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INFLUÊNCIA DO TAMANHO DE NINHADA NO SUCESSO REPRODUTIVO DA
ANDORINHA-DE-SOBRE-BRANCO: um experimento

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INFLUÊNCIA DO TAMANHO DE NINHADA NO SUCESSO REPRODUTIVO DA
ANDORINHA-DE-SOBRE-BRANCO: um experimento

Dissertação apresentada como requisito parcial à obtenção do grau de Mestre no Curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná.

Orientador: Prof. Dr. James Joseph Roper

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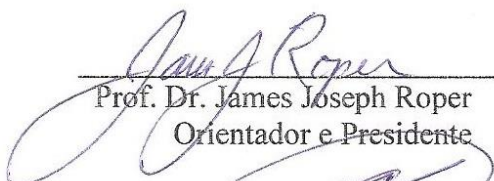
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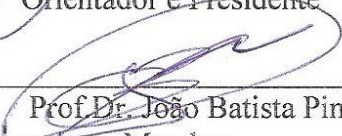
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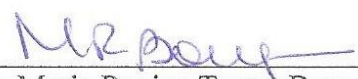


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*“To be the best in all possible worlds is not
biologically possible; to be well adapted to
even one world requires compromise.”*

David Reznick, 1985

RESUMO

A teoria de seleção natural prevê que o tamanho de ninhada mais comum em uma população deve ser também o mais produtivo (ótimo). Além disso, restrições de energia e tempo geram um *trade-off* entre reprodução atual e futura dos indivíduos. Assim, a quantidade de energia investida em uma ninhada (determinada, por exemplo, pelo número de filhotes) deve ser resultado das chances de sucesso reprodutivo futuro de um adulto e das chances de sobrevivência da prole. Aqui, investigamos se o tamanho das ninhadas da andorinha-de-sobrebranco (*Tachycineta leucorrhoa*, Aves) é ótimo. Uma vez que sua distribuição abrange desde áreas tropicais até temperadas do hemisfério sul, a espécie deve ser, em geral, mais longeva e ter maior dificuldade em coletar alimento durante a estação reprodutiva do que aves do hemisfério norte temperado. Logo, o esforço em criar ninhadas maiores é alto e os adultos devem privilegiar sua própria sobrevivência frente à de seus filhotes. Para testar essa predição, manipulamos tamanhos de ninhada de casais reproduzindo em caixas-ninho às margens de duas represas no Paraná. Medimos o crescimento dos ninhegos até a idade de 12 dias e a taxa de visitação pelos pais, como forma de avaliar o benefício para os filhotes e os custos para os pais do cuidado parental, respectivamente. No ano seguinte, avaliamos a taxa de retorno, a condição corporal e a fecundidade dos jovens e dos adultos, para verificar se deficiências de crescimento dos ninhegos e se o esforço parental resultaram em custos para sobrevivência e reprodução futura, como previsto pela teoria. Verificamos que filhotes de ninhadas aumentadas e controle cresceram igualmente; e que adultos intensificaram o cuidado a proles aumentadas, mantendo a taxa de alimentação por ninhego igual à natural. Descrevemos também um comportamento de visitação dos pais a ninhadas alheias, que provavelmente tem o objetivo de explorar locais futuros para ninhos e que é exibido principalmente por adultos com ninhadas reduzidas e controle. Não observamos nenhum efeito residual dos tamanhos de ninhada à fecundidade, condição corporal e taxa de retorno dos filhotes ou adultos. Em conjunto, esses resultados indicam que a) o esforço empregado durante a criação dos filhotes não gera custos reprodutivos, b) adultos conseguem criar ninhadas maiores que as naturais, logo, ninhadas não tem tamanho ótimo. Nesse caso, discute-se que talvez outras fases do ciclo reprodutivo restrinjam os tamanhos de ninhada naturais (por exemplo, a fase de postura e incubação dos ovos), ou a restrição é temporal e não energética. Ainda, deve-se avaliar o impacto da seleção de lugares para ninho para o sucesso reprodutivo futuro e de inconstâncias climáticas no sucesso ao longo da vida dos indivíduos.

ABSTRACT

The theory of natural selection predicts that the most common clutch size in a population is the most productive (optimum). In addition, time and energy restrictions cause a trade-off between current and future reproduction. Hence, the amount of energy invested in a clutch (determined, for example, by clutch size) should be a result of the chances of future breeding success of an adult and the chances of recruitment of its offspring. Here, we investigated if clutch sizes from the White-rumped Swallow (*Tachycineta leucorrhoa*) are optimal. Since its distribution ranges from tropical to temperate areas in the southern hemisphere, we predict that its lifespan is longer and it has more difficulty gathering food during the breeding season than birds from the temperate northern hemisphere. Therefore, the effort in rearing greater clutches is greater and adults should privilege their own survival, not that of their offspring. To test this prediction, we manipulated brood sizes from pairs breeding in nest boxes in two reservoirs in the state of Paraná. We measured nestling growth until 12 days of age and parental visiting rate, in order to evaluate offspring benefit and costs to adults of parental care. In the following year, we evaluated return rate, body condition and fecundity of first-year breeders and adults to assess if nestling growth deficiencies and parental effort resulted in costs to survival and reproduction, as predicted by theory. We verified that nestlings from enlarged and control broods grew similarly, and that adults increased parental care to enlarged broods, keeping nestling feeding rate similar to control broods. We described a visiting behavior by parents to nests of other pairs, which probably is to prospect for future breeding locations and is exhibited specially by adults with control and reduced broods. We observed no residual effect of brood size in survival, body condition, and fecundity of offspring and parents. Together, these results suggest that: a) the effort in rearing nestlings results in no reproductive costs; b) adults can rear broods greater than natural, and so, clutch size is not optimal. Therefore, we argue that perhaps other periods from the nestling cycle are the constraint to clutch sizes (e.g., laying and incubation), or the constraint is temporal rather than energetic. Additionally, future studies should evaluate the impact of nest site prospection in future reproductive success of birds breeding in natural cavities and the influence of climatic unpredictability in the success of an individual.

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1 INTRODUÇÃO GERAL

Tamanho de ninhada é uma característica de interesse central na compreensão da variabilidade em histórias de vida, e é especialmente estudada em aves. Em meados da década de 1940, estudos sobre a correlação entre tamanho de ninhada e latitude levaram à proposição de hipóteses que pretendiam explicar evolutivamente os tamanhos de ninhada baseando-se em componentes extrínsecos (ambientais) e intrínsecos aos organismos e populações (LACK, 1947; STEARNS, 2000).

Se o tamanho de ninhada é adaptativo, ele deve maximizar a aptidão de um organismo (WILLIAMS, 1966). Essa teoria foi amplamente testada experimentalmente e parece se adequar a alguns organismos, mas não a outros (revisão em LINDÉN; MØLLER, 1989). Uma das exceções é a andorinha norte-americana *Tachycineta bicolor*, cujo aumento experimental de esforço reprodutivo não parece gerar prejuízos à sobrevivência dos filhotes ou dos pais, ou seja, não há compensação (*trade-off*) aparente entre quantidade e qualidade de filhotes ou entre reprodução atual e futura, o que seria esperado conforme o princípio de alocação (CODY, 1966; SHUTLER et al., 2006).

Replicar esses estudos em uma espécie filogeneticamente próxima à andorinha norte-americana, porém em um contexto com diferentes pressões ambientais, permite compreender melhor as forças evolutivas agindo sobre os tamanhos de ninhada desse grupo de espécies. Adicionalmente, estudos experimentais avaliando a otimização de características reprodutivas ainda são incipientes na América do Sul (MARTIN, 1996; SOUZA; MARINI, 2012).

Dessa maneira, o objetivo deste trabalho é investigar a resposta da andorinha-de-sobre-branco *Tachycineta leucorrhoa* quando submetida a diferentes tamanhos de ninhada, de modo a avaliar se ninhadas são ótimas. Especificamente, serão avaliados o crescimento dos ninhegos e a taxa de cuidado parental resultantes de tamanhos de ninhada experimentalmente alterados, a fim de verificar se os custos reprodutivos são transferidos entre gerações (dos pais aos filhotes) ou absorvidos pelos pais (capítulo 2). Além disso, será descrito um comportamento de visitaç o de ninhadas alheias pela espécie, com suas possíveis motivações (capítulo 3). Por último, serão investigados os efeitos residuais dos tamanhos de ninhada modificados na taxa de retorno, condiç o corporal e desempenho reprodutivo dos adultos e filhotes na temporada reprodutiva seguinte (capítulo 4). O último capítulo discute brevemente os resultados dos capítulos precedentes diante da pergunta central do trabalho (capítulo 5). Ainda neste capítulo há uma breve revis o dos temas relevantes ao trabalho e uma descriç o

da área e espécie de estudo.

1.1 Revisão de literatura

1.1.1 Teorias que explicam tamanhos de ninhada

Derivando a ideia de seleção natural, que prevê que genótipos capazes de produzir um maior número de descendentes logo se tornam mais frequentes numa população, Lack propôs a primeira hipótese de otimização de ninhada. Segundo o autor, os tamanhos de ninhada observados na natureza seriam aqueles que produziriam um maior número de jovens deixando os ninhos (*fledglings*; LACK, 1947). Contudo, ele deixou de considerar filtros posteriores à sobrevivência e reprodução de tais filhotes e seus pais, que poderiam diminuir a frequência de seus genótipos na população. De fato, testes experimentais da hipótese de Lack demonstraram que ninhos contendo mais filhotes que o natural eram mais produtivos, ou seja, ninhadas naturais eram sub-ótimas (revisão em ROFF, 1992). Contudo, ao avaliar o tamanho corporal e a sobrevivência desses filhotes “extras”, percebeu-se que eles eram menores e tinham menor probabilidade de sobreviver para reproduzir no futuro (recrutamento), levando à proposta de uma nova hipótese de otimização baseada na chance de recrutamento dos filhotes de uma ninhada (PERRINS; MOSS, 1975). Ainda, em outras espécies o recrutamento em ninhadas aumentadas é maior que em ninhadas naturais, um resultado incoerente com as duas ideias de otimização expostas até agora (LINDÉN; MØLLER, 1989; ROFF, 1992). Com base nisso, propôs-se que o gargalo reprodutivo deveria estar nos adultos. Assim, aumentar o esforço empregado em uma determinada tentativa reprodutiva, diminui o valor reprodutivo residual, ou seja, as chances de sucesso reprodutivo futuro de um indivíduo. Dessa maneira, os tamanhos de ninhada naturais seriam os que produziram maior número de recrutas ao longo de toda a vida dos adultos (CHARNOV; KREBS, 1974; WILLIAMS, 1966).

Apesar de a hipótese de otimização ser suprema na teoria de história de vida, já há muito tempo uma concessão é feita à ideia de *bet-hedging*, ou seja, de diluição de risco. Em situações de imprevisibilidade ambiental, quando o organismo não consegue antever como as condições ambientais serão durante o resto do período reprodutivo, ele deve sempre decidir por um tamanho de ninhada menor do que o ótimo e estocar energia para uma nova tentativa reprodutiva, em caso de falha da primeira (BOER, 1968).

Atualmente, tem-se ainda tentado incorporar à teoria alguns fatores tradicionalmente ignorados, como seleção dependente de frequência ou densidade. Uma vez

que esses modos de seleção são modulados por características da população que flutuam temporalmente, questiona-se a existência de apenas um tamanho ótimo de ninhada por população. Por exemplo, demonstrou-se que duas guildas de fêmeas de lagartos co-ocorrem em uma população, uma delas K-estrategista (com poucos filhotes de alta qualidade) e a outra r-estrategista (com muitos filhotes de baixa qualidade; SINERVO; SVENSSON; COMENDANT, 2000). A frequência das fêmeas na população determina qual a estratégia mais vantajosa em um dado instante, sendo que à medida que a frequência de uma guilda aumenta, mais desvantajosa ela se torna. Paralelamente, a sobrevivência dos filhotes é mediada pela densidade desses. Filhotes de alta qualidade aumentam rapidamente em número em situações de alta densidade de filhotes, pois eles são bons competidores, enquanto filhotes de baixa qualidade são favorecidos em um ambiente menos denso. Esse exemplo demonstra claramente que o tamanho de ninhada ótimo varia ao longo do tempo de acordo com características populacionais, como densidade de indivíduos e frequência de uso de estratégias reprodutivas.

1.1.2 Fatores ambientais que influenciam os tamanhos ótimos de ninhada

Apesar de existir um componente herdável nos tamanhos de ninhada, há também plasticidade. Por um lado, temos algumas famílias de aves com postura fixa (e.g., Columbidae com dois ovos; LACK, 1947), por outro, temos aves cujos tamanhos de ninhada se baseiam em suas condições físicas ou no quão favorável o ambiente se apresenta no momento da reprodução (LLOYD, 1999). Por conseguinte, como todo genótipo, essa característica geralmente tem uma norma de reação, que dita os valores ótimos sob diferentes combinações ambientais (STEARNS, 2000). Abaixo, alguns fatores ambientais que, por variarem temporal ou espacialmente, são amplamente reconhecidos por influenciarem tamanhos de ninhada em aves.

Alimento

Inicialmente, imaginou-se que os tamanhos de ninhada seriam limitados pela quantidade de alimento que os pais eram capazes de suprir aos seus filhotes, também chamada de disponibilidade alimentar, dependente tanto da quantidade de alimento bruta no ambiente quanto da capacidade dos adultos em explorar esses recursos (LACK, 1947). A quantidade de alimento pode variar com a qualidade do território reprodutivo ou variar temporalmente, por

exemplo, em ambientes sazonais (HÖGSTEDT, 1980; KLUMP, 1970). A capacidade de forrageamento dos pais é afetada pelo número de horas disponíveis para a coleta de alimento (horas de luz) durante a temporada reprodutiva (LACK, 1947; ROSE; LYON, 2013) e já foi demonstrado que fêmeas com capacidade de forrageamento experimentalmente prejudicada (com asas aparadas) ou fêmeas muito jovens têm ninhadas menores (KLUMP, 1970; STUTCHBURY; ROBERTSON, 1988; WINKLER; ALLEN, 1995). Alternativamente, em áreas de clima mais ameno e menos sazonal, os tamanhos populacionais são mais estáveis, próximos à capacidade suporte do ambiente, e conseqüentemente, a competição por alimento é alta tornando-o menos disponível para cada indivíduo (ASHMOLE, 1963; SAMÁŠ et al., 2013). Também julga-se que em ambientes de alta diversidade de presas os adultos teriam maior dificuldade em localizá-las, devido à menor eficiência de imagens de procura (THIOLLAY, 1988).

Taxa de predação de ninhos

A predação de ninhos foi o segundo mecanismo proposto para explicar variações nos tamanhos de ninhada. Com base na baixa taxa de cuidado parental observada nos trópicos e na baixa sobrevivência de ninhos, propôs-se que pais visitariam pouco os ninhos, para fornecer menos pistas de sua localização aos predadores (SKUTCH, 1949). Logo, a quantidade de alimento que eles poderiam prover aos filhotes seria restrita, limitando os tamanhos de ninhada. Um segundo mecanismo pelo qual a predação poderia agir está relacionado a tentativas reprodutivas repetidas. Animais com longas temporadas reprodutivas, geralmente os mesmos que sofrem com alta predação de ninhos, têm a oportunidade de espalhar seus ovos em várias ninhadas pequenas ao longo da temporada, desse modo, um ninho malsucedido traz menos prejuízo (ROPER, 2005; ROPER; SULLIVAN; RICKLEFS, 2010). Confirmando a ideia de que taxas de predação influenciam tamanhos de ninhada, temos que aves nidificando em cavidades, especialmente as artificiais, possuem taxa menor de predação e maiores tamanhos de ninhada que aves de ninhos abertos da mesma comunidade (MARTIN; LI, 1992; MØLLER, 1989). Além disso, em aves de ninho aberto, a predação potencial poderia induzir a construção de ninhos menores e menos conspícuos, restringindo o número de ovos que poderiam conter (MØLLER, 1990).

Longevidade dos adultos

O ambiente pode influenciar a longevidade dos indivíduos devido à severidade do clima, escassez de recursos alimentares e à intensidade de predação e doenças (MCNAMARA et al., 2004). Merece destaque a concepção de que adultos sejam menos longevos em ambientes temperados, pois a sazonalidade climática e de recursos alimentares levaria muitos indivíduos à morte durante o inverno (ASHMOLE, 1963; MARTIN, 2004). Ainda que algumas espécies partam desses ambientes quando eles se tornam muito desfavoráveis, a migração é uma jornada árdua com altos riscos de mortalidade para os indivíduos (SILLETT; HOLMES, 2002).

Uma vez que a longevidade dos indivíduos pode ser vista como a chance que eles têm de sobreviver até a próxima temporada reprodutiva, indivíduos menos longevos devem investir mais energia na reprodução atual, de modo a garantir sua descendência. Logo, tais indivíduos devem ter ninhadas maiores e empregar mais energia na alimentação e proteção de seus filhotes (ver abaixo), mesmo que isso signifique prejudicar seu valor reprodutivo residual (CHARNOV; KREBS, 1974; GHALAMBOR; MARTIN, 2001).

1.1.3 Cuidado parental

Cuidado parental é um comportamento adaptativo, presente em 99% das aves (COCKBURN, 2006). Esse comportamento engloba desde atividades indiretas, como defesa de território, construção do ninho e alimentação da fêmea durante corte ou incubação, até atividades mais imediatas, como incubação de ovos e ninhegos, alimentação e proteção dos filhotes e acompanhamento de filhotes a locais de forrageamento (SILVER; ANDREWS; BALL, 1985).

