.6	<0.01	38.0
Φ(.)p(sx)pent(sx)N(.)	6	221.0	7.6	<0.01	38.0
Φ(t)p(.)pent(sx)N(.)	6	221.0	7.6	<0.01	38.0
Φ(Da)p(Da)pent(t)N(.)	7	221.0	7.6	<0.01	35.5
Φ(Da)p(Da)pent(r)N(.)	7	221.1	7.6	<0.01	35.5
Φ(Da)p(sx)pent(t)N(.)	7	221.1	7.7	<0.01	35.5
Φ(.)p(Da)pent(sx)N(.)	6	221.1	7.7	<0.01	38.1
Φ(Da)p(sx)pent(r)N(.)	7	221.1	7.7	<0.01	35.6
Φ(l)p(.)pent(rb)N(.)	6	221.2	7.7	<0.01	38.1
Φ(sx)p(Da)pent(rb)N(.)	7	221.2	7.8	<0.01	35.6
Φ(rb)p(.)pent(rb)N(.)	6	221.3	7.8	<0.01	38.2
Φ(sx)p(Da)pent(l)N(.)	7	221.3	7.9	<0.01	35.8
Φ(l)p(.)pent(l)N(.)	6	221.3	7.9	<0.01	38.3
Φ(rb)p(.)pent(l)N(.)	6	221.4	8.0	<0.01	38.4
Φ(sx)p(Da)pent(sx)N(.)	7	221.4	8.0	<0.01	35.9
Φ(r)p(s)pent(.)N(.)	8	221.4	8.0	<0.01	33.2
Φ(t)p(sx)pent(.)N(.)	6	221.4	8.0	<0.01	38.4
Φ(sx)p(s)pent(rb)N(.)	9	221.5	8.0	<0.01	30.5
Φ(Da)p(Da)pent(s)N(.)	9	221.5	8.1	<0.01	30.5
Φ(r)p(sx)pent(t)N(.)	7	221.5	8.1	<0.01	35.9
Φ(l)p(.)pent(sx)N(.)	6	221.5	8.1	<0.01	38.5
Φ(r)p(sx)pent(r)N(.)	7	221.5	8.1	<0.01	36.0
Φ(rb)p(.)pent(sx)N(.)	6	221.5	8.1	<0.01	38.5
Φ(t)p(Da)pent(.)N(.)	6	221.6	8.2	<0.01	38.6
Φ(sx)p(sx)pent(t)N(.)	7	221.6	8.2	<0.01	36.1
Φ(Da)p(s)pent(l)N(.)	9	221.6	8.2	<0.01	30.7
Φ(Da)p(sx)pent(s)N(.)	9	221.7	8.2	<0.01	30.7
Φ(sx)p(sx)pent(r)N(.)	7	221.7	8.2	<0.01	36.1
Φ(sx)p(s)pent(.)N(.)	8	221.8	8.4	<0.01	33.6
Φ(s)p(.)pent(.)N(.)	7	221.9	8.5	<0.01	36.3
Φ(.)p(s)pent(l)N(.)	8	221.9	8.5	<0.01	33.7

