UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

AUGUSTO FLORISVALDO BATISTELI

CONQUISTANDO O AMBIENTE URBANO: VALOR ADAPTATIVO E COMPORTAMENTO PARENTAL NOS NINHOS DE *TURDUS LEUCOMELAS* (AVES, TURDIDAE) EM EDIFÍCIOS

Orientador: Prof. Dr. Hugo Miguel Preto de Morais Sarmento

Coorientador: Prof. Dr. Marco Aurélio Pizo Ferreira

São Carlos

Março de 2020

UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

AUGUSTO FLORISVALDO BATISTELI

CONQUISTANDO O AMBIENTE URBANO: VALOR ADAPTATIVO E COMPORTAMENTO PARENTAL NOS NINHOS DE *TURDUS LEUCOMELAS* (AVES, TURDIDAE) EM EDIFÍCIOS

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais do Centro de Ciências Biológicas e da Saúde, Universidade Federal de São Carlos/SP, como parte dos requisitos necessários para obtenção do título de Doutor em Ciências, área de concentração Ecologia e Recursos Naturais.

São Carlos

Março de 2020

UNIVERSIDADE FEDERAL DE SÃO CARLOS

Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Folha de Aprovação

Assinaturas dos membros da comissão examinadora que avaliou e aprovou a Defesa de Tese de Doutorado do candidato Augusto Florisvaldo Batisteli, realizada em 06/03/2020:

Prof. Dr. Hugo Miguel Preto de Morais Sarmento
UFSCar

Mercival Roberto Francisco

Prof. Dr. Mercival Roberto Francisco
UFSCar

Prof. Dr. Augusto João Piratelli
UFSCar

Prof. Dr. César Cestari
UFU

Prof. Dr. Matheus Gonçalves dos Reis
Esfera Ambiental

Dedico essa tese à minha família, principalmente aos meus pais, Amélia e Antônio Batisteli, aos meus tios Geraldo, Cleide e Júlio (*in memorian*), minhas avós Maria Luiza e Ana Zanollo (*in memorian*).

AGRADECIMENTOS

Minha sincera e eterna gratidão a todos(as) que construíram quem sou e que colaboraram para essa conquista.

À Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES) pela bolsa de doutorado. À Universidade Federal de São Carlos pelos anos de enriquecimento pessoal e profissional, a todos os seus funcionários diretos e terceirizados, muitos dos quais se tornaram colaboradores e apoiadores. Ao Instituto Chico Mendes de Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), ao Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE) e à Comissão de Ética no Uso de Animais da UFSCar (CEUA) pela concessão das licenças para realização deste estudo.

Aos(às) docentes, funcionários(as) e aos(às) colegas discentes do Programa de Pós-Graduação em Ecologia e Recursos Naturais. Aos membros da banca de qualificação (Profs. Dr. Manoel Martins Dias Filho, Dr. Victor Satoru Saito e Drª. Odete Rocha) e de defesa da tese (Prof. Dr. Mercival Roberto Francisco, Prof. Dr. Augusto João Piratelli, Dr. César Cestari e Dr. Matheus Gonçalves dos Reis), que gentilmente prestaram valorosa contribuição à minha formação.

Aos Profs. Dr. Hugo Sarmento, pela orientação e valiosa amizade, e Dr. Marco Aurélio Pizo, pela inestimável parceria durante o doutorado. Vocês ocupam um lugar de destaque entre minhas referências profissionais e pessoais dentro da academia.

A todos(as) que, durante a caminhada do doutorado, incentivaram-me ou auxiliaram-me de qualquer forma. Às parceiras de trabalho de campo, Isadora e Talita, sem as quais esse trabalho não seria concluído, e também aos demais ajudantes. Ao Dr. José Carlos Nardy, a Vera e Cláudio Lavrador, ao Pe. Lourival, muito obrigado.

A todos(as) os(as) professores(as) de minha trajetória escolar e acadêmica. À Escola Recriart, todos os seus colaboradores, sem os quais eu não teria chegado até aqui, em especial Geni, Antônio, Gisele e Elizabeth Martinez.

A toda minha família. Minha preciosa vó Maria, tios, tias, primos e primas de Tabatinga e de São Paulo, todos muito amados e sempre presentes. Agradeço especialmente aos anjos que sempre me carregaram pela mão: tio Geraldo (tio Dito, meu guardião) e tia Cleide, primo Getúlio, irmã Ana Luiza, e sobrinhos Lívia e Felipe. Meu pai, Antônio, obrigado pelo exemplo de humildade, trabalho, e por dividir comigo sua paixão pelas aves. Minha mãe, Amélia, sem você não seria nada, não chegaria a lugar algum, não teria visto as maravilhas que pude ver, e não teria vivido os sonhos que sonhei.

Agradeço também por tudo que fizeram por mim o meu querido tio Júlio, o Ti, que hoje vive na paz de Deus, na companhia da saudosa vó Ana.

À minha companheira de todas as horas, Drª. Rosane Costa, que me mostrou novos horizontes, me apoiou incondicionalmente do início ao fim dessa jornada, e diariamente saboreou as alegrias e dividiu os fardos dessa difícil, mas prazerosa caminhada, incluindo inúmeras horas de ajuda em campo. Espero poder comemorar com você muitos outros passos.

Por fim, minha gratidão a todos os encantadores seres vivos que tive a honra de observar, tocar e estudar, em especial às aves. A Nossa Senhora Aparecida, minha mãe celestial. A Deus, que governa meus passos enquanto se faz humildemente presente em cada pequenina criatura e em cada centelha de natureza.

“O conhecimento serve para encantar as pessoas,
não para humilhá-las.”
Mário Sérgio Cortella

SUMÁRIO

ÍNDICE DE TABELAS

ÍNDICE DE FIGURAS

RESUMO

A reprodução é um estágio crucial da história de vida das espécies, e os conflitos energéticos envolvidos são especialmente importantes para aquelas com intenso cuidado parental, como as aves altriciais. A seleção do local de nidificação está diretamente ligada à aptidão dos adultos, podendo minimizar o custo energético do cuidado com a prole e o risco de predação, tanto da ninhada quanto dos adultos. No entanto, pouco se sabe sobre a influência de ambientes antrópicos sobre o comportamento reprodutivo das aves. Nesse estudo, avaliei o efeito da utilização de árvores e de edifícios como local de nidificação na incubação e na sobrevivência da ninhada no sabiá-barranco (Turdus leucomelas). Adicionalmente, investiguei as causas e consequências da troca de parceiros e da reutilização de ninhos, e a relação entre a nidificação em edifícios e a personalidade das fêmeas. As ninhadas em edifícios apresentaram maior sucesso devido a um efeito protetivo dos mesmos durante a fase de ovos. Nos edifícios, a temperatura interna dos ninhos permaneceu mais alta, de forma a compensar os recessos de incubação que as fêmeas realizam durante o dia. Como consequência, fêmeas de ninhos em edifícios apresentaram menor constância de incubação devido a recessos de incubação mais longos. Também encontrei que casais que permanecem juntos tiveram maior chance de reutilizar os ninhos e produziram mais filhotes. Os ninhos foram mais frequentemente reutilizados depois de uma ninhada de sucesso, especialmente dentro da mesma estação reprodutiva. A reutilização de ninhos, por sua vez, proporcionou economia de tempo no início da estação reprodutiva e diminuiu a chance de parasitismo da ninhada pelo chupim (Molothrus bonariensis). Por fim, a personalidade das fêmeas diferiu entre os tipos de suporte, com aquelas que nidificaram em edifícios sendo menos neofóbicas. Os resultados sugerem que casais que nidificam em edifícios tendem a apresentar maior aptidão em relação aos demais, tanto pela redução do investimento na incubação, quanto pela maior chance de sobrevivência da prole, essa última também ligada à maior chance de reutilização do ninho e suas vantagens. Ainda, a diferente personalidade das fêmeas que nidificam em edifícios indica que as vantagens da exploração deste recurso antrópico são dominadas por uma parcela específica da população. Assim, concluo que a nidificação em edifícios aumenta a performance reprodutiva do sabiá-barranco no ambiente urbano de múltiplas formas, contribuindo para a adaptação da espécie a esse contexto ambiental.

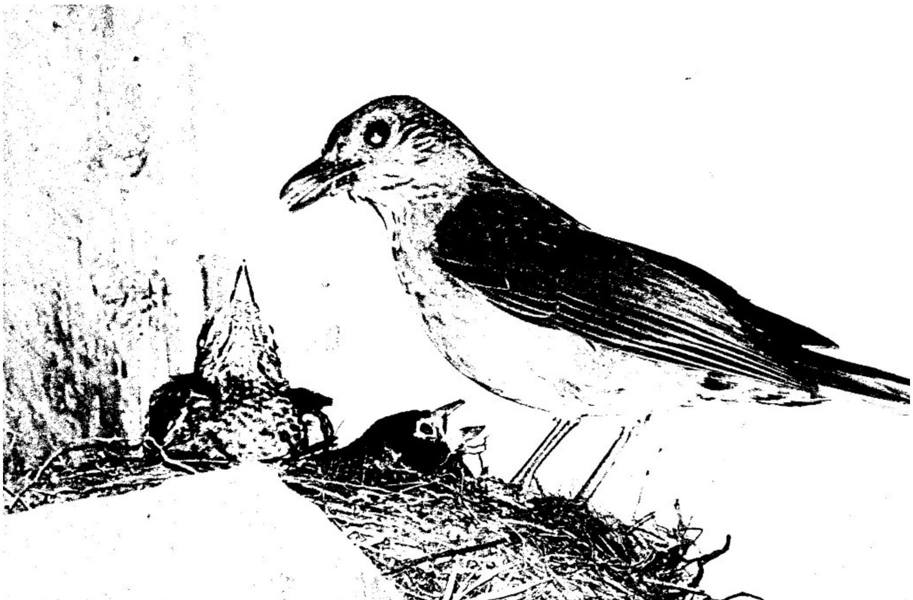
Palavras-chave: Ecologia comportamental, Neotrópico, plasticidade fenotípica, Turdidae, urbanização.

ABSTRACT

Reproduction is a crucial stage of the life cycle of all species, and the related energetic conflicts are especially important on species that present intense parental care, such as altricial birds. Nest site selection is directly linked to adult fitness by potentially minimizing the costs of offspring rearing and predation risk for both adults and young. However, the influence of anthropogenic environments on bird behavior and reproduction is still poorly known. Here, I address the effect of trees and buildings as nesting substrates on the incubation behavior and clutch survival in the Pale-breasted Thrush (Turdus leucomelas). I also assess the causes and consequences of mate change and nest reuse, and the relationship between the use of buildings as nesting substrates and female personality. Clutches on buildings had higher success due to a protective effect of buildings during the egg phase. The internal temperature of nests was higher on buildings, creating a compensatory effect for the incubation recesses took by females along the daytime. Consequently, females of nests on buildings showed lower nest attentiveness due to longer incubation recesses. I also found that pairs that stayed together had higher chance of nest reuse, and produced more fledglings. Nests were more often reused after a successful clutch, especially within the same breeding season. Nest reuse, in turn, enhanced earlier clutches at the beginning of the breeding season, and reduced the chance of brood parasitism by the Shiny Cowbird (Molothrus bonariensis). Finally, female personality differed between nesting support types, with those that nested on buildings were less neophobic. The results suggest that pairs that nest on buildings may have a higher fitness, by either lower incubation costs and higher clutch survival, the last also related to the increased chances of nest reuse and its advantages. Additionally, the difference on the personality of females that nested on buildings indicates that the advantages of exploiting that anthropogenic resource are dominated by a specific subset of the population. In conclusion, the use of buildings as nesting substrates increase the breeding performance of our study species in the urban environment in multiple ways, contributing to the adaptation of this species to this environmental context.

Keywords: Behavioral ecology, Neotropical, phenotypic plasticity, Turdidae, urbanization.

PREÂMBULO



PREÂMBULO

Esse estudo é um marco em um ciclo de curiosidade, fascínio, aprendizado, e gratidão que se iniciou há 33 anos. Os animais, em particular os passarinhos, fazem parte das minhas melhores lembranças de infância. Nessa época, ter uma gaiolinha de enfeite de 5 cm com um passarinho azul de pelúcia me tornava mais parecido com meu pai. Acompanhá-lo nas visitas aos demais criadores de pássaros era uma oportunidade muito aguardada, momento de contemplar belas formas, cores e cantos. Se meu pai sempre foi a faísca, minha mãe e meus tios foram um combustível infinito para uma paixão que reacende a todo bater de asas.

Desde o ensino médio, sempre soube onde queria estar e o que queria fazer no futuro, embora não soubesse muito bem como. Por isso, a graduação foi um grandioso desafio, com seus tropeços, como haveria de ser, porém, riquíssima em aprendizados. O fugaz mestrado foi decisivo para que eu conhecesse mais de perto as dificuldades e os prazeres de fazer pesquisa. O doutorado foi uma experiência única, um período intenso de trabalhos, descobertas, realizações e autoconhecimento, que passou mais rápido do que eu gostaria. Durante o doutoramento, tive o prazer de poder trabalhar com algo pelo qual sou apaixonado, e ainda descobrir novas paixões. Encerrar esse ciclo não me faz melhor que ninguém, apenas termino melhor que quando entrei. Descobri que o "como" não é o mais importante – na verdade, ainda estou descobrindo modos de fazer mais e melhor. E, mais do que nunca, não tenho vergonha de dizer "não sei, vamos estudar".

Nessa tese, está apresentada uma parte de tudo que pude documentar ao longo dos últimos quatro anos sobre a reprodução das aves em um ambiente urbano. A introdução geral aborda esse tema, fornecendo o contexto teórico necessário para a compreensão dos casos estudados. Os três capítulos que se seguem tratam da utilização de edifícios como locais para reprodução, suas consequências e das decisões comportamentais de duas populações urbanas de uma espécie de sabiá. A discussão geral conecta os resultados dos três capítulos e constrói um panorama sobre a possível abrangência dos resultados apresentados, os quais estão sintetizados na conclusão. Nos anexos I e II, apresento estudos desenvolvidos paralelamente durante o doutorado, relacionados ao tema da tese, abrangendo outras espécies no mesmo ambiente.

No primeiro capítulo, "*Anthropogenic nesting substrates increase brood survival in a Neotropical songbird*", abordei a sobrevivência das ninhadas, comparando ninhos em edifícios a ninhos em árvores, e testei se a frequência de cada tipo de suporte varia entre as fêmeas como uma preferência individual. No segundo capítulo, "*Buildings promote higher incubation temperatures and reduce nest attentiveness in a Neotropical thrush*", testei o efeito dos edifícios na temperatura interna dos ninhos e no comportamento de incubação das fêmeas. No terceiro capítulo, "*Causes and consequences of mate change and nest reuse in a Neotropical thrush*", investiguei as bases das decisões sobre a troca de parceiro e a reutilização de ninhos e seu efeito no sucesso reprodutivo. Por fim, no quarto capítulo, "*Female personality predicts the use of buildings as nesting sites*", testei se a personalidade das fêmeas que nidificam em edifícios difere daquelas que constroem seus ninhos em árvores.

Os resultados indicam benefícios do uso de edifícios como locais de nidificação por uma espécie de sabiá, do ponto de vista do sucesso reprodutivo e do investimento na prole, bem como a existência de longos vínculos entre os pares e uma maior chance de reutilização de ninhos após ninhadas de sucesso, e que fêmeas que nidificam em edifícios possuem personalidades distinta daquelas que constroem ninhos nas árvores. Juntos, esses efeitos sugerem que o uso de edifícios como locais de nidificação pode subsidiar a evolução do comportamento reprodutivo dessa e de outras espécies urbanas de hábitos similares.

INTRODUÇÃO GERAL

INTRODUÇÃO GERAL

CONTEXTUALIZAÇÃO

A ecologia comportamental, mais do que estudar o comportamento animal e suas bases fisiológicas, neurológicas e genéticas, investiga as causas de tais comportamentos, sejam causas imediatas ou evolutivas (Tinbergen 1963, Alcock 2005). Assim, é possível entender como determinados comportamentos passaram a ser um padrão dentro de um determinado grupo. Comportamentos herdáveis que aumentem a aptidão dos indivíduos, expressa na capacidade de deixar mais descendentes, devem ser favorecidos pelo mecanismo de seleção natural e consequentemente tornarem-se mais frequentes na população.

A reprodução é um processo crítico na história de vida das espécies animais, devido ao grande gasto energético envolvido em todas as suas fases, incluindo a busca por parceiros e/ou territórios e o investimento direto na prole (Ricklefs 2008). O chamado cuidado parental envolve uma série de comportamentos que aumentem a sobrevivência ou a qualidade da prole gerada (Alcock 2005). No entanto, tais comportamentos acarretam em prejuízos aos parentais, como piora da sua condição física, redução da fecundidade em eventos reprodutivos futuros e de sua expectativa de vida (Royle *et al.* 2012).

Os animais podem ser analisados sob um gradiente de variação entre dois extremos de investimento energético reprodutivo, marcado pelo antagonismo entre a alta fecundidade (número de descendentes a cada evento reprodutivo) e o cuidado parental intenso (Begon *et al.* 2006). Comparados a outros grupos animais, as aves são geralmente caracterizados por alto investimento no cuidado parental e, em contrapartida, uma prole relativamente pequena (Royle *et al.* 2012). Os ovos das aves constituem uma prole séssil e ectotérmica, sujeita a uma ampla gama de predadores especialistas e facultativos (Menezes & Marini 2017), o que exige grande esforço parental na transferência de calor e proteção da ninhada.

Entre as aves, temos dois grupos distintos com relação ao tipo de cuidado parental: espécies precoces e altriciais. Ao contrário das espécies precoces, nas quais os filhotes adquirem rapidamente a capacidade de locomoção, a prole das aves altriciais permanece no ninho até completar a maior parte de seu desenvolvimento corporal (Starck & Ricklefs 1998). Portanto, a seleção de um local adequado para a construção do ninho tem grande peso no sucesso reprodutivo das aves, especialmente nas altriciais, tanto do ponto de vista de um microclima favorável quanto da sobrevivência da prole e dos adultos associados aos ninhos (Martin 1993, Lima e Dill 1990).

A predação é considerada o mais importante fator de fracasso das ninhadas nas regiões tropicais (Skutch 1985). Para boa parte das espécies, a ação de parasitas de ninhada também incorre em diminuição do sucesso reprodutivo (e.g. Astié & Reboreda 2006, Borges & Marini 2010). Intempéries climáticas tem geralmente apenas uma modesta contribuição direta no fracasso dos ninhos, mas um microclima desfavorável pode resultar em um pior desempenho reprodutivo, aumentando o esforço parental e/ou diminuindo a qualidade da prole (Bryan & Bryant 1999, Mueller *et al.* 2019). Por meio da seleção do local de nidificação, os pais têm uma maior chance de contornar esses obstáculos ao sucesso da reprodução, bem como minimizar seu custo energético com a ninhada. Por exemplo, é esperado que as características dos locais selecionados propiciem a adultos e seus filhotes menores custos com termorregulação (Robertson *et al.* 2009) e com defesas passivas e ativas da ninhada (Cresswell 1997, Remeš 2005), além de menor risco de predação da prole (Young *et al.* 2017). Por isso, a seleção do local de nidificação é considerada uma resposta adaptativa às pressões ambientais, particularmente ao risco de predação (Mezquida & Marone 2002, Barrientos *et al.* 2009).

Os parâmetros de seleção do local de nidificação tendem a ser evolutivamente selecionados e mantidos dentro das linhagens de aves (Martin & Roper 1988, Brightsmith 2005), de forma que cada táxon pode ser relacionado a um local típico de nidificação. Essas preferências poder ser transmitidas verticalmente, tanto pela herdabilidade quanto pelo *imprinting* dos filhotes durante a fase de ninhegos, e horizontalmente, por meio da aquisição social pela cognição (Slagsvold *et al.* 2013). Por outro lado, os indivíduos podem apresentar flexibilidade em relação às preferências do local de construção do ninho, fruto de variações individuais e ontogenéticas, valendo-se de informações acumuladas em experiências anteriores (Lima e Dill 1990, Styrsky *et al.* 2005). Dessa forma, os indivíduos podem responder mais rapidamente (i.e. no tempo ecológico, não no evolutivo) às mudanças nas principais pressões ambientais sobre seu sucesso reprodutivo (Lima 2009).

Apesar de seu componente filogenético, e de ser uma resposta relativamente rápida às pressões ambientais, a seleção do local para nidificação é um processo complexo e multidirecional, porque as possíveis vantagens que o local do ninho pode proporcionar podem ser conflitantes em determinados contextos. Por exemplo, em ninhos extremamente encobertos pela vegetação, as proles estão mais protegidas de predadores visualmente orientados; o adulto, porém, tem menor visibilidade do entorno, o que prejudica sua capacidade de reagir antecipadamente a uma ameaça (Gómez-Serrano & López-López 2014). Da mesma forma, os locais de microclima mais favorável à construção do ninho podem ser mais vulneráveis à predação dos adultos ou da prole, quando a cobertura visual em torno do ninho impede a exposição demasiada ao sol, mas também prejudica a capacidade de o adulto reagir antecipadamente a predadores (Amat & Masero 2004). Por isso, a seleção do local de nidificação tende a um ponto de equilíbrio entre diversas pressões, as quais são fortemente dependentes do contexto ambiental (Forstmeier & Weiss 2004, Lomáscolo *et al.* 2010, Ibáñez-Álamo & Soler 2010).

A ocupação de novos ambientes pelas espécies de aves pode implicar em adaptações dos padrões de comportamento das espécies. Distúrbios antrópicos podem ser considerados como recentes na escala do tempo evolutivo e, de forma geral, induzem adaptações no comportamento reprodutivo de aves em relação ao cuidado parental e à seleção do sítio de nidificação (Yeh *et al.* 2007, Lomáscolo *et al.* 2010, Hanane *et al.* 2014, Mccarthy & Destefano 2011). Por exemplo, o uso de material e de substratos de origem antrópica na construção do ninho facilitam a reprodução e o estabelecimento de populações em áreas urbanas (Wang *et al.* 2009, 2015).

A CONQUISTA DO AMBIENTE URBANO E SEUS DESDOBRAMENTOS

A urbanização é uma das principais causas de conversão dos habitats naturais (Hahs *et al.* 2009), alterando de forma drástica e permanente os ecossistemas. Atualmente, 55,3% da população mundial vive em cidades, e esse percentual deve aumentar cerca de 23% em 30 anos, chegando a 68,4% em 2050 (Organização das Nações Unidas 2019). Como resultado de suas mudanças profundas na estrutura do ambiente, a urbanização cria uma barreira de permeabilidade seletiva às espécies, dependendo de seus traços funcionais (Croci *et al.* 2008). De acordo com seu grau de tolerância ao ambiente urbano, as espécies podem ser inicialmente consideradas nas categorias evitadora (“avoider”), usuária (“utilizer”) ou habitante (“dweller”) (Fischer et al. 2015). No entanto, essas categorias descrevem apenas de forma superficial as possíveis relações entre as espécies de aves e o meio urbano, uma vez que elas podem apresentar diferenças graduais quanto ao uso de recursos antropogênicos, como fontes de alimento, materiais para ninho e locais para nidificação (Kark *et al.* 2007, Galbraith *et al.* 2017, Batisteli *et al.* 2019).

Além de afetar negativamente a biodiversidade, criando um filtro ambiental, a urbanização também induz alterações no comportamento das espécies (Ditchkoff *et al.* 2006). O processo pelo qual as espécies desenvolvem sua tolerância ao ambiente urbano pode ser explicado por dois mecanismos não-excludentes: 1) linhagens urbanas podem ter se consolidado por seleção disruptiva, pela seleção dos fenótipos mais adaptados às pressões ambientais. Esse processo é evidenciado em outros grupos animais, como mariposas (Altermatt & Ebert 2016); alternativamente, 2) indivíduos podem se adaptar às alterações nas condições ambientais ao longo de suas vidas pela plasticidade de comportamento (Robertson & Olsen 2015). Embora ambos esses mecanismos possam contribuir efetivamente para a evolução de linhagens urbanas, há crescentes evidências de que a urbanização atua como filtro não apenas a nível de espécie, mas propicia maior sucesso para determinadas variantes morfológicas e comportamentais (Miranda *et al.* 2013, Samia *et al.* 2015, Lapiedra *et al.* 2017).

As decisões comportamentais buscam maximizar os retornos obtidos e minimizar os custos e riscos envolvidos em uma determinada situação (Alcock 2005). Além de dependerem do estado fisiológico e do contexto ambiental (Verdolin 2006, Moiron *et al.* 2019), essas decisões estão sujeitas à personalidade do indivíduo, as quais estabelecem patamares de resposta em situações de mesma natureza (Wolf & Weissing 2012). No entanto, ao contrário de alterações comportamentais nas decisões por conta de estímulos positivos ou negativos, as decisões pautadas pela personalidade são consistentes ao longo do tempo (Castanheira *et al.* 2013). Como consequência, dentro de uma mesma população, há indivíduos com personalidades bastante diferentes com relação, por exemplo, ao nível de agressividade contra coespecíficos, ou coragem frente a ameaças e situações novas (Wilson *et al.* 1993, Evans *et al.* 2010, Lapiedra *et al.* 2017). A coexistência desses diferentes fenótipos em uma população é garantida principalmente pelas variações nas pressões ambientais no espaço-tempo, as quais favorecem ora um, ora outro extremo de personalidade, como previsto pela teoria dos jogos (Smith & Price 1973, Niemelä *et al.* 2012). No entanto, alterações profundas e permanentes na estrutura dos habitats, como a urbanização, podem criar um direcionamento na seleção de determinadas personalidades capazes de lidar melhor com os riscos e recursos encontrados em ambientes antrópicos (Sol *et al.* 2011, Samia *et al.* 2015).

Portanto, a reprodução das aves em novos contextos ambientais, como o ambiente urbano, pode alterar os pontos de equilíbrio das demandas conflitantes do comportamento parental, levando a padrões comportamentais alternativos (Knight *et al.* 1987, Kunca &

Yosef 2016). Diversos estudos avaliam o desempenho reprodutivo e o comportamento das aves ao longo de gradientes (ou de extremos) de urbanização (veja as revisões de Vincze *et al.* 2017, Kettel *et al.* 2018, Reynolds *et al.* 2019). No entanto, relativamente poucos estudos avaliam, dentro de um mesmo grau de urbanização, o valor adaptativo das escolhas relacionadas ao local de construção do ninho (e.g. Møller 2010, Sumasgutner *et al.* 2014, Mainwaring 2015, da Silva *et al.* 2018), especialmente seus desdobramentos no comportamento parental das espécies (Knight *et al.* 1987, Kunca & Yosef 2016).

CARACTERIZAÇÃO DA ESPÉCIE

O gênero *Turdus* (Passeriformes, Turdidae) tem ampla distribuição geográfica, possuindo 65 espécies distribuídas na Europa, Ásia, América, África e Oceania (Collar 2005), das quais 26 ocorrem na região Neotropical (SACC 2015). Alimentam-se de frutos e invertebrados, especialmente artrópodes e minhocas, e as fêmeas constroem ninhos abertos utilizando plantas ou edificações humanas como suporte (Davanço *et al.* 2013, Wang *et al.* 2015). O sabiá-barranco *Turdus leucomelas* (Vieillot 1818) é uma espécie neotropical de tamanho mediano (~22 cm) que habita ambientes variados (Sick 2001), podendo, como outras espécies do gênero, ocorrer em regiões urbanizadas (Davanço *et al.* 2013, Wang *et al.* 2015). A reprodução ocorre entre agosto e janeiro, com 1 a 4 ovos por ninhada, e os períodos de incubação e permanência dos filhotes no ninho são, respectivamente, 12 a 15 dias e 13 a 18 dias (Davanço *et al.* 2013). O ninho do sabiá-barranco é constituído de fibras vegetais assentadas com barro e mede aproximadamente 13.2 × 10.2 cm (diâmetro externo × altura externa; Ruiz *et al.* 2017) (Fig. 1). A exemplo de outras espécies do gênero (Lichtenstein 2001, Astié & Reboreda 2006), o sabiá-barranco também é hospedeiro do parasita de ninhadas chupim (*Molothrus bonariensis* Gmelin 1789).