O cuidado parental melhora os prospectos de recrutamento de filhotes, embora possa gerar custos para os pais (WILLIAMS, 1966). Cabe ressaltar que o termo *custos reprodutivos* é limitado a situações em que o esforço reprodutivo, i.e. o direcionamento de recursos à reprodução, resulta em diminuição da longevidade e capacidade de reprodução futura dos pais (MARTIN, 1987).

O mecanismo por trás da redução de longevidade dos adultos pode estar simplesmente associado à maior exposição a situações de risco (predação, acidentes, combates), como também ao consumo de recursos do metabolismo somático do organismo. Esse consumo pode comprometer o sistema imune, esgotar reservas energéticas a ponto de

deteriorar tecidos vitais, como a musculatura de voo, e por último, levar à senescência acelerada, ao reduzir a taxa em que células e moléculas são renovadas (ARDIA, 2005; CALOW, 1979).

Durante o período de ninhego, o cuidado parental inclui a proteção do ninho, a incubação dos filhotes e a alimentação desses. Esse último comportamento é medido tradicionalmente em taxa de alimentação total à ninhada, representando o esforço do adulto, e em taxa de alimentação média por ninhego, indicando o benefício para o filhote. Adultos podem ajustar seu cuidado parental de diferentes formas quando expostos experimentalmente a diferentes tamanhos de ninhada (TABELA 1) e esse ajustamento pode ainda variar com a área de estudo, o ano, o sexo do adulto e a idade da ninhada (KLOMP, 1970; SANZ; TINBERGEN, 1999). A taxa de visitação à ninhada pode simplesmente aumentar linearmente com o número de ninhegos; pode acelerar, caso pais empreguem a mesma energia no cuidado de ninhadas reduzidas que já haviam previsto para suas ninhadas originais; ou pode desacelerar, caso exista um teto energético que os pais não conseguem ou escolhem não ultrapassar. Diversos padrões foram observados para a taxa de visitação por ninhego, e a relação dessa com a qualidade dos filhotes pode não ser linear, pois é modulada pela insulação do ninho (que aumenta com o número de filhotes, reduzindo o gasto metabólico desses) e pelo tamanho dos alimentos fornecidos pelos pais (que podem ter tamanho reduzido quando a taxa de visitação é elevada; NUR, 1984; ROYAMA, 1966).

1.2 A área de estudo

O trabalho foi realizado às margens de duas represas na cidade de Piraquara, Paraná (25°30'24"S 49°01'37"W, 908 m de altitude; e 25°30'22"S 49°04'42"W, 897 m de altitude; FIGURA 1). As áreas distam entre si em cerca de 5 km e ficam a 20 km da capital do estado, Curitiba.

O clima da região é temperado, com verões mornos e sem estação seca definida (FIGURA 2; PEEL; FINLAYSON; MCMAHON, 2007). Durante a estação reprodutiva (Out. – Jan.) de 2012, as médias de temperatura mínima e máxima diárias foram respectivamente 16.5°C (DP = 2.6, n = 122) e 26.1°C (DP = 4.0, n = 122), e a precipitação mensal variou de 69.4 mm a 254.6 mm (dados meteorológicos para Curitiba; INMET, 2013).

Apesar de as áreas estarem inseridas na Mata Atlântica, a vegetação é atípica, consistindo de gramados, brejos e bosques, com espécies nativas e exóticas, e é manejada pela companhia de saneamento de água responsável pelas represas, a SANEPAR. Por isso mesmo,

o habitat é ideal para a reprodução da espécie de ave estudada, já que ela prefere habitats aquáticos associados a áreas abertas (RIDGELY; TUDOR, 1989; SIGRIST, 2009).

TABELA 1 - Exemplos não-exaustivos de como o cuidado parental pode ser alterado frente a tamanhos de ninhada em aves e das consequências do cuidado para a qualidade dos filhotes (estimada através do tamanho ou da sobrevivência desses). Tamanhos de ninhada podem ser modificados para serem menores (reduzidos, R), iguais (controles, C) ou maiores do que os naturais (aumentados, A). No caso de estudos não experimentais, esses mesmos códigos representam tamanhos de ninhada pequenos (R), médios (C) ou grandes na população (A).

Taxa de alimentação total	Taxa de alimentação por ninhego	Qualidade dos ninhegos	Nome da hipótese, se houver (Referência)
$R < C < A$	$R = C = A$	$R = C = A$	(KLOMP, 1970; SKUTCH, 1949)
	$R > C > A$	$R > C > A$	(KLOMP, 1970; SHUTLER et al., 2006)
	$R > C = A$	$R > C > A^a$	(NUR, 1984)
$R < C = A$	$R = C > A$	$R = C > A$	Gibb-Lack hypothesis (NUR, 1984)
		$R = C = A^a$	Royama's hypothesis (NUR, 1984; ROYAMA, 1966)
	$R = C = A$	$R = C > A^b$	(SOUZA; MARINI, 2012)
	$R > C > A$	$R > C > A$	(MURPHY et al., 2000)
$R = C < A$	$R = C = A$	$R = C > A^c$	(SANZ; TINBERGEN, 1999)

Relação não linear entre taxa de alimentação por ninhego e qualidade de ninhegos é atribuída a: ^avariação do metabolismo basal dos ninhegos de acordo com tamanho da ninhada, sendo mais elevado em ninhadas pequenas; ^bvariação do tamanho das presas com taxa de alimentação total; ^cnenhuma explicação disponível.

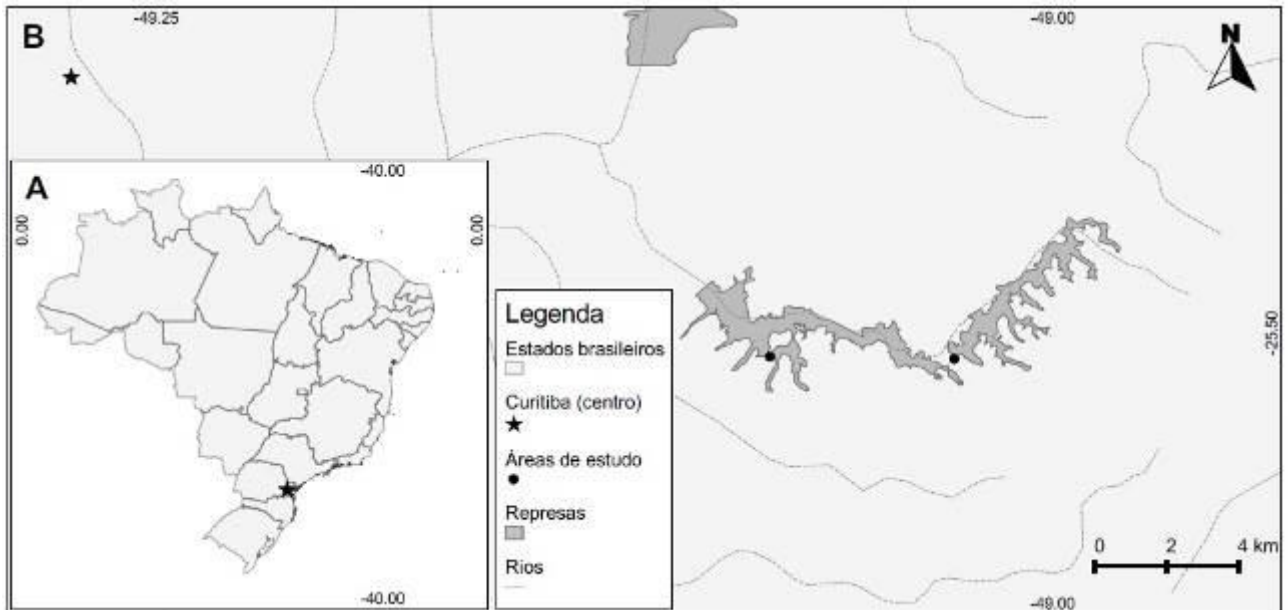


FIGURA 1 - Localização da área de estudo (*datum* WGS-84). O Painel A situa as represas no mapa político do Brasil, enquanto o painel B mostra a distância dessas à capital do estado do Paraná, Curitiba, e aos demais corpos d'água da região.

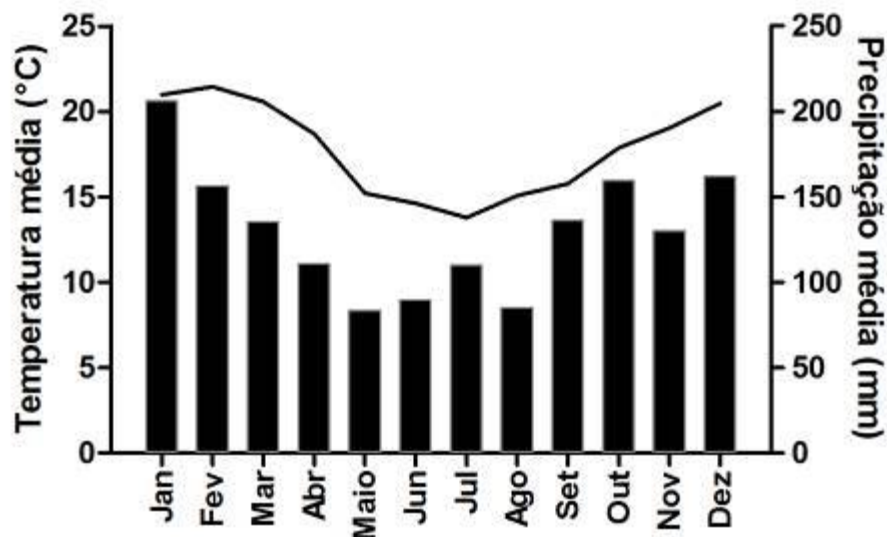


FIGURA 2 - Gráfico climatológico da área de estudo. A linha representa a temperatura mensal média e as barras representam a precipitação mensal média. Dados foram coletados de 2000 a 2013 na cidade de Curitiba, cerca de 20 km das áreas de estudo (INMET, 2013).

1.3 A andorinha-de-sobre-branco

A andorinha-de-sobre-branco (*Tachycineta leucorrhoa*, Hirundinidae, Aves) é uma espécie comum e localmente migratória, cuja distribuição restringe-se ao centro da

América do Sul em altitudes de 0 a 1.100 m (FIGURA 3; SIGRIST, 2009; STOTZ et al., 1996). Ocorre em áreas abertas, campos alagados, bordas de mata e áreas antropizadas como pastagens ou plantações, sempre associada a habitats aquáticos, tanto marinhos quanto continentais (RIDGELY; TUDOR, 1989; SIGRIST, 2009; STOTZ et al., 1996). Assim como as demais andorinhas, alimenta-se de plâncton aéreo e fornece bolas de insetos colados com saliva aos seus filhotes (SICK, 1997).

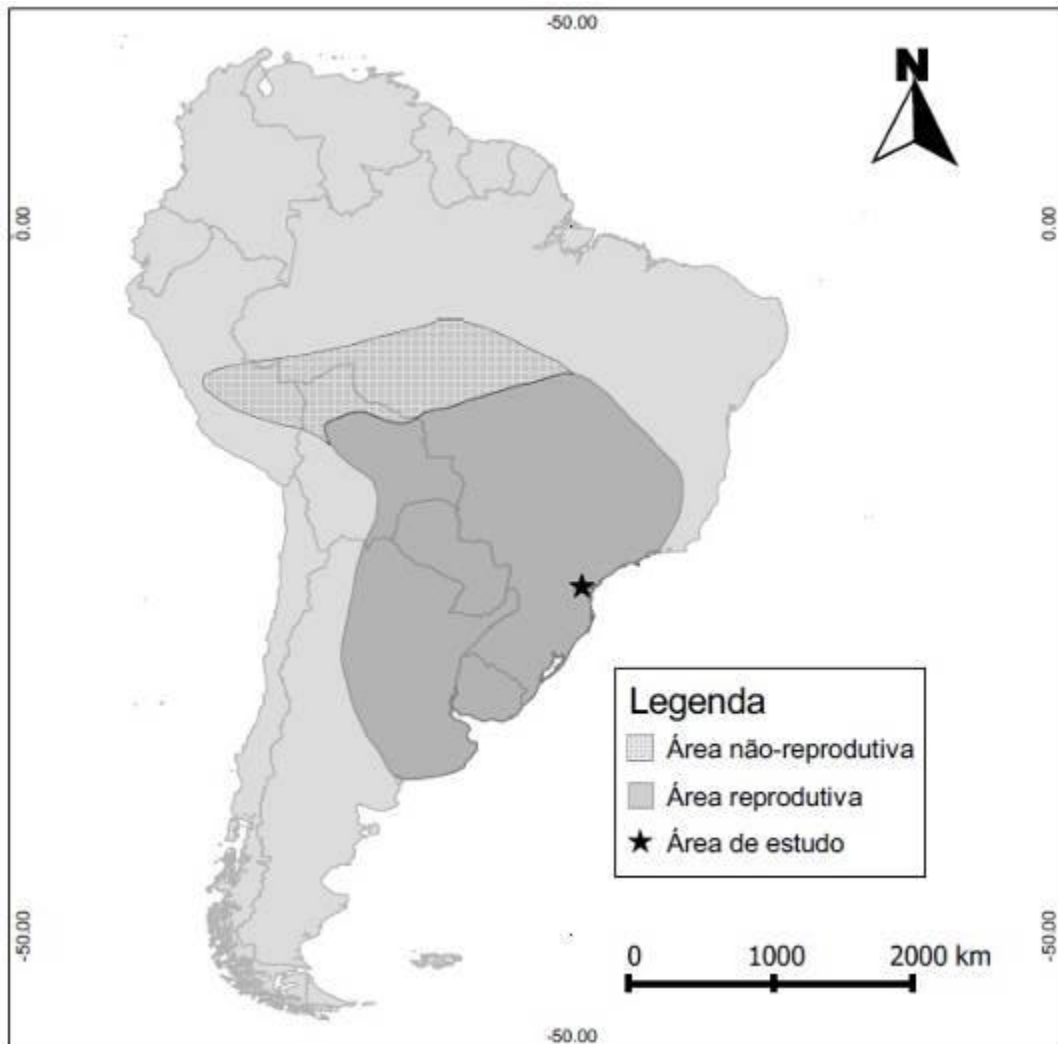


FIGURA 3 - Distribuição da andorinha-de-sobre-branco (*Tachycineta leucorrhoa*) na América do Sul (*datum* WGS-84). São destacados no mapa a área de estudo e a abrangência dos locais reprodutivos da espécie (RIDGELY et al., 2007).

Na área de estudo, o período reprodutivo da espécie (i.e. o período em que existem ninhos ativos) se estende de outubro a janeiro, e consiste em apenas um sucesso reprodutivo por casal (J. J. ROPER comunicação pessoal). Há formação de casais monogâmicos, porém paternidades extrapair são comuns (FERRETI et al., 2011). Apenas a

fêmea incuba os ovos, mas ambos os sexos cuidam dos filhotes (BULIT; PALMERIO; MASSONI, 2008). A espécie nidifica em cavidades secundárias (ou seja, ela não é escavadora) e constrói seus ninhos predominantemente com fibra vegetal e penas, mas também com outros materiais incomuns (lã de carneiro, fezes desidratadas de capivara, barbante, crina de cavalo, amora, escama de peixe; observação pessoal). Na Argentina, o tamanho de ninhada varia de 4 a 6, com incubação de 14 a 16 dias, eclosão assincrônica em 42% dos casos e período de ninhego de 21 a 27 dias (MASSONI; BULIT; REBORDA, 2007). Motivos de fracasso de ninho relatados são competição pelas caixas de ninho com outras espécies e condições meteorológicas desfavoráveis (MASSONI; BULIT; REBORDA, 2007).

Estudos com o gênero *Tachycineta* têm se tornado bastante comuns nas últimas décadas, o que pode ser explicado pela facilidade de estudo com essas espécies, que nidificam em caixas-ninho convenientemente dispostas pelos pesquisadores e que são facilmente observáveis e capturáveis (JONES, 2003). Além disso, o gênero ocorre em uma variedade de latitudes (do Alaska à Terra do Fogo; BIRDLIFE INTERNATIONAL, 2014), altitudes (de 0 a 3.200 m acima do nível do mar; DEL HOYO; ELLIOTT; CHRISTIE, 2004; STOTZ et al., 1996) e climas (tropicais, áridos, temperados, frio e polares; PEEL; FINLAYSON; MCMAHON, 2007) que privilegiam estudos comparativos de histórias de vida.

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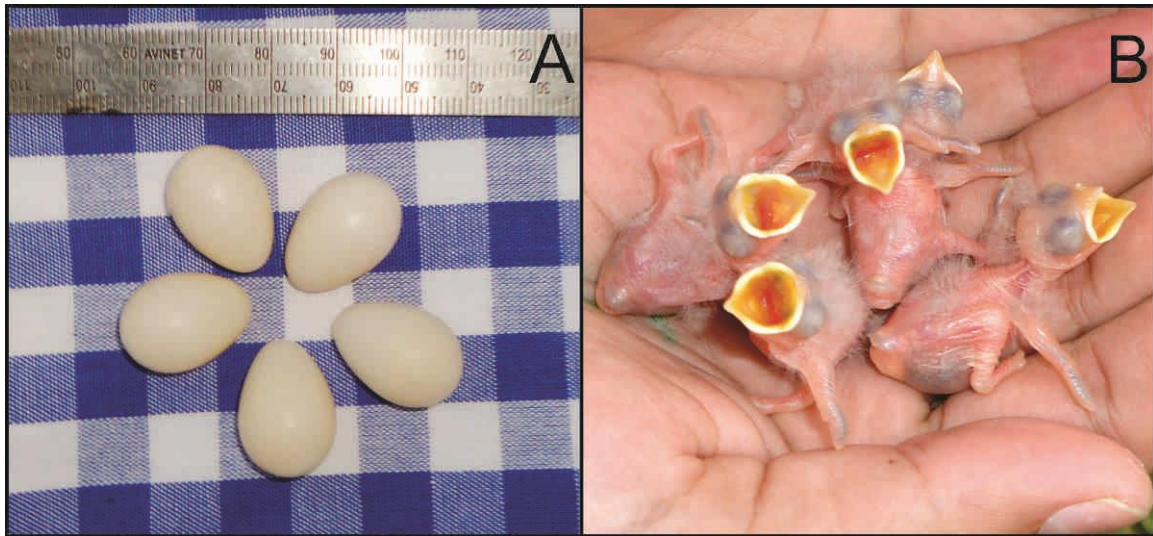
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2 ARE REPRODUCTIVE COSTS SHARED BY PARENTS AND OFFSPRING IN THE WHITE-RUMPED SWALLOW?