Φ(Da)p(s)pent(sx)N(.)	9	222.0	8.5	<0.01	31.0
Φ(r)p(Da)pent(t)N(.)	7	222.0	8.5	<0.01	36.4
Φ(l)p(sx)pent(.)N(.)	6	222.0	8.6	<0.01	39.0
Φ(r)p(Da)pent(r)N(.)	7	222.0	8.6	<0.01	36.4
Φ(t)p(s)pent(rb)N(.)	9	222.0	8.6	<0.01	31.0
Φ(r)p(sx)pent(s)N(.)	9	222.0	8.6	<0.01	31.1
Φ(rb)p(sx)pent(.)N(.)	6	222.1	8.6	<0.01	39.1
Φ(l)p(Da)pent(.)N(.)	6	222.1	8.7	<0.01	39.1
Φ(t)p(.)pent(t)N(.)	6	222.1	8.7	<0.01	39.1
Φ(.)p(s)pent(sx)N(.)	8	222.1	8.7	<0.01	33.9
Φ(rb)p(Da)pent(.)N(.)	6	222.1	8.7	<0.01	39.1
Φ(.)p(sx)pent(t)N(.)	6	222.1	8.7	<0.01	39.1
Φ(.)p(sx)pent(r)N(.)	6	222.2	8.8	<0.01	39.2
Φ(t)p(.)pent(r)N(.)	6	222.2	8.8	<0.01	39.2
Φ(sx)p(sx)pent(s)N(.)	9	222.2	8.8	<0.01	31.2
Φ(.)p(Da)pent(t)N(.)	6	222.2	8.8	<0.01	39.2
Φ(.)p(Da)pent(r)N(.)	6	222.3	8.9	<0.01	39.3
Φ(r)p(Da)pent(s)N(.)	9	222.3	8.9	<0.01	31.3
Φ(l)p(s)pent(rb)N(.)	9	222.3	8.9	<0.01	31.4
Φ(.)p(Da)pent(s)N(.)	8	222.4	9.0	<0.01	34.2
Φ(t)p(.)pent(s)N(.)	8	222.4	9.0	<0.01	34.2
Φ(.)p(sx)pent(s)N(.)	8	222.4	9.0	<0.01	34.2
Φ(t)p(sx)pent(rb)N(.)	7	222.4	9.0	<0.01	36.8
Φ(rb)p(s)pent(rb)N(.)	9	222.5	9.1	<0.01	31.5
Φ(t)p(Da)pent(rb)N(.)	7	222.6	9.2	<0.01	37.0
Φ(sx)p(Da)pent(t)N(.)	7	222.6	9.2	<0.01	37.0
Φ(t)p(sx)pent(l)N(.)	7	222.6	9.2	<0.01	37.1
Φ(sx)p(Da)pent(r)N(.)	7	222.6	9.2	<0.01	37.1
Φ(l)p(.)pent(t)N(.)	6	222.6	9.2	<0.01	39.6
Φ(rb)p(.)pent(t)N(.)	6	222.7	9.3	<0.01	39.7
Φ(Da)p(s)pent(t)N(.)	9	222.7	9.3	<0.01	31.7
Φ(l)p(.)pent(r)N(.)	6	222.7	9.3	<0.01	39.7
Φ(rb)p(.)pent(r)N(.)	6	222.7	9.3	<0.01	39.7

Φ(t)p(Da)pent(l)N(.)	7	222.8	9.4	<0.01	37.2
Φ(t)p(sx)pent(sx)N(.)	7	222.8	9.4	<0.01	37.3
Φ(r)p(s)pent(l)N(.)	9	222.8	9.4	<0.01	31.9
Φ(l)p(.)pent(s)N(.)	8	222.9	9.4	<0.01	34.6
Φ(.)p(s)pent(t)N(.)	8	222.9	9.5	<0.01	34.7
Φ(rb)p(.)pent(s)N(.)	8	222.9	9.5	<0.01	34.7
Φ(sx)p(s)pent(l)N(.)	9	222.9	9.5	<0.01	31.9
Φ(r)p(s)pent(sx)N(.)	9	222.9	9.5	<0.01	31.9
Φ(t)p(Da)pent(sx)N(.)	7	222.9	9.5	<0.01	37.4
Φ(sx)p(Da)pent(s)N(.)	9	222.9	9.5	<0.01	32.0
Φ(rb)p(s)pent(.)N(.)	8	223.0	9.6	<0.01	34.8
Φ(l)p(sx)pent(rb)N(.)	7	223.0	9.6	<0.01	37.4
Φ(s)p(.)pent(rb)N(.)	8	223.0	9.6	<0.01	34.8
Φ(Da)p(s)pent(r)N(.)	9	223.1	9.7	<0.01	32.1
Φ(t)p(s)pent(.)N(.)	8	223.1	9.7	<0.01	34.9
Φ(l)p(sx)pent(l)N(.)	7	223.1	9.7	<0.01	37.6
Φ(rb)p(sx)pent(rb)N(.)	7	223.2	9.7	<0.01	37.6
Φ(l)p(Da)pent(rb)N(.)	7	223.2	9.7	<0.01	37.6
Φ(s)p(.)pent(l)N(.)	8	223.2	9.8	<0.01	35.0
Φ(sx)p(s)pent(sx)N(.)	9	223.3	9.9	<0.01	32.3
Φ(rb)p(Da)pent(rb)N(.)	7	223.3	9.9	<0.01	37.7
Φ(.)p(s)pent(r)N(.)	8	223.3	9.9	<0.01	35.1
Φ(rb)p(sx)pent(l)N(.)	7	223.3	9.9	<0.01	37.7
Φ(l)p(Da)pent(l)N(.)	7	223.3	9.9	<0.01	37.8
Φ(s)p(.)pent(sx)N(.)	8	223.3	9.9	<0.01	35.1
Φ(l)p(s)pent(.)N(.)	8	223.3	9.9	<0.01	35.1
Φ(l)p(sx)pent(sx)N(.)	7	223.3	9.9	<0.01	37.8
Φ(rb)p(Da)pent(l)N(.)	7	223.4	10.0	<0.01	37.8
Φ(rb)p(sx)pent(sx)N(.)	7	223.4	10.0	<0.01	37.9
Φ(l)p(Da)pent(sx)N(.)	7	223.5	10.0	<0.01	37.9
Φ(rb)p(Da)pent(sx)N(.)	7	223.5	10.1	<0.01	37.9
Φ(r)p(s)pent(t)N(.)	9	223.8	10.3	<0.01	32.8
Φ(s)p(Da)pent(.)N(.)	8	223.8	10.4	<0.01	35.6