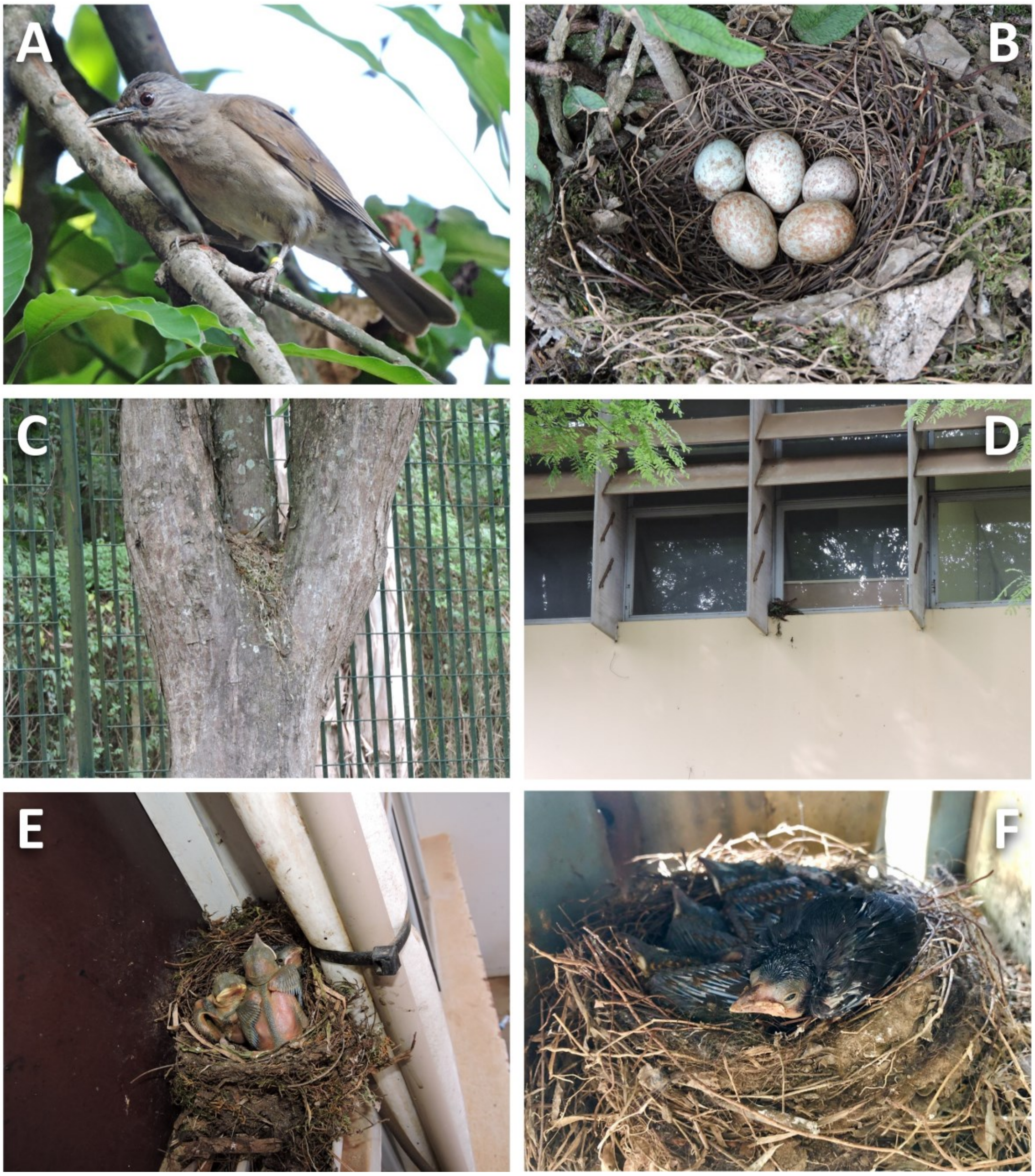


Fig. 1 Ninhos e ovos do sabiá-barranco (*Turdus leucomelas*) e do parasita de ninhadas chupim (*Molothrus bonariensis*). Sabiá-barranco adulto (A); Ninho com ovos de sabiá e de chupim (B); Ninho de sabiá em árvore (C) e na janela de um edifício (D); Ninho com dois ninhegos de sabiá e um de chupim (E); Ninho com três ninhegos de sabiá e um de chupim, em primeiro plano (F).

OBJETIVOS

Este estudo tem como objetivo investigar o comportamento reprodutivo do sabiá-barranco *Turdus leucomelas* (Vieillot, 1818) no meio urbano, sobretudo com relação à utilização de suportes antropogênicos para construção do ninho, seu valor adaptativo e seus desdobramentos na ecologia comportamental.

OBJETIVOS ESPECÍFICOS

Os objetivos específicos desse estudo são:

1- Testar se o uso de edifícios ao invés de árvores como substrato favorece a sobrevivência das ninhadas de sabiá-barranco, considerando separadamente as fases de ovos e de ninhegos.

2- Avaliar a variação da temperatura e o comportamento de incubação das fêmeas em ninhos localizados em edifícios e em árvores.

3- Investigar as causas e consequências da troca de parceiros e da reutilização de ninhos pelo sabiá-barranco.

4- Avaliar a relação entre o local de nidificação e a personalidades das fêmeas.

HIPÓTESES

No contexto dos objetivos, nós hipotetizamos que:

1- A sobrevivência da ninhada é maior em ninhos localizados em edifícios, devido à proximidade com elementos antropogênicos que funcionam como barreiras, dificultando a localização e o acesso de predadores aos mesmos.

2- Os ninhos em edifícios apresentam diferenças no regime de variação de sua temperatura interna, o que deve afetar o comportamento de incubação das fêmeas.

3- Casais que permanecem juntos tem maior sucesso reprodutivo devido, por exemplo, a uma maior sincronização das tarefas reprodutivas e que o sucesso da ninhada, por sua vez, aumenta a chance de reutilização do ninho dado o aspecto cognitivo dos parentais, que buscam a seleção de um local seguro para a reprodução.

4- Fêmeas que ocupam edifícios como local de nidificação tem personalidade distinta daquelas que nidificam em árvores, uma vez que, para estabelecerem-se nesses locais alternativos de nidificação, elas devem enfrentar rotineiramente situações desconhecidas inerentes à atividade humana.

REFERÊNCIAS

Alcock, J. (2005). *Animal behavior: an evolutionary approach*. Sinaeur Associates. Inc., Sunderland, Massachusetts.

Altermatt, F., & Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology letters*, *12*(4), 20160111.

Amat, J. A., & Masero, J. A. (2004). Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour*, 67(2), 293–300.

Astié, A. A., & Reboreda, J. C. (2006). Costs of egg punctures and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) at Creamy-bellied Thrush (*Turdus amaurochalinus*) nests. *The Auk*, 123(1), 23–32.

Barrientos, R., Valera, F., Barbosa, A., Carrillo, C. M., & Moreno, E. (2009). Plasticity of nest-site selection in the trumpeter finch: A comparison between two different habitats. *Acta Oecologica*, 35(4), 499–506.

Batisteli, A. F., Guilhermo-Ferreira, R., & Sarmento, H. (2019). Abundance and prevalence of plastic twine in nests of Neotropical farmland birds. *The Wilson Journal of Ornithology*, 131(1), 201-205.

Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology. From Individuals to Ecosystems*. Blackwell Publishing. MA, USA.

Borges, F. J. A., & Marini, M. Â. (2010). Birds nesting survival in disturbed and protected Neotropical savannas. *Biodiversity and Conservation*, 19(1), 223–236.

Brightsmith, D. J. (2005). Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes). *Journal of Avian Biology*, 36(1), 64–73.

Bryan, S. M., & Bryant, D. M. (1999). Heating nest–boxes reveals an energetic contraint on incubation behaviour in great tits, *Parus major*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1415), 157–162.

Castanheira, M. F., Herrera, M., Costas, B., Conceição, L. E., & Martins, C. I. (2013). Can we predict personality in fish? Searching for consistency over time and across contexts. *PLoS One*, 8(4), e62037.

Collar, N. J. (2005). Family Turdidae (thrushes). In del Hoyo J., Elliot A., and Sargatal J., eds. *Handbook of the birds of the world*. Pp. 514–807.

Cresswell, W. (1997). Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Animal Behaviour*, 53(1), 93–103.

Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits. *The Condor*, 110(2), 223–240.

da Silva, T. L., Cabral, R. B. G., Andrade, L. D. A. S., Nogueira, N. F., Oliveira, p+M. D. S., & Ferreira, I. (2018). Comparison of breeding biology aspects of *Fluvicola nengeta* (Aves: Tyrannidae) between two nesting sites. *Journal of Natural History*, 52(3–4), 225-235.

Davanço, P. V., Oliveira, L. S., Sousa, L. M., & Francisco, M. R. (2013). Breeding life-history traits of the Pale-breasted Thrush (*Turdus leucomelas*) in southeastern Brazil. *Ornitologia Neotropical*, 24, 401-411.

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban ecosystems*, 9(1), 5–12.

Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, 116(7), 588-595.

Fischer, J. D., Schneider, S. C., Ahlers, A. A., & Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology. Conservation Biology, 29(4), 1246-1248.

Forstmeier, W., & Weiss, I. (2004). Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, 104(3), 487–499.

Galbraith, J. A., Jones, D. N., Beggs, J. R., Parry, K., & Stanley, M. C. (2017). Urban bird feeders dominated by a few species and individuals. *Frontiers in Ecology and Evolution*, 5, 81.

Gómez-Serrano, M. Á., & López-López, P. (2014). Nest site selection by Kentish Plover suggests a trade-off between nest-crypsis and predator detection strategies. *PLoS One*, 9(9).

Hahs, A. K., McDonnell, M. J., McCarthy, M. A., Vesk, P. A., Corlett, R. T., Norton, B. A., ... & Williams, N. S. (2009). A global synthesis of plant extinction rates in urban areas. *Ecology letters*, 12(11), 1165–1173.

Hanane, S. (2014). Effects of human disturbance on nest placement of the woodpigeon (*Columba palumbus*): a case study from the Middle Atlas, Morocco. *Integrative Zoology*, 9(3), 349-359.

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: can anyone become an ‘urban exploiter'? *Journal of Biogeography*, 34(4), 638–651.

Kettel, E. F., Gentle, L. K., Quinn, J. L., & Yarnell, R. W. (2018). The breeding performance of raptors in urban landscapes: a review and meta-analysis. *Journal of Ornithology*, 159(1), 1–18.

Knight, R. L., Grout, D. J., & Temple, S. A. (1987). Nest-defense behavior of the American crow in urban and rural areas. *The Condor,* 89(1), 175–177.

Kunca, T., & Yosef, R. (2016). Differential nest-defense to perceived danger in urban and rural areas by female Eurasian sparrowhawk (*Accipiter nisus*). *PeerJ*, 4, e2070.

Lapiedra, O., Chejanovski, Z., & Kolbe, J. J. (2017). Urbanization and biological invasion shape animal personalities. *Global Change Biology*, 23(2), 592-603.

Lichtenstein, G. (2001). Low success of shiny cowbird chicks parasitizing rufous-bellied thrushes: chick–chick competition or parental discrimination? *Animal Behaviour*, 61(2), 401-413.

Lima, S. L. (2009). Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, 84(3), 485–513.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640.

Lomáscolo, S. B., Monmany, A. C., Malizia, A., & Martin, T. E. (2010). Flexibility in nest-site choice and nesting success of *Turdus rufiventris* (Turdidae) in a montane forest in northwestern Argentina. *The Wilson Journal of Ornithology*, 122(4), 674–680.

Mainwaring, M. C. (2015). The use of man-made structures as nesting sites by birds: A review of the costs and benefits. *Journal for Nature Conservation*, 25, 17–22.

Martin, T. E. (1993). Nest predation and nest sites. *BioScience*, 43(8), 523–532.

Martin, T. E., & Roper, J. J. (1988). Nest predation and nest-site selection of a western population of the Hermit Thrush. *The Condor, 90(1*), 51–57.

Mccarthy, K. P., & Destefano, S. (2011). Effects of spatial disturbance on common loon nest site selection and territory success. *The Journal of Wildlife Management*, 75(2), 289–296.

Menezes, J. C., & Marini, M. Â. (2017). Predators of bird nests in the Neotropics: a review. *Journal of Field Ornithology*, 88(2), 99–114.

Mezquida, E. T., & Marone, L. (2002). Microhabitat structure and avian nest predation risk in an open Argentinean woodland: an experimental study. *Acta Oecologica*, 23(5), 313-320.

Moiron, M., Araya-Ajoy, Y. G., Mathot, K. J., Mouchet, A., & Dingemanse, N. J. (2019). Functional relations between body mass and risk-taking behavior in wild great tits. *Behavioral Ecology*, 30(3), 617-623.

Møller, A. P. (2010). The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behavioral Ecology*, *21*(5), 913–918.

Mueller, A. J., Miller, K. D., & Bowers, E. K. (2019). Nest microclimate during incubation affects posthatching development and parental care in wild birds. *Scientific Reports*, 9(1), 1–11.

Niemelä, P. T., Vainikka, A., Forsman, J. T., Loukola, O. J., & Kortet, R. (2013). How does variation in the environment and individual cognition explain the existence of consistent behavioral differences? *Ecology and Evolution*, 3(2), 457-464.

Organização das Nações Unidas, Departamento de Assuntos Econômicos e Sociais. (2019). *World Urbanization Prospects: The 2018 Revision* (ST/ESA/SER.A/420). New York: United Nations.

Remeš, V. (2005). Nest concealment and parental behaviour interact in affecting nest survival in the blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behavioral Ecology and Sociobiology*, 58(3), 326–332.

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P., & Mainwaring, M. C. (2019). Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology*, 160, 841-860.

Ricklefs, R. E. (2008). *The economy of nature*. Macmillan.

Robertson, B. A. (2009). Nest-site selection in a postfire landscape: do parents make tradeoffs between microclimate and predation risk?. *The Auk*, 126(3), 500–510.

Robertson, E. P., & Olsen, B. J. (2015). Behavioral plasticity in nest building increases fecundity in marsh birds. *The Auk: Ornithological Advances*, 132(1), 37–45.

Royle, N. J., Smiseth, P. T., & Kölliker, M. (2012). *The evolution of parental care*. Oxford University Press.

Ruiz, N. L., Araújo, P., Lima, J., Ferreira, P., Andrade, L., & Pichorim, M. (2017). Breeding biology of Pale-breasted Thrush *Turdus leucomelas* (Turdidae) in the north of Atlantic Forest, Brazil. *Revista Brasileira de Ornitologia*, 25(2), 110-121.

SACC 2015. A classification of the bird species of South America. Consultado online em 12 de Abril de 2017. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm

Samia, D. S., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, 6, 8877.

Sick, H. (2001). *Ornitologia Brasileira*. Nova Fronteira, Rio de Janeiro, Brazil.

Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs*, 36, 575-594.

Slagsvold, T., Kleiven, K. W., Eriksen, A., & Johannessen, L. E. (2013). Vertical and horizontal transmission of nest site preferences in titmice. *Animal Behaviour*, 85(2), 323–328.

Smith, J. M., & Price, G. R. (1973). The logic of animal conflict. *Nature*, 246(5427), 15-18.

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS One*, 6(5).

Starck, J. M., & Ricklefs, R. E. (1998). Patterns of development: the altricial-precocial spectrum. *Oxford Ornithology Series*, 8, 3-30.

Styrsky, J. N. (2005). Influence of predation on nest-site reuse by an open-cup nesting neotropical passerine. *The Condor*, 107(1), 133-137.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H. W., & Gamauf, A. (2014). Hard times in the city–attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Frontiers in Zoology*, 11(1), 48.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für tierpsychologie*, 20(4), 410–433.

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, 60(4), 457-464.

Vincze, E., Seress, G., Lagisz, M., Nakagawa, S., Dingemanse, N. J., & Sprau, P. (2017). Does urbanization affect predation of bird nests? A meta-analysis. *Frontiers in Ecology and Evolution*, 5, 29.

Wang, Y., Chen, S., Blair, R. B., Jiang, P., & Ding, P. (2009). Nest composition adjustments by Chinese Bulbuls *Pycnonotus sinensis* in an urbanized landscape of Hangzhou (E China). *Acta Ornithologica*, 44(2), 185–192.

Wang, Y., Huang, Q., Lan, S., Zhang, Q., & Chen, S. (2015). Common blackbirds *Turdus merula* use anthropogenic structures as nesting sites in an urbanized landscape. *Current Zoology*, 61(3), 435–443.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107(3), 250.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452-461.

Yeh, P. J., Hauber, M. E., & Price, T. D. (2007). Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos*, 116(9), 1473–1480.

Young, C. M., Cain, K. E., Svedin, N., Backwell, P. R., & Pryke, S. R. (2017). Nesting success in crimson finches: chance or choice? *Ethology*, 123(1), 41–50.

Capítulo 1

ANTHROPOGENIC NESTING SUBSTRATES INCREASE BROOD SURVIVAL IN A NEOTROPICAL SONGBIRD

ANTHROPOGENIC NESTING SUBSTRATES INCREASE BROOD SURVIVAL IN A NEOTROPICAL SONGBIRD

ABSTRACT

Nest failure is a major obstacle to bird reproduction resulting in nest site choice being usually under strong selective pressure. Urban areas may offer safer nesting opportunities compared with non-urban areas, but the effect of anthropogenic structures as nesting sites on parental fitness is seldom studied. We studied the effect of anthropogenic substrates (hereafter "buildings") on nesting success of a Neotropical songbird, the Pale-breasted Thrush (*Turdus leucomelas*) using as covariates year and brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*). We also tested whether the prevalence of buildings as nesting substrates vary among females. We monitored 212 nests between 2010 and 2018, of which 86.3% were in buildings and 13.7% in plants. Apparent nest success (i.e., the percentage of nests that fledged at least one chick) was higher in buildings (55.2%) than in plants (34.5%). Egg success (survival from egg to fledgling) and hatching success (from egg to hatchling) were greater for nests in buildings, whereas fledging success (from hatching to fledgling) was not affected by nesting substrate type. Egg success, hatching success and fledging success decreased through study years and were not affected by cowbird parasitism. The frequency of buildings as nesting substrates differed among females. We highlight that nesting in buildings increases parental fitness in our study population, and that the repeatability of this choice suggests that some females accrue associated benefits more often than others do, favoring their settlement in urban areas and potentially driving the evolution of this breeding behavior.

Keywords: Behavioral ecology, Brazil, nest success, *Turdus*, urban ecosystem

RESUMO

Substratos de nidificação antropogênicos aumentam a sobrevivência da ninhada em um pássaro neotropical – O fracasso dos ninhos é um grande obstáculo à reprodução das aves, o que cria grande pressão de seleção sobre a escolha do local do ninho. Áreas urbanas podem oferecer oportunidades seguras de reprodução comparadas a áreas não urbanas, mas o efeito de estruturas antropogências como local de nidificação na aptidão dos parentais é pouco estudado. Nós estudamos o efeito de substratos antropogênicos (de agora em diante "edifícios") no sucesso de reprodução em um pássaro Neotropical, o sabiá-barranco (Turdus leucomelas), usando como covariáveis o ano e o parasitismo de ninhada pelo chupim (Molothrus bonariensis). Também testamos se a frequência do uso de edifícios como local de nidificação varia entre as fêmeas. Nós monitoramos 212 ninhos entre 2010 e 2018, dos quais 86,3% estavam em edifícios e 13,7% em plantas. O sucesso aparente dos ninhos (i.e., a porcentagem de ninhos em que ao menos um filhote sobreviveu até deixar o ninho) foi mais alta em edifícios (55,2%) que em plantas (34,5%). O sucesso dos ovos (porcentagem dos ovos que originaram filhotes que sobreviveram até abandonar o ninho) e o sucesso de eclosão (sobrevivência do ovo até a eclosão) foram maiores em edifícios, enquanto o sucesso dos ninhegos (sobrevivência entre a eclosão e o momento de abandonar o ninho) não foi afetado pelo tipo de substrato do ninho. O sucesso dos ovos, de eclosão e dos ninhegos decresceram ao longo dos anos de estudo, e não foram afetados pelo parasitismo por chupim. A frequência do uso de edifícios como local de nidificação diferiu entre as fêmeas. Nós destacamos que a nidificação em edifícios aumenta a aptidão dos parentais na população estudada, e que a repetibilidade dessa escolha sugere que algumas fêmeas acumulam esses benefícios mais do que outras, favorecendo o estabelecimento delas em áreas urbanas e potencialmente dirigindo a evolução desse comportamento reprodutivo.

Palavras-chave: Brazil, ecologia comportamental, ecossistemas urbanos, sucesso de ninhos, *Turdus*

INTRODUCTION

Nest failure is a major determinant of avian breeding performance (Martin 1993). Thus, behavioral traits that enhance brood survival are generally under strong selective pressure. For instance, parents actively select the site of nest construction to maximize their reproductive success (Ardia *et al.* 2006, Camprodon *et al.* 2008). Nest site can affect parental fitness in several ways, such as promoting an adequate microclimate for incubation and chick development (Ardia *et al.* 2006), reducing the predation risk of the incubating adult and its clutch (Gómez-Serrano & López-López 2014), and the chance of brood parasitism (Fiorini *et al.* 2009). Nest site preferences vary among species. While birds of some species rely on one or a few plant species to support their nests (Aguilar *et al.* 2008, Rovedder & Fontana 2012), others use a variety of plant species and even man-made structures as nesting substrates (de Oliveira *et al.* 2010, Wang *et al.* 2015). However, several studies have failed to find a clear relationship between nest site features and offspring survival because it depends on morphological and behavioral traits of each species, and the main causes of nest failure at a local scale, for instance, clutch predation, brood parasitism and starvation (Weidinger 2002, Borgmann & Conway 2015).

Predation is the commonest cause of nest failure and the list of potential nest predators comprises several groups of reptiles, mammals, and birds, which differ from each other in their habits, nest-searching behavior, and cognitive abilities (Menezes & Marini 2017). Nest placement determine the accessibility of nests to different guilds of predators, such as aerial/terrestrial and visually/olfactorily-oriented predators (Colombelli-Négrel & Kleindorfer 2009). Thus, depending on the predominant nest predators of a given locality, birds can alter their nest site preferences to reduce predation risk (Hanane 2014). Brood parasitism is another important cause of hatching failure and nestling mortality, for instance, by food competition with host chicks (Massoni & Reboreda 2002, Kilner 2003). Hatching failure caused by brood parasitic birds involves egg puncturing during nest inspections, heat competition with host eggs, and damage to host eggs caused by the thick shell of parasite eggs (Tuero *et al.* 2007, López *et al.* 2018). The relative importance of these and other factors that account for clutch failure vary broadly among species, nest phases, and ecological contexts (Stanley 2000, Okada *et al.* 2017).

Clutch survival rates in human-modified environments are variable, so that some studies reported urban areas as "safe nesting zones" because of high nesting success

(Gering & Blair 1999, Ibáñez-Álamo & Soler 2010), whereas others showed that urbanization increases nesting failure (Jokimäki & Huhta 2000). Furthermore, nesting success varies broadly between and within urban areas (e.g., López-Flores *et al.* 2009, Rivera-López & MacGregor-Fors 2016) depending on the local main nest predators, which can differ among regions and across urbanization gradients (Jokimäki *et al.* 2005, Rodewald & Kearns 2011). Similarly, the incidence of brood parasitism is affected by anthropogenic land uses (Chace *et al.* 2003, Burhans & Thompson 2006), and on a smaller scale by nest site (Moskát & Honza 2000, Saunders *et al.* 2003, Fiorini *et al.* 2009). Nevertheless, there are relatively few studies showing how nest site choices influence the patterns of clutch survival and brood parasitism in urban areas (e.g., Borgmann & Rodewald 2004, Muñoz *et al.* 2008, Mikula *et al.* 2014).

The typical nest site features of conspecifics or close-related species are shaped by natural selection in response to the main drivers of nesting success and adult survival (Nilsson 1984, Gómez-Serrano & López-López 2014), but nest placement is somewhat flexible so that individuals can exert their own choices under those evolutive constraints (Lomáscolo *et al.* 2010, Mainwaring 2017). Once a given choice increases parental fitness, it tends to spread within the population (Møller 2010, 2017), by either genetic inheritance or social learning (Slagsvold *et al.* 2013). In this sense, the differences in nest site preference among individuals allows population-level responses to environmental variations, enhancing the colonization of new areas (Yeh 2007, Lomáscolo *et al.* 2010). There is also evidence that the result of previous breeding attempts by individuals affects the choice of future nesting sites, but the role of cognition in managing clutch predation risk by changing nest site preferences has barely been explored in general (e.g., Eggers *et al.* 2005, Chen *et al.* 2011, Beckman *et al.* 2016). Long-term studies that could address the repeatability of nest site choices at individual level are rare too (e.g., Öst & Steele 2010).

Some bird species are considered urban dwellers, being able to use a variety of anthropogenic resources, such as food and nesting sites (Fischer *et al.* 2015, Wang *et al.* 2015). The use of man-made structures in nesting is widespread among birds (Tella *et al.* 2014, Dwyer & Rosa 2015, Wang *et al.* 2015, Pizo 2018, Reynolds *et al.* 2019), but the impacts of the use of such nesting sites on individual fitness have been rarely estimated, and with controversial findings (Mainwaring 2015). For instance, the use of anthropogenic nesting substrates and indoor breeding may increase nest survival (Møller 2010, da Silva *et al.* 2018, but see Muñoz *et al.* 2008), while nest proximity to human habitations and indoor nests reduce the chance of brood parasitism (Liang *et al.* 2013, Møller et al. 2016). However, anthropogenic nesting substrates may act as ecological traps (Schlaepfer & Sherman 2002) by decreasing the breeding performance of birds (Sumasgutner *et al.* 2014).

In this study, we assessed the effect of nesting substrate (natural versus anthropogenic) and brood parasitism on the nesting success of a neotropical songbird, the Pale-breasted Thrush (*Turdus leucomelas* Vieillot 1818) in an urban area of southeastern Brazil, and tested whether the frequency of nest substrate type use vary among females. We predicted that a) breeding success in nests placed on anthropogenic substrates would be greater due to the protective effect of man-made structures, reducing nest detectability and nest accessibility for both aerial and terrestrial (climbing) predators and brood parasitic birds, and b) the frequency of anthropogenic nesting substrates use should differ among females because of individual nest site preferences.

MATERIAL AND METHODS

Study area

This study was carried out on the campus of the Universidade Estadual Júlio de Mesquita Filho (UNESP), in Rio Claro municipality, São Paulo state, Brazil (22º23’43”S, 47º32’46”W, 628 m a.s.l). The regional climate is humid subtropical with dry winters and hot summers (Cwa) according to Köppen classification, with mean monthly temperature varying from 16.5ºC to 23ºC, and annual rainfall of approximately 1,344 mm (Alvares *et al.* 2013). The campus is a well-arborized periurban area with remnants of riparian native vegetation. The urbanized portion of the campus (ca. 50 ha out of 115.5 ha) has 198 plant species of which 60% are native from the Atlantic Forest (Potascheff *et al.* 2010).

Study species

The Pale-breasted Thrush occurs from northern South America to Paraguay and Argentina, inhabiting riparian forests to urbanized areas (Collar & Garcia 2016). Breeding season ranges from August to late December, and a single female can have up to three breeding attempts a year (Davanço *et al.* 2013). Only the female builds the nest and incubates the eggs, while both parents rear the chicks (Davanço *et al.* 2013). In the study area, clutch size is usually three eggs, with incubation and nestling phases lasting

12 and 15 days, respectively (MAP, unpubl. data). The potential predators of eggs and nestlings in the study area are birds, such as raptors (*Caracara planchus*, *Milvago chimachima*, *Rupornis magnirostris*, and *Ictinia plumbea*), owls (*Athene cunicularia*, *Tyto furcata*, and *Megaschops choliba*), the Toco Toucan (*Ramphastos toco*), and jays (*Cyanocorax cristatellus* and *Cyanocorax chrysops*), besides mammals, such as opossums (*Didelphis albiventris*), rodents (*Mus musculus* and *Rattus* spp.), and domestic cats (*Felis catus*). Similar to other Neotropical thrushes, the Pale-breasted Thrush is parasitized by the Shiny Cowbird (*Molothrus bonariensis* Gmelin 1789). Although cowbirds rarely remove host eggs, they usually puncture host eggs either during the laying or in following visits to parasitized and unparasitized nests, thus being treated as a potential predator of host eggs (Massoni & Reboreda 2002).

Field procedures

We monitored nests during nine breeding seasons (2010–2018) by active search and following adults carrying nesting material or food to the nestlings. We checked the nests using a pole with a mirror every 1–3 days to determine the nest status and content (the number of eggs or nestlings), hatching date, and nest fate. We classified each nest support as natural (plants) or anthropogenic, i.e., man-made structures such as roofs, walls, windows, air conditioners, concrete columns and other structures belonging to buildings. During the same years of nest searching and monitoring, we continuously captured birds with mist nets in random sites within the urban area of the campus, marking every captured bird with a metallic ring and a unique combination of colored plastic bands. Since adults are monomorphic, we collected blood samples from the toenail clip method (Owen 2011), and breeding birds were sexed by an outsourced laboratory (Unigen – Biologia pelo DNA, São Paulo) using PCR methodology. We recorded no nest abandonment immediately after the capture of breeding adults. Nests attended by unbanded females were included to estimate nesting success, but excluded from other statistical analyses.

Statistical analyses

We estimated apparent nesting success from the ratio between successful nests (i.e., nests that produced at least one fledgling) and the total number of nests monitored. Since nest reuse is higher in our study population, we used a generalized linear-mixed model (GLMM) to test whether the frequency of brood parasitism as a binary response variable differed between nesting substrate types, setting nest identity as a random factor. We calculated daily survival rates (DSR) according to Mayfield (1961), which consider the number of failed nests in an interval of *n* nest exposure days (i.e. four nests exposed during ten days = 40 exposure days), through the equation DSR = 1 - [depredated nests / exposure days]. We then tested whether the DSR differed between incubation and nestling phases following Hensler & Nichols (1981). This method confronts the critical z-value at a given α to the z-value from

$$\mathrm{z} = \frac{|\mathrm{DSR}_{\mathrm{incubation}} - \mathrm{S}^2_{\mathrm{incubation}}|}{\sqrt{\mathrm{DSR}_{\mathrm{nestling}} - \mathrm{S}^2_{\mathrm{nestling}}}}$$

where S^2 is the variance of DSR in each nest phase, given by

$$\mathrm{S}^2 = \frac{\mathrm{DSR}\ \times (1 - \mathrm{DSR})}{\text{exposure days}}$$

For each clutch, we estimated the hatching success (number of hatchlings/number of eggs laid), the fledging success (number of fledglings/number of hatchlings), and the egg success (number of fledglings/number of eggs) (Ricklefs and Bloom 1977). These ratios were used as response variables in generalized estimating equations (GEEs) with binomial error distribution using year, nesting substrate (plants vs. buildings), occurrence of brood parasitism as a binomial variable (yes/no), and the interaction between nesting substrate and brood parasitism as explanatory variables. Nest identity was set as a random factor. We tested whether the prevalence of nesting substrate types varied among females using a repeatability analysis (1000 bootstraps and 1000 permutations), setting nest substrate type as a binary response variable, female as a grouping variable, and the total number of clutches monitored for each female as a covariate. We conducted the analyses on the software R (R Core Team 2018) using the packages “geepack” for the GEEs (Halekoh *et al.* 2006) and “rptR” for the repeatability analysis (Stoffel *et al.* 2017).