Capítulo elaborado de acordo com normas do periódico The Auk: Ornithological Advances.



Aves são capazes de estimar tamanhos de ninhada ótimos? Na população estudada de andorinha-de-sobre-branco (*Tachycineta leucorrhoa*), a moda de ovos é cinco (A). Comumente, todos os ovos eclodem, dando origem a cinco ninhegos que demandam cuidado contínuo dos pais (B). Na imagem, os ninhegos possuem 3 dias de idade.

Reproductive costs in White-rumped Swallows

RESEARCH ARTICLE

Are reproductive costs shared by parents and offspring in the White-rumped Swallow?

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ABSTRACT

Clutch size in birds should be the result of a trade-off between current and future reproduction, but evidence is equivocal. For example, artificially increasing brood size in the Tree Swallow (*Tachycineta bicolor*) does not seem to incur a cost for offspring or breeding adults. To investigate this enigma, we manipulated brood size and compared nestling development and parental care among brood size treatments in the related species White-rumped Swallow (*T. leucorrhoa*), in subtropical Brazil. At this latitude, environmental conditions should result in greater between-season survival, smaller clutch size, and less available food, in comparison with more temperate latitudes. Thus, we predicted that parents faced with larger broods would increase care to a maximum, insufficient to cope with additional nestling demand. We found that parents were investing, with their natural clutch sizes, in quantity and not quality of offspring, as nestlings from reduced broods were larger. Also, nestling size was similar in control and enlarged broods and adults took on the additional foraging load required by a greater number of young. These results indicate that

these subtropical swallows adopt a mixed strategy. They transfer reproductive costs to their offspring even in broods of natural size, indicating that more nestlings of lower quality result in more recruits than less nestlings of better quality. At the same time, they lay fewer eggs than they are capable of rearing perhaps to bet-hedge for environmental unpredictability or to avoid costs to their future reproduction.

Keywords: brood size manipulation, nestling growth, optimum clutch size, PIT-tag, parental care, reproductive costs, South America, *Tachycineta leucorrhoa*

RESUMO

Tamanhos de ninhada em aves são, em teoria, resultado de uma compensação entre reprodução atual e futura, embora evidências disso sejam controversas. Por exemplo, aumentos nos tamanhos de ninhada da *Tachycineta bicolor* não geram custos aparentes à prole ou aos adultos. Para investigar esse enigma, manipulamos tamanho de ninhada e comparamos o desenvolvimento dos ninhegos e o cuidado parental entre tamanhos de ninhada da espécie aparentada *T. leucorrhoa* no Brasil subtropical. Nessa latitude, condições ambientais devem resultar em maior longevidade, tamanhos de ninhada menores e menor disponibilidade de alimento, em comparação com latitudes mais altas. Logo, previmos que adultos com tamanhos de ninhada maiores que o natural deveriam aumentar o cuidado com a prole até um máximo, que seria insuficiente para garantir o desenvolvimento normal dos ninhegos. Foi observado que adultos investem em quantidade, e não qualidade de filhotes, já que ninhegos em ninhadas reduzidas foram maiores. Além disso, ninhegos tiveram tamanho similar entre ninhadas controle e aumentadas, devido a um aumento do cuidado parental congruente com o número de ninhegos. Esses resultados indicam que essas andorinhas subtropicais adotam uma estratégia mista. Elas transferem custos reprodutivos à prole mesmo em ninhadas de tamanho natural, indicando que mais filhotes de pior qualidade resultam em

mais recrutas que menos filhotes de melhor qualidade. Ao mesmo tempo, os tamanhos de ninhada estão aquém de sua capacidade de criar filhotes e talvez elas estejam adotando uma estratégia de diluição de risco quando há imprevisibilidade ambiental ou evitando custos à própria reprodução futura.

INTRODUCTION

Clutch size in birds was thought to be a consequence of natural selection favoring the maximum number of offspring that parents are able to rear to fledging (optimum clutch size hypothesis, Lack 1947). Today, hypotheses of the evolution of clutch size include long term reproductive costs and optimal clutch size should be that which maximizes parental fitness and takes into account lifetime reproductive success of adults and their offspring (Charnov and Krebs 1974, Williams 1966). Thus, optimal clutch size should be a trade-off between current and future breeding opportunities based on individual traits (e.g., female age and provisioning capability, Perrins and Moss 1975, Slagsvold and Lifjeld 1988, Winkler and Allen 1995) and environmental characteristics (e. g., territory quality and food abundance, Perrins and Moss 1975, Högstedt 1980).

In higher latitudes, annual adult survival probabilities are relatively low due to harsh climate during winter for resident birds and long-distance migration for others (Martin 2004, Sillett and Holmes 2002). Moreover, in seasonal environments with a narrow window of favorable conditions for breeding, often only one brood per year is possible. As a result, birds at higher latitudes should favor current over future breeding opportunities (Charnov and Krebs 1974, Martin 2004). Thus, when challenged with artificially enlarged broods, birds should simply increase effort to meet the increased nestling demand for food, thereby maintaining offspring quality. At lower latitudes, on the other hand, where food is limiting during the breeding season and adult survival is greater, parents should favor their own

survival and not increase current reproductive effort when brood size is experimentally enlarged (Ashmole 1963, Martin 2004).

Trade-offs between offspring quantity and quality and between current and future reproduction have been observed (review in Lindén and Møller 1989), yet results are equivocal. For example, the short-lived, temperate, migratory, single-brooded Tree Swallow (*Tachycineta bicolor*) when faced with enlarged broods, increases effort and maintains constant offspring quality as well as adult survival (De Steven 1980, Wheelwright et al. 1991). Apparently, clutch size and parental care in the Tree Swallow are not food limited in these studies.

The South American White-rumped Swallow (*Tachycineta leucorrhoa*) is similar to northern temperate swallows due to its relatively short lifespan and large clutch size in the area and most breeding pairs raise only one successful brood during each breeding season (Bulit and Massoni 2011, Massoni et al. 2007). Hence, as with many temperate species, adults should accept greater reproductive costs and work harder with larger clutches (Nur 1984). On the other hand, the White-rumped Swallow migrates over smaller distances and breeds in the seasonally moderate tropics and subtropics (BirdLife International 2014). Thus, relative to northern temperate swallows, this species should have a lower mortality rate and food limitation should be more intense during breeding, so food gathering would require more effort (Ashmole 1963). The White-rumped Swallow, when faced with greater food demand by offspring, should increase effort up to some maximum that does not incur a survival cost for the adult and, if clutch size requires energy expenditure greater than that limit, parental care per offspring should decline, resulting in reduced offspring quality (Sanz and Tinbergen 1999). In other words, the trade-off should favor adult survival rather than reproductive success when costs are greater.

To test for this trade-off, we experimentally investigate how parental care varies with

brood size and how brood size influences nestling growth rate in the White-rumped Swallow. If adult survival is greater, and food is more limiting in this subtropical latitude, then we predict that parental care to enlarged broods will increase, albeit insufficiently to maintain constant parental care per offspring.

METHODS

Study Area

We carried out this study near 2 adjacent reservoirs in southern Brazil (S 25.51°, W 49.03°, 898 – 918 m and S 25.51°, W 49.08°, 893 – 900 m). During the breeding season of October 2012 to January 2013, average daily temperature was 20.2°C (SD = 2.9, temperature range = 9.8 – 34.2°C, $n = 122$ days). Monthly precipitation ranged from 69.4 mm in November to 254.6 mm in December (data for the city of Curitiba, ~20 km from study areas, INMET 2013). Vegetation around the reservoirs includes open grassy areas, trees, and marshes, with both native and exotic plants.

Study Species

The White-rumped Swallow (Hirundinidae) is a South American migrant that nests in natural cavities and artificial nest boxes. Argentinian birds have a lifespan of less than 3 years (Bulit and Massoni 2011). In Argentina, clutch size averaged 4.92 (SE = 0.05, $n = 106$), incubation lasts 14.8 days (SE = 0.2, $n = 82$) and the nestling stage lasts 23.3 days (SE = 0.2, $n = 44$, Massoni et al. 2007). Only females incubate eggs, but both sexes feed nestlings (Bulit et al. 2008). In previous years, we observed that breeding pairs arrived in our study area and began to nest in the last half of October, and usually left the area by mid January, after the completion of only one successful nest.

Adults were captured in nest boxes (see below) after egg-laying and before hatching by the use of a trap door. Measurements of adult birds followed *Golondrinas de las Americas*

protocol (weight to 1.0 g precision and flattened wing length to 1.0 mm, GDLA 2010). We banded birds with both a numbered metal band and, on the other leg, a PIT-tag (a passive integrated transponder with a unique code Cyntag 2x12 EM4102 12KhZ, see below) attached to a plastic band.

Nest Boxes

Nest boxes (17 x 13 x 25 cm, GDLA 2011) have been available on trees and posts near water since 2005 at one reservoir and 2010 in the other. During this study 121 nest boxes were available. Distances between boxes vary from 5 to 78 m, usually greater than 15 m. Nest box height varies from 1.5 to 2 m.

Once birds were observed in the study area, we checked boxes weekly. Once construction began, nests were checked every 4 days to determine the date of laying of the first egg. Nests were checked daily near estimated hatching date and hatching is synchronous in 58% of the nests of this species (Massoni et al. 2007). Hatching date was the first day on which half or more of the eggs in a clutch had hatched, and we considered it day zero of the nestling period.

PIT-tagging

We placed a circular antenna around the external entrance hole of the nest box with the data-logger and power supply underneath the nest box, before or on the day of brood size manipulation. Data-loggers recorded date, time and PIT-tag identification code at each visit by a tagged bird, with intervals greater than 15 s, between 0400 and 2100 hours. They were programmed with 500 ms poll interval (during which a tag may be read) and 500 ms pause interval (of no reading attempts). Each register was considered to be one visit, because arrivals and departures cannot be discerned due to the 15 s lag.

Brood Manipulation

Brood manipulation included control nests (in which we handled offspring but preserved

original clutch size) and enlarged or reduced broods (~50% larger or smaller than the original clutch size). Three-day-old nestlings were randomly exchanged between broods hatched on the same date (± 1 d). Control and reduced broods also contained cross-fostered nestlings (i.e. foreign nestlings) depending on the availability of other similar-aged nests for the exchange.

We clipped a claw on unique combinations of toes to identify each nestling until 12 days of age, when they were banded. Nestlings were weighed on a digital balance to the nearest 0.01 g and wing length was measured to 1.0 mm at 3, 6, 9, and 12 days of age. We did not open nests boxes after nestlings reached 12 days of age to avoid causing premature fledging. After 18 days, we checked nests daily through the entrance hole with a mirror and a flashlight to determine fledging date (when all nestlings had left the nest).

Statistical Analysis

Nestling growth and nest productivity. Daily growth was the difference between measurements (weight and wing length) every 3 days, divided by 3 and calculated for each individual. We used mean growth rate per brood at each period and mean nestling size per brood at age 12 days to compare treatments using analysis of variance (ANOVA). Nestling period length was compared among treatments using ANOVA. We used correlations between weight or wing length at age 12 and number of days until fledging to test the prediction that smaller nestlings remained in the nest longer to compensate for slower growth. Nest productivity (the number of fledglings) and fledging success (nest productivity divided by manipulated brood size) were correlated with brood size.

Parental care. Parental care was estimated as the number of visits of the tagged parent per hour recorded at nest boxes. We considered each visit to be a feeding trip (McCarty 2002). We divided the nestling period (from manipulation to the age when none of the broods had fledged) in 5 visitation periods of approximately equal length (ages 3-6, 7-9, 10-12, 13-15, and 16-18 days). Note that the first 3 visitation periods correspond to the

periods of growth. Parental care (total feeding rate) and parental care per nestling (total feeding rate divided by the number of nestlings) were compared among treatments using ANOVA. A level of significance of 0.05 was adopted in all analyses.

RESULTS

A total of 28 nests were used in the experiment. One nest in each treatment was abandoned (nestlings last seen alive at ages 3, 6, and 6 days) and excluded from analysis (Figure 1). All nests hatched near others in time, with one exception at the end of the breeding season, that we excluded. Treatments had similar temporal distributions in the breeding season based on hatching date (ANOVA, $F_{2,21} = 0.2$, $P = 0.86$).

Final sample size per treatment was 4 controls, 13 reduced, and 7 enlarged broods (Figure 1). Two control broods and 8 reduced broods included cross-fostered nestlings. Reduced broods without foreign nestlings were result of natural clutch reduction (partial hatching or predation). Experimental manipulation in reduced broods was 1 to 3 fewer nestlings and in enlarged broods was 2 additional nestlings (but in one nest, one nestling died early). We assumed that there were no effects due to the location (reservoir) of the nests.

Nestling Growth and Nest Productivity

Two nestlings died prior to age 12 and were excluded from analysis of growth. Mean nestling weight and wing length per brood were greater in reduced broods at age 12 days (Table 1). The relationship between daily growth rate and brood size treatment varied by age (Table 1 and Figure 2). At periods 3-6 and 6-9, weight gain and wing growth rates were greatest in reduced broods. At period 9-12, growth rate was similar among all treatments. Wing growth rate tended to increase with age, while weight gain rate remained relatively constant or slowed.

To better understand nestling size variation and nestling competition within broods,

we compared treatments based on samples containing only the smallest or only the largest nestlings from each brood. Nestling difference from the brood median over time was compared using repeated measures ANOVA (Table 2 and Figure 3). At the beginning of the nestling period, the smallest and largest nestlings were similar in size among all treatments. Differences increased with time in control and enlarged broods, but remained almost constant in reduced broods.

Reduced broods fledged ~3 days earlier than control and enlarged broods (Table 1). Since we recorded fledging date per brood, and not individual, the nestling period may sometimes be overestimated. Irrespective of treatment, length of the nestling period is shorter when weight is greater at age 12 days (reduced: $r = -0.40$, $n = 35$; control: $r = -0.53$, $n = 20$; enlarged: $r = -0.47$, $n = 48$; all $P < 0.02$). However, wing length was correlated with nestling period only in enlarged broods ($r = -0.55$, $n = 48$, $P < 0.001$). Fledging success was not correlated with manipulated brood size ($r = 0.03$, $n = 24$, $P = 0.91$) and nest productivity increased with manipulated brood size ($r = 0.90$, $n = 24$, $P < 0.001$).

Parental Care

All females and only 5 males from monitored nests were captured, therefore only female parental care was used in analysis. Records within one hour after our intervention at the nest box (nestling measurements and replacement of batteries from the PIT-tag readers), and sequences of 5 or more intervals of 15 s (because this suggests that the tagged parent was perched at the entrance hole) were excluded. Ten nestlings died before fledging and to compute parental care per nestling (which depends on how many nestlings are alive at the time) we estimated that they died in the middle of the interval between nest checks. This partial death sometimes caused a nest to change treatments, but it was always after age 20 days. The different sample sizes of nests in treatments were amplified due to the large number of hours in which parental care was recorded. So, to balance sample sizes, we randomly

sampled recording hours (without repetition) until an equal number of hours was reached in all treatments at each age period. We then compared the complete sample and the sub-sample with *t*-tests to see if the latter was representative of the former (all $P > 0.15$).

Total feeding rate peaked at ages 7-9 days in reduced broods, and 13-15 days in control and enlarged broods (Figure 4A). Control nests were visited less often than enlarged broods, except at ages 10-12 days (Table 3). Nests with reduced broods were visited more often than controls at ages 7-9 only. Feeding rate per nestling was greatest in the reduced treatment at all ages and was always similar among the control and the enlarged treatments. Feeding rate per nestling declined at the end of the period in reduced broods, but remained constant in control and enlarged broods (Figure 4B).

DISCUSSION

Adult White-rumped Swallows seem to favor their own survival over that of their young. They can easily rear fewer young to better fledging condition, but in control broods (their original clutch size) offspring body condition is compromised, in spite of their ability to increase parental care when needed, as seen in enlarged broods.

Offspring Quality and Quantity

Nestlings in control and enlarged broods were smaller than those in reduced broods, and so White-rumped Swallows seem to invest more in quantity than in quality of offspring. So, females are laying more eggs than they can rear at their ideal growth rates.

Reduced broods declined in weight gain near age 12, perhaps due to weight recession, common in aerial foraging species (Ricklefs 1968). Weight recession is primarily due to water loss, whereas dry mass and lipid content continue to accumulate, so acquired differences in weight during the nestling period are likely to be preserved after fledging (Ricklefs 1968, Wright et al. 2006). Even though control and enlarged broods might catch up with those from

reduced broods by postponing fledging, inferred from the inverse relationship we found between fledging date and nestling size, this longer time spent at the nest translates into migrating at a later date, which may be a secondary problem (Naef-Daenzer et al. 2001). In addition, similar results in the Tree Swallow led to the suggestion that the extra time at the nest may permit wing to reach the same size among treatments, but not weight (De Steven 1980). Therefore, survival of nestlings from reduced broods should be greater than that of enlarged and control broods (Naef-Daenzer et al. 2001, Schwagmeyer and Mock 2008). This trend was different from similar studies in which nestling size of Tree Swallows was independent of brood size, or controls were similar in size to reduced broods (Murphy et al. 2000, De Steven 1980, Wheelwright et al. 1991, Wiggins 1990).