Φ(s)p(sx)pent(.)N(.)	8	223.9	10.4	<0.01	35.6
Φ(rb)p(s)pent(l)N(.)	9	223.9	10.5	<0.01	32.9
Φ(t)p(sx)pent(t)N(.)	7	223.9	10.5	<0.01	38.4
Φ(t)p(sx)pent(r)N(.)	7	224.0	10.6	<0.01	38.4
Φ(s)p(s)pent(Da)N(.)	11	224.0	10.6	<0.01	27.2
Φ(r)p(s)pent(r)N(.)	9	224.0	10.6	<0.01	33.1
Φ(t)p(Da)pent(t)N(.)	7	224.1	10.7	<0.01	38.5
Φ(sx)p(s)pent(t)N(.)	9	224.1	10.7	<0.01	33.1
Φ(t)p(Da)pent(r)N(.)	7	224.1	10.7	<0.01	38.6
Φ(t)p(s)pent(l)N(.)	9	224.4	11.0	<0.01	33.4
Φ(t)p(Da)pent(s)N(.)	9	224.4	11.0	<0.01	33.5
Φ(sx)p(s)pent(r)N(.)	9	224.4	11.0	<0.01	33.5
Φ(t)p(sx)pent(s)N(.)	9	224.5	11.0	<0.01	33.5
Φ(l)p(sx)pent(t)N(.)	7	224.5	11.1	<0.01	38.9
Φ(s)p(.)pent(t)N(.)	8	224.5	11.1	<0.01	36.3
Φ(rb)p(s)pent(sx)N(.)	9	224.5	11.1	<0.01	33.5
Φ(l)p(sx)pent(r)N(.)	7	224.5	11.1	<0.01	39.0
Φ(s)p(.)pent(r)N(.)	8	224.5	11.1	<0.01	36.3
Φ(rb)p(sx)pent(t)N(.)	7	224.6	11.1	<0.01	39.0
Φ(l)p(s)pent(l)N(.)	9	224.6	11.2	<0.01	33.6
Φ(rb)p(sx)pent(r)N(.)	7	224.6	11.2	<0.01	39.1
Φ(l)p(Da)pent(t)N(.)	7	224.6	11.2	<0.01	39.1
Φ(t)p(s)pent(sx)N(.)	9	224.6	11.2	<0.01	33.6
Φ(rb)p(Da)pent(t)N(.)	7	224.7	11.2	<0.01	39.1
Φ(l)p(Da)pent(r)N(.)	7	224.7	11.2	<0.01	39.1
Φ(rb)p(Da)pent(r)N(.)	7	224.7	11.3	<0.01	39.1
Φ(l)p(s)pent(sx)N(.)	9	224.8	11.4	<0.01	33.8
Φ(l)p(Da)pent(s)N(.)	9	224.9	11.5	<0.01	34.0
Φ(l)p(sx)pent(s)N(.)	9	224.9	11.5	<0.01	34.0
Φ(rb)p(Da)pent(s)N(.)	9	225.0	11.6	<0.01	34.0
Φ(rb)p(sx)pent(s)N(.)	9	225.0	11.6	<0.01	34.1
Φ(s)p(sx)pent(rb)N(.)	9	225.1	11.7	<0.01	34.1
Φ(s)p(Da)pent(rb)N(.)	9	225.2	11.8	<0.01	34.2