RESULTS

We monitored 212 nests during the nine breeding seasons, of which 86.3% were in anthropogenic substrates, and 13.7% were built on plants, mainly on the lowest fork of tree trunks. Most of the nests were found before or during laying (42.5%) or incubation (55.7%), while the others were found during nestling phase. Apparent nesting success was 52.4% (n = 212 nests), being higher for nests in buildings (55.2%) than in plants (34.5%). Partial clutch loss occurred in 24.1% of these nests, being more common during the incubation (33.7%, n = 205 nests) than in the nestling phase (13.3%, n = 166 nests). In 96 (46.8%) of the clutches followed during incubation, all eggs successfully hatched. In most of the nests followed during nestling phase (54.2%), all the hatchlings survived to fledging. Brood parasitism by the Shiny Cowbird occurred in 33.5% of all nests (n = 212), being more frequent in nests placed in plants (41.4%) than in buildings (32.2%), but this difference was not significant (GLMM, $\chi^2 = 0.806$, p = 0.369).

The DSR was slightly higher during the egg phase (0.981 ± 0.003, 2,135 exposure days, n = 205 nests) than in the nestling phase (0.974 ± 0.004, 2,074 exposure days, n = 166 nests), but this difference was not significant (z = 0.994, p = 0.32). Nesting survival during incubation according to the Mayfield method was 78.2%, and during the nestling phase, 69.1%, resulting in an overall survival of 54.0% for the entire breeding attempt.

Nesting substrate and year influenced egg success. Egg success was higher for nests in anthropogenic substrates (Fig. 1-1A) and decreased across the study (Table 1-1, Fig. 1-2A). Similarly, hatching success was greater for nests placed in anthropogenic substrates (Fig. 1-1B), following a decreasing trend through the years (Fig. 1-2B). Fledging success also decreased throughout the years, but it was not influenced by nesting substrate (Fig. 1-1C, 1-2C). Brood parasitism and the interaction between nesting substrate and brood parasitism did not affect any of the nesting success parameters (Table 1). The frequency of buildings as nest substrate differed among females (R = 0.455, p = 0.005, n = 107 nests of 24 banded females) (Fig. 1-3).

Table 1-1. Results of generalized estimating equations of egg success (survival from egg to fledgling), hatching success (from egg to hatchling) and fledging success (from hatchling to fledgling) of the Pale-breasted Thrush (*Turdus leucomelas*) in relation to the nesting substrate (plants or buildings), the presence of brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*), study year (from 2010 to 2018), and the interaction between nesting substrate and brood parasitism.

	Estimate	SE	Wald χ^2	*P*
Egg success				
Intercept	435.938	134.572	10.490	0.001*
Nesting substrate	1.369	0.557	6.040	0.014*
Brood parasitism	0.316	0.750	0.180	0.673
Year	-0.217	0.067	10.540	0.001*
Nesting substrate × Brood parasistim	-0.676	0.770	0.770	0.380
Hatching success				
Intercept	322.212	119.797	7.230	0.007*
Nesting substrate	1.737	0.458	14.420	<0.001*
Brood parasitism	0.693	0.601	1.330	0.249
Year	-0.160	0.060	7.260	0.007*
Nesting substrate × Brood parasistim	-1.027	0.641	2.560	0.109
Fledging success				
Intercept	440.332	159.498	7.620	0.006*
Nesting substrate	0.213	0.834	0.070	0.799
Brood parasitism	0.461	1.119	0.170	0.680
Year	-0.218	0.079	7.610	0.006*
Nesting substrate × Brood parasistim	-0.756	1.164	0.420	0.516

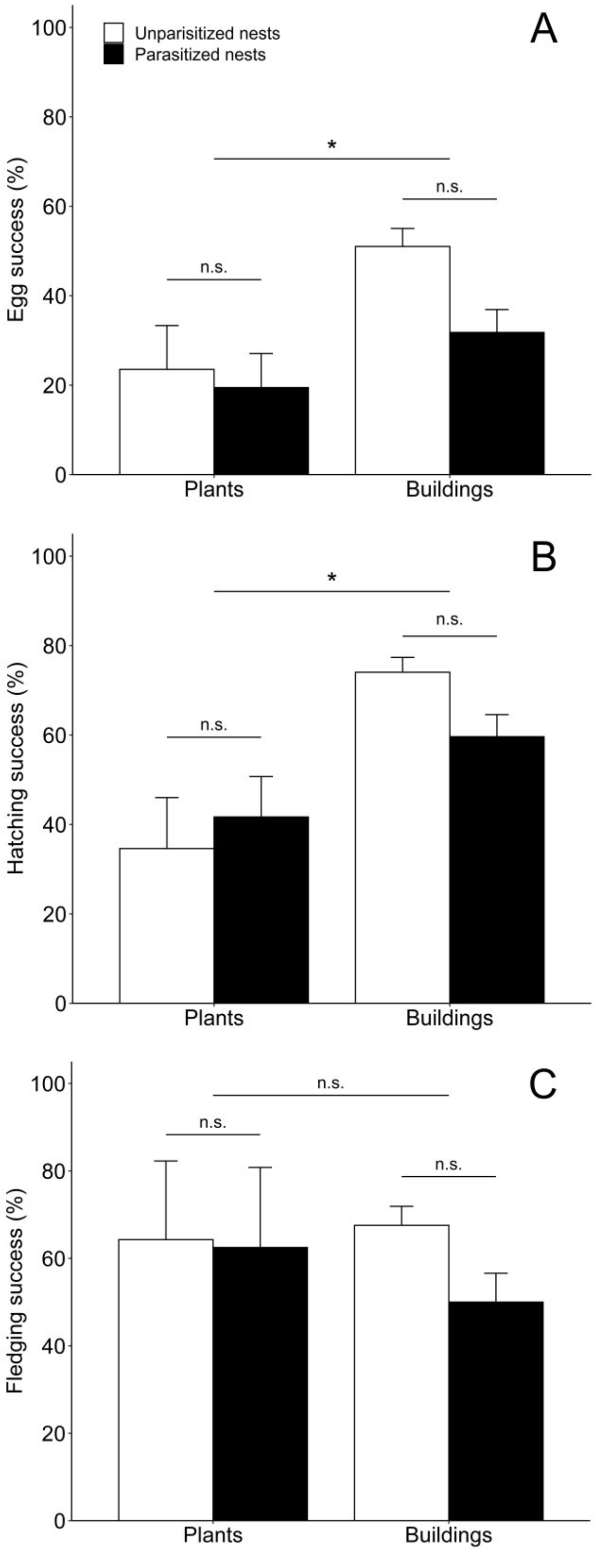


Fig. 1-1. Egg success (survival from egg to fledgling) (A), hatching success (from egg to hatchling) (B), and fledging success (from nestling to fledgling) (C) of Pale-breasted Thrush (*Turdus leucomelas*) nests built on different types of substrates in relation to the brood parasitism by *Molothrus bonariensis*. *: $p < 0.05$, n.s.: non-significant.

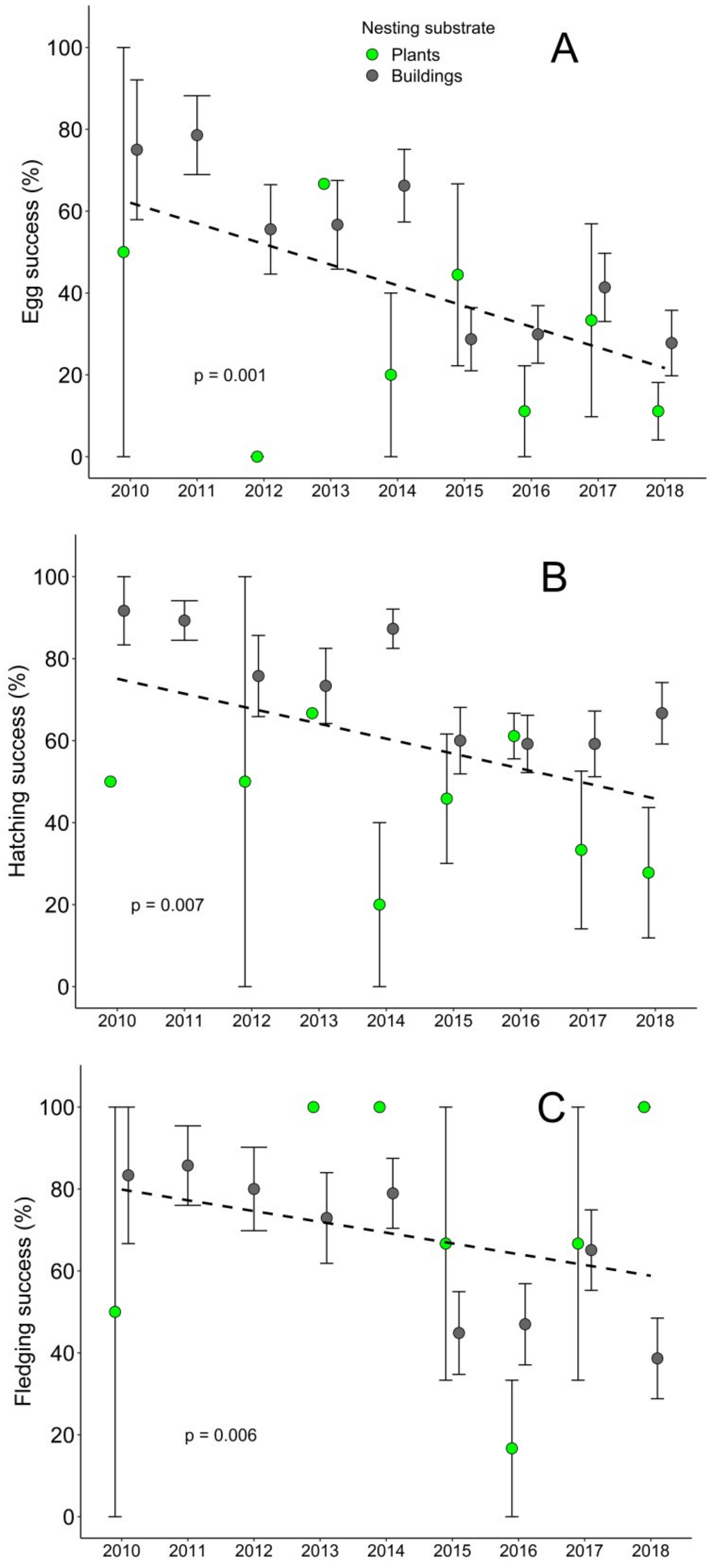


Fig. 1-2 Annual means of egg success (survival from egg to fledgling) (A), hatching success (from egg to hatchling) (B), and fledging success (from hatchling to fledgling) (C) of Pale-breasted Thrush (*Turdus leucomelas*) nests built over plants (green circles) and buildings (gray circles).

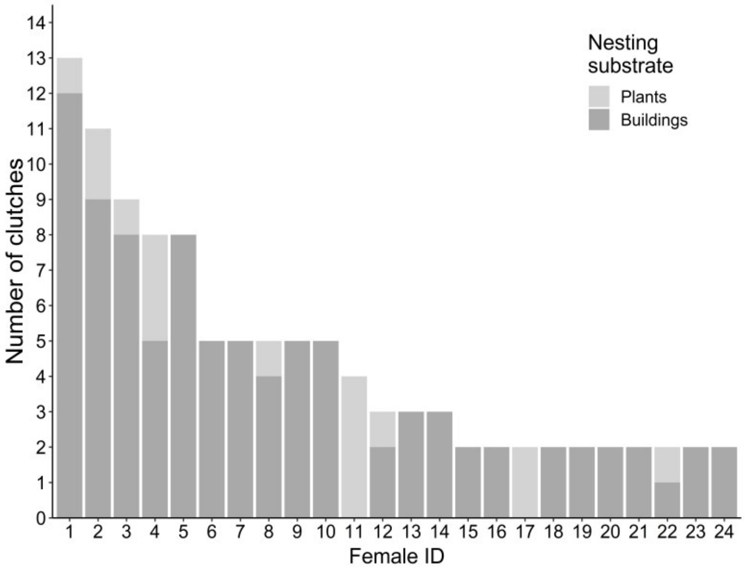


Fig. 1-3 Frequency of nest substrate types (plants and buildings) among Pale-breasted Thrush (*Turdus leucomelas*) females, ordered by the total number of clutches monitored for each individual.

DISCUSSION

We found that the type of nesting substrate affects the reproductive success of an urban thrush population irrespective of brood parasitism, and that the occurrence of nests in buildings is non-random among females. Clutches in nests placed on buildings had greater survival than those in nests constructed on plants, corroborating our hypothesis. Anthropogenic structures around nests in buildings help reduce the chance of clutch failure by restricting their visual exposure or limiting access to some predators unable to reach the sites where nests were placed. The visibility argument is plausible since most potential predators of thrush nests in the neotropics are birds, which are mostly diurnal and visually oriented (Menezes & Marini 2017). The role of nest concealment in reducing the predation risk by such predators, however, is less effective during the nestling period (Hatchwell 1996), when parents increase their activity at the nest and young provide additional (auditory and olfactory) cues for predators. Indeed, we found no effect of nesting substrate on clutch survival during the nestling phase, indicating that anthropogenic and natural substrates were likely equally accessible to predators. We predicted that nests in buildings would be safer from climbing predators such as opossums as well, but our data did not support this prediction since fledging success did not differ between nesting substrate types. Thus, the higher clutch survival for nests in buildings is probably as a consequence of reduced nest visual exposure. In addition, some major avian nest predators in our study area, such as corvids, avoid approximate or entering in buildings even if they are able to locate the nests (Møller 2010).

Higher survival rates during the egg than the nestling phase is commonly reported for Neotropical species (Auer *et al.* 2007). Nest attentiveness is greater during incubation since females spend most of the time in the nest, and their presence can repel opportunistic nest predators to some extent (Hu *et al.* 2017). In addition, male thrushes effectively reduce nest predation by guarding the nest during incubation recesses by sitting on the nest rim or nearby perches (Evans & Stutchbury 2012, Batisteli, pers. obs.), from where can detect and attack nest threats. On the other hand, constant parental arrivals and departures from the nest during the nestling phase, as well as the begging calls and the odor of nestlings, enhance nest detectability by predators. Both parental thrushes invest actively in nest defense to compensate for nest predation risk assessed by nest exposure (Remeš 2005), but their abilities to deter some predators such as avian raptors are limited (Schmidt & Whelan 2005, Batisteli & Sarmento 2016). Thus, features of the nesting site should offer special protection during the nestling period, when parents have fewer opportunities to defend the nest (Cresswell 1997, Remeš 2005). However, our data did not support that since the positive effect of the nesting substrate on clutch survival was restricted to the incubation phase. One likely alternative reason is that secondary causes of nest failure must be considered, especially in areas of reduced predation rates such as those found at our study site, which likely arise from the lower richness and abundance of nest predators. Partial clutch predation is uncommon in birds since nest predators usually take the entire nest contents (Martin 1993, França *et al.* 2009). Nevertheless, clutch size reduction occurred in a quarter of the monitored nests, suggesting additional causes of clutch failure other than predation, such as egg destruction by parasitic birds and starvation.

Egg damage by brood parasites is a typical cause of clutch reduction (Astié & Reboreda 2006). In our study, hatching success was not lower in parasitized nests, which suggests that costs related to the presence of parasite eggs (competition for heat and possible damage on host eggshells) did not play a major role in hatching failure. Thus, egg punctures were probably the main negative impact of cowbirds on the hatching success of thrushes. Egg puncturing is primarily a strategy carried out by the parasite to reduce competition from host chicks for food and thereby to promote parasitic chick survival (Astié & Reboreda 2009, Fiorini *et al.* 2014). However, the cost of egg punctures by cowbirds can be high even among unparasitized nests (Massoni & Reboreda 2002) as a way to obligate potential hosts to renesting, which provide a new opportunity of brood parasitism to cowbirds as described by the “farming hypothesis” (Swan *et al.* 2015). The presence of cowbird chicks also did not reduce the survival of thrush nestlings in our study, as reported for other thrushes (Astié & Reboreda 2006). This result may be a consequence of the larger body size of the thrush nestlings compared to cowbird nestlings (48.9 g vs. 29.8 g, respectively; AFB, unpubl. data), or parental discrimination in favor of their own nestlings (Lichtenstein 2001). Alternatively, starvation is a driver of nestling mortality in food-limited ecosystems (Astié & Luchesi 2012), as reported for an urban population of the Common Blackbird (*Turdus merula*) in Europe (Ibáñez-Álamo & Soler 2010). However, we have no data to test if food abundance in our study site may have been responsible for partial clutch reduction during the nestling phase.

We observed a decreasing temporal trend of brood survival caused by a progressive reduction in egg success. This trend is positively related to the continuous increase of brood parasitism by the Shiny Cowbird in the study area, where parasitized thrush nests ranged from 0% in 2010 and 2011 to a peak of 60.6% in 2017, even without marked changes in the parasite’s population size (MAP, unpubl. data). This increase may be related to host shift by cowbird females, since the Shiny Cowbird is a generalist that parasite that exploit approximately 100 different host species (Lowther 2018), but there are lineages of cowbird females that prefer certain hosts (Mahler 2007). Decreasing population trends in their preferred hosts might lead to increased parasitism of alternative hosts, but we have no data to test this possibility.

The frequency of buildings as nesting substrates in certain females may be effectively an individual preference or simply due to a higher availability of these nesting sites in the territories occupied by breeding pairs. In fact, the use of anthropogenic resources, such as nesting substrates and artificial nesting material, has been thought of as a simple consequence of their higher availability in relation to the natural elements in the breeding territory of urban birds (Wang *et al.* 2009, 2015, but see Batisteli *et al.* 2019). However, selection of nest site and nesting material may involve complex decision-making processes that include a genetic component, phenotypic plasticity, and individual lifetime experiences. For example, females Blue tits (*Cyanistes caeruleus*) have distinct individual preferences in selecting aromatic plants as nesting material (Mennerat *et al.* 2009). Although the causes beyond the likely individual preferences in nest site selection for the Pale-breasted Thrush remain unclear, it does not lessen the significance of the finding that females willing to use buildings as nesting substrates have increased fitness.

In conclusion, our data do not support the idea that anthropogenic nesting substrates could act as ecological traps at least regard to their effects on clutch survival, as also reported for other studies (Wallace *et al.* 2016, Da Silva *et al.* 2018). Instead, the choice of anthropogenic nesting substrates increased parental fitness in our study site by enhancing clutch survival. Moreover, the repeatability of the choice of this kind of nest substrate appears to apply to only certain females who accrue the benefits as a result. Considering the genetic and cognitive aspects of this reproductive trait (Slagsvold *et al.* 2013), we might infer that the use of buildings for nesting should be positively selected in this population (Møller 2010). Furthermore, nests in buildings probably reduce the parental investment in nest site selection and nest construction since they remain relatively preserved through the years and are frequently reused, while nests in trees are completely dismantled by weather between consecutive breeding seasons at our study site (MAP, pers. comm.). The use of buildings as nesting substrate may have costs that were not evaluated in this study, such as physiological stress caused by chronic anthropogenic noise (Kleist *et al.* 2018). Energetic investment in nest construction, incubation, and chick provisioning for nests in buildings are topics that should be addressed in further studies. Nevertheless, we highlight that the use of anthropogenic nesting substrates may favor the settlement of certain bird species in urban areas and potentially induce adaptive and non-adaptive responses in the nesting behavior of urban birds.

REFERENCES

Aguilar, T. M., Dias, R. I., Oliveira, A. C., & Macedo, R. H. (2008). Nest-site selection by Blue-black Grassquits in a Neotropical savanna: do choices influence nest success? *Journal of Field Ornithology*, 79(1), 24-31.

Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes, G., Leonardo, J., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6), 711-728.

Ardia, D. R., Pérez, J. H., & Clotfelter, E. D. (2006). Nest box orientation affects internal temperature and nest site selection by Tree Swallows. *Journal of Field Ornithology*, 77(3), 339-344.

Astié, A., & Luchesi, N. (2012). Reproductive success of the Creamy-bellied Thrush in a southern temperate zone. *The Wilson Journal of Ornithology*, 124(1), 133-138.

Astié, A. A., & Reboreda, J. C. (2006). Costs of egg punctures and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) at Creamy-bellied Thrush (*Turdus amaurochalinus*) nests. *The Auk*, 123(1), 23-32.

Astie, A. A., & Reboreda, J. C. (2009). Function of egg punctures by Shiny Cowbirds in parasitized and nonparasitized Creamy-bellied Thrush nests. *Journal of Field Ornithology*, 80(4), 336-343.

Audet, J. N., Ducatez, S., & Lefebvre, L. (2015). The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, 27(2), 637-644.

Auer, S. K., Bassar, R. D., Fontaine, J. J., & Martin, T. E. (2007). Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *The Condor*, 109(2), 321-333.

Batisteli, A. F., & Sarmento, H. (2016). Interspecific parental care by a Rufous-collared Sparrow (*Zonotrichia capensis*) at a nest of the Pale-breasted Thrush (*Turdus leucomelas*) parasitized by a cowbird (*Molothrus bonariensis*). *Ornitología Neotropical*, 27, 253-257.

Batisteli, A. F., Guilhermo-Ferreira, R., & Sarmento, H. (2019). Abundance and prevalence of plastic twine in nests of Neotropical farmland birds. *The Wilson Journal of Ornithology*, 131(1), 201-205.

Beckmann, C., & McDonald, P. G. (2016). Placement of re-nests following predation: are birds managing risk? *Emu*, 116(1), 9-13.

Borgmann, K. L., & Rodewald, A. D. (2004). Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecological Applications*, 14(6), 1757-1765.

Borgmann, K. L., & Conway, C. J. (2015). The nest-concealment hypothesis: New insights from a comparative analysis. *The Wilson Journal of Ornithology*, 127(4), 646-660.

Burhans, D. E., & Thompson III, F. R. (2006). Songbird abundance and parasitism differ between urban and rural shrublands. *Ecological Applications*, 16(1), 394-405.

Camprodon, J., Salvanyà, J., & Soler-Zurita, J. (2008). The abundance and suitability of tree cavities and their impact on hole-nesting bird populations in beech forests of NE Iberian Peninsula. *Acta Ornithologica*, 43(1), 17-31.

Chace, J. F., Walsh, J. J., Cruz, A., Prather, J. W., & Swanson, H. M. (2003). Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. *Landscape and Urban Planning*, 64(3), 179-190.

Chen, J. N., Liu, N. F., Yan, C., & An, B. (2011). Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. *Journal of Ornithology*, 152(3), 603-608.

Collar, N., & Garcia, E. F. J. (2016). Pale-breasted Thrush (*Turdus leucomelas*). In: del Hoyo J., Elliott A., Sargatal J., Christie D.A. & de Juana E. (eds.). *Handbook of the birds of the world alive*. Barcelona: Lynx Editions. http://www.hbw.com/node/58293 (access on 21 August 2019).

Colombelli-Negrel, D., & Kleindorfer, S. (2009). Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research*, 24(4), 921-928.

Cresswell, W. (1997). Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Animal Behaviour*, 53(1), 93–103.

da Silva, T. L., Cabral, R. B. G., Andrade, L. D. A. S., Nogueira, N. F., Oliveira, p+M. D. S., & Ferreira, I. (2018). Comparison of breeding biology aspects of *Fluvicola nengeta* (Aves: Tyrannidae) between two nesting sites. *Journal of Natural History*, 52(3–4), 225-235.

Davanço, P. V., Oliveira, L. S., Sousa, L. M., & Francisco, M. R. (2013). Breeding life-history traits of the Pale-breasted Thrush (*Turdus leucomelas*) in southeastern Brazil. *Ornitologia Neotropical*, 24, 401-411.

Dwyer, J. F., & Dalla Rosa, J. P. (2015). Use of Anthropogenic Nest Substrates by Crested Caracaras. *Southeastern Naturalist*, 14(1).

Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B: Biological Sciences*, 273(1587), 701-706.

Evans, M. L., & Stutchbury, B. J. (2012). Nest attendance and reproductive success in the Wood Thrush. *The Condor*, 114(2), 401-406.

Fiorini, V. D., Tuero, D. T., & Reboreda, J. C. (2009). Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by shiny cowbirds on chalk-browed mockingbirds. *Behaviour*, 146(10), 1387-1403.

Fiorini, V. D., Gloag, R., Kacelnik, A., & Reboreda, J. C. (2014). Strategic egg destruction by brood-parasitic cowbirds? *Animal Behaviour*, 93, 229-235.

Fischer, J. D., Schneider, S. C., Ahlers, A. A., & Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology. Conservation Biology, 29(4), 1246-1248.

França, L. F., Sousa, N. O., Santos, L. R. D., Duca, C., Gressler, D. T., Borges, F. J., Lopes, L. E., Manica, L. T., Paiva, L. V., de Medeiros, R. C. S., & Marini, M. Â. (2009). Passeriformes: nest predators and prey in a Neotropical Savannah in Central Brazil. *Zoologia (Curitiba)*, 26(4), 799-802.

Gering, J. C., & Blair, R. B. (1999). Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography*, 22(5), 532-541.

Gómez-Serrano, M. Á., & López-López, P. (2014). Nest site selection by Kentish Plover suggests a trade-off between nest-crypsis and predator detection strategies. *PLoS One*, 9(9), e107121.

Halekoh, U., Højsgaard, S., & Yan, J. (2006). The R package geepack for generalized estimating equations. *Journal of Statistical Software*, 15(2), 1-11.

Hanane, S. (2014). Effects of human disturbance on nest placement of the woodpigeon (*Columba palumbus*): a case study from the Middle Atlas, Morocco. *Integrative Zoology*, 9(3), 349-359.

Hatchwell, B. J., Chamberlain, D. E., & Perrins, C. M. (1996). The reproductive success of blackbirds *Turdus merula* in relation to habitat structure and choice of nest site. Ibis, 138(2), 256-262.

Hensler, G. L., & Nichols, J. D. (1981). The Mayfield method of estimating nesting success: a model, estimators and simulation results. *The Wilson Bulletin*, 93(1), 42-53.

Hu, Y. B., Zhao, Q. S., Lou, Y. Q., Chen, L. J., González, M. A., & Sun, Y. H. (2017). Parental attendance of Chestnut Thrush reduces nest predation during the incubation period: compensation for low nest concealment? *Journal of Ornithology*, 158(4), 1111-1117.

Ibáñez-Álamo, J. D., & Soler, M. (2010). Does urbanization affect selective pressures and life-history strategies in the common blackbird (*Turdus merula* L.)? *Biological Journal of the Linnean Society*, 101(4), 759-766.

Jokimäki, J., & Huhta, E. (2000). Artificial nest predation and abundance of birds along an urban gradient. *The Condor*, 102(4), 838-847.

Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Sorace, A., Fernández-Juricic, E., Rodriguez-Prieto, I., & Jimenez, M. D. (2005). Evaluation of the "safe nesting zone" hypothesis across an urban gradient: a multi-scale study. *Ecography*, 28(1), 59-70.

Kilner, R. M. (2003). How selfish is a cowbird nestling? *Animal Behaviour*, 66(3), 569–576.

Kleist, N. J., Guralnick, R. P., Cruz, A., Lowry, C. A., & Francis, C. D. (2018). Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proceedings of the National Academy of Sciences*, 115(4), E648-E657.

Liang, W., Yang, C., Wang, L., & Møller, A. P. (2013). Avoiding parasitism by breeding indoors: cuckoo parasitism of hirundines and rejection of eggs. *Behavioral Ecology and Sociobiology*, 67(6), 913-918.

Lichtenstein, G. (2001). Low success of shiny cowbird chicks parasitizing rufous-bellied thrushes: chick–chick competition or parental discrimination? *Animal Behaviour*, 61(2), 401-413.

Lomáscolo, S. B., Monmany, A. C., Malizia, A., & Martin, T. E. (2010). Flexibility in nest-site choice and nesting success of *Turdus rufiventris* (Turdidae) in a montane forest in northwestern Argentina. *The Wilson Journal of Ornithology*, 122(4), 674–680.

López, A. V., Fiorini, V. D., Ellison, K., & Peer, B. D. (2018). Thick eggshells of brood parasitic cowbirds protect their eggs and damage host eggs during laying. *Behavioral Ecology*, 29(4), 965-973.

López-Flores, V., MacGregor-Fors, I., & Schondube, J. E. (2009). Artificial nest predation along a Neotropical urban gradient. *Landscape and Urban Planning*, 92(2), 90-95.

Lowther, P. E. (2018). *Lists of victims and hosts of the parasitic cowbirds (Molothrus). Field Mueseum*. https://www.fieldmuseum.org/sites/default/files/cowbird-hosts-05sep2018.pdf. Accessed September 4, 2019

Mahler, B., Confalonieri, V. A., Lovette, I. J., & Reboreda, J. C. (2007). Partial host fidelity in nest selection by the shiny cowbird (*Molothrus bonariensis*), a highly generalist avian brood parasite. *Journal of Evolutionary Biology*, 20(5), 1918-1923.

Mainwaring, M. C. (2015). The use of man-made structures as nesting sites by birds: A review of the costs and benefits. *Journal for Nature Conservation*, 25, 17–22.