Comparisons of the smallest and largest nestlings among treatments suggest that provisioning was limited in control and enlarged broods. Also, the disparity of size between nestlings increased over time, implicating strong sibling competition when food is limited. Despite these potential costs for first year survival of young, fledging success was similar among treatments and nest productivity increased with brood size, so adults can raise broods larger than they lay, same as Tree Swallows (De Steven 1980, Wheelwright et al. 1991, Murphy et al. 2000).

Parental Care

As expected of a short-lived species, females increased total feeding rate when feeding more young, unlike other species in which feeding rate by females is maximum to natural-sized broods and any additional care is provided by males (Charnov and Krebs 1974, Leffelaar and Robertson 1986, Lombardo 1991, Low et al. 2011). In Tree Swallows, parental response to brood size seems to be dependent on food availability (Ardia 2007). So, total feeding rate in some studies have the same pattern we observed here (reduced = control < enlarged) but differs slightly in other studies, with greater feeding rates in control and enlarged broods or a

direct relationship between feeding rate and brood size (Leffelaar and Robertson 1986, Murphy et al. 2000, Ardia 2007).

Here, females usually invested the same care in reduced broods that they expected with their original clutch and ended up with fewer fledglings of greater quality, suggesting that this is the maximum amount of care without costs to the adult. Total feeding rate was occasionally greater in reduced than in control broods, when theory predicts equal or lower rates (Sanz and Tinbergen 1999). This trend comes exclusively from a control female responsible for one fifth of the sample with extremely low feeding rate (maximum number of visits per hour was lower than mean from other control females). If, contrary to appearance, she represents a normal individual in the population, a biological explanation for the higher rates in reduced broods would be that perhaps nestlings with few nest mates lose more heat (due to reduced insulating quality of siblings) and so require more food (Royama 1966). Yet, here reduced broods were visited more often at ages 7-9 days, when they should be capable of thermoregulating (Dunn 1979).

From the nestling perspective, each nestling in enlarged broods received the same amount of care as nestlings from control broods, indicating that the increase in female reproductive effort resulted in more fledglings of adequate quality, same as observed in other short-lived species (e.g., the Great tit *Parus major*, Sanz and Tinbergen 1999). In contrast, feeding rate per nestling declines with brood size in Tree Swallows (Leffelaar and Robertson 1986, Murphy et al. 2000, Shutler et al. 2006). Thus, White-rumped swallows invested more in young from enlarged broods than Tree Swallows, despite the higher effort to find food and the potential costs for future reproduction for the female (but see Murphy et al. 2000).

Parental care normally peaks around the middle of the nestling period and gradually declines until fledging (Leffelaar and Robertson 1986, Lombardo 1991, Low et al. 2011). Feeding rate per nestling varied little over time in control and enlarged broods, but declined as

expected near the end of the period in reduced broods. Because provisioning should be a consequence of demand by the young, the constant feeding rate over time in control and enlarged broods suggests that demand was constant and females were working at their maximum rate.

The lack of differential survival of parents or fledglings for enlarged broods in Tree Swallows led to the suggestion that reproduction is cost free (Murphy et al. 2000, Shutler et al. 2006, De Steven 1980, Wheelwright et al. 1991, Wiggins 1990). If true, why don't they raise more young? Explanations may depend upon 1) costs of egg formation and incubation (Monaghan and Nager 1997, but see Shutler et al. 2006), 2) elevated post-fledging care (Morehouse and Brewer 1968), 3) bet-hedging due to environmental unpredictability (Stearns 2000); or 4) timing in the breeding season (i.e. parents that start incubation earlier win an advantage on the nestling and post-fledging period, however, lower food supplies at the beginning of the breeding season restrain the number of eggs; Murphy et al. 2000, Shutler et al. 2006). Here, we can rule out the fourth hypothesis because clutch and egg size were constant over time (personal observation), in contrast to places with strong seasonal effects on food (Liljeström et al. 2012, Massoni et al. 2007, Winkler and Allen 1996). Nevertheless, unpredictably cold and rainy days are common. Thus, we suggest that the third option, bet-hedging, is likely. The first and second hypotheses remain to be tested and may act in concert with bet-hedging.

In conclusion, adult White-rumped Swallows seem to favor their own survival at the cost of offspring quality, but to confirm this, further studies will need to investigate return rates of offspring from broods of different sizes to examine costs for first-year survival. Though provision rate was lower than possible in control broods, increasing parental care appears to be costly and may only be worth the effort when greater numbers of young fledge. So, the reproductive value of any brood is determined by a combination of numbers and

survival probability, which suggests that more young of lower survival probability can yield greater future reproductive success than fewer young of greater survival probability.

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Figure 1. Nesting sequence of the experimentally manipulated nests of the White-rumped Swallow during the breeding season of 2012-2013 in southern Brazil. Bars indicate the number of nests that hatched during that week in each brood-size treatment or those that were abandoned or excluded from analyses (left y-axis). Circles indicate broods that fledged at least one fledging (right y-axis).

Figure 2. Daily growth rate of A) weight and B) wing length was estimated in time intervals of 3 days for each nestling and averaged within broods. Nestlings were part of a brood manipulation experiment with White-rumped Swallows. Symbols are mean daily growth for treatments and whiskers are 95% confidence intervals.

Figure 3. Comparison in weight and wing-length between smallest and largest nest-mates in the brood manipulation experiment in the White-rumped Swallow. Individual weight and wing length were subtracted from the median of the brood at nestling age 3, 6, 9, and 12 days (mean and 95% confidence intervals).

Figure 4. Comparison of female care in the White-rumped Swallow between experimental brood size manipulation treatments (means, 95% confidence interval). A) is total feeding rate, and B) is feeding rate per nestling. For ANOVA results and sample sizes (equalized among treatments at each nestling age) refer to Table 3.

Figure 1

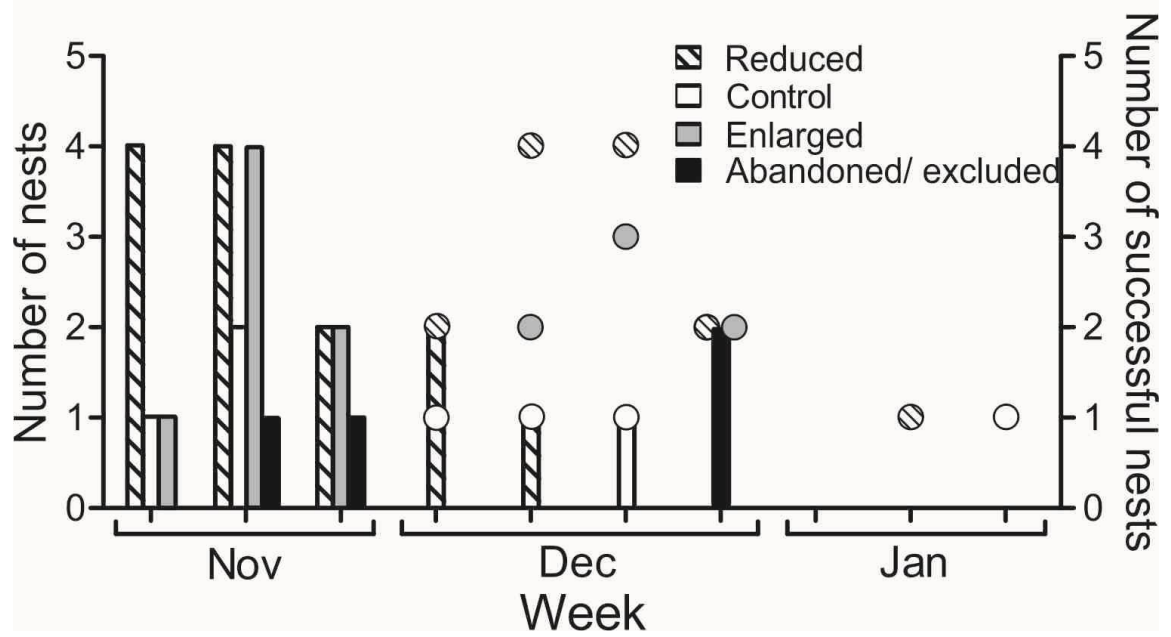


Figure 2

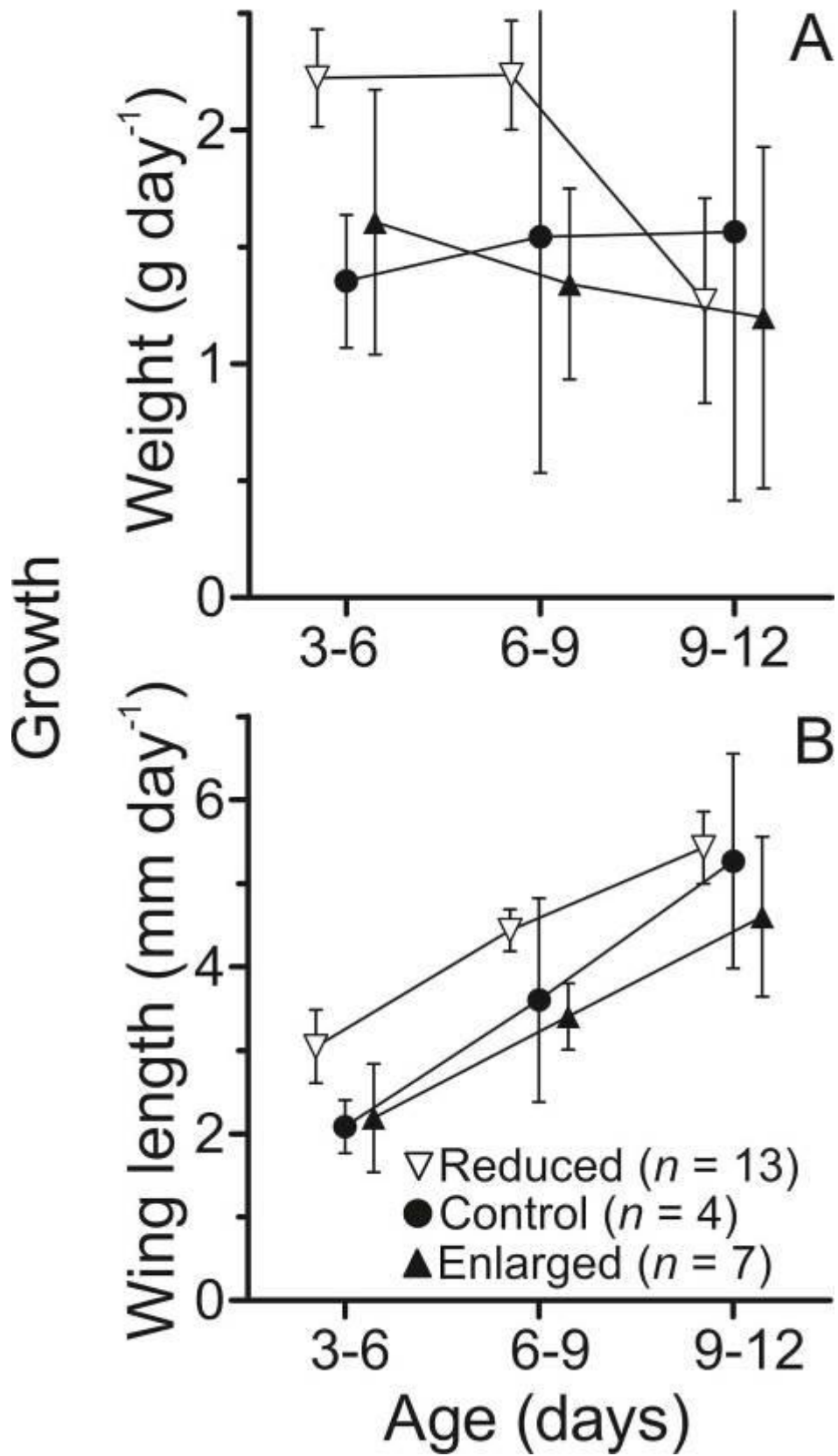


Figure 3

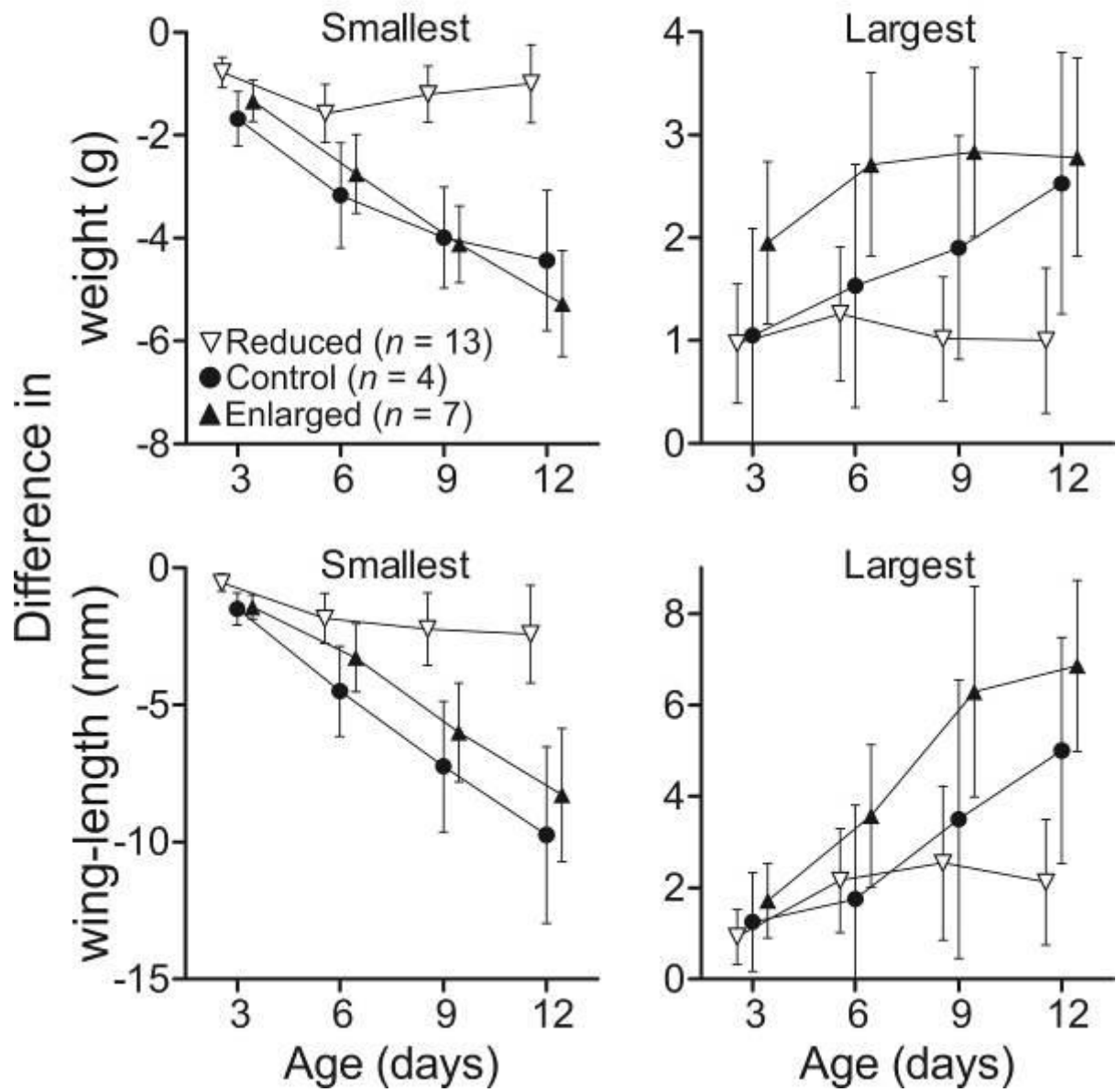


Figure 4

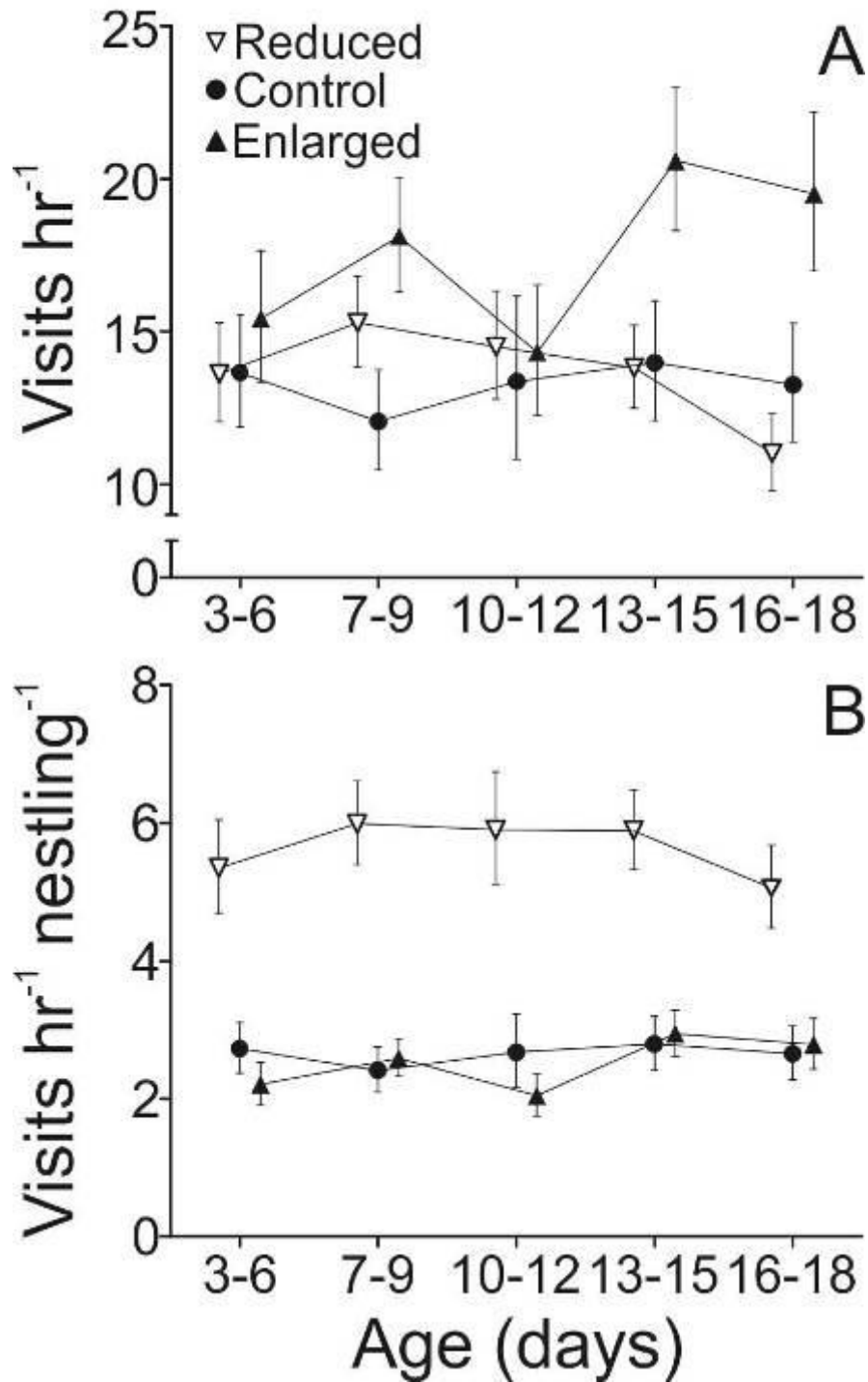


Table 1. Effects of brood size manipulation in White-rumped Swallows on mean nestling size at age 12 days, on mean and nestling growth per brood in 3 growth periods, and on length of the nestling period. Brood size treatments are reduced ($n = 13$ nests), control ($n = 4$), and enlarged ($n = 7$). Values are means (SE in parenthesis), F is the f-statistic, P is the p -value or * when <0.001 , and r^2 is the coefficient of determination.