Φ(rb)p(s)pent(t)N(.)	9	225.2	11.8	<0.01	34.2
Φ(s)p(sx)pent(l)N(.)	9	225.3	11.9	<0.01	34.3
Φ(s)p(Da)pent(l)N(.)	9	225.3	11.9	<0.01	34.3
Φ(s)p(.)pent(s)N(.)	10	225.3	11.9	<0.01	31.5
Φ(t)p(s)pent(t)N(.)	9	225.3	11.9	<0.01	34.4
Φ(s)p(Da)pent(sx)N(.)	9	225.4	11.9	<0.01	34.4
Φ(.)p(s)pent(s)N(.)	10	225.4	11.9	<0.01	31.5
Φ(Da)p(s)pent(s)N(.)	11	225.4	12.0	<0.01	28.6
Φ(s)p(sx)pent(sx)N(.)	9	225.4	12.0	<0.01	34.4
Φ(l)p(s)pent(t)N(.)	9	225.6	12.2	<0.01	34.6
Φ(rb)p(s)pent(r)N(.)	9	225.6	12.2	<0.01	34.6
Φ(t)p(s)pent(r)N(.)	9	225.8	12.4	<0.01	34.8
Φ(s)p(s)pent(rb)N(.)	11	225.9	12.5	<0.01	29.1
Φ(l)p(s)pent(r)N(.)	9	226.0	12.6	<0.01	35.0
Φ(r)p(s)pent(s)N(.)	11	226.1	12.7	<0.01	29.3
Φ(s)p(s)pent(.)N(.)	10	226.5	13.1	<0.01	32.7
Φ(s)p(Da)pent(t)N(.)	9	226.5	13.1	<0.01	35.6
Φ(s)p(sx)pent(t)N(.)	9	226.6	13.1	<0.01	35.6
Φ(sx)p(s)pent(s)N(.)	11	226.6	13.1	<0.01	29.7
Φ(s)p(Da)pent(r)N(.)	9	226.6	13.2	<0.01	35.6
Φ(s)p(sx)pent(r)N(.)	9	226.6	13.2	<0.01	35.6
Φ(s)p(Da)pent(s)N(.)	11	227.5	14.1	<0.01	30.7
Φ(s)p(sx)pent(s)N(.)	11	227.7	14.3	<0.01	30.8
Φ(s)p(s)pent(l)N(.)	11	227.7	14.3	<0.01	30.8
Φ(t)p(s)pent(s)N(.)	11	228.0	14.6	<0.01	31.1
Φ(rb)p(s)pent(s)N(.)	11	228.0	14.6	<0.01	31.2
Φ(s)p(s)pent(sx)N(.)	11	228.2	14.8	<0.01	31.4
Φ(l)p(s)pent(s)N(.)	11	228.3	14.8	<0.01	31.4
Φ(s)p(s)pent(t)N(.)	11	228.9	15.5	<0.01	32.1
Φ(s)p(s)pent(r)N(.)	11	229.4	16.0	<0.01	32.5
Φ(s)p(s)pent(s)N(.)	13	232.1	18.7	<0.01	28.9

Considerações finais

No primeiro capítulo foi demonstrado que não houve diferenciação na dieta das duas espécies na área estudada. Além disto, foi possível observar que *Metachirus nudicaudatus* e *Didelphis aurita* dividem o uso do espaço ao longo do tempo. Estes resultados indicam que a divisão do nicho espacial na escala temporal seria o mecanismo para contornar a competição por recurso, permitindo assim a coocorrência das espécies. As conclusões obtidas a partir deste capítulo inovam ao demonstrar que a dieta de *M. nudicaudatus* tem um potencial mais generalista do que previa a literatura. Esperamos que a metodologia de análise proposta neste estudo, que combina as análises de nicho isotópico e redes de inivíduo-recurso, contribua para estudos futuros sobre a dieta dos marsupiais brasileiros e outras espécies.

No segundo capítulo foi demonstrado que, na ausência de predadores, é esperado o aumento na abundância de *D. aurita* e a expansão de seu nicho trófico realizado. Como consequência da competição por recurso, a abundância da população e o nicho trófico realizado de *M. nudicaudatus* devem diminuir. Por outro lado, em áreas onde ocorrem predadores de topo, é esperado que ocorra o cenário oposto. As conclusões obtidas a partir deste capítulo inovam ao demonstrar que a ausência de predadores de topo é capaz de alterar não apenas a abundância de mesopredadores, mas também o seu nicho trófico realizado. Como direção futura, é necessário testar a aplicabilidade do modelo proposto para outros grupos de organismos.