Mainwaring, M. C. (2017). Causes and consequences of intraspecific variation in nesting behaviors: insights from blue tits and great tits. *Frontiers in Ecology and Evolution*, 5, 39.

Martin, T. E. (1993). Nest predation and nest sites. *BioScience*, 43(8), 523–532.

Massoni, V., & Reboreda, J. C. (2002). A neglected cost of brood parasitism: egg punctures by Shiny Cowbirds during inspection of potential host nests. *The Condor*, 104(2), 407-412.

Mayfield, H. (1961). Nesting success calculated from exposure. The Wilson Bulletin, 73(3), 255-261.

Mennerat, A., Perret, P., & Lambrechts, M. M. (2009). Local individual preferences for nest materials in a passerine bird. PLoS One, 4(4), e5104.

Menezes, J. C., & Marini, M. Â. (2017). Predators of bird nests in the Neotropics: a review. *Journal of Field Ornithology*, 88(2), 99–114.

Mikula, P., Hromada, M., Albrecht, T., & Tryjanowski, P. (2014). Nest site selection and breeding success in three Turdus thrush species coexisting in an urban environment. *Acta Ornithologica*, 49(1), 83-92.

Møller, A. P. (2010). The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behavioral Ecology*, *21*(5), 913–918.

Møller, A. P., Díaz, M., & Liang, W. (2016). Brood parasitism and proximity to human habitation. *Behavioral Ecology*, 27(5), 1314-1319.

Møller, A. P. (2017). Fashion and out of fashion: appearance and disappearance of a novel nest building innovation. *Avian Research*, 8(1), 14.

Moskát, C., & Honza, M. (2000). Effect of nest and nest site characteristics on the risk of cuckoo *Cuculus canorus* parasitism in the great reed warbler *Acrocephalus arundinaceus*. *Ecography*, 23(3), 335-341.

Muñoz, A. M., McCleery, R. A., Lopez, R. R., & Silvy, N. J. (2008). Nesting ecology of mourning doves in an urban landscape. *Urban Ecosystems*, 11(3), 257-267.

Nilsson, S. G. (1984). The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica*, 15(3), 167-175.

Okada, S., Lindenmayer, D. B., Wood, J. T., Crane, M. J., & Pierson, J. C. (2017). How does a transforming landscape influence bird breeding success? *Landscape Ecology*, 32(5), 1039-1048.

de Oliveira, L. S., Sousa, L. M., Davanco, P. V., & Francisco, M. R. (2010).

Breeding behaviour of the Lined Seedeater (*Sporophila lineola*) in southeastern Brazil. *Ornitologia Neotropical*, 21, 251-261.

Öst, M., & Steele, B. B. (2010). Age-specific nest-site preference and success in eiders. *Oecologia*, 162(1), 59-69.

Owen, J. C. (2011). Collecting, processing, and storing avian blood: a review. *Journal of Field Ornithology*, 82(4), 339-354.

Pizo, M. A. (2018). A Narrow-billed Woodcreeper, Lepidocolaptes angustirostris, nesting in a mailbox. *Ornithology Research*, 26(3), 189-191.

Potascheff, C. D. M., Lombardi, J. A., & Lorenzi, H. (2010). Angiosperm trees and shrubs on the campus of the São Paulo State University Júlio de Mesquita, Rio Claro (SP), Brazil. *Bioikos*, 24(1), 21-30.

R Core Team. 2018. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Remeš, V. (2005). Nest concealment and parental behaviour interact in affecting nest survival in the blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behavioral Ecology and Sociobiology*, 58(3), 326–332.

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P., & Mainwaring, M. C. (2019). Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology*, 160, 841-860.

Ricklefs, R. E., & Bloom, G. (1977). Components of avian breeding productivity. *The Auk*, 94(1), 86-96.

Rivera-López, A., & MacGregor-Fors, I. (2016). Urban predation: a case study assessing artificial nest survival in a neotropical city. *Urban Ecosystems*, 19(2), 649-655.

Rodewald, A. D., & Kearns, L. J. (2011). Shifts in dominant nest predators along a rural-to-urban landscape gradient. *The Condor*, 113(4), 899-906.

Rovedder, C. E., & Fontana, C. S. (2012). Nest, eggs, and nest placement of the Brazilian endemic Black-bellied Seedeater (*Sporophila melanogaster*). *The Wilson Journal of Ornithology*, 124(1), 173-176.

Saunders, C. A., Arcese, P., & O'Connor, K. D. (2003). Nest site characteristics in the song sparrow and parasitism by brown-headed cowbirds. *The Wilson Bulletin*, 24-28.

Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17(10), 474-480.

Schmidt, K. A., & Whelan, C. J. (2005). Quantifying male Wood Thrush nest-attendance and its relationship to nest success. *The Condor*, 107(1), 138-144.

Slagsvold, T., Kleiven, K. W., Eriksen, A., & Johannessen, L. E. (2013). Vertical and horizontal transmission of nest site preferences in titmice. *Animal Behaviour*, 85(2), 323–328.

Stanley, T. R. (2000). Modeling and estimation of stage-specific daily survival probabilities of nests. *Ecology*, 81(7), 2048-2053.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639-1644.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H. W., & Gamauf, A. (2014). Hard times in the city–attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Frontiers in Zoology*, 11(1), 48.

Swan, D. C., Zanette, L. Y., & Clinchy, M. (2015). Brood parasites manipulate their hosts: experimental evidence for the farming hypothesis. *Animal Behaviour*, 105, 29-35.

Tella, J. L., Canale, A., Carrete, M., Petracci, P., & Zalba, S. M. (2014). Anthropogenic nesting sites allow urban breeding in burrowing parrots *Cyanoliseus patagonus*. *Ardeola*, 61(2), 311-321.

Tuero, D. T., Fiorini, V. D., & Reboreda, J. C. (2007). Effects of Shiny Cowbird *Molothrus bonariensis* parasitism on different components of House Wren *Troglodytes aedon* reproductive success. *Ibis*, 149(3), 521-529.

Wallace, Z. P., Kennedy, P. L., Squires, J. R., Olson, L. E., & Oakleaf, R. J. (2016). Human-made structures, vegetation, and weather influence ferruginous hawk breeding performance. *The Journal of Wildlife Management*, 80(1), 78-90.

Wang, Y., Chen, S., Jiang, P., & Ding, P. (2008). Black-billed Magpies (*Pica pica*) adjust nest characteristics to adapt to urbanization in Hangzhou, China. *Canadian Journal of Zoology*, 86(7), 676-684.

Wang, Y., Chen, S., Blair, R. B., Jiang, P., & Ding, P. (2009). Nest composition adjustments by Chinese Bulbuls *Pycnonotus sinensis* in an urbanized landscape of Hangzhou (E China). *Acta Ornithologica*, 44(2), 185–192.

Wang, Y., Huang, Q., Lan, S., Zhang, Q., & Chen, S. (2015). Common blackbirds *Turdus merula* use anthropogenic structures as nesting sites in an urbanized landscape. *Current Zoology*, 61(3), 435–443.

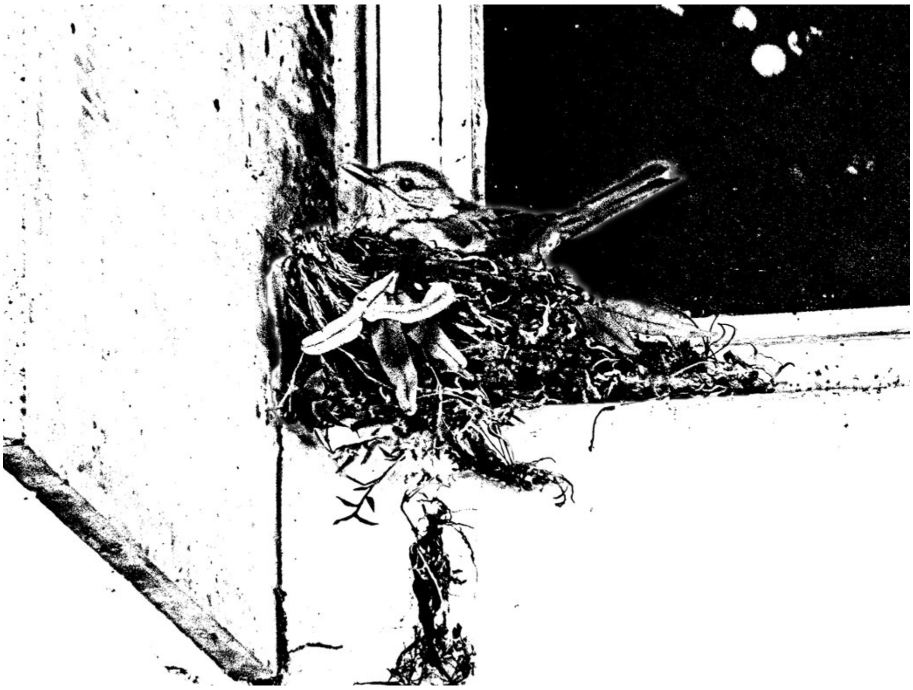
Weidinger, K. (2002). Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology*, 71(3), 424-437.

Yeh, P. J., Hauber, M. E., & Price, T. D. (2007). Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos*, 116(9), 1473–1480.

Capítulo 2

BUILDINGS PROMOTE HIGHER INCUBATION TEMPERATURES AND REDUCE NEST ATTENTIVENESS IN A NEOTROPICAL THRUSH

Submitted for publication in Ibis



BUILDINGS PROMOTE HIGHER INCUBATION TEMPERATURES AND REDUCE NEST ATTENTIVENESS IN A NEOTROPICAL THRUSH

ABSTRACT

Incubation is an energetically costly parental task of breeding birds. Incubating parents respond to environmental variations and nesting site features to adjust the balance between the time spent incubating (i.e., nest attentiveness) and foraging to supply their own needs. Non-natural nesting substrates, such as human buildings, impose new environmental contexts that may affect time allocation of incubating birds, but this is still an underexplored topic. Here, we tested whether nesting substrate type (buildings vs. trees) affect the temperature inside the incubation chamber, hereafter 'nest temperature', in the Pale-breasted Thrush *Turdus leucomelas*, either during "daytime" (with eventual incubation recesses) and "night" periods (representing uninterrupted female presence at the nest). We also tested if nesting substrate type affect the incubation budget (nest attentiveness, on- and off-bout duration), using air temperature and the day of the incubation cycle as covariates. Nest temperature, when controlled for microhabitat temperature, was higher at night and in nests placed in buildings, but did not differ between daytime and night for nests in buildings, indicating that buildings partially compensate females incubation recesses due to nest temperature stability. Females from nests placed in buildings exhibited lower nest attentiveness and longer off-bouts. Higher air temperatures were significantly correlated with shorter on-bouts and longer off-bouts, but without affecting nest attentiveness. We suggest that the longer off-bouts took by females of nests in buildings is a consequence of higher nest temperatures promoted by man-made structures around these nests. Therefore, the use of buildings as nesting substrate may increase the parental fitness due to a relaxed incubation budget, and potentially drive the evolution of incubation behavior in certain urban bird populations.

Keywords: Anthropogenic nesting sites, behavioral plasticity, nest microclimate, parental behavior, urban birds.

RESUMO

Edifícios promovem temperaturas de incubação maiores e reduzem a constância de incubação em um sabiá Neotropical – A incubação é uma tarefa de alto custo energético do cuidado parental das aves. Os pais em incubação respondem a variações ambientais e às características do local do ninho ajustando o balanço entre o tempo gasto incubando (i.e., constância de incubação) e o forrageio para suprir suas próprias necessidades. Substratos de nidificação artificiais, como edificações humanas, impõem novos contextos ambientais, que podem afetar a alocação do tempo em aves em incubação, mas esse ainda é um assunto pouco explorado. Neste estudo, testamos se o tipo de substrato de nidificação (edifícios vs. árvores) afeta a temperatura da câmara de incubação (de agora em diante "temperatura do ninho") no sabiá-barranco (Turdus leucomelas), durante o dia (com eventuais recessos de incubação) e à noite (representando a presença constante da fêmea no ninho). Também testamos se o tipo de substrato de nidificação afeta o ritmo de incubação (constância de incubação, duração das sequências e dos recessos de incubação), usando a temperatura atmosférica e o dia do ciclo de incubação como covariáveis. A temperatura do ninho, quando controlada pela temperatura do micro-habitat, foi mais alta durante a noite e em ninhos em edifícios, mas não diferiu entre o dia e a noite ninhos em edifícios, indicando que os edifícios compensam parcialmente os recessos de incubação das fêmeas quanto à estabilidade da temperatura do ninho. Fêmeas de ninhos em edifícios exibiram menor constância de incubação e recessos mais longos. Temperaturas atmosféricas mais altas estiveram significativamente correlacionadas com sequências de incubação mais curtas e recessos mais longos, mas sem afetar a constância de incubação. Nós sugerimos que os recessos mais longos das fêmeas com ninhos em edifícios é uma consequência das temperaturas mais altas dentro dos ninhos promovidas pelas estruturas antrópicas em volta dos mesmos. Portanto, o uso de edifícios como local de nidificação pode aumentar a aptidão parental por meio de um ritmo mais ameno de incubação, e potencialmente dirigir a evolução do comportamento de incubação em certas populações de aves urbanas.

Palavras-chave: Aves urbanas, comportamento parental, microclima do ninho, substratos antropogênicos de nidificação, plasticidade comportamental.

INTRODUCTION

Parental care in bird embraces a suit of energetically costly tasks, including nest construction, incubation, nestling provisioning, and nest defense. Although these activities usually increase parental fitness through enhancing offspring survival (Schmidt & Whelan 2005, Evans & Stutchbury 2012), the engagement in parental tasks worse adult body condition and reduce their life expectancy (Fast *et al.* 2007, Santos & Nakagawa 2012). The evolution of parental care strategies seeks to maximize this trade-off between the gain in offspring production and the immediate and long-term costs to parents (Ghalambor & Martin 2001). The optimal equilibrium point of this trade-off is influenced by variations in environmental contexts, such as food availability and habitat structure, and can be actively altered by behavioral decisions of breeding birds, such as nest placement choices (Burhans & Thompson III 2001, Eggers *et al.* 2008, Fan *et al.* 2017). Nest attentiveness (i.e., the percentage of time birds spend incubating) represents a remarkable conflict for passerine species with uniparental incubation, in which the incubating bird, usually the female, must equate nest attendance and self-maintenance activities. The presence of an incubating bird at the nest have multiple functions, such as warm the brood and passively defend the nest against opportunistic predators (Halupka & Greeney 2009). Thus, features of the nest site that reduce brood exposition to predators and adverse weather conditions are expected to directly affect the incubation behavior (Weidinger 2002, Hu *et al.* 2017).

Nest site selection is a complex decision that involves inherited, cognitive and personality aspects (Chen 2001, Breen *et al.* 2016), and has direct influence on the parental care-survival trade-off by changing the predation risk for breeding adults and their brood (Miller et al 2007). Birds usually show intraspecific plasticity on nest site preferences in response to nest predators and their local abundance (Forstmeier & Weiss 2004, Yeh *et al.* 2007). Certain nest site features, such as nest concealment, are taken into account by birds in the selection of nest sites as a proxy to minimize reproductive costs related to predation risk, nest attentiveness, and the parental investment on nestling provisioning (Robertson 2009, Węgrzyn & Leniowski 2011, Latif *et al.* 2012). Nest concealment also has important effects on nest microclimate and therefore in thermoregulatory costs to parents and offspring (Amat & Masero 2004, Robertson 2009).

The correct development of bird embryos requires eggs to be kept under a narrow, species-specific thermal range (Ricklefs & Brawn 2013, Robinson *et al.* 2014). Even small variations in the mean incubation temperature influence the length of the incubation period, nestling physiology, and their life expectancy (Berntsen & Bech 2016, Griebel *et al.* 2018, Vedder *et al.* 2018). Parental birds are expected to cope with natural oscillations in environmental temperature primarily through the selection of a nesting site that minimizes incubation costs (Robertson 2009, Bueno-Enciso *et al.* 2016, but see Lloyd & Martin 2004). Further, incubating birds modulate the incubation behavior in response to air temperatures. This topic has been extensively studied (reviewed by Conway & Martin 2000), and most studies report that higher air temperatures are related to shorter incubation sessions (hereafter "on-bouts") and longer incubation recesses ("off-bouts"). The effect of nest site microclimate in incubation behavior, however, is seldom studied (e.g., Bryan & Bryant 1999, Ardia *et al.* 2009, Álvarez & Barba 2014, Bueno-Enciso *et al.* 2016, Mueller *et al.* 2019), especially among open-cup nesting birds (Lloyd & Martin 2004, Londoño *et al.* 2008, Robertson 2009).

The colonization of novel habitats, such as urban areas, imposes new challenges in the adjustment of the trade-offs faced by breeding birds. Urban birds experience changes in nest predator community (Rodewald & Kearns 2011) and opportunities to explore new resources, such as alternative food sources and artificial nesting sites (Møller *et al.* 2015, Wang *et al.* 2015). The exploitation of those new resources shapes an urban behavioral profile, which include high levels of problem-solving skills, boldness, and higher tolerance to human proximity in urban than in rural conspecifics (Evans *et al.* 2010, Audet *et al.* 2015, Møller *et al.* 2015). The use of anthropogenic nesting sites enhances the settlement of bird breeding territories in urban areas where natural nesting substrates are limited or absent (Møller 2010, Tella *et al.* 2014, Reynolds *et al.* 2019). Although some studies have reported the impact of these man-made structures on breeding success (reviewed by Mainwaring 2015), the likely behavioral adjustments of individuals using those nesting sites have been rarely studied.

In this study, we aimed to test if the occupation of anthropogenic nesting structures affects the incubation behavior in females of an open-cup nesting Neotropical passerine, the Pale-breasted Thrush (*Turdus leucomelas* Vieillot 1818). We tested whether 1) the temperature inside the incubation chamber (hereafter "nest temperature") is affected by nesting substrate type (buildings vs. trees) and the presence of incubating females at the nest ("daytime", with eventual incubation recesses, and "night", when the female is uninterruptedly at the nest), and 2) the incubation budget (nest attentiveness, on- and off-bout durations) is affected by nesting substrate type, using as covariates air temperature and the day of the incubation cycle. We predicted that the use of buildings as nesting substrates permits the maintenance of higher nest temperatures, which may somewhat enable females take longer off-bouts without harming embryonic development. Therefore, female attentiveness should be lower for nests placed in buildings, because of the thermal benefits provided by man-made structures. We also predicted that an increase in air temperature should affect negatively on-bout duration and positively off-bout duration, because of the narrow range of incubation temperature required to adequate embryo development, which imposes differences in thermoregulatory costs to incubating females.

MATERIALS AND METHODS

Study area

This study was conducted in two periurban areas in São Paulo State, southeastern Brazil: the campus of the Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP) in Rio Claro municipality (22º23’43”S, 47º32’46”W, 628 m a.s.l), and the campus of the Universidade Federal de São Carlos (UFSCar) in São Carlos municipality (21º59’02”S, 47º52’58”W, 848 m a.s.l.). Study sites are 60 km distant from each other and have similar climatic conditions. The regional climate is subtropical with dry winters and wet, hot summers (Alvares *et al.* 2013). Mean annual rainfall is about 1344 mm in Rio Claro, and 1435 mm in São Carlos, with rains concentrated between October and March in both sites. Monthly mean temperatures are 20.2 ºC in Rio Claro (range: 16.5–23 ºC), and 19.9 ºC in São Carlos (range: 16.2–22.4 ºC). Both sites held green urbanized portions and patches of native vegetation (Brazilian savanna in São Carlos and Atlantic Forest in Rio Claro) (Potascheff *et al.* 2010, Lessi *et al.* 2016).

Temperature survey

During the breeding season of 2012 (between August and December), nests of the Pale-breasted Thrush were searched at UNESP by carefully inspecting buildings and trees, and following adults carrying nesting material. Once located, we installed a pair of data loggers Ibuttons/Maxim® programed to take temperature measurements every 2 min. Before installation, all data loggers were waterproofed by wrapping them in pieces of latex gloves, and camouflaged with mud to resemble the nesting material. In each nest, we positioned one ibutton in the bottom of the incubation chamber to register the temperature inside the nest (hereafter "nest temperature"), and another outside the nest (~30 cm) to capture variations in microhabitat temperature. We used a nylon wire to attach the internal ibutton to the nest structure and to the nest substrate to prevent females of removing it. We installed loggers in nine active nests (four in trees and five in buildings). Ibutton installation took 5–10 min and no nest abandonment occurred after this procedure. We discarded temperature data before the next 0:00 h after ibutton installation to allow some hours of female habituation. Nest status was checked daily, and we also discarded all temperature records after 0:00 h of hatching day or the day when the nest was depredated to assure that incubation was in course during data collection.

Incubation behavior

From August to December 2017 and 2018, we searched for nests in UFSCar every other day in the same way as described above. Once located, nests were checked every 1–3 days using a pole with a mirror until the chicks hatched or the nest was depredated. Daily nest checking near the expected hatching date allowed us to infer the day of the incubation cycle in each of our behavioral observations during incubation (see below). We performed sessions of direct observations (1 h duration) of the incubation behavior following the animal focal method (Altmann 1974). Each nest was observed six times (twice each day, once between 7:00–9:00 and once between 12:00–14:00, for three days), in morning and afternoon periods to survey female behavior under a wide range of air temperatures. To sample possible variation in female behavior across the incubation cycle, each day of observations in the same nest was spaced 2–3 days from the next observations. All observations were carried out in non-rainy days, from places of wide pedestrian flow at a minimum distance of 10 m from the nest. Since most of the nests were located close to pedestrian passages, we assumed that the presence of the observer did not drive special attention by the females, which were presumably habituated to human activity near the nest. Nevertheless, we waited for 5 min before starting data collection in each observation session to avoid a possible observer effect. Some nests were depredated early in the incubation phase or could not be repeatedly observed due to bad weather, leading to missing data. We included in the analysis only data from nests observed at least in four of the expected six observation sessions.

During each observation session, we recorded the time when a given female left the nest or resume incubation. We estimated nest attentiveness as the percentage of time that females stayed incubating during each 1-h observation session. We assumed the first incubation day as the day when the second egg was laid. For nests found after clutch completion, we inferred the incubation day at a given observation session by backdating from the hatching day, considering that the incubation period of the Pale-breasted Thrush in the region lasts 14 days (AFB, unpubl. data). Air temperatures were retrieved from automatic meteorological station located at UFSCar to the nearest 0.1 ºC. Nesting substrate was classified in buildings (any man-made structure belonging to buildings, such as walls, concrete columns, windows and air conditioners) or trees.

Statistical analyses

To assess the influence of microhabitat temperature in the thermic balance of the incubation chamber, we built a linear mixed-effects model with the nest temperature as a continuous dependent variable. Explanatory variables were nesting substrate (tree/building), period of the day (daytime/night), microhabitat temperature, and the interaction between nesting substrate × period of the day. Nest ID was set as a random factor. Temperature measurements in brief intervals (i.e., 2 min) often incur in violation of sample independence. Thus, we tested for temporal autocorrelation in the data by adding an auto-regressive correlation structure to the model, which improved it significantly. Given the temporal autocorrelation (Phi = 0.986), degrees of freedom of the linear mixed-effects model were corrected based on the effective sample size according Zuur *et al.* (2009). The residuals were graphically checked and supported model validation. The Tukey post-hoc test was used to address differences indicated by the statistical significance of the interaction term.

Since the age of the nests where we conducted behavioral observations were not normally distributed, we used a Wilcoxon test to detect a possible temporal bias in female behavioral observations across incubation, comparing the day of incubation cycle for observations of nests in trees and in buildings. Nest attentiveness and the duration of on- and off-bouts did not achieve normal distribution even after statistical transformations. Accounting for this non-normality, we built generalized estimating equations (GEE) to assess whether the female attentiveness to the nest (a continuous variable with Gamma distribution), on-bout, and off-bout durations were affected by nesting substrate type, incubation day, air temperature, and all possible interactions between these terms. The conceptual model proposed by Conway & Martin (2000) suggests a complex, non-linear variation of the incubation behavior under a wide range of daytime environmental temperatures (from -8 ºC to 45 ºC). However, we tested a linear relationship between incubation behavior and air temperatures due to the absence of such extreme daytime temperatures in our study site (air temperature = 22.9 ± 4.5 ºC, mean ± SD, range 14.1 – 34.0 ºC). Only complete on- and off-bouts were included in analysis, discarding events intercepted by the start or the end of observation sessions. In all GEE's, nest ID was set as a random factor. The best model was selected from a full factorial model employing a backward stepwise selection until all non-significant interactions or single terms had been removed (Zuur *et al.* 2009). To assess whether possible differences in incubation budget between nests in trees and in buildings would affect egg survival, we built a generalized linear model (GLM) with binomial distribution to compare hatching success (the number of hatchlings divided by the clutch size) between nesting substrate types (Zuur *et al.* 2009). All analyses were conducted in the software R (R Development Core Team 2019) using the packages "nlme" (linear mixed-effects model, Pinheiro *et al.* 2017) and "geepack" (GEE, Højsgaard *et al.* 2016).

RESULTS

We obtained 43,915 nest temperature measurements over 63 nest-days (6.77 ± 4.17 [mean ± SD] survey days each nest). Nest temperature averaged 28.2 ± 4.3 ºC (range: 15.1–37.5 ºC), and was positively influenced by microhabitat temperature and period of the day (Table 2-1), being higher at night, when female presence on the nest is uninterrupted. Nest temperature was higher in buildings than trees (buildings: 31.3 ± 3.7 ºC, n = 17,071, trees: 25.5 ± 2.6 ºC, n = 19,644; Table 2-1). Nest temperature in buildings was in general 6.0 ºC warmer than microhabitat temperature, while this difference was near zero (0.03 ºC) for nests in trees. The interaction term (nesting substrate type × period of the day) was significant (Table 2-1). The Tukey post-hoc test revealed that the nest temperature at a given microhabitat temperature did not differ between nests placed in trees at night (when the female was continuously at the nest) and in buildings either during daytime or night (Fig. 2-1).

We performed direct observation of female behavior for 81 h in 15 nests placed in trees (5.40 ± 0.82 h each nest), and for 108 h in 21 nests in buildings (5.14 ± 0.85 h each nest). The day of incubation cycle did not differ between observations of nests in trees and in buildings, discarding a bias in nest detection (Wilcoxon test, W = 4326, p = 0.898). Nest attentiveness during observation sessions averaged 76.5 ± 14.7 %, ranging from 21.6% to 100%. Nest attentiveness was affected by nesting substrate type (Table 2-2), being lower for nests placed in buildings (74.0 ± 16.0 %) than in trees (80.0 ± 12.0 %) (Fig. 2-2A). There was a slight but significant decrease in nest attentiveness as incubation progressed, while air temperature did not affect nest attentiveness (Table 2-2).

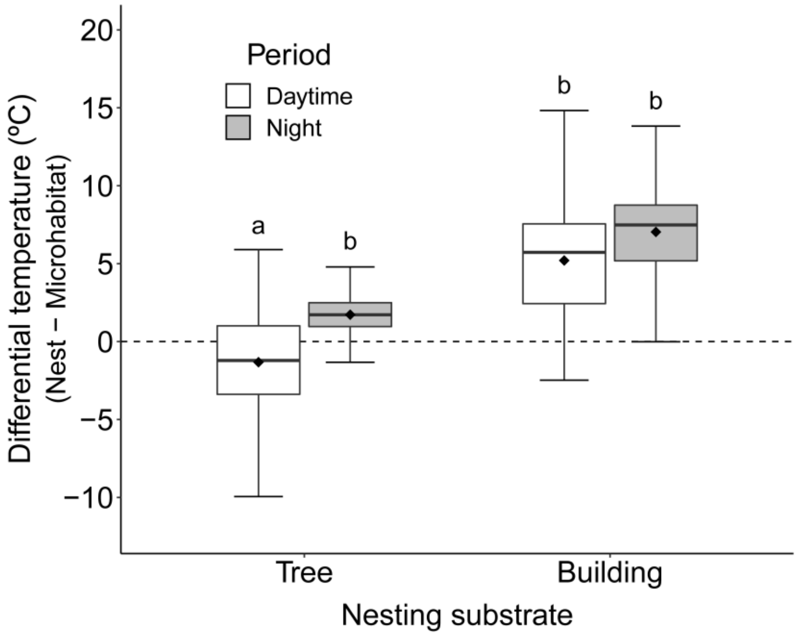


Fig. 2-1 Differential temperature (the difference between the temperature inside the nest incubation chamber and microhabitat temperature) in relation to nesting substrate type and period of day in nests of Pale-breasted Thrush (*Turdus leucomelas*). The dashed line represents equal nest and microhabitat temperature, boxplots show interquartile ranges, whiskers denote standard errors, diamonds represent means of differential temperatures, and lowercase letters indicate statistically significant differences after Tukey post-hoc test.

Table 2-1. Results of the linear mixed-effects model on the temperature inside nests of the Pale-breasted Thrush *Turdus leucomelas* in relation to nest substrate type (buildings/trees), period of the day (daytime/night), the interaction nest substrate type × period of the day, and microhabitat temperature. Degrees of freedom were calculated based on the effective sample size due to temporal autocorrelation in temperature, resulting in n = 4020.457 independent samples out of 36,715 temperature measurements (see details in Methods). *: statistical significance at α = 0.05.