Variable	Reduced	Control	Enlarged	F	P	r^2
Weight at age 12 days (g)	23.2 (0.6)	19.1 (1.6)	17.8 (1.0)	12.3	*	0.54
Wing length at age 12 days (mm) ^L	48.9 (1.0)	42.6 (1.1)	39.8 (1.1)	11.3	*	0.52
Weight growth (g day ⁻¹)						
Age 3-6 days	2.2 (0.1)	1.4 (0.1)	1.6 (0.2)	8.8	0.002	0.46
Age 6-9 days	2.2 (0.1)	1.5 (0.3)	1.3 (0.2)	10.4	*	0.50
Age 9-12 days	1.3 (0.2)	1.6 (0.4)	1.2 (0.3)	0.3	0.72	
Wing length growth (mm day ⁻¹)						
Age 3-6 days	3.0 (0.2)	2.1 (0.1)	2.2 (0.3)	5.3	0.01	0.34
Age 6-9 days	4.4 (0.1)	3.6 (0.4)	3.4 (0.2)	11.9	*	0.53
Age 9-12 days	5.4 (0.2)	5.3 (0.4)	4.5 (0.4)	2.3	0.12	
Nestling period (days)	22.9 (0.4)	26.3 (0.3)	26.7 (0.4)	28.4	*	0.73

^LBased on the natural logarithm to normalize residuals.

Table 2. Simplified repeated measures ANOVA table for Figure 3 contrasting the difference in size from the smallest and largest nestling from each brood to the brood median in reduced, control, and enlarged broods of the White-rumped Swallow measured at ages 3, 6, 9, and 12 days. *df* are the numerator and denominator degrees of freedom, *F* is the f-statistic and *P* is the *p*-value or * when <0.001.

Variable	Nestling	Effects								
		Age ^a			Age * treatment ^a			Treatment		
		df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Weight	Smallest	1.8, 38.1	32.8	*	3.6, 38.1	12.1	*	2, 21	28.0	*
	Largest	1.5, 31.2	4.0	0.04	1.7, 31.2	1.6	0.21	2, 21	6.4	0.007
Wing length	Smallest	2.1, 43.8	40.0	*	4.2, 43.8	6.5	*	2, 21	15.4	*
	Largest	2.3, 47.3	22.0	*	4.5, 47.3	4.6	0.002	2, 21	5.0	0.02

^aGreenhouse-Geisser correction was used due to violation of sphericity.

Table 3. Simplified ANOVA table from analysis shown in Figure 4 comparing total feeding rate and feeding rate per nestling among control, reduced, and enlarged broods of the White-rumped Swallow at 5 age periods. All $P < 0.001$ except total feeding rate at 3-6 days, when $P = 0.31$, and at 10-12 days, when $P = 0.74$. df are the denominator degrees of freedom. Numerator degrees of freedom always equals 2. Variables were square-root transformed to obtain normality of residuals.

Variable	Age period (in days)	df	F	r^2
Total feeding rate	3-6	282	1.2	
	7-9	300	13.1	0.08
	10-12	246	0.3	
	13-15	306	15.3	0.09
	16-18	312	19.3	0.11
Feeding rate per nestling	3-6	282	50.7	0.26
	7-9	300	89.2	0.37
	10-12	246	50.0	0.29
	13-15	306	57.1	0.27
	16-18	312	32.0	0.17

3 STRANGERS IN THE NEST

Capítulo submetido ao periódico Acta Ethologica.



Se cuidar dos próprios filhotes deve trazer contribuições maiores à aptidão de um indivíduo, por que visitar outros ninhos? Na foto, um adulto de andorinha-de-sobre-branco (*Tachycineta leucorrhoa*) alimentando um ninhego com 22 dias de idade. O equipamento que registra a taxa de visitação está afixado abaixo da caixa-ninho e conectado à antena ao redor da entrada. Crédito da imagem: F. MARQUES-SANTOS, 2013.

SHORT COMMUNICATION

Strangers in the nest

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ABSTRACT

White-rumped Swallows (Hirundinidae, Aves) visit nests that are not their own. Using birds tagged with passive-integrated transponders (PIT-tags) breeding in nest boxes in southern Brazil, we found that: 1) nest boxes are often visited by apparently unrelated birds (54% of nests were visited at least once), 2) adults visit nests of other pairs while tending their own, 3) visitors tend to have small broods, 4) visitors do not appear to select nests to visit based on the number of nestlings they contain, 5) parental care is more intense in the visited nests, and 6) visited nest boxes are more distant from failed than from successful visitor's nests. These patterns do not suggest a clear explanation for nest visiting, and we offer that inspecting other nests occurs when time is available (small visitor brood size) and may be prospecting for future nest-site availability.

KEYWORDS: nest intruder, non-parental visit, nest site inspection, prospective behavior,

Tachycineta leucorrhoa

INTRODUCTION

During the breeding season, birds are often seen visiting conspecific nests of others and several explanations for this behavior have been suggested. Visitors may be helpers that benefit from both inclusive fitness and improving their own parental skills (Cockburn 1998, Lombardo 1986). An adult without a mate or territory may search for breeding opportunities through cuckoldry or nest parasitism (Lenda et al. 2012). Subordinate birds without nests or territories may search for vacancies throughout the breeding season and occupy breeding territories as they become available (Stutchbury and Robertson 1987). Recently fledged young may attempt to receive food from other breeders (Czechowski and Zduniak 2005). Competition for nest sites, common in non-excavating cavity nesters, may possibly result in infanticide and active nest usurpation (Holroyd 1975; Lombardo 1987b; Waltman and Beissinger 1992). Additionally, as site quality influences reproductive success, visitors at nests might simply be examining potential nest sites for the future, perhaps to understand availability or identify better breeding locations for the next breeding season (Eadie and Gauthier 1985; Lombardo 1987a). Though many birds search for breeding sites immediately before nesting, some are known to search later in the breeding season, while having active nests (Eadie and Gauthier 1985). Breeders that prospect in the late season have the advantage of using public information (in this case, information on reproductive performance of conspecifics) to access site quality (Valone and Templeton 2002).

The above hypotheses have been offered for this behavior in swallows, sometimes without clearly testing the predictions (Czechowski and Zduniak 2005; Lombardo 1987a; Petrie and Møller 1991, Skutch 1961; Stutchbury 1991; Stutchbury and Robertson 1987). Here, we describe visit behavior to nests of other individuals in the White-rumped Swallow (*Tachycineta leucorrhoa*, Hirundinidae, Aves).

METHODS

The White-rumped Swallow is migratory and nests in secondary cavities or boxes we provide at two neighboring reservoirs in southern Brazil (25° 30' 24" S, 49° 1' 37" W and 25° 30' 22" S, 49° 4' 42" W). In the breeding season of Oct. 2012 to Jan. 2013, 121 nest boxes (17 x 13 x 25 cm; GDLA 2011) are available for nesting (79 in one area, 42 in the other). We recorded for every nest built inside boxes the laying, hatching and fledging dates. This study was concurrent with another that involved brood size manipulation, carried out at nestling age of three days. Modal clutch size is five, and experimental brood sizes resulted in two to seven nestlings per nest (chapter 2).

Nesting adults, usually females (sexed by the presence of a brood patch), were captured in the boxes. Captured birds were banded with a numbered metal band and a plastic band with a PIT-tag (uniquely coded passive integrated transponder Cyntag 2x12 EM4102 12KhZ). To enter boxes, birds passed through circular antennas constructed of magnetic wire (connected to the data-logger) at the entrance, and consequently their PIT-tag code, the time, and the date were logged. Data-loggers were programmed with 500 ms poll interval (during which a tag may be read) and 500 ms pause interval (of no reading attempts), and to record PIT-tags with a 15 s minimum lag, and so do not distinguish between arrivals and departures. Monitoring equipment was mounted at most three days after hatching and removed after fledging.

Since the term “visitor” may imply visiting one's own nest or that of a different pair, we will avoid confusion by calling the visitor to a nest of another pair, the “inspector” and we will call the visit an “inspection.” We may use the term “visit” when a bird arrives at or enters its own nest. In the following breeding season (Oct. 2013 – Jan. 2014), returning adults and the boxes they occupied were identified.

RESULTS

We recorded visits during the nestling period at 26 nest boxes, in 4261 recording hours with 33 females and 5 males tagged. Twelve females and one male inspected ($n = 71$ inspections) active nests of other breeding pairs (each bird inspected from 1 to 8 nests, Fig. 1 and 2a). Boxes were inspected by the same bird up to seven times (Fig. 2a). When a box was inspected more than once by the same bird, it was on the same day ($n = 28$ revisits), or the next day ($n = 6$) or three days later ($n = 3$). The interval between inspections on the same day ranged from 15 s – 6.5 h (median = 73 s). Fourteen of the 26 monitored nest boxes (54%) were inspected at least once (Fig. 2a). Most inspectors had their own nests with nestlings when they inspected ($n = 49$ visits) and eight inspections were after the inspector's nest failed ($n = 2$ birds), and 14 were after the inspector's success ($n = 4$ birds, Fig. 2b).

Inspections began around sunrise and declined around 15:00 h, while parental visits were almost constant during daylight hours (Fig. 3). The shortest time interval between leaving its own nest and inspecting another was 25 s, in a straight-line distance of 71 m. The shortest interval for an inspector to return to its own box was 7 s (also 71 m away). The duration of the nestling period varied with brood size, from 19 – 28 d (chapter 2). The age of nestlings in boxes being inspected ranged from 7 – 23 d (median = 18, $n = 43$ visits) and the age of the inspector's nestlings on the inspection date ranged from 13 - 23 d (median = 20, $n = 18$ visitors once a day; Fig. 4a). Inspections were distributed over more than one month, different birds inspected on the same day and a female that performed most inspections tended to concentrate them in few days (Fig. 4b). Inspectors with fledged young inspected other nests from 1 - 12 days after fledging (median = 10, $n = 14$ visits) and inspectors whose nest failed inspected from 5 – 10 days after failure (median = 6, $n = 8$ visits).

Inspector brood size ranged from 2 - 5 (median = 3, $n = 10$ active inspector broods, Fig. 5), though one inspector successfully fledged seven young (Fig. 1). One female with two

nestlings was responsible for 41% of all inspections and only when included in the analyses, was inspector's brood size inversely correlated with the number of nests inspected (including birds that did not inspect: $r_s = -0.37$, $n = 31$, $p = 0.04$), or with the number of inspections ($r_s = -0.34$, $n = 31$, $p = 0.05$). Inspected boxes had 2 - 7 nestlings (median = 7, $n = 34$ broods visited by a new bird, disregarding repeat inspections, Fig. 5). No preference for any particular brood size was noted, because inspectors did not consistently visit any to the exclusion of others, nor did they return preferentially to any box after their first inspection (Fig. 6).

The female of an inspected nest box was more attentive of her nest (estimated as the number of entries in her own box during the hour prior to the inspection, mean = 12.3 entries hr^{-1} , SE = 1.1, $n = 63$ hours) than the inspecting female (mean = 6.3 entries hr^{-1} , SE = 1.1, $n = 39$ hours, t -test entries h^{-1} , $t_{100} = 3.42$, $p < 0.001$). Recorded number of entries into boxes was not normally distributed and so was \log_{10} transformed to meet the assumptions of the tests. Yet, the number of visits per nestling was similar (visited mean = 2.4 visits hr^{-1} nestling $^{-1}$, SE = 1.2, $n = 63$ hours, inspector mean = 2.5 entries hr^{-1} nestling $^{-1}$, SE = 1.2, $n = 39$ hours, t -test entries per nestling hour, $t_{100} = 0.29$, $p = 0.77$), and so, inspectors did not neglect their own nests during that time.

Distance between an inspector's own and the inspected nest box averaged 5118 m when the inspector's nest attempt failed (range = 4855 – 5327 m, $n = 4$ visits, disregarding repeats) and 121 m when successful (range = 20 – 274 m, $n = 31$ visits; Fig. 1). With only successful nests, the distance was similar during (mean = 119, range = 20 – 274 m, $n = 24$ visits) or after (mean = 130, range = 73 – 198 m, $n = 7$ visits) the inspector nestling period.

The availability of nest boxes was not limited during this study. In four years of study with this population, nest boxes were reused in the same season only five times. Three times, the same female that used the box, that previously failed; and once probably by the same

female, because laying began again three days after predation while laying. The last was at a box occupied 11 days after failure by a female with unknown previous attempts. Of the 121 nest boxes available at the study sites, 56 were occupied in 2012 or 2013, and so a surplus of 65 suggests that boxes are not limiting. Also, 19 adequate boxes were not used in 2012 (if only these 56 are considered adequate by the swallows), also suggesting that boxes are not limiting.

Only nine females (plus two found dead in nest boxes at the beginning of the 2013 season) and three males returned to our study areas (Table 1), corresponding to a return rate of 37%. Of these, only four females and one male inspected in 2012. Only one female nested in an inspected box (that contained a brood of two), though another two females and one male nested in monitored boxes. Another three females nested in boxes not being monitored in 2012 and we do not know if they were visited during that season.

DISCUSSION

A surprisingly large number of White-rumped Swallow nest boxes were inspected by others (54%), and this underestimates the true visit rate because we only counted visits by marked birds during the nestling period. Swallows caring for their own broods inspected others, sometimes repeatedly, and this is the first study to our knowledge to register this behavior in this species.

Inspectors are unlikely helpers, because when raising their own broods simultaneously, fitness returns from parental care would be higher if invested in their own broods. Considering that, there is a considerable rate of extrapair mating in this species (58% of offspring are extrapair; Ferretti et al. 2011), males might be caring for their young in other nests, but the same does not apply to females.

If inspectors were floaters and trying to get a breeding opportunity, they should visit

nests during egg-laying (when cuckoldry or egg dumping are possible) and not visit nests repeatedly during the nestling period when there are no more chances to breed. Moreover, all the registries of inspections were by breeding birds, and by definition, not floaters. Likewise, inspection is unlikely a search for nest box vacancies because boxes were inspected when many were still vacant.

Birds with small broods were more likely to inspect others, although this trend comes only from one female, with two young, that alone accounts for 41% of all inspections. Nonetheless, only one inspector had seven young, and inspected another box only once, after its young had fledged. Considering that 31% of all nest boxes had seven nestlings, we would expect more inspections from this group of females if inspections were not influenced by their brood size. Thus, parents with fewer nestlings apparently had reduced parental demands and consequently had free time for other activities. This is supported by the observation that female inspectors, though providing the same care to each nestling, entered their own nests at a lower rate than did the female owners of the nests being inspected.

Inspections began around the middle of the nestling period, after nestlings can thermoregulate (4-6 d after hatching, Dunn 1979). Also, the time required to inspect and return from neighboring nests (less than one minute) is so brief that inspection probably does not engender a cost for the nestlings. Apparently, therefore, parents begin inspecting as the nestling demand for care declines (from the middle of the nestling period onwards, Lombardo 1991).