No terceiro capítulo foi possível observar que na área estudada, a abundância de *D. aurita* influenciou negativamente todos os parâmetros populacionais de *M. nudicaudatus*. Fica evidente que nesta área, em uma curta escala de tempo, há uma relação negativa dependente de densidade entre *M. nudicaudatus* e *D. aurita.* Porém, tendo em vista a influência dos predadores de topo sobre a proporção das abundancias das duas espécies, e que na área estudada não ocorre a maioria dos predadores de *D. aurita*, seria interessante realizar este mesmo estudo em áreas onde a comunidade de predadores seja diversa e abundante, para avaliar se o padrão aqui apresentado irá se repetir.

A partir dos três estudos apresentados nesta tese, fica claro que *D. aurita* afeta negativamente diferentes aspectos ecológicos de *M. nudicaudatus*. Acreditamos que é a semelhança entre seus nichos tróficos que faz com que a abundância de *D. aurita* influencie *M. nudicaudatus* no uso do espaço, determine a amplitude de seu nicho trófico realizado, e afete negativamente seus parâmetros populacionais. Os mecanismos pelos quais estas interações ocorrem ainda são desconhecidos. Provavelmente um deles seja o reconhecimento interespecífico das substâncias químicas secretadas pelas glândulas paracloacais de ambas as espécies. Desta forma, são necessários estudos comportamentais sobre a interação entre os indivíduos, para uma melhor compreensão de como são gerados os padrões aqui descritos. Até o momento não havia na literatura estudos que demonstrassem a interferência negativa de *D. aurita* sobre aspectos ecológicos de nenhuma espécie. Assim, os resultados desta tese lançam uma nova perspectiva sobre o papel ecológico deste mesopredador da Mata Atlância.

Apêndice

Bem-estar de pequenos mamíferos capturados em armadilhas de grade

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Título curto: Bem-estar de pequenos mamíferos

Resumo

Prezar pelo bem-estar dos animais capturados envolve questões éticas e implica diretamente na qualidade do dado coletado. Pouco se discute sobre o bem-estar dos animais capturados em armadilhas de grade. O presente trabalho tem como objetivo apresentar algumas sugestões práticas para o uso destas armadilhas na captura de pequenos mamíferos, visando um maior bem-estar dos indivíduos capturados. O foco do trabalho foi nas dificuldades peculiares às áreas tropicais, especialmente as com altos índices de pluviosidade. Porém, esperamos que os pontos apresentados aqui sirvam também para provocar a discussão sobre o bem-estar de pequenos mamíferos em outros cenários.

Palavras chave: boas práticas, marsupial, roedor, Tomahawk, Young,

Abstract

Welfare issues related to animal capture directly implicate on data quality. However, little is discussed about the welfare of wild animals caught in livetraps. This paper aims to present some practical suggestions for the use of these traps in capturing small mammals, seeking for the welfare of captured individuals. Although this work has focused on how to overcome peculiar challenges of tropical areas, especially with high rates of rainfall, we wish that the issues that we point out here could also serve to provoke discussions about small mammals' welfare in other scenarios.

Key words: marsupial, rodent, Tomahawk, welfare, Young.

O bem-estar animal engloba a saúde do animal, seus estados afetivos (e.g. dor, medo, sofrimento), e sua capacidade para viver na maneira à qual são adaptados (Fraser et al., 1997). Para garantia deste bem-estar todos os animais devem ser livres de medo e estresse crônico (distress), livres de fome e sede, de desconforto, de dores, e doenças (FAWEC, 2012). A fundamentação destes direitos surgiu com base no bem-estar dos animais de criação (Broom, 2011). Já o bem-estar e a ética que envolvem os animais de vida livre ainda são pouco discutidos (Fauvel et al., 2012; Funk et al., 2005; Minteer & Collins, 2005). O bem-estar dos indivíduos em ambiente natural ainda é comumente negligenciado em detrimento de um benefício último para as suas populações (Fraser, 2010). O estudo das populações de espécies em vida livre pode levar a mudanças de comportamento dos indivíduos, evasão das áreas estudadas em função das capturas, e até mesmo causar lesões a longo prazo (Krag, 2008; Wilson & McMahon, 2006). Infelizmente, a dificuldade de registrar as conseqüências sobre os indivíduos acaba por subsidiar esta idéia de que os efeitos negativos causados aos indivíduos são insignificantes (Krag, 2008; Wilson & McMahon, 2006). Além disto, durante o planejamento das pesquisas em campo, custos e prazos tendem a ser vistos como prioridade sobre o bem-estar e a ética animal (Parris et al., 2010).