	Estimate	Std error	df	t	p
Intercept	15.510	1.239	4008.457	12.523	<0.001*
Nest substrate	6.464	1.842	7	3.560	0.001*
Period of the day	0.901	0.120	4008.457	7.481	<0.001*
Nest substrate × Period of the day	0.835	0.179	4008.457	4.667	<0.001*
Microhabitat temperature	0.640	0.030	4008.457	135.301	<0.001*

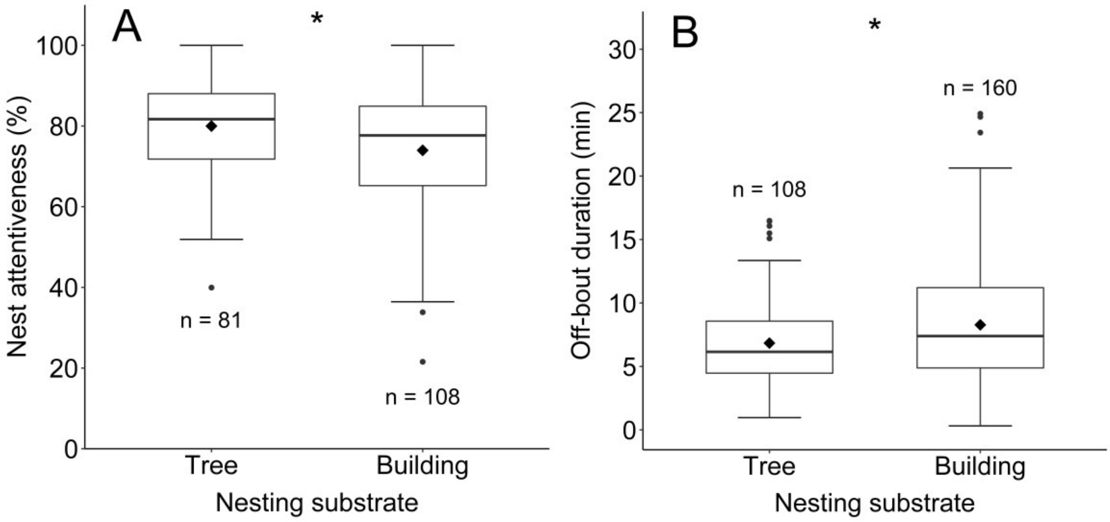


Fig. 2-2 Nest attentiveness by Pale-breasted Thrush (*Turdus leucomelas*) females (A) and off-bout duration (B) in nests placed in trees and buildings. Boxplots show interquartile ranges, whiskers denote standard errors, diamonds represent means, and dots indicate outliers. * Statistical significance at α = 0.05.

Table 2-2. Results of generalized estimating equations assessing the incubation behavior (nest attentiveness, on-bout and off-bout duration) of Pale-breasted Thrush (*Turdus leucomelas*) in relation to nesting substrates types (trees and buildings), air temperature and day of the incubation cycle. Final models were selected from full models containing all the possible interactions through a stepwise backward method, dropping the non-significant terms based on likelihood-ratio tests. Estimates, standard error, and degrees of freedom ('df') not shown for explanatory variables absent from final models. * statistical significance at $\alpha = 0.05$.

	Estimate	Std. error	df	Wald χ^2	*P*
Nest attentiveness (%)					
Intercept	1.152	0.048	153	574.690	<0.001*
Nest substrate	0.109	0.050	33	4.680	0.031*
Air temperature				0.001	0.989
Incubation day	0.013	0.005	153	5.020	0.025*
On-bout duration					
Intercept	1.341	0.700	100	3.670	0.055
Nest substrate				2.390	0.122
Air temperature	0.079	0.035	100	5.100	0.024*
Incubation day				2.150	0.142
Off-bout duration					
Intercept	14.464	1.623	212	79.390	<0.001*
Nest substrate	-1.614	0.558	33	8.380	0.004*
Air temperature	-0.267	0.070	212	14.260	<0.001*
Incubation day				1.330	0.248

On-bouts lasted 1186 ± 653 s, ranging from 67 s to 3121 s (n = 135 on-bouts in 101 h). On-bouts were shorter under higher air temperatures (Table 2-2, Fig. 2-3A), but their duration was not affected by nesting substrate or incubation day (Table 2-2). We obtained the duration of 268 off-bouts (108 for nests in trees and 160 for nests in buildings), which averaged 268 ± 270 s (range: 19 – 1927 s). Off-bout duration differed between nesting substrate types (Table 2-2, Fig. 2-2B), being greater for nests in buildings. Off-bout duration was positively related to air temperature (Table 2-2, Fig. 2-

3B), but not to incubation day (Table 2-2). Despite the differences in incubation budget, hatching success did not differ between nests in buildings and in trees (GLM, z = 0.286, p = 0.775).

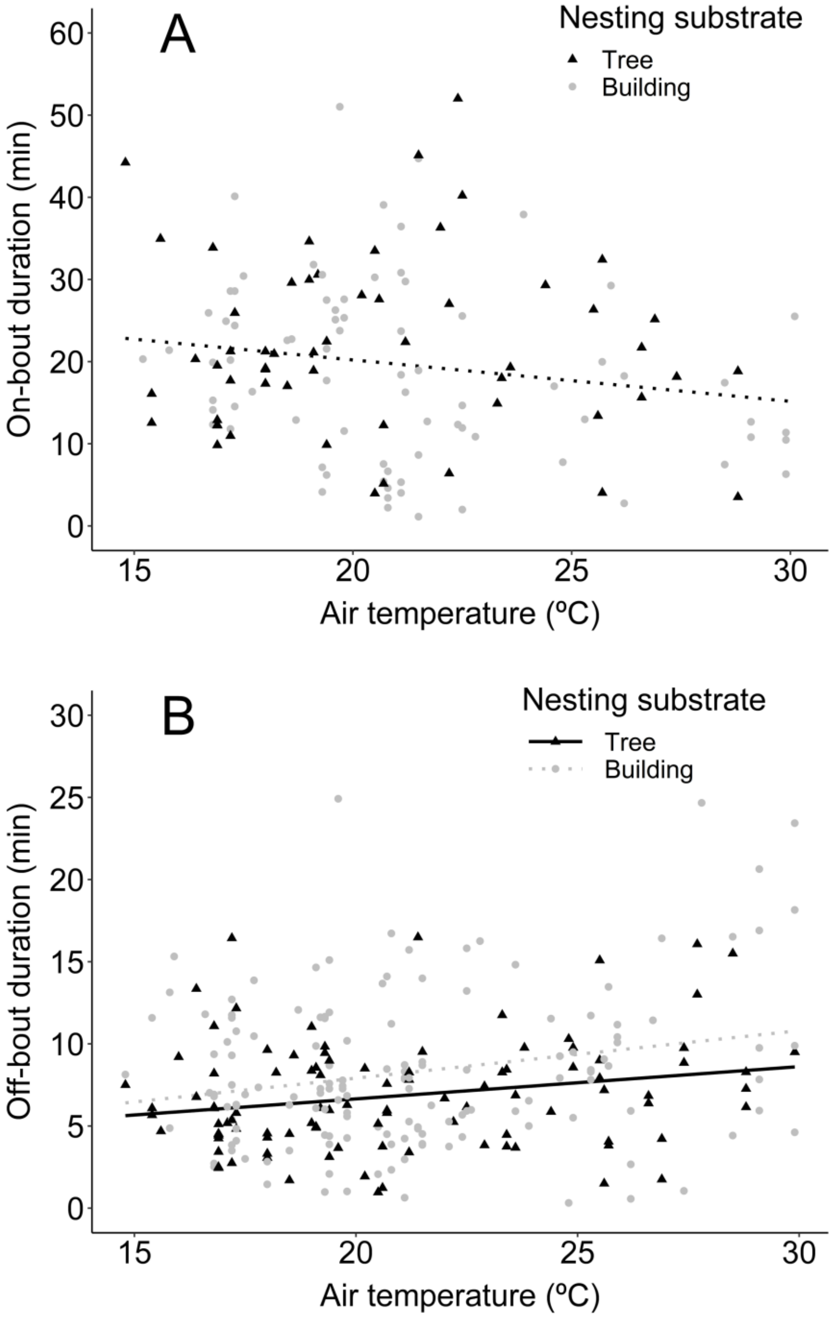


Fig. 2-3 Duration of on-bouts (A) and off-bouts (B) of Pale-breasted Thrush (*Turdus leucomelas*) females incubating in nests placed in trees (triangles) and buildings (circles) in relation to air temperature. (A) Dashed line represent a general tendency of the linear relationship between variables. (B) Dashed and continuous lines indicate linear relationships between variables for nests in buildings and in trees respectively.

DISCUSSION

The use of buildings as nesting substrate by the Pale-breasted Thrush promoted greater nest temperatures at a given microhabitat temperature and allowed a reduction in female nest attentiveness compared to nests in trees, corroborating our hypothesis. During daytime, even with incubation recesses, buildings kept nest temperature at a level comparable to that observed for nests placed in both trees and buildings with constant female presence (i.e., during the night). Therefore, the lower nest attentiveness in buildings we observed was likely enhanced by warmer nest temperatures provided by man-made structures around the nests, enabling longer off-bouts without prejudice to hatching success.

The energetic-bottleneck hypothesis states that the time an incubating bird spent at the nest is energetically limited by its own demand for self-maintenance (Yom-Tov & Wright 1993). One prediction that stem from this hypothesis is that female in artificially heated nests should benefit from this extra energy and increase their nest attentiveness, as experimentally demonstrated for cavity nesters, such as great tits (*Parus major*) and tree swallows (*Tachycineta bicolor*), and for the ground nester pectoral sandpiper in the artic (*Calidris melanotos*) (Bryan & Bryant 1999, Cresswell *et al.* 2004, Ardia *et al.* 2009). However, our data did not support such prediction, since females take longer off-bouts under warmer nests (i.e., buildings). Similarly, higher nest temperature is related to lower nest attentiveness in both cavity- and open-cup nesters (Londoño *et al.* 2008, Robertson 2009, Álvarez & Barba 2014, Amininasab *et al.* 2016, Bueno-Enciso *et al.* 2016). These differences indicate that nest temperature may elicit adjustments in female incubation behavior in species-specific ways (Mueller *et al.* 2019). Some species canalize any extra energy (either food or heat) to increase the time devoted to the current clutch (Ardia *et al.* 2009, Vafidis *et al.* 2018), while others may invest more in self-maintenance and consequently in future breeding attempts. One likely reason for these alternative strategies is related to specific life-history traits. Tropical species as the Pale-breasted Thrush have lower adult mortality probability, and parents might prioritize the possibility of future breeding attempts rather than invest in the current clutch (Ghalambor & Martin 2001, Martin *et al.* 2015). Such a relaxed incubation budget did not harmed hatching success, which is actually higher for nests in buildings in our study region when considering a more robust sample size (Batisteli, in prep.).

Off-bout duration was greater for nests in buildings regardless of air temperature, likely as an effect of the higher nest temperature in buildings. The physical barriers around nests in buildings provide better nest concealment, and their lower exposition to wind sustains greater differences between nest and microhabitat temperatures (Hilton *et al.* 2004). It could be argued that buildings would be suboptimal nesting microhabitats where energy expenditure of incubating females is higher than in trees, which would require longer foraging times to replace their energetic reserves, resulting in longer off-bouts. If true, we should have observed shorter on-bouts for nests in buildings than in trees due to a more rapid depletion of female reserves (Yom-Tov & Wright 1993). However, on-bout duration did not differ between nesting substrate types, rejecting this explanation to our findings. Therefore, longer off-bouts are more likely a benefit rather than an obligation for females that nest in buildings, enabling greater foraging time. Females that nest in buildings spent 7.5% less time incubating, which corresponds to 0.9–1.01 h a day considering the duration of the photoperiod during the breeding season of the Pale-breasted Thrush in the region (12–13.5 h). The extra energetic resource acquired during this time can improve parental efforts either in the current or future breeding attempts (Reid *et al.* 2000, Robertson 2009).

Lower nest attentiveness may be an ecological-time response to lower nest predation risk (Fontaine & Martin 2006). All nests studied regard to the female behavior were in the same area, therefore experiencing the same predator community. Thus, the particular features of each nesting substrate type may be responsible for the variation in nest attentiveness as a response to the perceived nest predation risk. Corvids are important predators in both study areas, but usually avoid the proximity to or entering buildings (Møller 2010). In our study populations, females frequently reuse successful nests within and between breeding seasons, as reported for the European Blackbird (*Turdus merula*) (Wysocki 2004). The reuse of successful nesting sites may enable them to accumulate previous experiences about nesting site security and adjust their behavior to optimize the balance between self-maintenance and incubation. Thus, more than thermal benefits, thrush females that nest in buildings may take advantage of the visual protection of man-made structures around the nest, leading the nest unattended during greater intervals.

Air temperature affected both on-bout and off-bout duration, corroborating our hypothesis. Prolonged on-bouts under lower air temperatures suggest an effect of temperature on incubation efficiency (Capp *et al.* 2018). Even when an open-cup nesting bird is incubating, the external air is continuously penetrating in the nest cup through nest walls in a convection flow (Deeming 2016). From this point of view, the warmer the external air, the higher is the efficiency of the incubating female in keeping eggs at optimal temperatures, except in extremely hot environments where air exceeds the upper lethal temperature for the embryos. Prolonged off-bouts under warmer temperatures is justifiable since air temperature provides an indirect assessment of egg cooling rates to incubating females, which respond reducing their latency to return to the nest (Reneerkens *et al.* 2011, Forrester & Londoño 2016).

Incubation efforts usually increase with incubation progress for tropical birds (Ruggera & Martin 2010, Martin *et al.* 2017), but our results showed an opposite pattern. The relationship between nest attentiveness and incubation progress is highly variable among species, with studies reporting increasing (Endo & Ueda 2016), decreasing (Cooper & Voss 2013, Forrester & Londoño 2016), or constant nest attentiveness across the incubation period (Biancucci & Martin 2008, Bueno-Enciso *et al.* 2016). This unclear relationship may also be affected by spatiotemporal fluctuations on food availability and nest predation risk (Vafidis *et al.* 2018). Incubating passerines continuously lose mass during the course of incubation (Suárez *et al.* 2005, Blem & Blem 2006, Redfern 2010). Thus, the need of ameliorating their body condition to invest on nestling care from hatching onwards may be related to the decreasing nest attentiveness across incubation course, as observed in our study population.

Three explanations other than the insulation/protection effects provided by man-made structures might apply to the differences in female behavior between substrate types but are not supported by our data. First, lower nest attentiveness in building nests might be a consequence of human proximity and frequent perturbation, eliciting escaping behavior of incubating females. If true, human movements should have induced repeated trips from and to the nest, resulting on shorter on-bout periods, since incubation would be prematurely interrupted (McGowan & Simons 2006). However, on-bout duration did not differ between nesting substrate types, thus refuting this argument. Additionally, birds that breed in disturbed sites such as our urban areas are usually habituated to human disturbance (Baudains & Lloyd 2007, Piratelli *et al.* 2015). Second, nests in buildings are generally surrounded by man-made structures, which imply a poor view of the surroundings and a supposed high predation risk to incubation females (Burhans & Thompson III 2001, Gómez-Serrano & López-López 2014). The need of constantly leaving incubation to monitor nest vicinity for self-protection should have produced shorter on-bouts in nests in buildings, as discussed above, which was not the case.

Therefore, it is unlikely that the poor view of nest surroundings has been responsible for lower nest attentiveness of females nesting on buildings. Last, the longer off-bouts for females that nest in buildings might also be related to lower food availability in the surroundings of buildings, requiring a longer foraging time to supply female energetic demands. In fact, several experimental studies reported that increased food availability enable passerine females to spend more time on the nest (Londoño *et al.* 2008, Lothery *et al.* 2014, Vafidis *et al.* 2018), either prolonging on-bouts (Pearse *et al.* 2004) or shortening off-bouts (Chalfoun & Martin 2007, Amininasab *et al.* 2016). We are not able to test this hypothesis, but nests in both substrate types were uniformly distributed, and close enough from each other to dismiss strong differences in patch quality related to each nesting substrate surroundings.

We concluded that the use of buildings as nesting substrates enable a reduction in the energetic costs associated to nest attentiveness for incubating females of the Pale-breasted Thrush due to longer off-bouts. Although each part of this study have been conducted in a different site, the strong similarities and proximity between study areas allow us to infer that such behavioral adjustments are possible due to the insulation provided by the buildings itself. Extended off-bouts enhance greater foraging time for females, which may result in a better body condition over the breeding season. The use of anthropogenic nesting substrates may ultimately promote the settlement of birds in urbanized areas (Møller 2010, Reynolds *et al.* 2019). This advantage related to reduced breeding costs may contribute to increase parental fitness of the subset of individuals using human buildings as nesting sites, and potentially drive the evolution of the incubation behavior in urban bird populations.

REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 227-266.

Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes, G., Leonardo, J., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6), 711-728.

Álvarez, E., & Barba, E. (2014). Behavioural responses of great tits to experimental manipulation of nest temperature during incubation. *Ornis Fennica*, 91(4), 220-230.

Amat, J. A., & Masero, J. A. (2004). Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour*, 67(2), 293-300.

Amininasab, S. M., Kingma, S. A., Birker, M., Hildenbrandt, H., & Komdeur, J. (2016). The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behavioral Ecology and Sociobiology*, 70(9), 1591-1600.

Ardia, D. R., Pérez, J. H., Chad, E. K., Voss, M. A., & Clotfelter, E. D. (2009). Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. *Journal of Animal Ecology*, 78(1), 4-13.

Audet, J. N., Ducatez, S., & Lefebvre, L. (2015). The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, 27(2), 637-644.

Baudains, T. P., & Lloyd, P. (2007). Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation*, 10(3), 400-407.

Berntsen, H. H., & Bech, C. (2016). Incubation temperature influences survival in a small passerine bird. *Journal of Avian Biology*, 47(2), 141-145.

Biancucci, L., & Martin, T. E. (2008). First description of the breeding biology and natural history of the Ochre-breasted Brush Finch (*Atlapetes semirufus*) in Venezuela. *The Wilson Journal of Ornithology*, 120(4), 856-863.

Blem, C. R., & Blem, L. B. (2006). Variation in mass of female Prothonotary Warblers during nesting. *The Wilson Journal of Ornithology*, 118(1), 3-13.

Breen, A., Guillette, L. M., & Healy, S. D. (2016). What can nest-building birds teach us? *Comparative Cognition & Behavior Reviews*, 11, 83-102.

Bryan, S. M., & Bryant, D. M. (1999). Heating nest–boxes reveals an energetic contraint on incubation behaviour in great tits, *Parus major*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1415), 157-162.

Bueno-Enciso, J., Ferrer, E. S., Barrientos, R., & Sanz, J. J. (2016). Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. *Journal of Ornithology*, 157(3), 759-772.

Burhans, D. E., & Thompson III, F. R. (2001). Relationship of songbird nest concealment to nest fate and flushing behavior of adults. *The Auk*, 118(1), 237-242.

Capp, E., Liebl, A. L., Cones, A. G., & Russell, A. F. (2018). Advancing breeding phenology does not affect incubation schedules in chestnut-crowned babblers: Opposing effects of temperature and wind. *Ecology and Evolution*, 8(1), 696-705.

Chalfoun, A. D., & Martin, T. E. (2007). Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Animal Behaviour*, 73(4), 579-585.

Chen, J. N., Liu, N. F., Yan, C., & An, B. (2011). Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. *Journal of Ornithology*, 152(3), 603-608.

Clauser, A. J., & McRae, S. B. (2017). Plasticity in incubation behavior and shading by King Rails *Rallus elegans* in response to temperature. *Journal of Avian Biology*, 48(4), 479-488.

Conway, C. J., & Martin, T. E. (2000). Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution*, 54(2), 670-685.

Cooper, C. B., & Voss, M. A. (2013). Avian incubation patterns reflect temporal changes in developing clutches. *Plos one*, 8(6), e65521.

Cresswell, W., Holt, S., Reid, J. M., Whitfield, D. P., Mellanby, R. J., Norton, D., & Waldron, S. (2004). The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behavioral Ecology*, 15(3), 498-507.

Deeming, D. C. (2016). How does the bird-nest incubation unit work? *Avian Biology Research*, 9(2), 103-113.

Eggers, S., Griesser, M., & Ekman, J. (2008). Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behavioral Ecology*, 19(5), 1056-1062.

Endo, S., & Ueda, K. (2016). Factors affecting female incubation behavior in the Bull-headed Shrike. *Ornithological Science*, 15(2), 151-161.

Evans, M. L., & Stutchbury, B. J. (2012). Nest attendance and reproductive success in the Wood Thrush. *The Condor*, 114(2), 401-406.

Fan, L. Q., Chen, G. L., Da, X. W., Luo, J. J., Xian, L. L., Ren, Q. M., ... & Du, B. (2017). Seasonal variation in food availability influences the breeding strategy of White-collared Blackbirds *Turdus albocinctus* on the Tibetan Plateau. *Ibis*, 159(4), 873-882.

Fast, P. L., Grant Gilchrist, H., & Clark, R. G. (2007). Experimental evaluation of nest shelter effects on weight loss in incubating common eiders *Somateria mollissima*. *Journal of Avian Biology*, 38(2), 205-213.

Fontaine, J. J., & Martin, T. E. (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters*, 9(4), 428-434.

Forrester, T. R., & Londoño, G. A. (2016). Breeding biology and egg temperatures of Black-faced Brush-finches (*Atlapetes melanolaemus*), Neotropical montane songbirds. *Journal of Field Ornithology*, 87(3), 260-272.

Forstmeier, W., & Weiss, I. (2004). Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, 104(3), 487-499.

Ghalambor, C. K., & Martin, T. E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, 292(5516), 494-497.

Gómez-Serrano, M. Á., & López-López, P. (2014). Nest site selection by Kentish Plover suggests a trade-off between nest-crypsis and predator detection strategies. *PLoS One*, 9(9), e107121.

Griebel, I. A., Fairhurst, G. D., Marchant, T. A., & Clark, R. G. (2018). Effects of parental and nest-site characteristics on nestling quality in the Tree Swallow (*Tachycineta bicolor*). *Canadian Journal of Zoology*, 97(1), 63-71.

Halupka, K., & Greeney, H. F. (2009). The influence of parental behavior on vulnerability to nest predation in tropical thrushes of an Andean cloud forest. *Journal of Avian Biology*, 40(6), 658-661.

Hilton, G. M., Hansell, M. H., Ruxton, G. D., Reid, J. M., & Monaghan, P. (2004). Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. *The Auk*, 121(3), 777-787.

Højsgaard, S., Halekoh, U., &Yan, J. (2014). geepack: Generalized estimating equation package. *R package version*, 1-2.

Hu, Y. B., Zhao, Q. S., Lou, Y. Q., Chen, L. J., González, M. A., & Sun, Y. H. (2017). Parental attendance of Chestnut Thrush reduces nest predation during the incubation period: compensation for low nest concealment? *Journal of Ornithology*, 158(4), 1111-1117.

Latif, Q. S., Heath, S. K., & Rotenberry, J. T. (2012). How avian nest site selection responds to predation risk: testing an ‘adaptive peak hypothesis’. *Journal of Animal Ecology*, 81(1), 127-138.

Lessi, B. F., Pires, J. S. R., Batisteli, A. F., & MacGregor-Fors, I. (2016). Vegetation, urbanization, and bird richness in a Brazilian periurban area. O*rnitología Neotropical*, 27, 203-210.

Lloyd, J. D., & Martin, T. E. (2004). Nest-site preference and maternal effects on offspring growth. *Behavioral Ecology*, 15(5), 816-823.

Londoño, G. A., Levey, D. J., & Robinson, S. K. (2008). Effects of temperature and food on incubation behaviour of the northern mockingbird, *Mimus polyglottos*. *Animal Behaviour*, 76(3), 669-677.

Lothery, C. J., Thompson, C. F., Lawler, M. L., & Sakaluk, S. K. (2014). Food supplementation fails to reveal a trade-off between incubation and self-maintenance in female house wrens. *PloS one*, 9(9), e106260.

Mainwaring, M. C. (2015). The use of man-made structures as nesting sites by birds: A review of the costs and benefits. *Journal for Nature Conservation*, 25, 17-22.

Martin, T. E., Oteyza, J. C., Boyce, A. J., Lloyd, P., & Ton, R. (2015). Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. *The American Naturalist*, 186(2), 223-236.

Martin, T. E., Ton, R., & Oteyza, J. C. (2017). Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines. *The Auk: Ornithological Advances*, 135(1), 101-113.

McGowan, C. P., & Simons, T. R. (2006). Effects of human recreation on the incubation behavior of American Oystercatchers. *The Wilson Journal of Ornithology*, 118(4), 485-494.

Miller, D. A., Grand, J. B., Fondell, T. F., & Anthony, R. M. (2007). Optimizing nest survival and female survival: consequences of nest site selection for Canada geese. *The Condor*, 109(4), 769-780.

Møller, A. P. (2010). The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behavioral Ecology*, 21(5), 913-918.

Møller, A. P., Tryjanowski, P., Díaz, M., Kwieciński, Z., Indykiewicz, P., Mitrus, C., ... & Polakowski, M. (2015). Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behavioral Ecology*, 26(3), 861-865.

Mueller, A. J., Miller, K. D., & Bowers, E. K. (2019). Nest microclimate during incubation affects posthatching development and parental care in wild birds. *Scientific Reports*, 9(1), 5161.

Pearse, A. T., Cavitt, J. F., & Cully, J. F. (2004). Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *The Wilson Journal of Ornithology*, 116(1), 23-31.

Pinheiro, J., Bates, D., Saikat, D., Sarkar, D., & R Development Core Team. (2011). Linear and nonlinear mixed-effects models (nlme). R package version 3.1-101.

Piratelli, A. J., Favoretto, G. R., & Maximiano, M. F. (2015). Factors affecting escape distance in birds. *Zoologia (Curitiba)*, 32(6), 438-444.

Potascheff, C. D. M., Lombardi, J. A., & Lorenzi, H. (2010). Angiosperm trees and shrubs on the campus of the São Paulo State University Júlio de Mesquita, Rio Claro (SP), Brazil. *Bioikos*, 24(1), 21-30.

Redfern, C. P. (2010). Brood-patch development and female body mass in passerines. *Ringing & Migration*, 25(1), 33-41.

Reid, J. M., Monaghan, P., & Ruxton, G. D. (2000). Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1438), 37-41.

Reneerkens, J., Grond, K., Schekkerman, H., Tulp, I., & Piersma, T. (2011). Do uniparental Sanderlings *Calidris alba* increase egg heat input to compensate for low nest attentiveness? *PLOS one*, 6(2), e16834.

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P., & Mainwaring, M. C. 2019. Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology*, 160, 841-860.

Ricklefs, R. E., & Brawn, J. (2013). Nest attentiveness in several Neotropical suboscine passerine birds with long incubation periods. *Journal of Ornithology*, 154(1), 145-154.

Robertson, B. A. (2009). Nest-site selection in a postfire landscape: do parents make tradeoffs between microclimate and predation risk? *The Auk*, 126(3), 500-510.

Robinson, W. D., Austin, S. H., Robinson, T. R., & Ricklefs, R. E. (2014). Incubation temperature does not explain variation in the embryo development periods in a sample of Neotropical passerine birds. *Journal of Ornithology*, 155(1), 45-51.

Rodewald, A. D., & Kearns, L. J. (2011). Shifts in dominant nest predators along a rural-to-urban landscape gradient. *The Condor*, 113(4), 899-906.

Ruggera, R. A., & Martin, T. E. (2010). Breeding biology and natural history of the Slate-throated Whitestart in Venezuela. *The Wilson Journal of Ornithology*, 122(3), 447-454.

Santos, E. S. A., & Nakagawa, S. (2012). The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology*, 25(9), 1911-1917.

Schmidt, K. A., & Whelan, C. J. (2005). Quantifying male Wood Thrush nest-attendance and its relationship to nest success. *The Condor*, 107(1), 138-144.

Suarez, F., Traba, J., & Herranz, J. (2005). Body mass changes in female tawny pipits *Anthus campestris* during the nesting stage. *Journal of Ornithology*, 146(4), 372-376.

Tella, J. L., Canale, A., Carrete, M., Petracci, P., & Zalba, S. M. (2014). Anthropogenic nesting sites allow urban breeding in burrowing parrots *Cyanoliseus patagonus*. *Ardeola*, 61(2), 311-322.

Vafidis, J. O., Facey, R. J., Leech, D., & Thomas, R. J. (2018). Supplemental food alters nest defence and incubation behaviour of an open-nesting wetland songbird. *Journal of Avian Biology*, 49, e01672.

Vedder, O., Verhulst, S., Zuidersma, E., & Bouwhuis, S. (2018). Embryonic growth rate affects telomere attrition: an experiment in a wild bird. *Journal of Experimental Biology*, 221(15), jeb181586.

Wang, Y., Huang, Q., Lan, S., Zhang, Q., & Chen, S. (2015). Common blackbirds *Turdus merula* use anthropogenic structures as nesting sites in an urbanized landscape. *Current Zoology*, 61(3), 435-443.

Węgrzyn, E., & Leniowski, K. (2011). Nest site preference and nest success in Blackcaps *Sylvia atricapilla* in Poland. *Ardeola*, 58(1), 113-125.

Weidinger, K. (2002). Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology*, 71(3), 424-437.

Wiebe, K. L., & Martin, K. (1997). Effects of predation, body condition and temperature on incubation rhythms of White-tailed Ptarmigan *Lagopus leucurus*. *Wildlife Biology*, 3(3/4), 219-228.

Wysocki, D. (2004). Nest re-use by Blackbirds—the way for safe breeding? *Acta Ornithologica*, 39(2), 164-168.

Yeh, P. J., Hauber, M. E., & Price, T. D. (2007). Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos*, 116(9), 1473-1480.