In the Tree Swallow (*Tachycineta bicolor*), conspecific inspectors were not helpers nor did they pose any threats to the nest being inspected, since encounters with parents were usually non-aggressive (Lombardo 1986, 1987b). So perhaps they are checking potential nest sites for the future (Lombardo 1987a). Prospecting is especially likely for migratory birds or those that nest in secondary cavities, if breeding seasons are short and nest sites are limited

(Lombardo 1987a). If nest box location is associated with nesting area quality, we expect birds whose nest failed to examine nests farther from that failed nest than those with successful nests (Greenwood and Harvey 1982), which is indeed what happened. However, birds with successful nests also probably remained nearby because they were caring for their fledglings. Also, failed breeders did not inspect other boxes immediately after nest failure while successful birds inspected immediately.

On the other hand, if public information is used to access site quality, individuals should be more attracted to nests with higher parent visit rate or more nestlings, and nest in them in the following season (Pärt and Doligez 2003). Indeed, more nests with broods of seven were inspected by naive birds, yet they were also more available than other brood sizes and their location, some in the center of boxes distribution, might have privileged inspection by being in foraging routes. Also, if greater broods sizes were actively selected, we would expect that once having been inspected by a bird they would receive more repeat visits than boxes with less nestlings, which was not the case. On the contrary, boxes with both small and large broods were inspected repeatedly and independently. Also, returning birds should prefer boxes with larger broods in the previous season, but only one returning bird in 2013 nested in an inspected box, which had a small brood in 2012. Some returning birds nested in boxes not monitored in 2012 and so we do not know whether they were visited. Others nested in monitored nests that were not visited and so inspection does not result in future use.

In conclusion, we found that inspector breeding condition (brood size and nest success) was associated with the intensity, and perhaps distance, of nest-box inspection. We found no support for the idea that visitors are helpers, floaters or are searching for box vacancies, and found limited support for the hypothesis that they are checking, not selectively, potential nest sites in anticipation of future breeding opportunities.

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ETHICAL STANDARDS

This study complies with the current ethical standards and laws of Brazil.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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Table 1 Number of banded White-rumped Swallows (*Tachycineta leucorrhoa*) that nested in southern Brazil in 2012 and 2013. The box chosen in 2013 by a bird that nested in 2012 can be: 1) the same, 2) a monitored box used by a different individual that it inspected, 3) a monitored box used by a different individual that it did not inspect, and 4) an unmonitored box.

Status	Female	Male
Nested in 2012 but not in 2013	24	2
Nested in 2012 and 2013	9	3
Inspected in 2012	4	1
Same nest	1	0
Different monitored and inspected box	1	0
Different monitored but not inspected box	0	1
Not monitored	2	0
Did not inspect in 2012	5	2
Same nest	2	2
Different monitored but not inspected box	2	0
Not monitored	1	0

Figure 1 Maps of the two study areas, approximately 5 km from each other (datum WGS 84). Circles indicate White-rumped Swallows (*Tachycineta leucorrhoa*) nests that were monitored with passive integrated transponder (PIT) equipment and numbers indicate brood sizes. Absences of a number are boxes with nestlings that died prior to three days of age, when data loggers were usually installed. Filled circles indicate successful and open circles failed nests. Arrows indicate the direction the bird moved from its own to an inspected box. Dashed arrows indicate movement between study areas.

Figure 2 Histograms of inspection patterns by White-rumped Swallows (*Tachycineta leucorrhoa*). A) The x-axis is the frequency of different nests inspected by an individual ($n = 13$), the number of inspections of the same nest by an individual ($n = 71$), or the number of different birds that inspected the same nest ($n = 34$). B) The number of inspections ($n = 71$) divided among birds based on the status of their own nest (active, after success, or after failure).

Figure 3 Frequency of inspections and of parental visits to their own nest, by time of day at nest boxes of White-rumped Swallows (*Tachycineta leucorrhoa*, $n = 71$). Frequency was controlled by the number of inspectors or parents, and by the number of days with records.

Figure 4 Histograms of inspections based A) on nestling age (own nestlings and those in the inspected nest) and B) on day of the year. In panel A repeated inspections from a bird to a nest were excluded if on the same day. In panel B, repeated inspections are represented and we draw attention to the female that performed most of the inspections.

Figure 5 Brood size of all monitored nests, inspected nests (the first time they were ever inspected and inspections by any new bird), and active nests of inspectors of White-rumped Swallows.

Figure 6 Sequence of inspections with respect to brood size in the inspected nest (y-axis). Each panel indicates the number of young of the inspector and each line is a different

inspector. Arrows indicate fledging from the inspector nest. Black circles indicate inspections to a previously not inspected nest and open circles indicate repeat inspections.