Um dos aspectos mais discutidos sobre o bem-estar de animais de vida livre na pesquisa científica são as metodologias de marcação individual (e.g. Loretto et al. 2013). Já existem trabalhos que avaliam as conseqüências destas marcações para as populações (e.g. Gauthier-Clerc et al., 2004), para os indivíduos (e.g. Walker et al., 2011), e também para a conservação das espécies (e.g. Funk et al., 2005). Entretanto, ainda são escassos na literatura trabalhos que avaliem aspectos de bem-estar animal relacionados a diferentes metodologias de captura. A captura pode gerar grande estresse aos indivíduos levando a mudanças na sua fisiologia, como por exemplo: aumentos na produção de adrenalina, na taxa metabólica, na temperatura corporal, e nas frequências cardíaca e respiratória (Giese, 1996; Weimerskirch et al., 2002).

Especificamente para pequenos mamíferos, sabe-se pouco sobre o impacto das capturas, manipulações, e marcações individuais, sobre o bem-estar dos indivíduos estudados (Fisher & Blomberg, 1995). Alguns documentos, como as diretrizes da Sociedade Americana para o uso de mamíferos em pesquisas, indicam condutas metodológicas que visam assegurar o bem-estar dos animais capturados (Sikes et al., 2011; Trajano & Silveira, 2008). As diretrizes são simples e podem ser facilmente adotadas para um trabalho de campo mais ético. Alguns exemplos das boas práticas sugeridas são: cobrir a gaiola assim que se aproximar dela, para diminuir o estresse do indivíduo capturado enquanto o material necessário para a manipulação é preparado; cobrir os olhos do indivíduo enquanto ele é manipulado; e utilizar um número de armadilhas condizente com a capacidade do pesquisador de monitorá-las. Além disto, sempre que possível, verificar freqüentemente as armadilhas para minimizar o agravamento de ferimentos e a mortalidade dos indivíduos.

Apesar da existência destas diretrizes gerais, cada espécie, em cada bioma, possui necessidades diferentes e suas particularidades devem ser priorizadas para garantia de seu bem-estar durante o estudo (Do et al., 2013; Drickamer & Paine,1992; Rychlik et al., 2012; Shonfield et al., 2013). Além disto, o pesquisador deve estar atento também às particularidades de cada metodologia de captura e aos respectivos riscos que elas expõem aos indivíduos capturados. A captura através de armadilhas de interceptação e queda (pitfalls), em função das altas taxas de mortalidade geradas, é a metodologia de captura de pequenos mamíferos mais discutida na literatura (Cáceres et al., 2012; Ferguson & Forstner, 2006; Karraker, 2001; Kogut, 1997; Padgett-Flohrge & Jennings, 2001; Pearce et al., 2005; Peter, 2015). Por outro lado, quase não se discute a exposição e a diminuição de bem-estar que os animais estão expostos quando capturados em armadilhas de grade. Desta forma, o presente trabalho tem como objetivo apresentar algumas sugestões práticas para o uso destas armadilhas em campo, visando um maior bem-estar dos indivíduos capturados.

Os modelos Tomahawk e Young são armadilhas de grade que consistem basicamente de uma gaiola de arame que se fecha através de uma alavanca que é destravada assim que o animal tenta acessar a isca. Estes modelos são amplamente utilizados na captura de pequenos mamíferos para as mais diversas finalidades: pesquisas científicas, inventário de espécies, resgate de fauna, monitoramento ambiental, entre outros. As armadilhas de grade são capazes de capturar uma variedade de espécies, desde grandes marsupiais como Didelphis spp. que podem chegar a pesar 2kg, até pequenos roedores que pesam menos de 100g. (Cáceres et al., 2011; Santos-Filho et al. 2006).