Tov, Y. Y., & Wright, J. (1993). Effect of heating nest boxes on egg laying in the Blue Tit (*Parus caeruleus*). *The Auk*, 110(1), 95-99.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

Capítulo 3

CAUSES AND CONSEQUENCES OF MATE CHANGE AND NEST REUSE IN A NEOTROPICAL THRUSH

CAUSES AND CONSEQUENCES OF MATE CHANGE AND NEST REUSE IN A NEOTROPICAL THRUSH

ABSTRACT

Most bird species are socially monogamous and pairs realize non-random nest site choices as a way to escape from nest predators – the major source of nest failure. However, different mating systems and breeding behavioral decisions evolved from the demand for maximizing offspring production at a given reproductive cost. Nest reuse is a potential strategy to save time and energy, but is rare among open-cup nesting passerines. Few studies have addressed the causes and consequences of divorce and nest reuse in birds, and the way they interplay to affect reproductive output. Here, we studied an urban population of the Pale-breasted Thrush (*Turdus leucomelas* Vieillot, 1818) with an unusual high rate of nest reuse to test whether a) mate change occurs more within or between breeding season and depends on the fate of the last clutch, b) mate change and nest reuse are adaptive strategies considering fledgling production in the following clutch. We also tested whether nest reuse c) is enhanced by pair stability and the fate of the last clutch both within and between breeding seasons, d) allows earlier first clutches each year or shorter renesting interval, and f) reduces the chance of brood parasitism by the Shiny Cowbird (*Molothrus bonariensis* [Gmelin, 1788]). Mate change occurred more frequently between than within breeding seasons, regardless of the fate of last clutch, and newly bonded pairs produced less fledglings than stable pairs. Nest reuse was more frequent after a successful clutch, in accordance with predicted by "win stay, loose switch" strategy, but the reuse of successful nests did not assure higher nest success. Females that reuse nests had earlier clutches but did not have shorter renesting intervals, and clutches in reused nests were less parasitized by cowbirds. Our results supported the idea that both long-term bond duration and nest reuse are adaptive behavioral strategies for the Pale-breasted Thrush from the point of view of fledgling production.

Keywords: divorce, nesting behavior, pair bond duration, social monogamy, *Turdus leucomelas*.

RESUMO

Causas e consequências da troca de parceiros e da reutilização de ninhos em um sabiá Neotropical – A maior parte das espécies de aves são socialmente monogâmicas e os pais realizam escolhas orientadas do local de nidificação como uma forma de escapar de predadores de ninhada – a maior causa de fracasso dos ninhos. Entretanto, diferentes sistemas de acasalamento e decisões do comportamento reprodutivo evoluíram pela demanda de maximizar a produção de descendentes a um dado custo reprodutivo. A reutilização de ninhos é uma estratégia potencialmente capaz de economizar tempo e energia, mas é rara entre os passeriformes de ninhos abertos. Poucos estudos tem investigado as causas e consequências do divórcio e do reuso de ninhos em aves, e a forma com que eles interagem e afetam a performance reprodutiva. Estudamos uma população urbana do sabiá-barranco (*Turdus leucomelas* Vieillot, 1818) com uma taxa anormal de reutilização de ninhos para testar se a) a troca de parceiros ocorre mais dentro ou entre estações reprodutivas e depende do destino na última ninhada, b) a troca de parceiros e a reutilização de ninhos são estratégias adaptativas considerando a produção de filhotes na ninhada subsequente. Também testamos se a reutilização de ninhos c) é favorecida pela estabilidade do casal e pelo destino da última ninhada tanto dentro quanto entre estações reprodutivas, d) viabiliza a antecipação das primeiras ninhadas no início da estação reprodutiva ou menores intervalos entre as ninhadas, e f) reduz a chance de parasitismo pelo chupim (*Molothrus bonariensis* Gmelin, 1788). A troca de parceiros ocorreu mais frequentemente entre do que na mesma estação reprodutiva, independentemente do destino da última ninhada, e pares recém-formados produziram menos filhotes. A reutilização do ninho foi mais frequente após uma ninhada de sucesso (corroborando a estratégia "vencer ficar, perder mudar"), mas a reutilização de ninhos após o sucesso da ninhada não resultou em maior sucesso da próxima ninhada. Fêmeas que reutilizaram ninhos tiveram ninhadas antecipadas no início da estação mas não tiveram intervalos mais curtos entre as ninhadas, e ninhadas em ninhos reutilizados foram menos parasitadas pelo chupim. Nossos resultados suportam a ideia de que a longa duração dos laços entre pares reprodutivos e a reutilização de ninhos são estratégias comportamentais adaptativas para o sabiá-barranco do ponto de vista da produção de filhotes.

Palavras-chave: Comportamento reprodutivo, divórcio, duração do par reprodutivo, monogamia social, *Turdus leucomelas.*

INTRODUCTION

The wide diversity of animal reproductive strategies must counterbalance the demand to maximize offspring production and the energetic investment in reproduction (Alcock & Rubenstein 2019). Part of the solution to this trade-off is expressed in the evolution of different mating systems and parental care behavior, which are adjusted to specific life-history traits (Reynolds 1996, Royle *et al.* 2012). The social monogamy with biparental care, which involves offspring provisioning and nest defense by both parents, is the commonest mating system among birds (Cockburn 2006). However, sexual conflicts lead to specialization and sexual asymmetry in breeding tasks. Males, for instance, risk more in active nest defense (Trivers 1972), whereas the cost of some passive defenses such as covering the eggs and nestlings is usually devoted to females (Auer 2007).

Numerous advantages emerge from long-term pair bonds in socially monogamous birds, from early nest initiation to enhanced breeding success (Griggio & Hoi 2011, Sánchez-Macouzet *et al.* 2014). The scarcity of nearby unpaired mates and mortality risks associated with looking for a new mate contribute to constraint mate change (Freed 1987, Jankowiak *et al.* 2018). Nevertheless, several hypothesis have been proposed to explain how mate change in monogamous passerines may be adaptive – at least for one mate or a third bird – under particular circumstances, such as mate incompatibility, mate usurpation, and the choice for a higher quality mate (the "better option hypothesis", Choudhury 1995). Sex-biased mortality due to asymmetry in breeding costs may impute higher rates of mate change initiation to a given sex (Kraaijeveld 2003, Liker & Székely 2005; but see Cézilly 2000).

A major barrier for successful breeding, that has potential impacts on bird population dynamic and avian community structuring is nest failure (Martin 1988, Thompson 2007). Predation, in turn, is the commonest cause of nest failure in a variety of species and ecosystems (Sanders & Maloney 2002, Auer 2007, Marini *et al.* 2017). Eggs and nestlings are usually defenseless and attract a variety of specialized or opportunistic nest predators (Menezes & Marini 2017). Brood parasitic birds have also an important negative effect on nesting success, through damages on host eggs and nestling-nestling competition (Kilner 2003, Astié & Reboreda 2006). The strong evolutionary pressure over nesting success favors the emergence of parent behavioral mechanisms that increase the chance of clutch success, for instance, by nest site selection (Lima 2009).

Certain features of a potential nest site, such as the degree of nest concealment and habitat structure, are used by breeding birds as proxy to lower the risk of both brood predation and parasitism (Saunders *et al.* 2003, Fiorini *et al.* 2009, Young *et al.* 2017, Guilherme *et al.* 2018). However, such strategies to select a safe nest site are not unidirectional processes, because its efficacy in precluding nest location depends on the behavior and cognitive abilities of the main nest predators at local scale, which vary with space and time (Jokimäki *et al.* 2005, Sperry *et al.* 2008). To cope with such constant changes in environmental pressures, individuals can develop life-time behavioral responses to manage predation risk, using information gathered on their previous breeding attempts to decide where to build their nests (Chalfoun & Martin 2010, Chen *et al.* 2011). Nest site selection, thus, is a complex process in which parents integrate inherited and cognitive aspects (Slagsvold *et al.* 2013).

Some individuals/couples may use existing nests from previous reproductive seasons or rebuild nests in previous nesting sites, in order to save time and energy ("time/energy saving hypothesis", Cancellieri & Murphy 2013). The benefits related to reuse of nests can be expressed in earlier clutch initiation (Cavitt 1999, Herzog *et al.* 2018), increased fledgling production (McIvor & Healy 2017), and shortened nest replacement (Cancellieri & Murphy 2013). Nest reuse, however, is rare among open cup nesting passerines. The change of nest location enables breeding birds to avoid repeated nest failures due to short-term predator memory (Martin *et al.* 2000, Weidinger & Kočvara 2010). In fact, it is expected that a positive breeding experience (i.e., a successful nest) reinforce nest site fidelity, while a failure should induce changes in nesting site (the "win stay loose switch" strategy), from the microhabitat to patch scales (Chalfoun & Martin 2010). For instance, pairs may disperse farther after a failed rather than a successful clutch (Chalfoun & Martin 2010, Fisher & Wiebe 2006), which will depend on the predator type and its home range (Powell & Frasc 2000). More frequently, nesting failures induce only small changes in nest site characteristics, such as nest height above ground and nest concealment (Beckmann & McDonald 2016, Hunter *et al.* 2016). However, most studies have failed to corroborate the idea that the reuse of a successful nest increases the survival chance for the following clutch (Herzog *et al.* 2018).

Pair bond stability, nest site fidelity and breeding success are potentially interrelated, but few studies investigated causes and consequences of mate change and nest site reuse concomitantly, especially for open nesting passerines. In this paper, we use an urban population of the Pale-breasted Thrush (Turdus leucomelas) with an unusual high rate of nest reuse to test whether a) mate change is more common between than within breeding seasons, and depends on the fate of the last clutch, b) mate change is adaptive considering fledgling production in the first breeding attempt of newly bonded pairs, as predicted by the "better option hypothesis", c) nest reuse is enhanced by pair stability and the fate of the last clutch ("win stay, loose switch" strategy) both within and between breeding seasons, d) nest reuse permits the anticipation of the laying date in the beginning of the breeding season or reduce the interval between consecutive nesting attempts in a given breeding season (hereafter "renesting interval"), e) the reuse of successful nests favors the success of the following clutch, and f) nest reuse in consecutive clutches reduces the chance of cowbird parasitism.

MATERIALS AND METHODS

Study area

The study was conducted at the campus of the Universidade Estadual Paulista Júlio de Mesquisa Filho (UNESP) in Rio Claro, São Paulo state, Brazil (22º23'43"S, 47º32'46"W, 628 m a.s.l.). The campus is a suburban area of approximately 115 ha, of which ca. 52 ha consist of an urban area rich in unpaved spaces, such as lawns, gardens with exotic shrubs and trees, and small (<1 ha) woodlands of native vegetation of the semidecidual seasonal forest of the Atlantic Forest domain (Potaschef *et al.* 2010).

Study species

The Pale-breasted Thrush is a Neotropical resident, monomorphic, and socially monogamous passerine (Sick 1997). Adults (ca. 23.4 cm in body length) weigh around 69.1 g, and females are slightly heavier than males (Moraes *et al.* 2018). This species is widely distributed in South America, with exception of its southern portion, Amazonian Forest, and Andean regions (Sick 1997). It inhabits riparian forests to green urban areas, where it benefits from exotic plants as food sources and human buildings as nesting substrates (Gasperin & Pizo 2009, Batisteli & Sarmento 2016). In the study region, Pale-breasted Thrushes breed typically from September to December, and each couple have up to three nesting attempts, but not more than two successful broods a year (Davanço *et* *al.* 2013). The nest is a robust and low cup of ca. 13.2 cm in external diameter and 10.2 cm height, composed by a mix of vegetal material (mainly roots, moss, and fibers) and mud (Ruiz *et al.* 2017). Clutch size is usually of three eggs, ranging from one to four (Davanço *et al.* 2013). Although females solely build the nest, incubate the eggs, and brood the nestlings, both parents share nestling provisioning, nest sanitation, and nest defense (Batisteli, unpubl. data). As other Neotropical thrushes, the Pale-breasted Thrush is a host for the brood parasite Shiny Cowbird (*Molothrus bonariensis*) (Lowther 2018).

Field procedures

Our nest search was restricted to the urbanized portion of the campus to assure an accurate monitoring of breeding adults, because precise data on the breeding history of specific pairs was more important to our study than a high number of breeding pairs without good breeding history. We conducted nest search every other day from middle August to late December from 2013 to 2019. We found nests by following adult thrushes and inspecting all potential nesting sites (trees and human buildings). During the whole study period, we captured adult thrushes with mist nests, and marked captured birds with a unique combination of colored leg bands and a metallic ring. Nestlings were also banded during the whole study period. We collected blood samples of each captured adult or nestlings following the toenail clip method (Owen 2011), and used them to sex birds in an outsourced laboratory (UNIGEN – Biologia pelo DNA, São Paulo, Brazil) through the polymerase chain reactions method.

We assigned a numeric code for each nest when discovered. In the non-breeding season, some old nests were inadvertently removed by university staff or fall down to the ground due to unknown causes. When any female returned to use one of these vacated nesting sites, we assigned a new number to the new nest built. Thus, we only classified nests as reused when females had consecutive breeding attempts in the same nest structure. Otherwise, exclusively to test if an old nest would save time and energy in the beginning of the breeding season and between consecutive clutches, we used “nest reuse” in a broad sense (i.e., females that reuse any old nest structure). Undiscovered clutches in the start of the breeding season might inflate laying date estimates of new nests if we incorrectly assign a second clutch as a first one. To reduce this potential problem, we only considered nests found within the first 30 days after the start of the breeding season when analyzing the effect of nest reuse on laying date. We chose this threshold because only two of 43 known second clutches have laying dates within the first 30 days of the start of the breeding season.

We checked all nests every 1-3 days to monitor nest content and nest fate by recording the number of eggs and nestlings of the thrush and the cowbird. Parasite and thrush eggs are discernible by size, shape and eggshell coloration, and parasite hatchlings differ from thrush ones by a black down in the back and more rosy skin. We recorded the date of the first egg laying of each clutch (hereafter "laying date") assuming that females laid one egg per day. For nests found after clutch completion, we estimated the laying date backdating from hatching day, considering a 14-day interval between the first egg laying and hatching date. For each breeding season, we assumed the earliest laying date of all nests as the day 1 of the breeding season. The renesting interval was calculated by the difference between the estimated fledging date or the day when a clutch was preyed and the laying date of the next clutch of the same female.

A clutch was considered successful when at least one nestling (either thrush or cowbird) survived until fledging. Otherwise, a clutch was considered failed when eggs or nestlings disappeared from the nest before the expected fledging date (likely due to predation), when nestlings died in the nest, or when eggs remained in the nest without any signal of adult presence during three consecutive monitoring visits. For the purpose of this study, we were not able to differentiate causes of nesting failure, but the majority of failed clutches fitted the characteristics of predation events. We defined mate change as an adult bird nesting with a different mate in relation to the previous breeding attempt, regardless if it had been caused by widowhood. In opposition, we defined a stable pair when an adult remained bonded with the same mate in consecutive clutches. Nests attended by unbanded pairs were excluded from analyses.

Statistical analyses

Since our data contained repeated observations of breeding pairs and nests, we built linear mixed-effects models (LMMs) and generalized mixed-effects models (GLMMs) to test our predictions. Numeric transformations, model structure, and data subsets used in each analysis are summarized below:

1) We built GLMMs to test whether mate change is more common after failed clutches and between rather than within breeding seasons (all binary variables). Data from

banded males and females were analyzed separately to maximize our sample size, and adult ID was set as a random factor in both models.

2) Cowbird parasitism reduces the number of fledglings per clutch (see Results). We discarded parasitized clutches, and built a linear mixed-effects model (LMM) testing whether the number of fledglings (square-root-transformed) is affected by pair stability (0 = stable pairs, 1 = recently bonded pairs), time of mate change (0 = within, 1 = between breeding seasons), and the interaction between these variables. Clutch size (i.e., the number of eggs) was used as a covariate, whereas pair ID and nest number were set as random factors.

3) We built a binomial GLMM to test whether the decision for nest reuse is affected by the last clutch outcome (0 = failed, 1 = successful), pair stability, the interval between clutches (within vs. between breeding seasons), and all possible interactions between these binary variables, using female ID as a random factor. Non-significant terms were dropped by stepwise backward selection, comparing nested models by a chi-square test (Zuur *et al.* 2009).

4) To test whether nest reuse is in line with the predictions of time/energy save hypothesis, we built LMMs using laying date and renesting interval as continuous response variables (both square root-transformed). Nest reuse (coded 0 = reuse of any old nest structure, 1 = new) and year were set as categorical explanatory variables, whereas female ID and nest number were set as random factors in both models.

5) Recently bonded pairs produced less fledglings (see Results). Thus, we used only data on stable pairs in a LMM to test whether the number of fledglings (square-root-transformed) is affected by nest reuse either within or between breeding seasons, setting the presence of cowbirds as another explanatory binary variable, clutch size as a covariate, and female ID and nest number as random factors.

6) Finally, we used a GLMM to test whether brood parasitism by the cowbird is less common in nests reused both within and between breeding seasons (all binary variables), employing female ID and nest number as random factors.

The analyses were conducted in the software R (R Development Core Team 2019) using the packages “lme4” (Bates *et al.* 2014) and “lmerTest” (Kuznetsova *et al.* 2015), with $\alpha = 0.05$.

RESULTS

We banded 469 individuals (323 adults and 146 nestlings), of which 96 (52 males and 44 females) were recorded forming breeding pairs during the study. From 262 monitored clutches, 169 had at least one banded individual, from which we could obtain data on 130 renesting events. Considering data from banded females (the larger subset), nest reuse occurred in 69 of 99 clutches. Among pairs in which both birds were banded, only nine out of 45 males and ten out of 35 females were seen with more than one mate during the study. Mate change occurred more between than within breeding seasons, either considering data from banded females or males, and was not related to the last clutch outcome for any parental sex (Table 3-1, Fig. 3-1).

Newly bonded pairs produced significantly less fledglings in their first clutch irrespective of clutch size (Table 3-2, Fig. 3-2). Time of mate change (within or between breeding seasons) and its interaction with pair composition were absent from the final model ($p = 0.182$ and $p = 0.192$, respectively), indicating that the lower breeding success of newly bonded pairs is consistent regardless of the time when mate change occurred.

Nest reuse was more frequent among pairs that remained together and after successful clutches, either comparing nesting attempts within or between breeding seasons (hereafter "inter-clutch time", Table 3-1). However, the predisposition of reusing the nest after a successful clutch was restricted to clutches within the same breeding season (last clutch outcome × inter-clutch time in Table 3-1, Fig. 3-3). In most cases of nest reuse, the old nest structure remained relatively intact during the interseasonal period because of the protection provided by buildings. Females that reuse these nests either just lined the old structure or, more rarely, built a new nest on the top of the old one.

Table 3-1. Results of generalized linear mixed-effects models assessing the effect of binary variables on the occurrence of divorce (including possible widowhood cases) and nest reuse, and the relationship between nest reuse and brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*) in the Pale-breasted Thrush (*Turdus leucomelas*). Time of year = within/between breeding seasons; last clutch outcome = failure/success; inter-clutch time = consecutive nesting attempts within/between breeding seasons; pair stability = stable/newly bonded pairs. * statistical significance at $\alpha = 0.05$.

	Estimate	Std. error	z	p
Divorce among banded females				
Intercept	-1.747	0.541	-3.228	0.001*
Time of year	1.603	0.615	2.605	0.009*
Last clutch outcome	-0.375	0.599	-0.627	0.531
Divorce among banded males				
Intercept	-2.924	0.895	-3.266	0.001*
Time of year	2.411	0.881	2.736	0.006*
Last clutch outcome	0.123	0.778	0.159	0.874
Nest reuse				
Intercept	1.818	0.952	1.909	0.056
Last clutch outcome	-2.963	1.117	-2.654	0.008*
Inter-clutch time	-1.506	1.349	-1.116	0.264
Pair stability	2.653	1.265	2.098	0.036*
Last clutch outcome × Inter-clutch time	3.812	1.787	2.133	0.033*
Brood parasitism				
Intercept	-1.302	0.444	-2.931	0.003*
Inter-clutch time	-0.170	0.479	-0.356	0.722
Nest reuse	2.024	0.516	3.923	0.000*

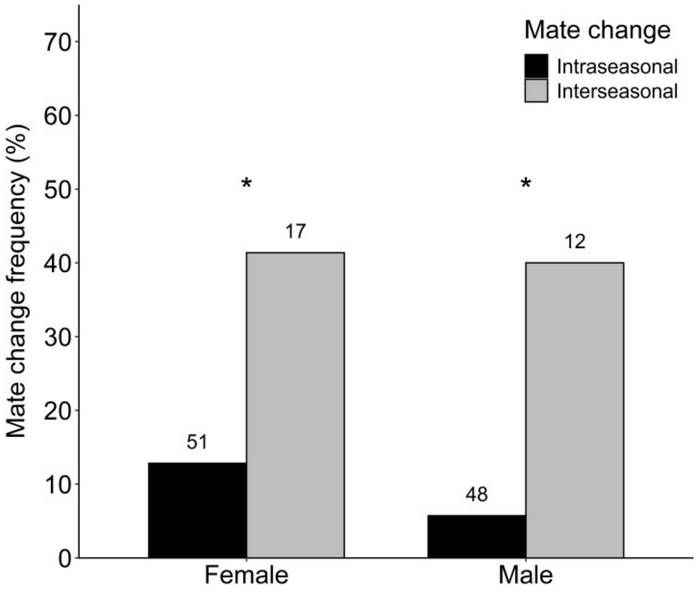


Fig. 3-1 Frequency of mate change among Pale-breasted Thrush (*Turdus leucomelas*) pairs within (black bars) and between breeding seasons (grey bars) (from 2013 to 2019), separately from banded females and males. Numbers above bars represent sample size, and asterisks indicate statistical significance at α = 0.05.

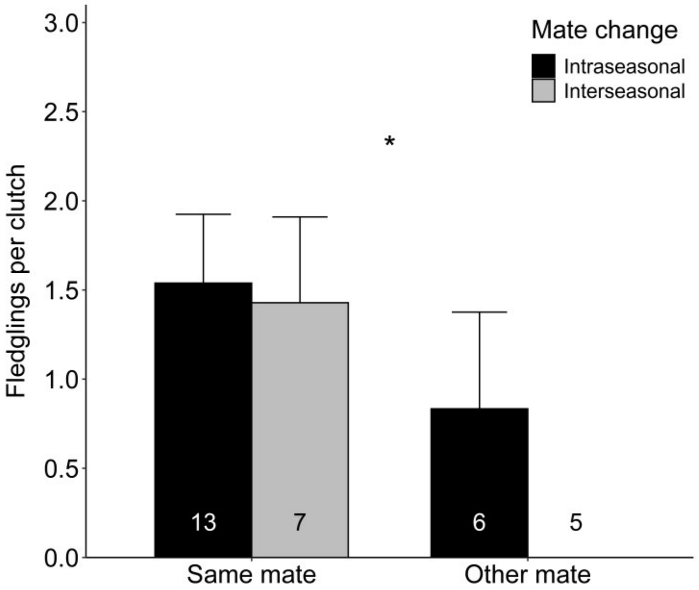


Fig. 3-2 Number of fledglings produced per clutch in relation to pair composition and time of mate change (within or between breeding seasons represented by black and grey bars, respectively) in an urban population of the Pale-breasted Thrush (*Turdus leucomelas*). Numbers inside bars represent sample size, whiskers denote standard errors, and asterisk indicates statistical significance at α = 0.05.

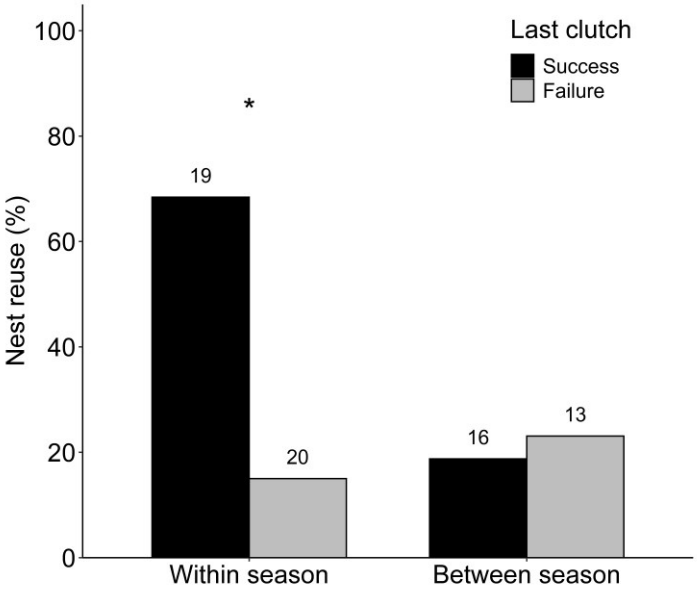


Fig. 3-3 Frequency of nest reuse within and between breeding seasons (black and grey bars, respectively) in relation to the fate of the last clutch in an urban population of the Pale-breasted Thrush (*Turdus leucomelas*). Numbers above bars represent sample size for each group, and asterisk indicates statistical significance at α = 0.05.

The laying date of the first clutch of each female at each year was earlier among reused nests compared to new ones, and did not vary significantly among years (Table 3-2, Fig. 3-4A) (n = 78 clutches of 25 banded females in 63 different nests). On the other hand, the renesting interval did not differ between reused (either the same or another reused nest) and new nests (Table 3-2, Fig. 3-4B), nor among the years of the study (n = 49 clutches of 21 banded females in 42 different nests).

Among pairs that stayed together between consecutive clutches, however, the number of fledglings produced in the latter clutch was not affected by nest reuse, neither by the number of eggs or inter-clutch time (Table 3-2). However, the number of fledglings was lower in clutches parasitized by the cowbird (Table 3-2, Fig. 3-5). The number of fledglings in reused nests did not differ between intra- or interseasonal nest reuse (inter-clutch time × nest reuse, Table 3-2). Cowbird parasitism, in turn, was less frequent when consecutive clutches are in the same nest, and this pattern did not vary within and between breeding seasons (Table 3-1, Fig. 3-6).

Table 3-2. Results of linear mixed-effects models assessing the effect of divorce, nest reuse, pair stability (stable/newly bonded pairs) and time of divorce (within/between breeding seasons) on the number of fledglings, using clutch size as a covariate, and the consequence of nest reuse in laying date and renesting interval through years of study in the Pale-breasted Thrush (*Turdus leucomelas*). * statistical significance at $\alpha = 0.05$.

	Estimate	Std. error	df	t	p
Number of fledglings vs. divorce (unparasitized nests only)					
Intercept	0.216	0.554	26.531	0.390	0.699
Clutch size	0.290	0.204	26.393	1.423	0.167
Pair stability	-0.751	0.275	22.856	-2.729	0.012*
Time of divorce					0.182
Pair stability × Time of divorce					0.192
Number of fledglings vs. nest reuse (clutches of stable pairs only)					
Intercept	0.463	0.434	39.820	1.067	0.293
Clutch size	0.199	0.151	39.511	1.318	0.195
Nest reuse	0.166	0.297	34.585	0.559	0.580
Inter-clutch time	0.020	0.337	26.915	0.059	0.953
Brood parasitism	-0.668	0.237	36.685	-2.822	0.008*
Nest reuse × Inter-clutch time	-0.281	0.432	34.258	-0.649	0.520
Laying date					
Intercept	-78.336	143.568	8.852	-0.546	0.599
Nest reuse	-1.195	0.353	73.493	-3.382	0.001*
Year	0.041	0.071	8.888	0.572	0.582
Renesting interval					
Intercept	-51.603	175.468	45.937	-0.294	0.770
Nest reuse	-0.372	0.315	44.347	-1.179	0.244
Year	0.027	0.087	45.935	0.314	0.755

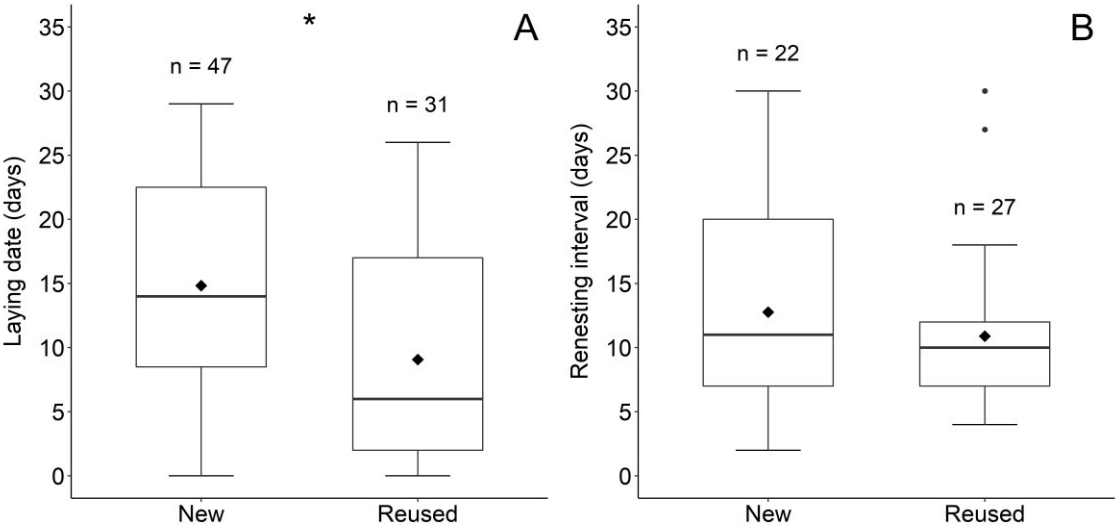


Fig. 3-4 The effect of nest reuse on the laying date of the first clutch (A), and on the renesting interval between consecutive clutches within the same breeding season (B) in an urban population of the Pale-breasted Thrush (*Turdus leucomelas*). Diamonds represent means and asterisk indicates statistical significance at α = 0.05.