Figure 1

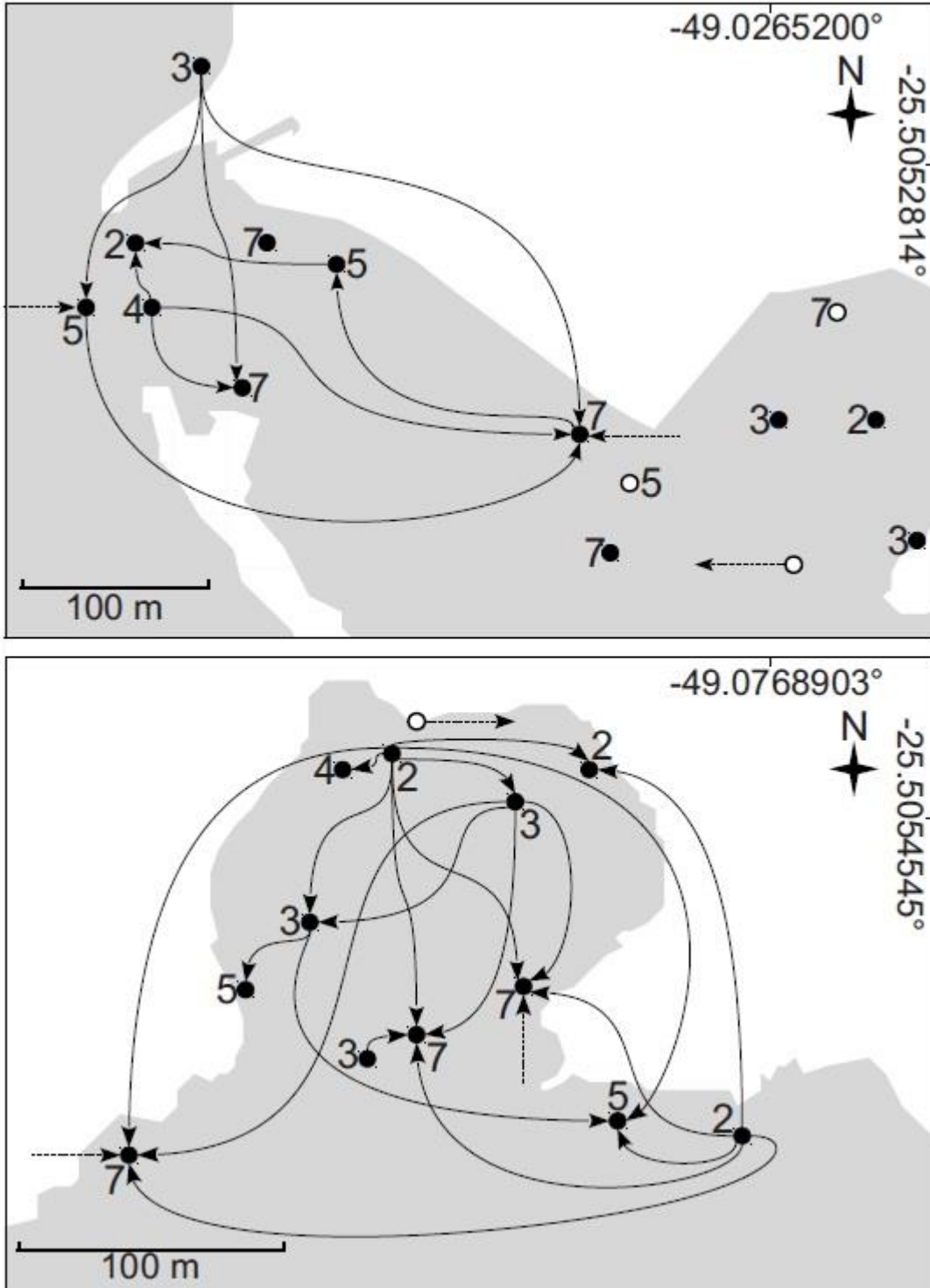


Figure 2

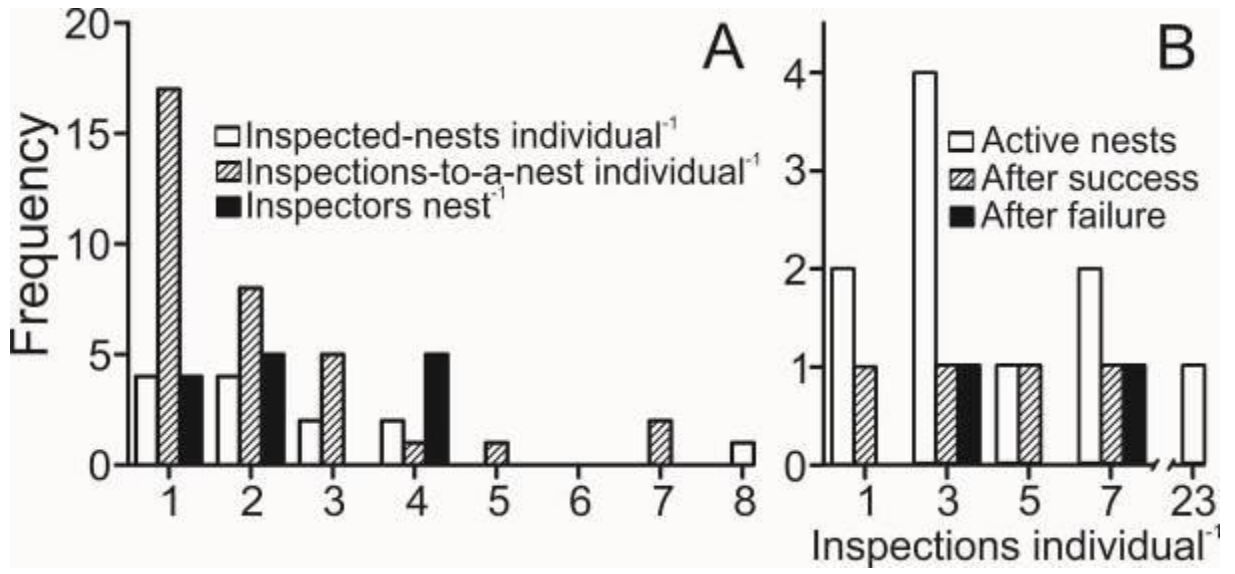


Figure 3

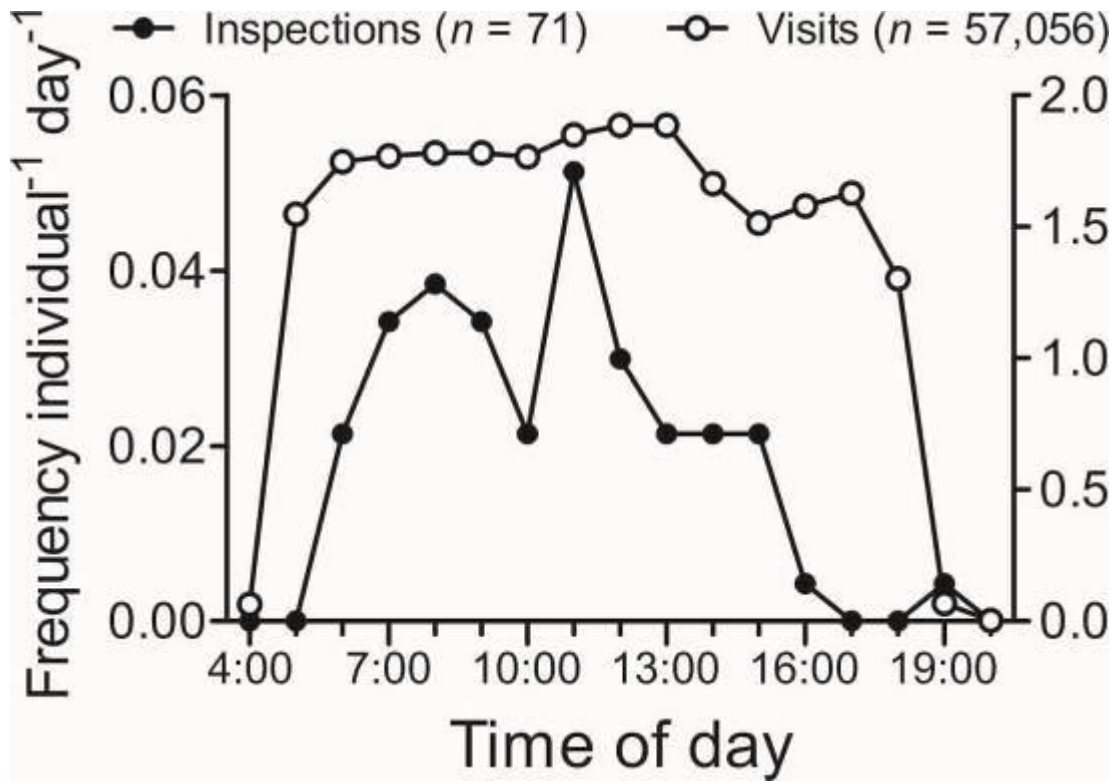


Figure 4

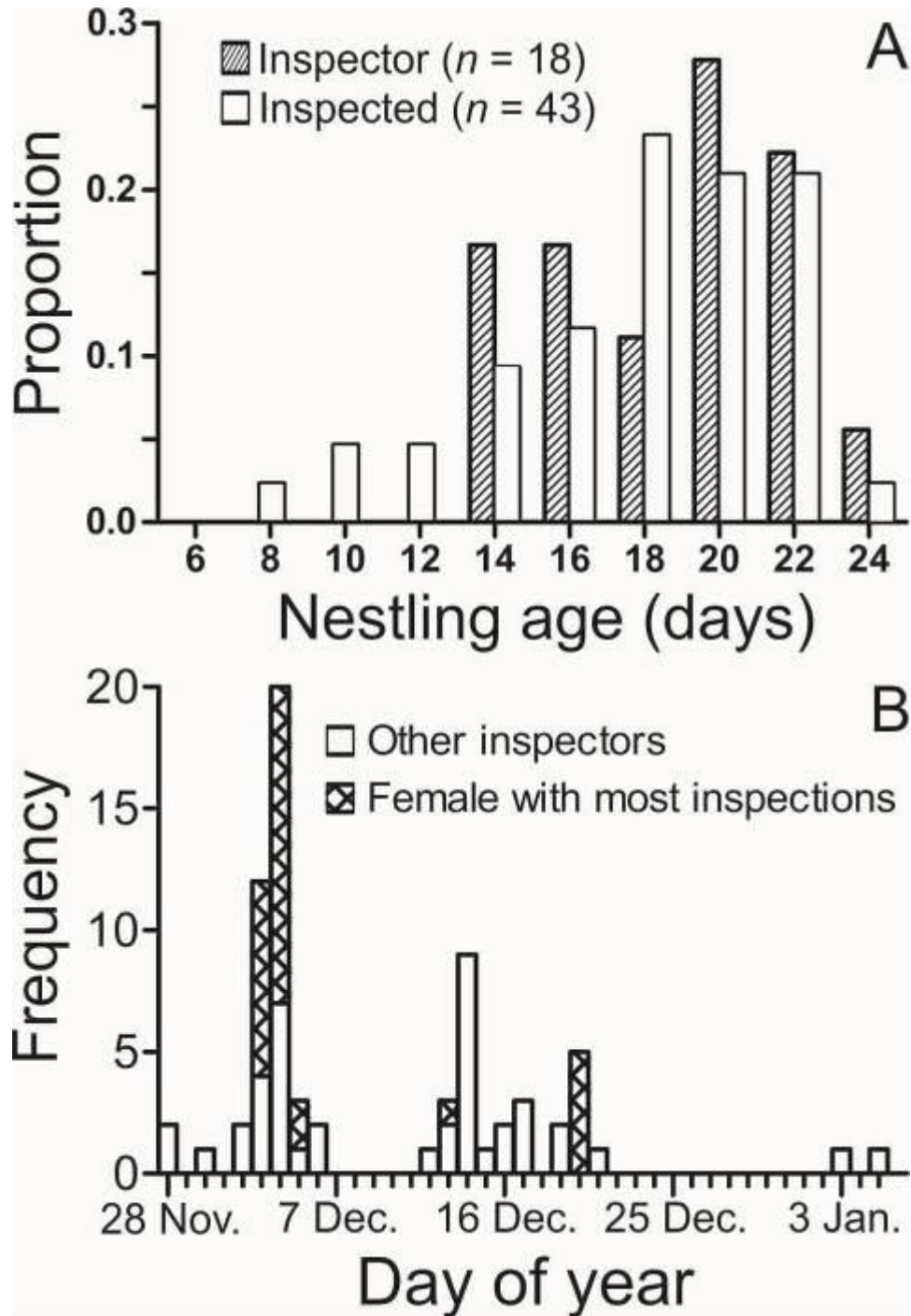


Figure 5

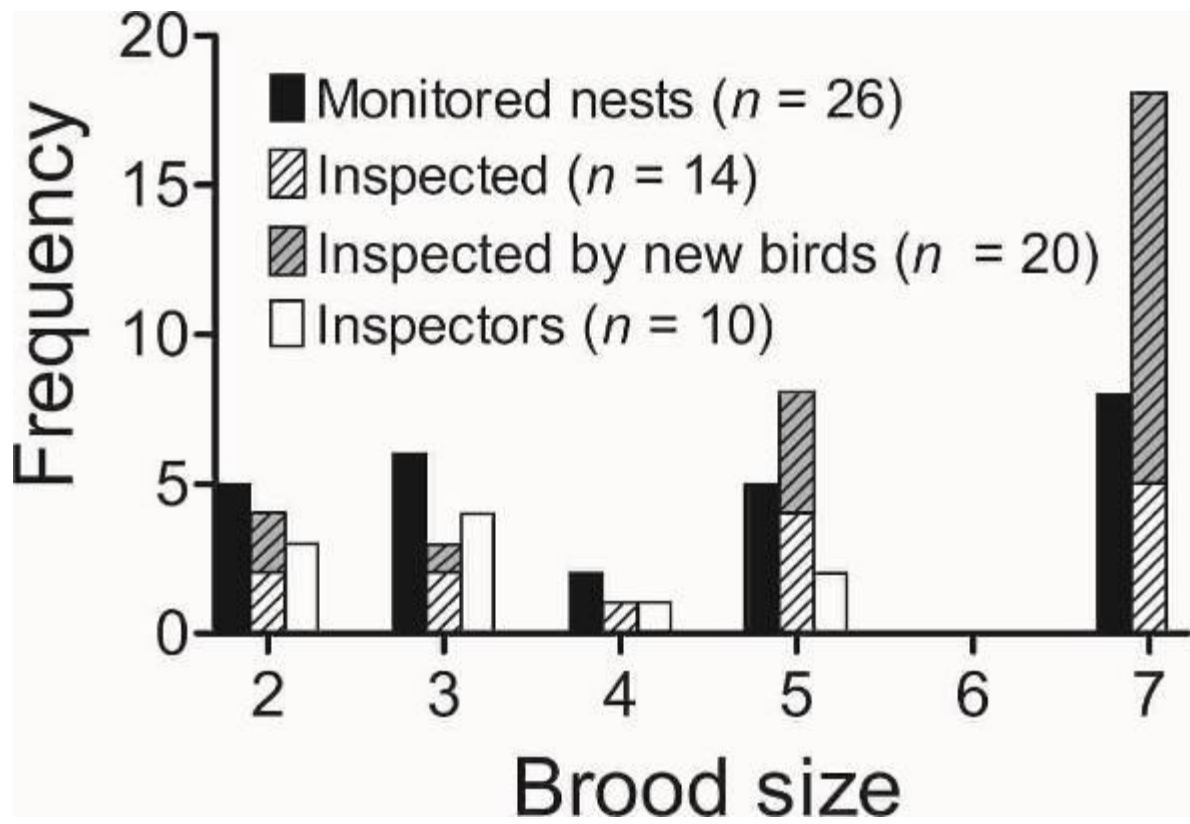
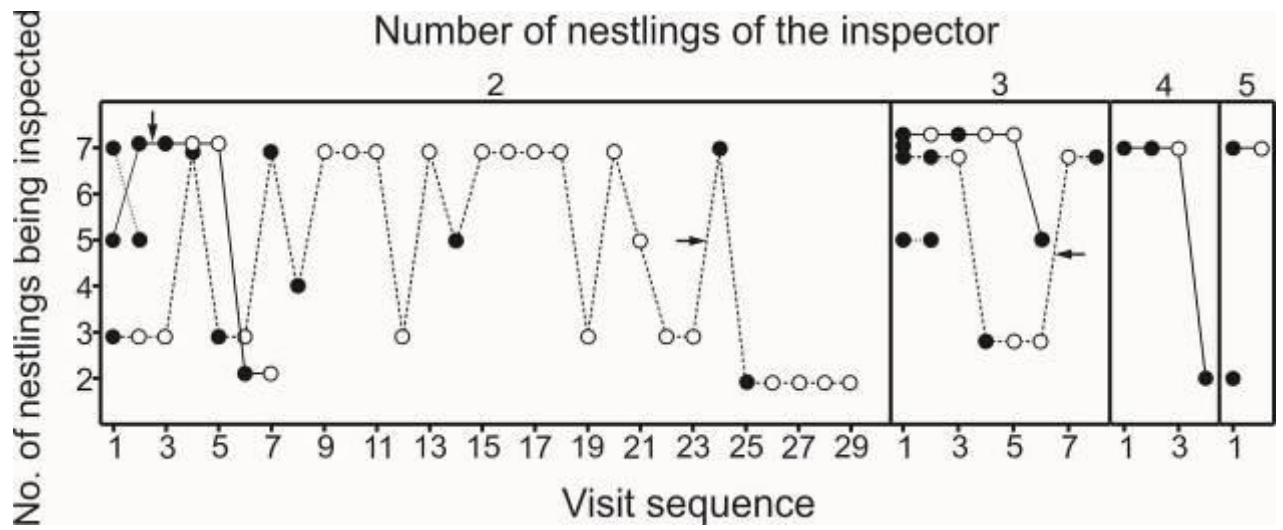


Figure 6



4 DOES BROOD SIZE COME WITH A COST? RESIDUAL EFFECTS OF EXPERIMENTALLY VARIABLE BROOD SIZE IN THE WHITE-RUMPED SWALLOW

Capítulo elaborado de acordo com normas do periódico Journal of Field Ornithology.



A migração sazonal de aves é extenuante e muitos morrem na jornada. Aqueles com melhores reservas energéticas tem chances maiores de retornarem à mesma área reprodutiva em temporada seguintes. Esses indivíduos são identificados pela anilha metálica numerada que carregam em uma das patas (seta).

Crédito da imagem: F. MARQUES-SANTOS, 2013.

Wischhoff et al.

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Residual effects in White-rumped Swallow breeding

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Does brood size come with a cost? Residual effects of experimentally variable brood size in
the White-rumped Swallow

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1 ABSTRACT. Clutch size in birds, if optimal, should maximize present and future
2 reproductive success. Thus, increasing the number of nestlings in a brood should incur costs
3 to offspring or to adult survival or physical condition, and thereby reduce future reproductive
4 success. We investigated these predicted costs in the White-rumped Swallow (*Tachycineta*
5 *leucorrhoa*) one year after experimentally manipulating brood size. Three fledglings returned
6 to the study area the year following brood manipulation and were from both enlarged and
7 reduced broods. Those from enlarged broods showed no sign of poorer body condition or
8 diminished fecundity. Eleven females whose broods were manipulated the previous year also
9 returned (38% from enlarged and 42% from control and reduced broods). Probability of adult
10 return, as well as body condition and fecundity were independent of the brood size they raised
11 the previous year. Though sample sizes were relatively small, results suggest the absence of
12 reproductive costs associated with brood size in a given year. Costs may exist only in years of
13 unpredictably low food availability or clutch size may be constrained by time or by energetic
14 demands during other stages of the breeding cycle.

15 KEY WORDS: brood size manipulation, fecundity, return rate, recruitment, reproductive
16 costs, survival, *Tachycineta leucorrhoa*

17 That greater reproductive effort leads to poorer survival is almost a paradigm in ecology
18 (Orton 1929). This idea implies a trade-off between current and future reproduction, so that an
19 increase in current breeding effort should produce long-term costs to fecundity and survival of
20 adults and young (Williams 1966, Charnov and Krebs 1974, Calow 1979, Ardia 2005). Costs
21 of reproduction have been investigated through observations (based on correlations between
22 life-history traits) and experiments (in which traits are manipulated, Lindén and Møller 1989,
23 Santos and Nakagawa 2012), with equivocal conclusions.

24 Costs of reproduction were absent in the Tree Swallow (*Tachycineta bicolor*,
25 Hirundinidae), a migratory bird that nests in North America. Birds with experimentally
26 increased effort in one year had equal or greater return rates in the subsequent year than
27 control birds, with no consequences for fecundity (De Steven 1980, Wiggins 1990,
28 Wheelwright et al. 1991, Murphy et al. 2000, Shutler et al. 2006). In addition, growth and
29 recruitment of young were independent of brood size (De Steven 1980, Wheelwright et al.
30 1991, Shutler et al. 2006). This lack of a cost is intriguing because trade-offs are the essence
31 of life-history theory (Cody 1966, Martin 2004).

32 The related White-rumped Swallow (*Tachycineta leucorrhoa*) in South America,
33 provides an opportunity to further investigate this enigma. Natural selection should favor
34 current over future reproduction in species in circumstances that impose relatively greater
35 mortality (as a result of severe climate or seasonal food shortage) or migratory species, due to
36 lower probabilities of surviving to breed in the future (Charnov and Krebs 1974, Sillett and
37 Holmes 2002, McNamara et al. 2004). Thus, the more tropical White-rumped Swallow, which
38 migrates over shorter distances, should tend to favor future over current reproduction in
39 comparison to the Tree Swallow (BirdLife International 2014, Martin 1996). Moreover,
40 competition for food is presumably stronger during the breeding season for the White-rumped
41 Swallow, and consequently, parental care should be more costly (Ashmole 1963, Martin

42 1996).

43 Contrary to expectations, however, we found that parental care increased in
44 experimentally enlarged broods, resulting in nestlings within the range of average size
45 (chapter 2). Although size is usually an indicative of offspring quality and recruitment
46 probability, the development of the immune system can lag behind structural development,
47 and so, to better understand reproductive costs to offspring, recruitment should be measured
48 directly (Perrins 1965, Garnett 1981, Mauck et al. 2005). Because expected costs to rearing
49 larger broods are greater in White-rumped Swallows in comparison to its northern relative, we
50 predict that we will be able to detect residual effects on return rate, body condition or
51 fecundity of either parents or offspring from increased broods.

52

53 METHODS

54 *Study area*

55 This study was carried out in southern Brazil, where 121 nest boxes (17 x 13 x 25 cm, GDLA
56 2011) were available in two neighboring reservoirs (25°30'24"S, 49°01'37"W, 908 m and
57 25°30'22"S, 49°04'42"W, 897 m). Climate is C_f in Köppen classification, that is, temperate
58 with warm summers and without a dry season (Peel et al. 2007). During the breeding season
59 (Oct. - Jan.) monthly precipitation averages 150.1 mm (SD = 80.1, min. = 2.4, max. = 473.8,
60 $N = 208$) and daily temperature, 20.1°C (SD = 3.1, min. = 7.1, max. = 28.5, $N = 18,385$; data
61 for the city of Curitiba, about 20 km from reservoirs, INMET 2014). The area includes open
62 grassy areas, marshes and trees.

63 *Study species*

64 We studied the White-rumped Swallow (Hirundinidae), a South American migrant that nests
65 in natural cavities or artificial nest boxes in the tropics and subtropics. In Argentina, its
66 lifespan is of less than three years (Bulit and Massoni 2011) and clutch size averages 4.9 eggs

67 (Massoni et al. 2007).

68 We captured adults, especially females, in the nest boxes by use of a trap door after
69 clutch completion (GLDA 2011). Birds were measured (weight to 1.0 g, flattened wing length
70 to 1.0 mm) and banded with a numbered metal band and a plastic band with a passive
71 integrated transponder (Cyntag 2x12 EM4102 12KhZ), which was used to monitor nest
72 visitation rate (chapter 2).

73 *Reproduction monitoring and brood manipulation experiment*

74 During the breeding season of 2012, we monitored reproduction and experimentally
75 manipulated brood size (see below). In 2013, we monitored reproduction and identified
76 returning females. We determined dates of laying and hatching, recorded clutch sizes and
77 weighed eggs with an electronic scale to the nearest 0.01 g. Nestlings were weighed (to 0.01
78 g) and wing length was measured (to 1.0 mm) when we banded them at 12 days of age. Nest
79 boxes were checked weekly after birds arrived in the study areas; every four days after nest
80 construction began, in order to determine date of laying of the first egg of a clutch; and daily
81 near the estimated hatching date. Hatching date was the day when half or more of the eggs
82 hatched and was the day zero of the nestling period.

83 Brood size manipulation consisted of adding or subtracting ~50% of nestlings
84 from broods, while control broods maintained original clutch size. Control and reduced
85 broods contained, when possible, foreign nestlings to control for manipulation effects, should
86 they occur. Nestlings were randomly exchanged at three days of age among nests with the
87 same hatching date (± 1 d).

88 *Statistical analysis*

89 With one sample *t*-tests, we compared body condition (weight and wing length) at age 12
90 days of nestlings that returned to those that did not, and body condition of these first-year
91 females in 2013 to the population of older females. We also compared reproductive effort of

92 first-year females to that of the population. We expected that first-year females from enlarged
93 broods were lighter, had shorter wings, smaller clutches and lighter eggs than the older female
94 average; we expected the opposite for first-year females from reduced broods.

95 Fisher's exact test was used to compare the number of older females that returned
96 versus did not return in relation to brood size treatment in 2012 (one-sided: reduced + control
97 > enlarged). To check for residual effects of brood size manipulation on subsequent older
98 female body condition and fecundity, we compared the differences between years in weight,
99 clutch size, mean egg weight per clutch, and laying date among treatments (enlarged vs.
100 reduced + control) with *t*-tests.

101

102 RESULTS

103 We experimentally manipulated 28 broods, three of which were abandoned. Manipulation
104 resulted in reduced broods with 2 to 4 nestlings ($n = 15$), control broods with 5 nestlings ($n =$
105 5), and enlarged broods with 7 nestlings (but in one nest, one nestling died early; $n = 8$). Only
106 one female had two broods manipulated, none of which was successful (for analysis we
107 considered the treatment of her second nest, because it lasted longer).

108 We banded 27 females and 101 fledglings in 2012. Three females born in nest boxes
109 in 2012 returned to nest in 2013 (3% of banded fledglings). One was from reduced and two
110 from enlarged brood treatments. The return rate of older females whose broods were
111 manipulated was 41% ($N = 11$). Two of the returning older females were found dead in nest
112 boxes prior to the beginning of nest construction. In 2012, one raised a reduced brood with
113 fledging success (number of fledglings per number of nestlings) of 75%, and the other an
114 enlarged brood with 100% fledging success. The proportion of returning older females was
115 similar when we compared the combined sample of 19 birds that raised control and reduced
116 broods (42% returned) with the eight that raised enlarged broods (38% returned, Fisher's

117 exact test $P = 0.59$).

118 All first-year females were of average or above average size as nestlings (Table 1
119 and Fig. 1). Contrary to expectations, only one of the first-year females that came from an
120 enlarged brood had weight and wing length smaller than average for females (Table 1 and
121 Fig. 1). In addition, the first-year female from a reduced brood did not have better body
122 condition than average females. Treatment in 2012 also had no effect on weight of older
123 females that returned in 2013 ($t_7 = 1.2$, $P = 0.29$, Fig. 2A).

124 Reproductive effort was apparently similar among first-year females. We had
125 predicted that effort (either egg size, clutch size, or both) from first-year females from the
126 enlarged treatment would be smaller than average in relation to all other females. Although
127 one had a small clutch size, her eggs were particularly heavy (Table 1, Fig. 3). The first-year
128 female from a reduced brood had clutch and egg sizes smaller than expected. She laid her
129 eggs between the dates of the other two first-year females, and only the first-year female with
130 better body condition and a 5-egg clutch started laying prior to the median laying date of the
131 sample. For returning older females, clutch size ($t_7 = 0.1$, $P = 0.90$ Fig. 2B), mean egg weight
132 per clutch ($t_7 = 0.2$, $P = 0.84$, Fig. 2C), and the outset of laying in 2013 ($t_6 = 0.1$, $P = 0.92$,
133 Fig. 2D) were independent of brood size treatment in 2012.

134

135 DISCUSSION

136 White-rumped Swallows are enigmatic in that there is no evidence of a cost to rearing
137 enlarged brood sizes. Although the number of returning females was not large, we suggest
138 that the lack of evidence indicates a true absence of reproductive costs, because results are
139 consistent with other studies with Tree Swallows. Here, condition of nestlings did not
140 influence body condition or fecundity of recruits. Thus, though nestlings from enlarged
141 broods were on average in poorer body condition than nestlings from reduced broods (chapter

142 2), that difference disappeared over the course of the year. The critical period in which
143 condition is most likely to influence survival is prior to the first migration (Naef-Daenzer et
144 al. 2001). So, we expected to have more returns of birds from the reduced treatment, but the
145 only three females that were recruited in monitored nest boxes showed no such tendency. No
146 effect of brood size on recruitment was found in the Tree Swallow either (De Steven 1980,
147 Wheelwright et al. 1991, Shutler et al. 2006).

148 Older females return rate, body condition and fecundity were also independent of
149 brood size in 2012. Though one could argue that our sample size was small, these results were
150 similar to other studies with Tree Swallows that did not find costs to adult survival (return
151 rate) or fecundity (clutch size and breeding date; De Steven 1980, Wiggins 1990,
152 Wheelwright et al. 1991, Shutler et al. 2006). Because one of these studies increased brood
153 sizes from the same females for three consecutive seasons, and another pooled 14 years of
154 data that also measured incubation costs, the lack of evidence for reproductive costs is not the
155 consequence of small effect and sample sizes, and so we believe that our results simply agree
156 with theirs. So far, only one study with Tree Swallows found different adult return rates
157 among brood size treatments, but not in the direction that would indicate a cost (Murphy et al.
158 2000). Return rates are consequences not only of survival, but also of site fidelity and the
159 probability of encounter (Bulit and Massoni 2011). Hence, the greater return rate for females
160 with enlarged broods in that study perhaps was due, not to greater survival, but to their
161 perceived success, as unsuccessful females disperse more (Bulit and Massoni 2011).