Durante a noite, normalmente o período mais frio do dia, é que a maioria das espécies de pequenos mamíferos está ativa. Quando capturados, ao invés de passarem a noite ativos, passam a noite presos e expostos às intempéries. Pequenos mamíferos possuem uma alta relação corpórea de superfície/volume, o que dificulta a manutenção da sua temperatura (Schmidt-Nielsen 2002). A estrutura vazada destas armadilhas dificulta a manutenção dessa temperatura, o que pode levar os indivíduos à morte por hipotermia (obs. pess.). Uma alternativa para diminuir as chances de hipotermia seria ensacar as gaiolas com sacos plásticos. A menos que a porção dos sacos que fica em contato ao solo seja furada, esta técnica não é recomendada, pois quando há chuva intensa a água que escorre pelo solo pode se acumular dentro do saco. O acúmulo da água pode ocorrer até mesmo com a entrada da gaiola posicionada a favor do declínio do terreno. Como não é fácil encontrar no comércio sacos plásticos com apenas um lado furado, e furar manualmente demanda certo tempo, sugerimos que a gaiola seja apenas coberta por um plástico. O plástico deve ser de tamanho suficiente para tampar as laterais e a parte superior da armadilha, desta forma o animal fica protegido do sereno e da chuva (Figura 1). A revisão das armadilhas será facilitada se o plástico for transparente, o que permite verificar a curtas distâncias se algum indivíduo foi capturado ou se ainda há isca disponível.

Figura 1. Armadilha de captura modelo Tomahawk coberta por plástico para proteger o indivíduo capturado da chuva e do sereno, e apoiada sobre placa de mdf para proteger o indivíduo capturado da umidade do solo.

Outra técnica que pode ser adotada para diminuir as chances de hipotermia é colocar as armadilhas sobre placas de fibra de madeira de média densidade (mdf, Figura 1). Estas placas permitem que a armadilha fique isolada do contato com o solo frio e úmido. O uso do mdf possui vantagens como: o custo deste material é baixo; não é pesado, o que permite ser carregado com facilidade; é reutilizável; é fácil de higienizar, com um borrifador de álcool e uma escovinha é possível remover as fezes com facilidade; e não diminui o sucesso de captura. A utilização dos sacos plásticos e do mdf também proporcionam ao pesquisador outras vantagens. Por exemplo, em dias chuvosos a cobertura das gaiolas pelos sacos plásticos protege a isca da água da chuva, prolongando a sua durabilidade o que aumenta o sucesso de captura e diminui os custos da pesquisa. Além disto, o mdf também isola as fezes do contato com o solo, o que é ideal para estudos de parasitologia e dieta.

Dependendo da duração do esforço amostral os animais podem ficar debilitados em função das recapturas. Graipel & Santos-Filho (2006) relatam que uma fêmea de Didelphis aurita Wied-Neuwied, 1826 foi sucessivamente recapturada ao longo do estudo. As recapturas deixaram o indivíduo extremamente debilitado, e após a oitava recaptura no mesmo mês, a fêmea já tinha perdido cerca de 13% do seu peso original, e morreu na gaiola. O planejamento do esforço amostral é ainda mais relevante quando os estudos visam obter dados da dinâmica populacional. Cáceres e colaboradores (2012) sugerem que o esforço de amostragem para estudos populacionais de pequenos mamíferos não deve ultrapassar 5 dias consecutivos.

Tendo em vista que os indivíduos capturados muitas vezes chegam a ficar mais de 12 horas consecutivas presos na gaiola, é de extrema importância que sejam utilizadas iscas com algo valor energético e que estas sejam ofertadas em quantidade suficiente. Além da escolha da isca adequada, também é importante fazer um planejamento do número de armadilhas e do tamanho da área amostrada, que leve em conta a fragilidade dos indivíduos frente ao estresse que a captura proporciona. Para o cálculo do esforço amostral deve ser considerado o tempo necessário para visitar todas as armadilhas. O ideal é minimizar ao máximo o tempo que os indivíduos capturados ficarão nas gaiolas. Dessa forma, é indicado que a revisão das armadilhas seja feita nas primeiras horas do dia. Nos casos em que as armadilhas estão posicionadas em áreas que não possuem uma cobertura arbórea para proteção do calor do sol, é importante considerar o tempo que o animal ficará exposto ao sol, principalmente por que os indivíduos capturados não terão acesso à água. Locais sem cobertura devem ser evitados tanto pela exposição ao sol, mas também pela exposição à chuva.