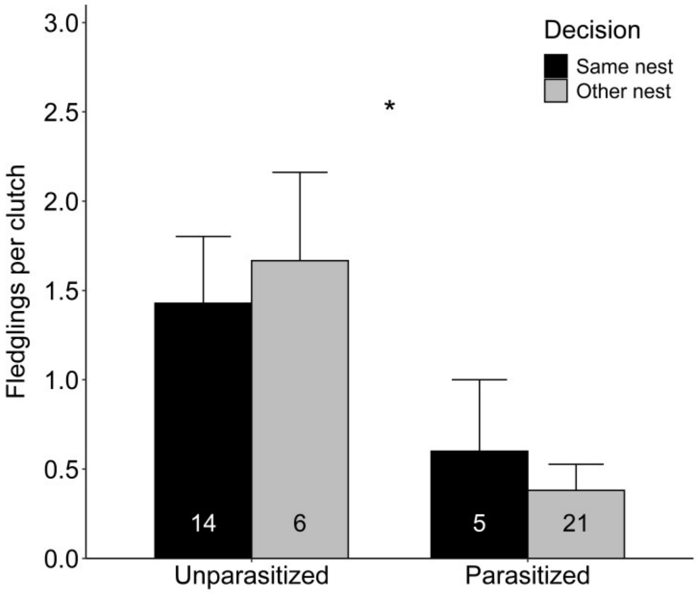


Fig. 3-5 Number of fledglings produced per clutch in the presence and absence of the brood parasite Shiny Cowbird (*Molothrus bonariensis*) and its relationship with nest reuse in an urban population of the Pale-breasted Thrush (*Turdus leucomelas*). Numbers inside bars represent sample size and asterisk indicate statistical significance at α = 0.05.

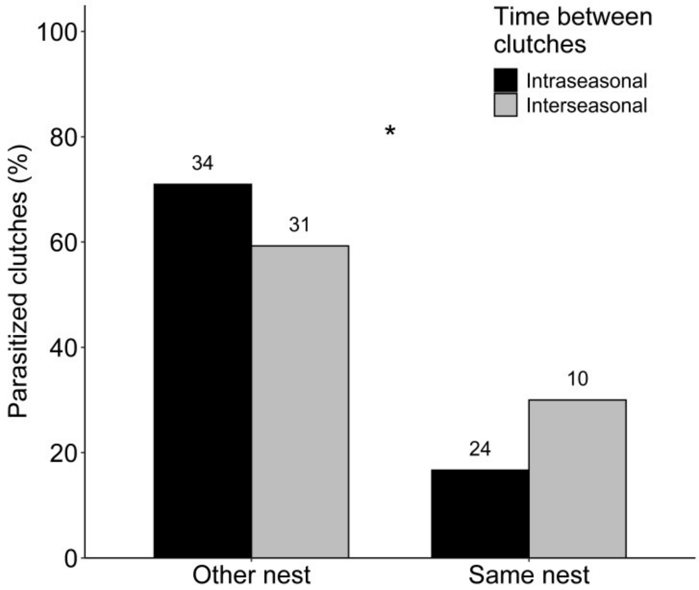


Fig. 3-6 Frequency of clutches parasitized by the Shiny Cowbird (*Molothrus bonariensis*) in relation to nest reuse within and between breeding seasons in an urban population of the Pale-breasted Thrush (*Turdus leucomelas*). Numbers above bars represent sample size and asterisk indicate statistical significance at α = 0.05.

DISCUSSION

We found that pair stability and nest reuse enhance the fitness of adult Pale-breasted Thrushes. Moreover, we found that these two behavioral features were mutually connected: stable pairs had more fledglings per clutch than newly bonded ones and were more prone to reuse nests. Nest reuse, in turn, enhanced earlier laying dates in the first clutch of each female and reduced the chance of brood parasitism by *Molothrus bonariensis*, which ultimately increased breeding success.

The Pale-breasted Thrush fits to the characteristics that favor long-duration pair bonds, namely long adult life expectancy, absence of sexual dichromatism and ornamentation, territoriality, and continuous rather than breeding-time partnerships (Jeschke & Kokko 2008). In fact, the low number of birds recorded with multiple mates across the study indicates that Pale-breasted thrushes tend to a strong, long-term social monogamy bond, which is more often broken from one breeding season to the other. Mate change is also more frequent between than within breeding seasons in Blackbirds *Turdus merula* (Wysocki 2004b). Since the Pale-breasted Thrush is a multi-brooded species (Davanço *et al.* 2013), the lower rate of mate change within the breeding season may be a strategy to seize the breeding time and maximize renesting opportunities.

Pairs remain together irrespective of the failure of the last clutch, reinforcing that the advantages of pair bond stability in the Pale-breasted Thrush emerge from multiple breeding attempts. In blackbirds, for instance, pair-bond duration is proportional to breeding season length and consequently to the amount of breeding opportunities (Jankowiak & Wysocki 2015), while searching for a new mate implies greater death risk (Jankowiak *et al.* 2018), besides the chance that there are no available mate. Our data support that the maintenance of the pair bond is also beneficial to offspring survival, likely due to a greater coordination in parental tasks (Evans & Stutchbury 2012, Leniowski & Węgrzyn 2018). Mate change, instead, may delay clutch initiation, reduce clutch mass, and increase the levels of the stress hormone corticosterone in nestlings, as experimentally showed in the socially monogamous zebrafinch *Taeniopygia guttata* (Crino *et al.* 2017). Our results did not corroborate the better option hypothesis as an explanation to mate change, which we found to be maladaptive, since newly married pairs produced less fledglings, as in blackbirds (Wysocki 2006).

We found a link between pair stability and nest reuse, which may have been driven by the domain a pair exerts on a given breeding territory and the nesting sites within that area. On the other hand, females with new mates were more prone to change nest location. Most open cup passerines build ephemeral nest structures, so that nest reuse is rare and usually occurs within the same breeding season (Aguilar & Marini 2007, Ellison 2008, but see Cavitt 1999). Nest reuse between consecutive years requires that the nest be protected from dismantling by the weather (Wysocki 2004a). In this sense, nests placed on human buildings are more likely to be reused, since they are in general more protected from bad weather than those placed on trees. However, nest integrity is not enough to induce nest reuse, as in the Eurasian blackcap *Sylvia atricapilla* (Zieliński 2012), because nest reuse depends on other factors such as the fate of last clutch and pair stability, as we found in our study.

In our studied population, nest reuse occurred more often after a successful clutch, in agreement with the "win stay, loose switch" strategy, as reported for blackbirds (Wysocki 2004a), the Neotropical Spotted Antbird *Hylophylax naevioides* (Styrsky 2005), and Dark-eyed juncos *Junco hyemalis* (Yeh 2007). Additionally, this strategy was restricted to consecutive clutches within the same breeding season, likely because the repeatability of nest fate at a given nest-site depends on a short time lapse between clutches (Weidinger & Kočvara 2010). However, reusing a successful nest did not assure great breeding success for the next clutch. This finding corroborates previous studies

(Antonov & Atanasova 2003, Wysocki 2004, Styrsky 2005), with rare exceptions, as the Vermilion Flychatcher *Pyrocephalus rubinus* in Texas (Ellison 2008). In the neotropics, nest predators and their nest searching methods are highly diverse (Menezes & Marini 2017), which helps to explain the unrelated fates of consecutive clutches in reused nests (Weidinger & Kočvara 2010).

Nest reuse, although rare among open-cup nesters, can save time and energy, enhancing earlier laying dates at the start of the breeding season and a shorter interval between intra-seasonal consecutive clutches. In our study, females that reused an old nest anticipated their first laying date each year, as in Brown Thrashers *Toxostoma rufum* (Cavitt 1999) and Magpies *Pica pica* (Antonov & Atanasova 2003). However, we failed to support the same time/energy saving benefits of nest reuse in relation to renesting interval, as well as reported for blackbirds (Wysocki 2004a) and for the Eastern Kingbird *Tyrannus tyrannus* (Cancellieri & Murphy 2013). One likely reason is that the renesting interval is subject to several factors that were not accounted for, such as adult experience (Roper 2005), the physiology of breeding adults, the remaining time for the breeding season (Nilsson 2000), and the duration of post-fledging care (Tarwater & Brawn 2010). Thus, anticipating of the laying date in the beginning of the breeding season is the mechanism by which nest reuse promotes time saving in our study population.

Most studies suggest that host activity near the nest increase the chance of brood parasitism by cowbirds (Robinson & Robinson 2001, Fiorini & Reboreda 2006, Svageli *et al.* 2009). Clutches in new nests were more parasitized than in reused ones, suggesting that cowbirds discover nests more by following parental behavioral cues than revisiting previously parasitized nests. Moreover, this difference suggests that cowbirds probably rely on specific host behaviors to locate their nests, such as nest site probing and nest building (Batisteli, pers. obs.). Apparently, the lower chance of parasitism in reused nests is related to a possible lower requirement of nest lining compared to build an entirely new nest. If so, the construction of a new nest implies that cowbirds have more opportunities to find the nest due to the higher number of building trips.

In conclusion, we found that Pale-breasted Thrushes tends to have long-term pair bonds, which lead to higher fledgling production and a greater chance of nest reuse. Clutch success enhances the probability of nest reuse, which in turn allows earlier clutches in the beginning of the breeding season, lower risk of brood parasitism, and higher fledgling production in successful nests. Our results support that pair bond stability and nest reuse are both adaptive behavioral strategies from the point of view of offspring production in the Pale-breasted Thrush.

REFERENCES

Aguilar, T. M., & Marini, M. Â. (2007). Nest and nest-site reuse within and between breeding seasons by three neotropical flycatchers (Tyrannidae). *Brazilian Journal of Biology*, 67(3), 537-540.

Alcock, J., & Rubenstein, D. R. (2019). *Animal behavior*. Sunderland, MA, USA: Sinauer Associates.

Antonov, A., & Atanasova, D. (2003). Re-use of old nests versus the construction of new ones in the Magpie *Pica pica* in the city of Sofia (Bulgaria). *Acta Ornithologica*, 38(1), 1-5.

Astié, A. A., & Reboreda, J. C. (2006). Costs of egg punctures and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) at Creamy-bellied Thrush (*Turdus amaurochalinus*) nests. *The Auk*, 123(1), 23-32.

Auer, S. K., Bassar, R. D., Fontaine, J. J., & Martin, T. E. (2007). Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *The Condor*, 109(2), 321-333.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R package version*, 1(7), 1-23.

Batisteli, A. F., & Sarmento, H. (2016). Interspecific parental care by a Rufous-collared Sparrow (*Zonotrichia capensis*) at a nest of the Pale-breasted Thrush (*Turdus leucomelas*) parasitized by a cowbird (*Molothrus bonariensis*). *Ornitología Neotropical*, 27, 253-257.

Beckmann, C., & McDonald, P. G. (2016). Placement of re-nests following predation: are birds managing risk? *Emu*, 116(1), 9-13.

Cancellieri, S., & Murphy, M. T. (2013). Experimental examination of nest reuse by an open-cup-nesting passerine: time/energy savings or nest site shortage? *Animal Behaviour*, 85(6), 1287-1294.

Cavitt, J. F., Pearse, A. T., & Miller, T. A. (1999). Brown Thrasher nest reuse: a time saving resource, protection from search-strategy predators, or cues for nest-site selection? *The Condor*, 101(4), 859-862.

Cézilly, F., Préault, M., Dubois, F., Faivre, B., & Patris, B. (2000). Pair-bonding in birds and the active role of females: a critical review of the empirical evidence. *Behavioural Processes*, 51(1-3), 83-92.

Chalfoun, A. D., & Martin, T. E. (2010). Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? *Oecologia*, 163(4), 885-892.

Chen, J. N., Liu, N. F., Yan, C., & An, B. (2011). Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. *Journal of Ornithology*, 152(3), 603-608.

Choudhury, S. (1995). Divorce in birds: a review of the hypotheses. *Animal Behaviour*, 50(2), 413-429.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences*, 273(1592), 1375-1383.

Crino, O. L., Buchanan, K. L., Fanson, B. G., Hurley, L. L., Smiley, K. O., & Griffith, S. C. (2017). Divorce in the socially monogamous zebra finch: hormonal mechanisms and reproductive consequences. *Hormones and Behavior*, 87, 155-163.

Davanço, P. V., Oliveira, L. S., Sousa, L. M., & Francisco, M. R. (2013). Breeding life-history traits of the Pale-breasted Thrush (*Turdus leucomelas*) in southeastern Brazil. *Ornitologia Neotropical*, 24, 401-411.

Ellison, K. S. (2008). Nest reuse by vermilion flycatchers in Texas. *The Wilson Journal of Ornithology*, 120(2), 339-345.

Evans, M. L., & Stutchbury, B. J. (2012). Nest attendance and reproductive success in the Wood Thrush. *The Condor*, 114(2), 401-406.

Fiorini, V. D., & Reboreda, J. C. (2006). Cues used by shiny cowbirds (*Molothrus bonariensis*) to locate and parasitise chalk-browed mockingbird (*Mimus saturninus*) nests. *Behavioral Ecology and Sociobiology*, 60(3), 379-385.

Fiorini, V. D., Tuero, D. T., & Reboreda, J. C. (2009). Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by shiny cowbirds on chalk-browed mockingbirds. *Behaviour*, 146(10), 1387-1403.

Fisher, R. J., & Wiebe, K. L. (2006). Breeding dispersal of Northern Flickers *Colaptes auratus* in relation to natural nest predation and experimentally increased perception of predation risk. *Ibis*, 148(4), 772-781.

Freed, L. A. (1987). The long-term pair bond of tropical House Wrens: Advantage or constraint? *The American Naturalist*, 130(4), 507-525.

Gasperin, G., & Pizo, M. A. (2009). Frugivory and habitat use by thrushes (*Turdus* spp.) in a suburban area in south Brazil. *Urban Ecosystems*, 12(4), 425.

González-Solís, J., Wendeln, H., & Becker, P. H. (1999). Within and between season nest-site and mate fidelity in Common Terns (*Sterna hirundo*). *Journal für Ornithologie*, 140(4), 491-498.

Griggio, M., & Hoi, H. (2011). An experiment on the function of the long-term pair bond period in the socially monogamous bearded reedling. *Animal Behaviour*, 82(6), 1329-1335.

Guilherme, J. L., Burnside, R. J., Collar, N. J., & Dolman, P. M. (2018). Consistent nest-site selection across habitats increases fitness in Asian Houbara. *The Auk: Ornithological Advances*, 135(2), 192-205.

Herzog, P., Saalfeld, S. T., Kaatz, H. H., & Lanctot, R. B. (2018). Nest reuse in arctic-breeding shorebirds: an analysis of potential benefits and factors affecting the occurrence of this rare behavior. *Journal of Avian Biology*, 49(7), e01737.

Hunter, E. A., Nibbelink, N. P., & Cooper, R. J. (2016). Threat predictability influences seaside sparrow nest site selection when facing trade-offs from predation and flooding. *Animal Behaviour*, 120, 135-142.

Jankowiak, Ł., & Wysocki, D. (2015). Do individual breeding experience and parental effort affect breeding season length in blackbirds? *Behavioral Ecology*, 27(3), 829-834.

Jankowiak, Ł., Cholewa, M., & Wysocki, D. (2018). Survival costs of within-and between-season mate change in the European blackbird *Turdus merula*. *Journal of Avian Biology*, 49(6): e01643.

Jeschke, J. M., & Kokko, H. (2008). Mortality and other determinants of bird divorce rate. *Behavioral Ecology and Sociobiology*, 63(1), 1-9.

Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Sorace, A., Fernández-Juricic, E., Rodriguez-Prieto, I., & Jimenez, M. D. (2005). Evaluation of the “safe nesting zone” hypothesis across an urban gradient: a multi-scale study. *Ecography*, 28(1), 59-70.

Kilner, R. M. (2003). How selfish is a cowbird nestling? *Animal Behaviour*, 66(3), 569-576.

Kraaijeveld, K. (2003). Degree of mutual ornamentation in birds is related to divorce rate. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1526), 1785-1791.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). Package 'lmertest'. *R package version*, 2(0), 1-30.

Leniowski, K., & Węgrzyn, E. (2018). Synchronisation of parental behaviours reduces the risk of nest predation in a socially monogamous passerine bird. *Scientific Reports*, 8(1), 1-9.

Liker, A., & Székely, T. (2005). Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*, 59(4), 890-897.

Lima, S. L. (2009). Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, 84(3), 485-513.

Lowther, P. E. (2018). Lists of victims and hosts of the parasitic cowbirds (Molothrus). Field Mueseum. https://www.fieldmuseum.org/sites/default/files/cowbird-hosts-05sep2018.pdf. Accessed November 28, 2019

Marini, M. Â. (2017). Nesting success of birds from Brazilian Atlantic Forest fragments. *Revista Brasileira de Ornitologia*, 25(2), 77-83.

Martin, T. E. (1988). Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology*, 2(1), 37-50.

Martin, T. E., Scott, J., & Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1459), 2287-2293.

McIvor, G. E., & Healy, S. D. (2017). Nest site selection and patterns of nest re-use in the Hooded Crow *Corvus cornix*. *Bird Study*, 64(3), 374-385.

Menezes, J. C., & Marini, M. Â. (2017). Predators of bird nests in the Neotropics: a review. *Journal of Field Ornithology*, 88(2), 99-114.

Moraes, A. L., Da Silveira, N. S., & Pizo, M. A. (2018). Nocturnal roosting behavior of the Pale-breasted Thrush (*Turdus leucomelas*) and its relation with daytime area of use. *The Wilson Journal of Ornithology*, 130(3), 828-833.

Nilsson, J. Å. (2000). Time-dependent reproductive decisions in the blue tit. *Oikos*, 88(2), 351-361.

Otterbeck, A., Selås, V., Nielsen, J. T., Roualet, É., & Lindén, A. (2019). The paradox of nest reuse: early breeding benefits reproduction, but nest reuse increases nest predation risk. *Oecologia*, 190(3), 559-568.

Owen, J. C. (2011). Collecting, processing, and storing avian blood: a review. *Journal of Field Ornithology*, 82(4), 339-354.

Potascheff, C. D. M., Lombardi, J. A., & Lorenzi, H. (2010). Angiosperm trees and shrubs on the campus of the São Paulo State University Júlio de Mesquita, Rio Claro (SP), Brazil. *Bioikos*, 24(1), 21-30.

Powell, L. A., & Frasch, L. L. (2000). Can nest predation and predator type explain variation in dispersal of adult birds during the breeding season? *Behavioral Ecology*, 11(4), 437-443.

Redmond, L. J., Murphy, M. T., & Dolan, A. C. (2007). Nest reuse by Eastern Kingbirds: adaptive behavior or ecological constraint? *The Condor*, 109(2), 463-468.

Reynolds, J. D. (1996). Animal breeding systems. *Trends in Ecology & Evolution*, 11(2), 68-72.

Robinson, W. D., & Robinson, T. R. (2001). Is host activity necessary to elicit brood parasitism by cowbirds? *Ethology Ecology & Evolution*, 13(2), 161-171.

Roper, J. J. (2005). Try and try again: nest predation favors persistence in a neotropical bird. *Ornitologia Neotropical*, 16(2), 253-262.

Royle, N. J., Smiseth, P. T., & Kölliker, M. (Eds.). (2012). *The evolution of parental care*. Oxford University Press.

Ruiz, N. L., Araûjo, P., Lima, J., Ferreira, P., Andrade, L., & Pichorim, M. (2017). Breeding biology of Pale-breasted Thrush *Turdus leucomelas* (Turdidae) in the north of Atlantic Forest, Brazil. *Revista Brasileira de Ornitologia*, 25(2), 110-121.

Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: pair bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society B: Biological Sciences*, 281(1786), 20132843.

Sanders, M. D., & Maloney, R. F. (2002). Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biological Conservation*, 106(2), 225-236.

Saunders, C. A., Arcese, P., & O'Connor, K. D. (2003). Nest site characteristics in the song sparrow and parasitism by brown-headed cowbirds. *The Wilson Bulletin*, 24-28.

Slagsvold, T., Kleiven, K. W., Eriksen, A., & Johannessen, L. E. (2013). Vertical and horizontal transmission of nest site preferences in titmice. *Animal Behaviour*, 85(2), 323-328.

Sick, H. (2001). *Ornitologia Brasileira*. Edição revisada e ampliada por J. F. Pacheco, 2001. Ed. Nova Fronteira, Rio de Janeiro.

Sperry, J. H., Peak, R. G., Cimprich, D. A., & Weatherhead, P. J. (2008). Snake activity affects seasonal variation in nest predation risk for birds. *Journal of Avian Biology*, 39(4), 379-383.

Styrsky, J. N. (2005). Influence of predation on nest-site reuse by an open-cup nesting neotropical passerine. *The Condor*, 107(1), 133-137.

Svagelj, W. S., Fernández, G. J., & Mermoz, M. E. (2009). Effects of nest-site characteristics and parental activity on cowbird parasitism and nest predation in Brown-and-yellow Marshbirds. *Journal of Field Ornithology*, 80(1), 9-18.

Tarwater, C. E., & Brawn, J. D. (2010). The post-fledging period in a tropical bird: patterns of parental care and survival. *Journal of Avian Biology*, 41(4), 479-487.

Thompson III, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis*, 149, 98-109.

Trivers R. L. 1972. Parental investment and sexual selection. In: Campbell B. (ed.). *Sexual Selection and the Descent of Man 1871–1971*. Aldine, Chicago, pp. 136–179.

Weidinger, K., & Kočvara, R. (2010). Repeatability of nest predation in passerines depends on predator species and time scale. *Oikos*, 119(1), 138-146.

Wysocki, D. (2004). Nest re-use by Blackbirds—the way for safe breeding? *Acta Ornithologica*, 39(2), 164-168.

Wysocki, D. (2004). Within-season divorce rate in an urban population of European Blackbird *Turdus merula*. *Ardea*, 92(2), 219-228.

Wysocki, D. (2006). Factors affecting the between-season divorce rate in the urban populations of European Blackbird *Turdus merula* in north-western Poland. *Acta Ornithologica*, 41(1), 71-78.

Yeh, P. J., Hauber, M. E., & Price, T. D. (2007). Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos*, 116(9), 1473-1480.

Young, C. M., Cain, K. E., Svedin, N., Backwell, P. R., & Pryke, S. R. (2017). Nesting success in crimson finches: chance or choice? *Ethology*, 123(1), 41-50.

Zieliński, J. (2012). Nest reuse by Eurasian blackcap *Sylvia atricapilla*. *Ardea*, 100(1), 98-101

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

Capítulo 4

FEMALE PERSONALITY PREDICTS THE USE OF BUILDINGS AS NESTING SITES

FEMALE PERSONALITY PREDICTS THE USE OF BUILDINGS AS NESTING SITES

ABSTRACT

Behavioral decisions, although depend on physiological state and environmental context, are subject to individual personality, which states a baseline of expected responses consistent through time in similar conditions. Anthropogenic disturbances as urbanization act not only as a selective barrier to the settlement of wild species, but are also associated to changes in animal behavior by selecting personality traits. Neophobia (i.e., the degree of avoidance in face of an unknown situation) is a personality dimension that may predict the ability of exploit new resources, enhancing the settlement of urban populations. However, despite raising information on the use of man-made structures as substrates for bird nests, the hypothesis that their use is related to specific personality traits has never been tested. We conducted a neophobia experiment to address the relationship between female personality and the use of buildings as nesting sites in an urban population of the Pale-breasted Thrush (*Turdus leucomelas* Vieillot, 1818). We placed a novel object (a textured colored ball or a magic cube) near active nests and measured the latency time to incubating females reengage on breeding duties – return to nest vicinity, perch on nest rim, and resume incubation – comparing nests placed on buildings and on trees. We found a significant relationship between nesting substrate and female personality. For all the three studied behaviors, females of nests placed on trees showed higher latency times in neophobia tests than in control trials, while females of nests in buildings presented an unexpected opposite pattern. Therefore, a novel object near the nest repealed females that nested on trees, but attracted females that nested on buildings instead, probably by eliciting a nest defense behavior. Less neophobic individuals tend to more exploratory and innovative behaviors, which should enhance the use of buildings as nesting sites by fearless females. We concluded that less neophobic females are more prone to use buildings as nesting substrates in the Pale-breasted Thrush. Our findings contribute to link the exploitation of anthropogenic resources to the predominance of certain animal personalities in anthropic environments, showing that urbanization may affect species evolution by selecting behavioral traits.

Keywords: Anthropogenic resources, behavioral syndromes, neophobia, Thrush, urban bird.

RESUMO

Personalidade das fêmeas prediz o uso de edifícios como local de nidificação – Decisões comportamentais, apesar de dependerem do estado fisiológico e do contexto ambiental, estão sujeitas à personalidade dos indivíduos, que estabelece um padrão de respostas esperadas em situações semelhantes, o qual é consistente ao longo do tempo. Distúrbios antrópicos como a urbanização, além de agirem como uma barreira seletiva ao estabelecimento de espécies, também são associados a mudanças no comportamento das mesmas através da seleção de traços de personalidade. A neofobia (i.e., o grau de hesitação frente a uma situação nova) é uma dimensão da personalidade que pode predizer a habilidade de explorar novos recursos, o que favorece o estabelecimento de populações urbanas. Entretanto, apesar dos crescentes estudos sobre o uso de estruturas antrópicas como substratos para ninhos de aves, a hipótese de que o uso dos mesmos está relacionado a traços específicos de personalidade nunca foi testada. Nós conduzimos um experimento de neofobia para investigar a relação entre a personalidade das fêmeas e o uso de edifícios para nidificação em uma população urbana do sabiá-barranco (*Turdus leucomelas* Vieillot, 1818). Colocamos um objeto novo (uma bola colorida com texturas ou um cubo mágico) próximo de ninhos ativos e medimos o tempo de latência até as fêmeas em incubação voltarem às suas tarefas reprodutivas – retornar às proximidades do ninho, pousar na borda do ninho e retomar a incubação – comparando ninhos em edifícios e em árvores. Encontramos uma relação significativa entre o tipo de substrato do ninho e a personalidade das fêmeas. Para os três comportamentos avaliados, as fêmeas de ninhos em árvores apresentaram maiores tempos de latência nos testes de neofobia que nos controles, enquanto fêmeas de ninhos em edifícios exibiram inesperadamente o padrão oposto. Portanto, um objeto desconhecido próximo ao ninho repeliu as fêmeas que nidificaram em árvores, mas atraiu aquelas que nidificaram em edifícios, provavelmente por incitar a defesa do ninho. Indivíduos menos neofóbicos tendem a realizar mais comportamentos inovadores e de exploração, o que deve ter propiciado a nidificação em edifícios por fêmeas mais destemidas. Concluímos que as fêmeas menos neofóbicas são mais inclinadas a nidificar em edifícios no sabiá-barranco. Nosso resultado contribui para ligar a exploração de recursos antropogênicos à predominância de certas personalidades nas populações de animais em ambientes antrópicos, mostrando que a urbanização pode afetar a evolução das espécies selecionando traços comportamentais.

Palavras-chave: Ave urbana, neofobia, recursos antropogênicos, sabiá, síndromes comportamentais.

INTRODUCTION

Animal decisions tend to maximize the relationship between the potential risks and benefits. These trade-offs usually depend on the individual physiological state and environmental context, because the gains and risks are relative to intrinsic factors, such as body condition (Moschilla *et al.* 2018, Moiron *et al.* 2019), and external factors, such as resource availability and predation risk (Heithaus & Dill 2002, Verdolin 2006). However, behavioral responses in similar contexts vary among individuals as a consequence of personality traits, which impose to each individual different baselines of expected responses in a given context (Wolf & Weissing 2012). Unlike ephemeral alterations in behavioral decisions caused by a positive or negative stimulus (Dugatkin 1997, Fuxjager & Marler 2010), responses based on personality are consistent through time (Castanheira *et al.* 2013). A classical axis of personality is the shy-bold continuum (Wilson *et al.* 1993), which have been supported by numerous empirical evidence in a wide range of animal taxa (Wilson *et al.* 1994, Toms *et al.* 2010, Mather & Logue 201).

Several facets of the animal behavior linked to personality axes, such as the level of aggressiveness, boldness and problem-solving skills are usually correlated within individuals, shaping behavioral syndromes (Groothuis & Carere 2005, Evans *et al.* 2010, Lapiedra *et al.* 2017). Individuals with high levels of aggression against conspecifics, for instance, tend to risk more facing threats, present higher exploratory behavior, and are less neophobic than shyer individuals (Kortet & Hedrick 2007, Barnett *et al.* 2012, Thys *et al.* 2017). The persistence of individuals with such different reaction norms within populations is thought to be sustained by assortive mating and fluctuations with environmental pressures in time and space (Groothuis & Carere 2005, Niemelä *et al.* 2012), as predicted by game theory (Smith & Price 1973). Nevertheless, in particular contexts, extreme variants of personality traits may be favored, leading to the predominance of certain behavioral syndromes (Samia *et al.* 2015).

Anthropogenic disturbance is a known driver of changes in animal behavior (Ditchkoff *et al.* 2006), and ultimately promotes the selection of specific behavioral syndromes (Samia *et al.* 2015, Lapiedra *et al.* 2017). Urbanization, for instance, induces differences in behavioral syndromes between urban and rural populations in different groups (Bókony *et al.* 2012, Samia *et al.* 2015, Lapiedra *et al.* 2017). Urban dwellers are frequently exposed to novel resources, threats and disturbances, so that lineages able to deal with abnormal experiences should prosper in urban areas (Samia *et al.* 2015, Tryjanowski *et al.* 2015). Neophobia (i.e., the degree of reluctance to face an unknown situation) can predict the ability of an individual to solve problems and discover new resources (Webster & Lefebvre 2001, Sol *et al.* 2011), which in turn enhance its persistence in highly mutable environments, such as urban areas (Sol *et al.* 2011).