162 This absence of measurable costs in short- and long-term studies with Tree
163 Swallows suggests that years with extreme conditions and detectable reproductive costs are
164 unlikely to drive clutch size evolution (Shutler et al. 2006). White-rumped Swallows may
165 provide a useful system to further investigate this idea, because rainfall in this region, that
166 strongly influences food supply for aerial foragers, is variable and unpredictable both within-

167 and between-years (Williams 1961, Marques et al. 2004, pers. obs.). Within-year
168 unpredictability should favor bet-hedging strategies, which will result in suboptimal
169 individual clutch size in any year (Stearns 2000). Also, evidence shows that the accuracy of
170 individual optimization is low, because females cannot predict food availability during the
171 brood rearing period and clutch size is a direct consequence of food intake during laying, not
172 of their physiological condition (Winkler and Allen 1995, Winkler and Allen 1996, Török et
173 al. 2004, Dunn et al. 2011). So, different clutch sizes of females laying near in time are not
174 based on their ability to predict environmental conditions and estimate own reproductive
175 residual value. Hence, we would expect little adjustment in clutch size of individual females.
176 Consequently, between-year variation in food abundance should cause fluctuating selection
177 and maintain an adaptive variability of clutch sizes (Török et al. 2004).

178 Alternatively, individual clutch sizes may indeed be optimal, but the consequence of
179 other constraints (e.g., calcium for egg laying, time). In Tree Swallows time instead of
180 reproductive costs are believed to constrain clutch sizes. It is suggested that breeding early
181 improves offspring recruitment chances, but limits clutch size and can incur a starvation risk
182 to parents, due to low food abundance at the beginning of the season (Murphy et al. 2000,
183 Shutler et al. 2006). Here, in both years of study, dead adults (in nest boxes) were found prior
184 to the beginning of nest construction (one male in 2012, two females and one of undetermined
185 sex in 2013). This would be evidence for the existence of this possible time constraint,
186 because it suggests that food availability was a problem when birds arrived from migration.
187 Still, clutch and egg size were constant over the breeding season in our study (unpubl. data),
188 in contrast to places with strong seasonal variation in food abundance (Winkler and Allen
189 1996, Massoni et al. 2007, Liljeström et al. 2012).

190 Evidence does not support the idea of reproductive costs in the White-rumped
191 Swallow. Future studies with *Tachycineta* should focus on optimization based on constraints

192 other than effort during the nestling period, evaluate yearly variation in breeding success and
 193 look for alternative processes to clutch size optimization by which clutch sizes might evolve.

194

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Table 1. Results of *t*-tests contrasting body condition and fecundity of first-year females that were recruited in our study to other nestlings that were not recruited and to older females.

Variable (sample)	First-year female (bar pattern in Fig. 1 and 3)	<i>t</i>	df	<i>P</i> -value	Alternative hypothesis ^a
Weight (nestlings) ^b	Enlarged (black)	5.6	94	< 0.001	=
	Enlarged (gray)	5.2		< 0.001	=
	Reduced (hatched)	16.8		< 0.001	=
Wing length (nestlings) ^b	Enlarged (black)	3.5	94	< 0.001	=
	Enlarged (gray)	1.4		0.16	=
	Reduced (hatched)	6.9		< 0.001	=
Weight (adults) ^c	Enlarged (black)	1.3	52	0.11	>
	Enlarged (gray)	16.0		< 0.001	>
	Reduced (hatched)	10.4		1.0	<
Wing length (adults)	Enlarged (black)	4.6	52	1.0	>
	Enlarged (gray)	19.1		< 0.001	>
	Reduced (hatched)	7.3		1.0	<
Clutch size	Enlarged (black)	2.3	40	0.99	>
	Enlarged (gray)	18.6		< 0.001	>
	Reduced (hatched)	8.2		1.0	<
Egg weight	Enlarged (black)	3.4	34	1.0	>
	Enlarged (gray)	7.3		1.0	>
	Reduced (hatched)	3.2		1.0	<

^aAlternative hypotheses: > mean of the sample is greater than the value of the young female; < mean is less than the tested value; = mean is equal to the tested value.

^bOriginal variable was squared to fulfill the normality assumption.

^cOriginal variable was square-rooted to fulfill the normality assumption.

Figure 1. Body condition of nestlings from 2012 (brood size treatment of origin represented in bar pattern) that returned to breed in our study areas in the following year. At the left, size at age 12 days in comparison to other nestlings that fledged ($N = 101$). At the right, size at maturity in comparison to other females captured in 2012 and 2013 (if any of these older females were recaptured between years, we only represented their size in 2013; $N = 56$).

Figure 2. Comparison of female weight (A), clutch size (B), mean egg weight per clutch (C), and date of laying in relation to the first clutch of the season (D) among years from female White-rumped Swallows that returned to nest in our study areas in the year after an experimental brood size manipulation. Lines are individual females and line patterns represent brood size treatment in 2012. In (A) some lines were nudged to prevent overlap. In (D) we excluded a female with two breeding attempts at a season; also note the y-axis break. The variation on these variables between years was independent of brood size treatment in 2012 (see Results).

Figure 3. Breeding effort of first-year females in 2013 that were born in manipulated broods (brood size treatment of origin represented in bar pattern). (A) Clutch size ($N = 44$) and (B) mean egg weight ($N = 38$) per clutch in comparison to all clutches from 2013.

Figure 1

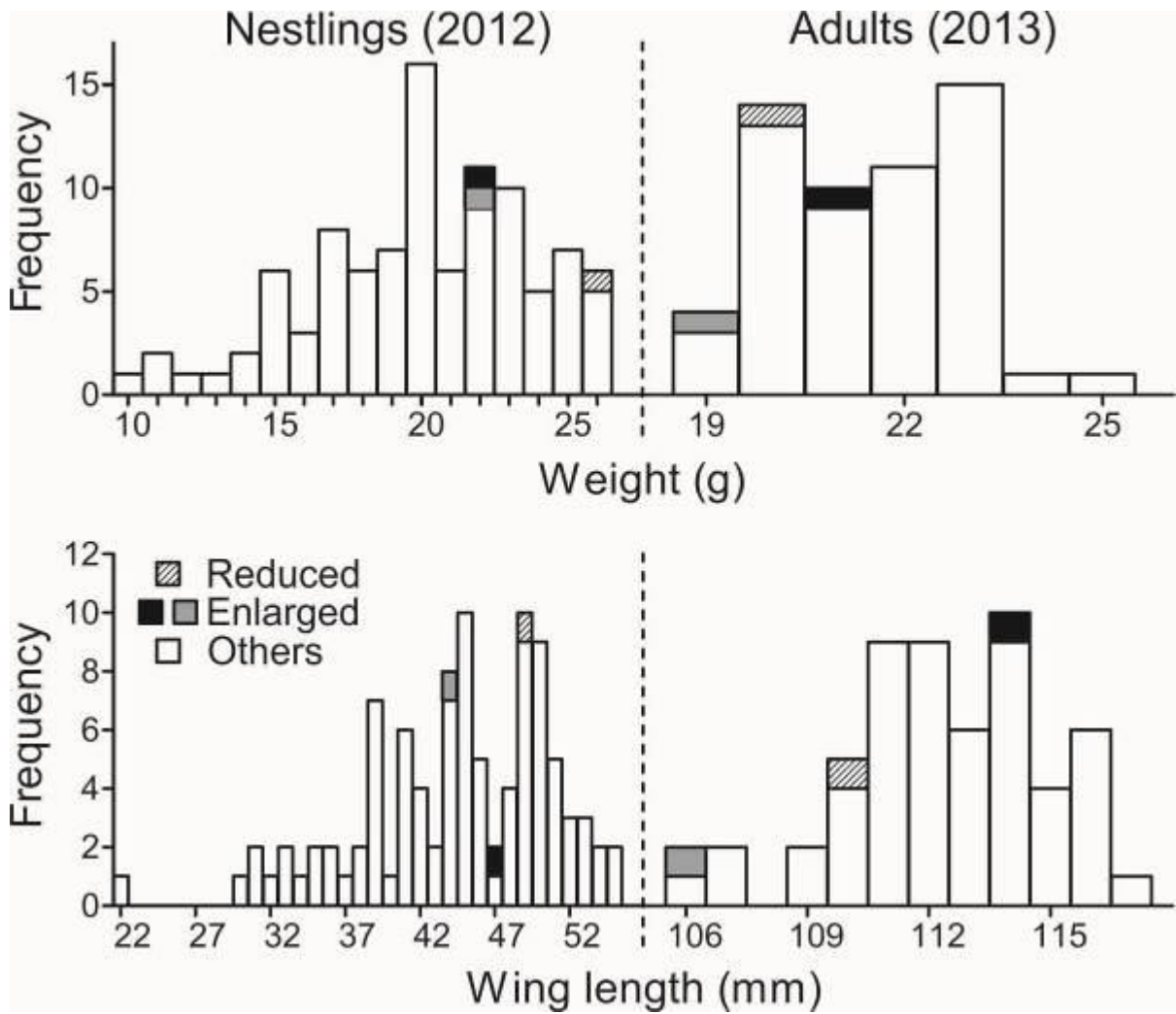


Figure 2

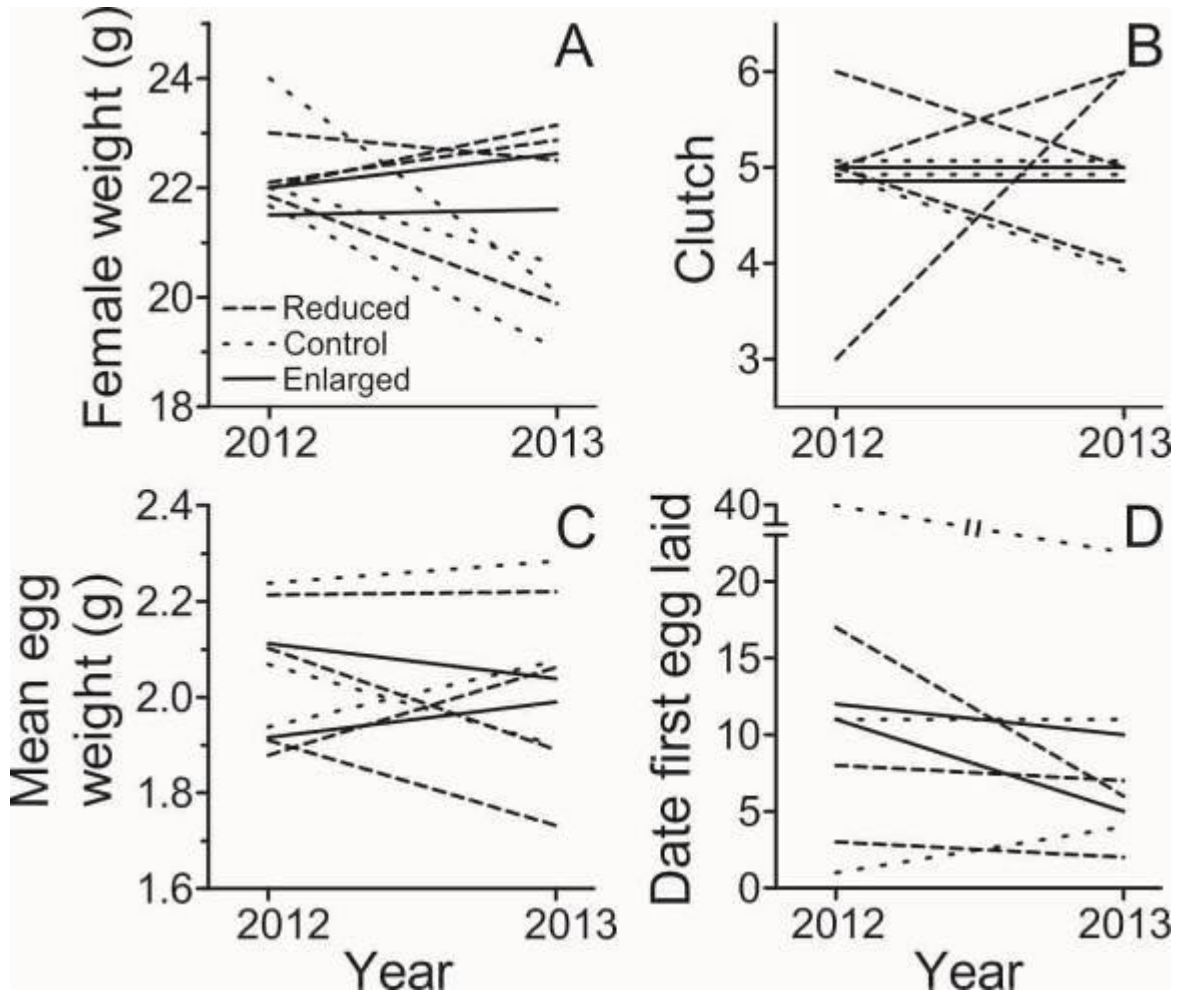
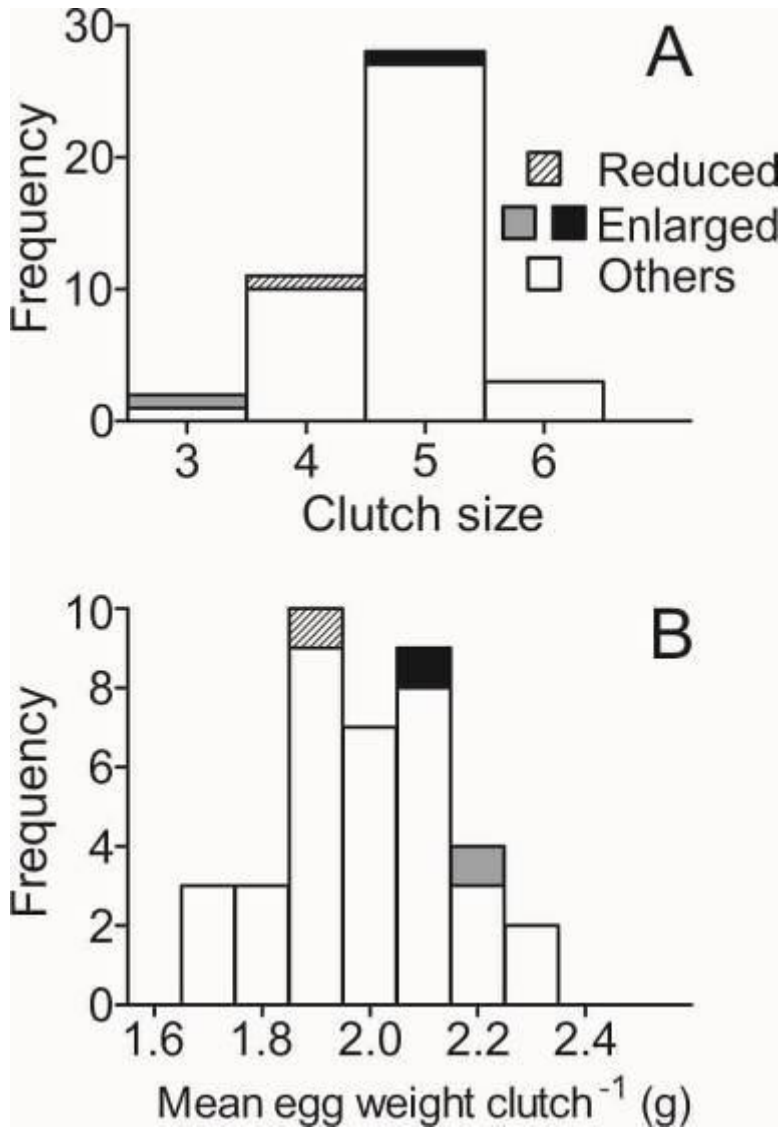


Figure 3



5 CONSIDERAÇÕES FINAIS

No segundo capítulo, vimos que fêmeas foram capazes de intensificar o cuidado parental em ninhadas aumentadas de modo que cada filhote recebesse em média a mesma atenção que em ninhadas controle. Assim, os tamanhos que os filhotes atingiram na idade 12 dias foram também similares entre esses tratamentos. Esses resultados indicam que, caso existam custos reprodutivos em ninhadas maiores que o natural, esses custos devem ser absorvidos pelos adultos.

No terceiro capítulo, vimos que adultos com ninhadas aumentadas não visitaram ninhadas alheias em igual intensidade àqueles que criaram ninhadas reduzidas e controle. Dentre as hipóteses disponíveis para esse comportamento de visitação, nossas evidências apontam para a exploração de futuros locais para ninho. Se isso for verdade, adultos com ninhadas aumentadas não tiveram oportunidade equivalente aos seus competidores de se preparar para a temporada reprodutiva seguinte, o que em um ambiente natural (ou seja, em que cavidades naturais existem em número reduzido e possuem qualidade variável) pode trazer prejuízos reprodutivos futuros.

No quarto capítulo, verificamos que o maior esforço com cuidado de filhotes pelas fêmeas de ninhadas aumentadas em 2012 não diminuiu a taxa retorno dessas fêmeas à nossa área de estudo, nem gerou efeitos residuais na condição corporal ou fecundidade delas em 2013. Desse modo, as ninhadas da andorinha-de-sobre-branco parecem não ser ótimas se considerarmos o esforço reprodutivo empregado durante o período de criação de filhotes (ninhgos e *fledglings* - estes últimos avaliados indiretamente). Contudo, conforme já discutido nos capítulos anteriores, o gargalo energético pode ainda encontrar-se em fases do ciclo reprodutivo não avaliadas aqui (como postura e incubação); ou a otimização reprodutiva pode estar relacionada a limitações de tempo, e não de recursos. É importante também avaliar o impacto de substratos naturais de ninhos no sucesso reprodutivo de um adulto, de modo a verificar se adultos que não exibiram o comportamento de visitação a outros ninhos teriam menor sucesso reprodutivo na temporada seguinte que os demais. Uma última alternativa é que ninhadas de um indivíduo não são ótimas, e outros fatores evolutivos, como diluição de risco (*bet-hedging*) ou seleção flutuante causados por imprevisibilidade e variabilidade ambiental gerem os tamanhos de ninhada observados.