Infelizmente, mesmo com a adoção de boas práticas em campo, alguns indivíduos são mais frágeis do que outros e mais propensos à desnutrição ou hipotermia. Durante o inverno, ou nas épocas chuvosas, as chances de hipotermia aumentam ainda mais. Uma alternativa para reverter quadros de hipotermia é levar para campo uma bolsa de látex com água quente. Estas bolsas são ideais, pois são capazes de conservar o calor por até seis horas. A bolsa deve ser envolta em um pano para evitar queimaduras, e caso aconteça algum caso de hipotermia, basta apoiar o animal por alguns minutos em cima da bolsa para ele se recuperar.

Além da hipotermia, outra questão relevante ao bem-estar dos animais capturados em armadilhas de grade são as lesões causadas pelas tentativas de fuga. Alguns modelos possuem reentrâncias ou folgas (Figura 2a) que o animal é capaz de empurrar para forçar a saída e acaba se machucando. Além dos ferimentos na pele (Figura 2b) alguns indivíduos chegam a ficar com os dentes presos por entre as grades destas reentrâncias de tanto forçar a saída (Kuhnen obs. pess.). Modelos com folga nas portas ou que apresentem algum tipo de reentrâncias, como exemplificado na figura 2a, devem ser evitados para prevenir lesões.

As feridas causadas pelas tentativas de fuga são portas para infecções. Sempre que um animal capturado apresentar qualquer tipo de ferimento, este precisa ser tratado antes da soltura. Sobre os machucados existentes é recomendado utilizar álcool iodado 7% (Forattini et al., 1972). Além das feridas, o tempo em que o animal está cativo dentro da armadilha já o expõe à parasitas oportunistas (Figura 3). Esta exposição diminui consideravelmente o bem-estar dos indivíduos, podendo levar à morte (obs. pess.). Porém, não existem estudos dos impactos causados aos indivíduos pelas parasitoses obtidas durante o período de captura. A vulnerabilidade à parasitas durante o tempo em que o animal está na gaiola é um sério fator de bem-estar animal, e deveria receber mais atenção pela comunidade científica. A utilização de armadilhas modelo Sherman dificulta o acesso de insetos, reduzindo a incidências de parasitoses. Porém, este tipo de armadilha não costuma ser utilizado para captura de espécies de maior porte, como por exemplo marsupiais do gênero Didelphis. Além disto, a coleta das fezes e a limpeza destas armadilhas são mais trabalhosas do que armadilhas de grade.

Figura 2. a) Armadilha de captura com reentrância na porta que favorece com que o indivíduo capturado se machuque nas tentativas de fuga; b) Indivíduo de *Metachirus nudicaudatus* lesionado pelas tentativas de fuga da armadilha da figura a.

Figura 3. a) *Trinomys iheringi* capturado em armadilha Tomahawk e sendo parasitado por díptero; b) Detalhe da oviposição dos dípteros.

Prezar pelo bem-estar dos animais capturados não envolve apenas questões éticas, mas implica também na qualidade do dado coletado. Pequenas ações como as aqui apresentadas são de baixo custo, não aumentam o tempo despedido em campo, além de aumentarem as chances de sobrevivência e o bem-estar dos indivíduos capturados. Práticas que aumentem o bem-estar deveriam ser naturalmente incorporadas no desenho amostral e nos planejamentos dos trabalhos de campo. Esperamos que nossas sugestões aprimorem o trabalho de campo em pesquisas, levantamento e monitoramentos de pequenos mamíferos. Apesar das sugestões apresentadas aqui terem maior aplicabilidade em áreas que apresentem baixas temperaturas e altos índices de pluviosidade, gostaríamos que este trabalho servisse para provocar a discussão sobre o bem-estar de pequenos mamíferos também em outros cenários.

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Anexos

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Presidente
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Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **ECOLOGY OF THE MARSUPIALS Didelphis aurita AND Metachirus nudicaudatus - ECOLOGIA DOS MARSUPIAIS Didelphis aurita E Metachirus nudicaudatus**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 03 de março de 2016.

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Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada "***ECOLOGY OF THE MARSUPIALS Didelphis aurita AND Metachirus nudicaudatus - ECOLOGIA DOS MARSUPIAIS Didelphis aurita E Metachirus nudicaudatus***", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

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