Despite birds are successful in colonizing urban areas worldwide, urban avifauna has a narrow functional trait composition (Croci *et al.* 2008), and the performance of each urban species depends on its habits (Kark *et al.* 2007). Urban bird personality has also been the focus of many studies comparing urban and rural populations (Bókony *et al.* 2012, Minias *et al.* 2018). In this context, urban bird colonization is associated to the persistence of certain phenotypes, such as more aggressive, sedentary, human-tolerant, and less neophobic individuals (Miranda *et al.* 2013, Møller *et al.* 2014, Minias *et al.* 2018, Weaver *et al.* 2018). These traits apparently enhance the exploitation of anthropogenic resources, such as food and nesting sites (Sol *et al.* 2011).

Nest site selection is the major response against selective pressures on breeding birds (Mainwaring *et al.* 2015), and it is a passive way by which breeding adults deal with the costs of offspring rearing (Bueno-Enciso *et al.* 2016, Mueller *et al.* 2019). The main characteristics of a potential nest site are relatively well conserved phylogenetically, by which most avian taxa are associated to typical nest site features (Sheldon & Winkler 1999). Despite such genetic heritability, individual can exert their own preferences on nest site selection according to lifetime experiences and personality (Slagsvold *et al.* 2013, Seltmann *et al.* 2014). In birds breeding outside cavities, nesting substrate (i.e., the plant or surface where the nest is attached) is key to nest site selection, directly affecting clutch survival (Donâzar *et al.* 1994, Rodewald *et al.* 2010). Some bird species rely on one or a few plant species to support their nests, while others are able to nest in a wide variety of anthropogenic substrates (Reynolds *et al.* 2019). However, despite increasing information on the use of anthropogenic nesting sites by urban birds (see the reviews by Mainwaring 2015, Reynolds *et al.* 2019), to the best of our knowledge no study addressed possible differences in the personality of individuals nesting in natural and anthropogenic substrates in urban areas.

Here, we address the relationship between the occupancy of anthropogenic substrates and female personality in females of the Pale-breasted Thrush (*Turdus leucomelas* Vieillot, 1818), a Neotropical open-cup nesting passerine. We conducted neophobia experiments to test whether the latency time to reengage in parental tasks (expressed by return to nest vicinity, perch on the nest rim, and resume incubation) vary between incubating females of nests on buildings and on trees in a same urban setting. We predicted that females nesting on buildings should be less neophobic than those nesting on trees, since they were able to build their nests close to pedestrian flow and other sources of disturbance.

MATERIALS AND METHODS

Study area

This study took place at the campus of the Federal University of São Carlos (21º59'02"S, 47º52'58"W), São Carlos municipality, São Paulo State, Brazil. The regional climate is subtropical, with mean monthly temperatures between 16.2ºC and 22.4ºC, and annual rainfall around 1,435 mm (Alvares *et al.* 2013). São Carlos is located on the southern portion of the Cerrado domain (Brazilian savanna), and the campus (645 ha) occupies a periurban area. The campus comprises a mosaic of unmanaged vegetation types (cerrado stricto sensu, riparian forests, *Eucalyptus* and *Pinus* stands, and anthropic fields dominated by invasive grasses), and its urbanized portion (ca. 96 ha) present low building density surrounded by lawns, with abundant native and exotic shrubs and trees (Lessi *et al.* 2017). The activities related to this study were restricted to the urbanized portion of the campus.

Study species

The Pale-breasted Thrush is a medium-sized omnivore passerine (22 cm, 63 g) that occurs from northern South America to Paraguay and Argentina (Collar & Garcia 2016, Moraes *et al.* 2018). This monomorphic, resident bird inhabits a variety of habitats, from undisturbed native vegetation to urban areas (Sick 1997). The nest consists in a bulky low cup measuring 13.2 × 10.2 cm (external diameter × external height) built with roots and other vegetal fibers firmly cemented with mud (Ruiz *et al.* 2017). Breeding attempts in the study region are concentrated from September to December, and clutch size is usually three eggs (Davanço *et al.* 2013). Both parents raise the nestlings, but female solely is responsible for nest construction, incubation and nestling brooding (Ruiz *et al.* 2017). The nest is usually attached to a large, lower tree trunk bifurcations, but this species also use buildings as nesting substrates (Davanço 2009, Ruiz *et al.* 2017).

Field procedures

We caught adult thrushes with mist nets weekly from September 2017 to August 2019. Each captured bird received a metallic ring and a unique combination of colored bands. Individuals were sexed through field observations during the breeding period, assuming that singing and incubation are performed exclusively by male and female, respectively. During the breeding season, we searched for nests by inspecting all trees and buildings and by following adults. Once located, nests were monitored every 2–3 days using a pole with a mirror to determine laying date. Females in the study area were presumably habituated to the perturbation caused by nest monitoring, since these field procedures have been conducted since 2017 as part of other studies.

Neophobia experiment

During the 2019 breeding season, we conducted neophobia experiments as a way to address the personality of incubating females. The experiment consisted in two rounds of paired trials (a neophobia test and a control trial), which were conducted in the morning (9:00–12:00 h) of sunny days. In each nest, paired trials were realized two hours apart in the same morning to reduce the interference of the female reaction to the first trial in the next response. Rounds in each nest were spaced from two or three days, depending on weather conditions, to assure that female responses were consistent through time. We adopted this interval to prevent differences in female response due to the increasing cumulative value of the clutch across incubation. As novel objects, we choose a textured yellow ball (5 cm diameter) and a magic cube (5 cm edge). For each nest, we randomized the order of treatments within rounds, and the novel object used in the first round. To assure that each observed nest was an independent replicate, unbanded females were included only if their nests were concomitant with each other or at least 200 m apart from any other studied unbanded female.

Prior to the beginning of the experiment, we make sure that females were on the nests. In neophobia tests, AFB walked directly to the nest from its most visible angle holding the same pole used in nest monitoring, placed a novel object in a point 30 cm far from the nest, and then retrieved 20 m away from the nest to a hidden place. We attached a receptacle in the empty extremity of the pole to aid placing the novel object near to the nest. Control trials were conducted in the same manner, but no object was left near the nest.

We estimated the latency time to return to nest vicinity (i.e., within a 2 m radius from the nest), perch on the nest rim, and resume incubation, from the instant the female flushed from the nest in each trial. We recorded no nest abandonment attributed to either nest monitoring or procedures related to this experiment. The experiment was conducted under a federal banding license (SISBIO 59414-1, CEMAVE 4216/1), and our field protocol was previously approved by the ethical committee of animal research of the university (code 1958100718).

Statistical analyses

To address whether females were individually consistent in their responses to the neophobia tests, as expected for behavioral syndromes, we used Pearson correlation to test if latency times were correlated between the two trials. We then use latency time to return to nest vicinity, perch on the nest rim, and resume incubation as response variables in generalized mixed-effects models (GLMMs) with Poisson error distribution (Tryjanowski *et al.* 2015) to test for differences in female behavioral syndromes among nesting substrates. In all models, we set the treatment (neophobia vs. control), nesting substrate (buildings vs. trees) and the interaction treatment × nesting substrate as factorial explanatory variables, and female ID as a random factor. When the interaction term was significant, we ran Dunn post-hoc tests to compare the variation in latency time among treatments within nesting substrates. All analyses were conducted in the software R (R Core Team 2018), using the package “lme4” (Bates *et al.* 2014). Values are presented as mean ± standard deviation.

RESULTS

We carried out the neophobia experiment in females of 19 nests, 12 in buildings and seven in trees. The latency time of each female was positively correlated between the two neophobia tests to either return to nest vicinity ($r = 0.503$, $p = 0.033$), perch on the nest rim ($r = 0.492$, $p = 0.032$), or resume incubation ($r = 0.483$, $p = 0.036$). Such positive correlations indicated that female responses were consistent at individual level. We found a significant difference in female response between treatments. In control trials, females took significantly less time to return to nest vicinity, perch on the nest rim, and resume incubation than in neophobia tests (Table 4-1), which implies that novel objects were in fact perceived and inhibited female return to nests.

We did not find significant differences in latency time between nesting substrates for none of the tested responses (Table 4-1), which lead us to conclude that females are equally prone to return to their nests regardless of nesting substrate. However, we found a significant interaction between treatment × nesting substrate for latency to returning to nest vicinity, to perching on the nest rim, and to resuming incubation (Table 4-1). Females showed opposite responses to the treatments in each substrate type. For trees, females showed higher latency times for neophobia tests than control trials, whereas females of nests placed on buildings had greater latency times in control than in neophobia tests. This opposite pattern held to the latency time for all the behaviors studied (Fig. 4-1).

Table 4-1. Results of generalized linear mixed-effects models assessing the latency of incubating females of the Pale-breasted Thrush (*Turdus leucomelas*) in different nesting substrates (trees, n = 7, and buildings, n = 12) to return to nest vicinity, perch on the nest rim, and resume incubation during neophobia tests and control trials ("Treatment") and the interaction between these two factorial variables. * statistical significance at α = 0.05.

	Estimate	SE	Wald χ^2	*P*
Return to nest vicinity				
Intercept	2.716	1.262	2.153	0.031*
Treatment	0.609	0.024	25.028	<0.001*
Nesting substrate	2.120	1.530	1.385	0.166
Nesting substrate × Treatment	-0.399	0.029	-13.546	<0.001*
Perch on the nest rim				
Intercept	5.310	0.302	17.574	<0.001*
Treatment	0.585	0.020	29.123	<0.001*
Nesting substrate	0.146	0.380	0.384	0.701
Nesting substrate × Treatment	-0.335	0.025	-13.139	<0.001*
Resume incubation				
Intercept	5.374	0.273	19.685	<0.001*
Treatment	0.558	0.020	28.213	<0.001*
Nesting substrate	0.166	0.343	0.482	0.630
Nesting substrate × Treatment	-0.291	0.025	-11.597	<0.001*

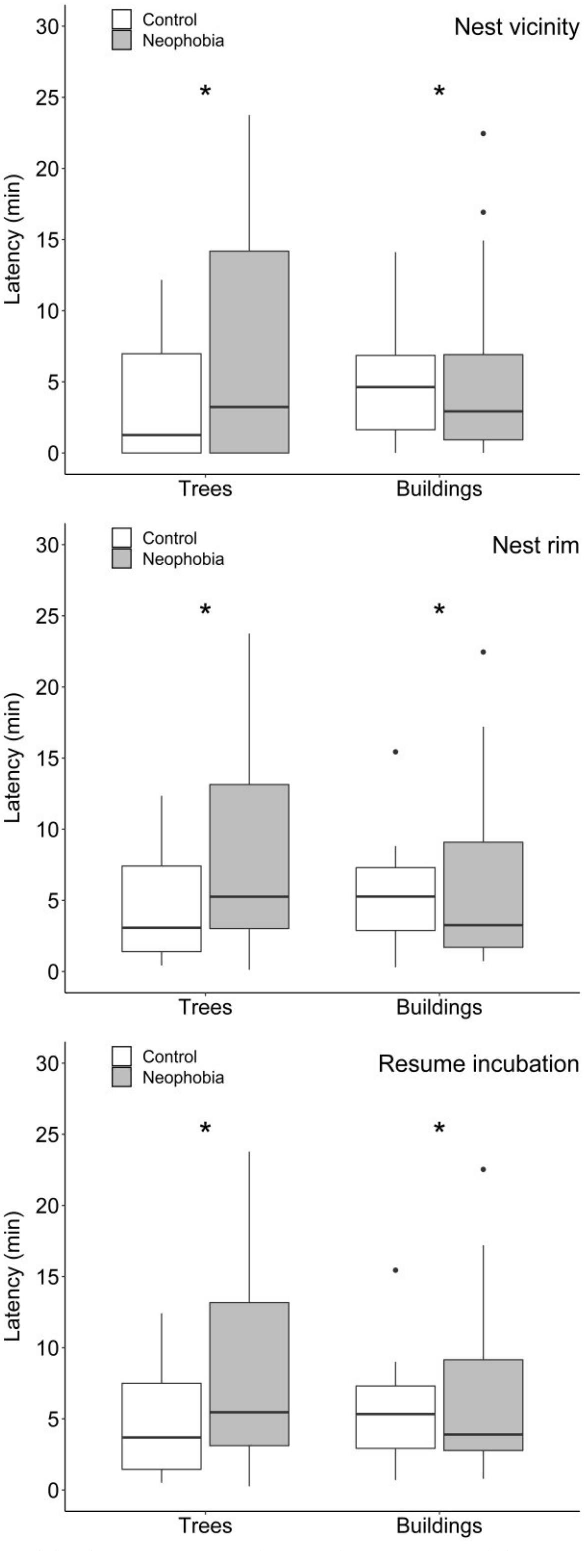


Fig. 4-1. The relationship between nesting substrates and latency time to returning to nest vicinity (a 2-m radius from the nest), perching on the nest rim, and resuming incubation in neophobia tests and control trials in females of an urban population of the Pale-breasted Thrush (*Turdus leucomelas*). Whiskers: standard errors; boxes:

interquartile ranges; horizontal segments: medians; dots: outliers. Asterisks represent statistical significance at $\alpha = 0.05$

DISCUSSION

We found different levels of neophobia between females nesting on trees and on buildings in an urban habitat, suggesting that female behavioral syndromes are related to nest site choices in the Pale-breasted Thrush. Moreover, we found an opposite trend in latency time between treatments for nesting substrates types. Females of nests placed on trees presented longer latency times in neophobia tests than in control trials, whereas females in buildings returned to nest vicinity, perched on the nest rim, and resumed incubation more quickly in neophobia tests than in control trials. These results show that, while a novel object near the nests repealed females that nested on trees, it attracted females that nested on buildings instead.

Individuals with lower levels of neophobia usually tend to realize more exploratory and innovative behaviors (Greenberg 2003, Overington *et al.* 2011, Ducatez *et al.* 2017, Biondi *et al.* 2020), which should have contributed to less neophobic females to discover and use buildings as nesting sites. The earlier return of females in buildings to their breeding duties in neophobia tests is likely a decision for defending their nests face an unknown threat (the novel object). Such a shorter latency in neophobia tests versus control trials is an uncommon pattern (see references cited below). One likely cause for this unexpected response is that novel objects are usually presented near a source of food (e.g., Boogert *et al.* 2006, Fox & Millam 2007, Apfelbeck & Raess 2008, Bókony *et al.* 2012, Miranda *et al.* 2013, Audet *et al.* 2015), while our neophobia tests were conducted near active nests. Thus, unlike simply losing a foraging opportunity, the females we studied probably account for the value of the current offspring in terms of invested energy. Neophobia and boldness are generally inversely related in birds (e.g., Ducatez *et al.* 2017). Therefore, the more fearless, bolder females inclined to defend their nests should promptly return to their breeding duties, and probably were the responsible for the unusual shorter latency in neophobia than in control trials for nests in buildings.

Individuals of urban bird populations are known to be in general less neophobic that their counterparts in rural or natural habitats (Bókony *et al.* 2012, Ducatez *et al.* 2017, Biondi *et al.* 2020), although some studies revealed an opposite trend (Miranda *et al.* 2013, Audet *et al.* 2015). In the same urban context, we found considerable variation in neophobia even among individuals of an urban population. In agreement with other studies, our result suggest that individuals that exhibit certain personality traits are more prone to the benefits of living close to humans. Less neophobic individuals, for instance, are more prone to exploit novel food sources (An *et al.* 2011). Additionally, higher tolerance to human proximity is typical among vertebrate populations in urban and other human-disturbed habitats (Samia *et al.* 2015), and may incur in greater protection against predators of adult birds (Møller *et al.* 2012). Also, the proximity to human buildings is known to enhance breeding success, diminishing clutch susceptibility to brood parasitic birds and predators (Møller 2010, Møller *et al.* 2016). Thus, the potential benefits provided by human presence, including the exploitation of anthropogenic nesting substrates and food sources, tend to be heterogeneously experienced by individuals within a given bird population.

Parental personality effects in bird breeding performance are known to affect offspring success and quality, because behavioral syndromes are correlated to the engagement on nest defense and nestling provisioning (Barnett *et al.* 2012, Colchester & Harrison 2016, Li *et al.* 2020). Parents must deal to repeated human perturbation in urban environments, and those who present lower latency times to resuming parental tasks should have better breeding success. Recent evidence pointed out the role of the personality of breeding adults in affecting subtle features of nest site choices, which are expected to interact with modulations of the parental effort in predicting clutch success (Seltmann *et al.* 2014, Zhao *et al.* 2016). For instance, adults able to react more aggressively against threats can choose better concealed nest sites, where clutch survival is higher, despite the potential increasing in predation risk for themselves (Seltmann *et al.* 2014). Our study showed that innovations regarding the choice of nesting substrates are also elicited by intraspecific variation in personality. Despite the potential role of both sexes in nest site selection in our study species (Batisteli, pers. obs.), we focused on the link between female personality and nesting substrate. Although the personality of males in our study population was not assessed in this study, we believe their influence on nest site selection is limited because females solely built the nest, incubate the eggs, and brood the nestlings in this species (Ruiz *et al.* 2017), being therefore the sex exposed to higher predation risk at the nest and the ones that pay the main thermoregulatory costs related to nest site. Thus, it seems unfeasible that females would accept to nest in sites radically different from their own preferences.

Individual preferences in nest site selection are primarily vertically transmitted by both an inherited and a cognitive (imprinting) component (Slagsvold *et al.* 2013). In the same way, behavioral syndromes are largely inheritable (van Oers *et al.* 2004, Groothuis & Carere 2005). Based on these two assumptions, we might suppose a strong potential for the heritability of the use of buildings as nesting substrates. Nests in buildings are related to multiple advantages in our study context, such as higher clutch survival and lower nest attentiveness (Batisteli, in prep.). Thus, we strongly suspect that females able to nest in buildings are more prone to establish urban lineages, but this topic requires further studies.

We conclude that the use of nesting substrates by the Pale-breasted Thrush is related to female personality and that less neophobic females are more prone to nest in building. Our results may help to link the differential access to anthropogenic resources to the predominance of certain behavioral syndromes in anthropic environments, contributing to shape animal behavior in these habitats.

REFERENCES

Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes, G., Leonardo, J., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6), 711-728.

An, Y. S., Kriengwatana, B., Newman, A. E., MacDougall-Shackleton, E. A., & MacDougall-Shackleton, S. A. (2011). Social rank, neophobia and observational learning in black-capped chickadees. *Behaviour*, 148(1), 55-69.

Apfelbeck, B., & Raess, M. (2008). Behavioural and hormonal effects of social isolation and neophobia in a gregarious bird species, the European starling (S*turnus vulgaris*). *Hormones and Behavior*, 54(3), 435-441.

Audet, J. N., Ducatez, S., & Lefebvre, L. (2015). The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, 27(2), 637-644.

Barnett, C. A., Thompson, C. F., & Sakaluk, S. K. (2012). Aggressiveness, Boldness and Parental Food Provisioning in Male House Wrens (*Troglodytes aedon*). *Ethology*, 118(10), 984-993.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R package version* 1.1-7.

Biondi, L. M., Fuentes, G. M., Córdoba, R. S., Bó, M. S., Cavalli, M., Paterlini, C. A., ... & García, G. O. (2020). Variation in boldness and novelty response between rural and urban predatory birds: the Chimango Caracara, *Milvago chimango* as study case. *Behavioural Processes*, 104064.

Bókony, V., Kulcsár, A., Tóth, Z., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PloS one*, 7(5): e36639.

Boogert, N. J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, 72(6), 1229-1239.

Bueno-Enciso, J., Ferrer, E. S., Barrientos, R., & Sanz, J. J. (2016). Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. *Journal of Ornithology*, 157(3), 759-772.

Castanheira, M. F., Herrera, M., Costas, B., Conceição, L. E., & Martins, C. I. (2013). Can we predict personality in fish? Searching for consistency over time and across contexts. *PLoS One*, 8(4), e62037.

Colchester, C., & Harrison, N. M. (2016). Personality in blue tits (*Cyanistes caeruleus*) and its effect on their breeding success. *Ethology*, 122(8), 695-701.

Collar, N., & Garcia, E. F. J. (2016). Pale-breasted Thrush (*Turdus leucomelas*). In: del Hoyo J., Elliott A., Sargatal J., Christie D.A. & de Juana E. (eds.). *Handbook of the birds of the world alive*. Barcelona: Lynx Editions. http://www.hbw.com/node/58293 (access on 13 January 2020).

Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits. *The Condor*, 110(2), 223–240.

Davanço, P. V. (2009). Biologia reprodutiva do Sabiá-barranco (*Turdus leucomelas*) na região sudeste do Brasil. Undergraduate thesis. Universidade Federal de São Carlos.

Davanço, P. V., Oliveira, L. S., Sousa, L. M., & Francisco, M. R. (2013). Breeding life-history traits of the Pale-breasted Thrush (*Turdus leucomelas*) in southeastern Brazil. *Ornitologia Neotropical*, 24, 401-411.

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems*, 9(1), 5-12.

Donâzar, J. A., Ceballos, O., Travaini, A., Rodriguez, A., Funes, M., & Hiraldo, F. (1994). Breeding performance in relation to nest-site substratum in a Buff-necked Ibis (*Theristicus caudatus*) population in Patagonia. *The Condor*, 96(4), 994-1002.

Ducatez, S., Audet, J. N., Rodriguez, J. R., Kayello, L., & Lefebvre, L. (2017). Innovativeness and the effects of urbanization on risk-taking behaviors in wild Barbados birds. *Animal Cognition*, 20(1), 33-42.

Dugatkin, L. A. (1997). Winner and loser effects and the structure of dominance hierarchies. *Behavioral Ecology*, 8(6), 583-587.

Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, 116(7), 588-595.

Fox, R. A., & Millam, J. R. (2007). Novelty and individual differences influence neophobia in orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, 104(1-2), 107-115.

Fuxjager, M. J., & Marler, C. A. (2010). How and why the winner effect forms: influences of contest environment and species differences. *Behavioral Ecology*, 21(1), 37-45.

Greenberg, R. S. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Reader, S. M., & Laland, K. N. (Eds.). (2003). *Animal innovation* (Vol. 10). Oxford: Oxford University Press.

Groothuis, T. G., & Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews*, 29(1), 137-150.

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83(2), 480-491.

Ibáñez-Álamo, J. D., & Soler, M. (2010). Does urbanization affect selective pressures and life-history strategies in the common blackbird (*Turdus merula* L.)? *Biological Journal of the Linnean Society*, 101(4), 759-766.

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: can anyone become an ‘urban exploiter’? *Journal of Biogeography*, 34(4), 638–651.

Kortet, R., & Hedrick, A. N. N. (2007). A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biological Journal of the Linnean Society*, 91(3), 475-482.

Lapiedra, O., Chejanovski, Z., & Kolbe, J. J. (2017). Urbanization and biological invasion shape animal personalities. *Global Change Biology*, 23(2), 592-603.

Lessi, B. F., Bataghin, F. A., & Pires, J. S. R. (2017). Diversity and distribution of trees on the Federal University of São Carlos campus, Brazil: implications for conservation and management. *Revista da Sociedade Brasileira de Arborização Urbana*, 12(1), 92-104.

Li, J. C., Gao, L. F., Fan, L. Q., Zhang, H. Y., Zhang, W., & Du, B. (2020). Field study of the relationship between personality and reproductive strategy in the White-collared Blackbird *Turdus albocinctus*. *Ibis*, 162(1), 245-249.

Mainwaring, M. C., Reynolds, S. J., & Weidinger, K. (2015). *The influence of predation on the location and design of nests*. In: Deeming, D. C. & Reynolds, S. J. (eds.) Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, Oxford. Pp 50-64.

Mainwaring, M. C. (2015). The use of man-made structures as nesting sites by birds: A review of the costs and benefits. *Journal for Nature Conservation*, 25, 17-22.

Mather, J. A., & Logue, D. M. (2013). *The bold and the spineless: invertebrate personalities*. In: Carere, C. & Maestripieri, D. Animal personalities: behavior, physiology, and evolution. The University of Chicago Press, Chicago. Pp 13-35.

Minias, P., Jedlikowski, J., & Włodarczyk, R. (2018). Development of urban behaviour is associated with time since urbanization in a reed-nesting waterbird. *Urban Ecosystems*, 21(6), 1021-1028.

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*, 19(9), 2634-2644.

Moiron, M., Araya-Ajoy, Y. G., Mathot, K. J., Mouchet, A., & Dingemanse, N. J. (2019). Functional relations between body mass and risk-taking behavior in wild great tits. *Behavioral Ecology*, 30(3), 617-623.

Møller, A. P. (2010). The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behavioral Ecology*, 21(5), 913–918.

Møller, A. P. (2012). Urban areas as refuges from predators and flight distance of prey. *Behavioral Ecology*, 23(5), 1030-1035.

Møller, A. P., Díaz, M., & Liang, W. (2016). Brood parasitism and proximity to human habitation. *Behavioral Ecology*, 27(5), 1314-1319.

Møller, A. P., Jokimäki, J., Skorka, P., & Tryjanowski, P. (2014). Loss of migration and urbanization in birds: a case study of the blackbird (*Turdus merula*). *Oecologia*, 175(3), 1019-1027.

Moraes, A. L., Da Silveira, N. S., & Pizo, M. A. (2018). Nocturnal roosting behavior of the Pale-breasted Thrush (*Turdus leucomelas*) and its relation with daytime area of use. *The Wilson Journal of Ornithology*, 130(3), 828-833.

Moschilla, J. A., Tomkins, J. L., & Simmons, L. W. (2018). State-dependent changes in risk-taking behaviour as a result of age and residual reproductive value. *Animal Behaviour*, 142, 95-100.

Mueller, A. J., Miller, K. D., & Bowers, E. K. (2019). Nest microclimate during incubation affects posthatching development and parental care in wild birds. *Scientific Reports*, 9(1), 1–11.

Niemelä, P. T., Vainikka, A., Forsman, J. T., Loukola, O. J., & Kortet, R. (2013). How does variation in the environment and individual cognition explain the existence of consistent behavioral differences? *Ecology and Evolution*, 3(2), 457-464.

Overington, S. E., Cauchard, L., Côté, K. A., & Lefebvre, L. (2011). Innovative foraging behaviour in birds: what characterizes an innovator? *Behavioural Processes*, 87(3), 274-285.

R Core Team. 2018. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P., & Mainwaring, M. C. (2019). Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology*, 160, 841-860.

Rodewald, A. D., Shustack, D. P., & Hitchcock, L. E. (2010). Exotic shrubs as ephemeral ecological traps for nesting birds. *Biological Invasions*, 12(1), 33-39.

Ruiz, N. L., Araújo, P., Lima, J., Ferreira, P., Andrade, L., & Pichorim, M. (2017). Breeding biology of Pale-breasted Thrush *Turdus leucomelas* (Turdidae) in the north of Atlantic Forest, Brazil. *Revista Brasileira de Ornitologia*, 25(2), 110-121.

Samia, D. S., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, 6, 8877.

Seltmann, M. W., Jaatinen, K., Steele, B. B., & Öst, M. (2014). Boldness and stress responsiveness as drivers of nest-site selection in a ground-nesting bird. *Ethology*, 120(1), 77-89.

Sheldon, F. H., & Winkler, D. W. (1999). Nest architecture and avian systematics. *The Auk*, 116(4), 875-877.

Sick, H. (2001). *Ornitologia Brasileira*. Edição revisada e ampliada por J. F. Pacheco, 2001. Ed. Nova Fronteira, Rio de Janeiro.

Smith, J. M., & Price, G. R. (1973). The logic of animal conflict. *Nature*, 246(5427), 15-18.

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS One*, 6(5).

Thys, B., Pinxten, R., Raap, T., De Meester, G., Rivera-Gutierrez, H. F., & Eens, M. (2017). The female perspective of personality in a wild songbird: repeatable aggressiveness relates to exploration behaviour. *Scientific Reports*, 7(1), 1-10.

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. International *Journal of Comparative Psychology*, 23(1).

Tryjanowski, P., Morelli, F., Skórka, P., Goławski, A., Indykiewicz, P., Møller, A. P., ... & Zduniak, P. (2015). Who started first? Bird species visiting novel birdfeeders. *Scientific Reports*, 5, 11858.

van Oers, K., de Jong, G., Drent, P. J., & van Noordwijk, A. J. (2004). A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behavior Genetics*, 34(6), 611-619.

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, 60(4), 457-464.

Weaver, M., Ligon, R. A., Mousel, M., & McGraw, K. J. (2018). Avian anthrophobia? Behavioral and physiological responses of house finches (*Haemorhous mexicanus*) to human and predator threats across an urban gradient. *Landscape and Urban Planning*, 179, 46-54.

Webster, S. J., & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, 62(1), 23-32.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9(11), 442-446.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107(3), 250.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452-461.

Zhao, Q. S., Hu, Y. B., Liu, P. F., Chen, L. J., & Sun, Y. H. (2016). Nest site choice: a potential pathway linking personality and reproductive success. *Animal Behaviour*, 118, 97-103.

DISCUSSÃO GERAL

DISCUSSÃO GERAL

Neste estudo, avaliei o efeito de diferentes tipos de suporte (edifícios e árvores) na aptidão, no comportamento reprodutivo e na personalidade dos indivíduos de sabiá-barranco dentro de um mesmo contexto urbano. Ninhos em prédios proporcionaram maior sobrevivência das ninhadas, apresentaram temperaturas internas mais altas e viabilizaram uma menor constância de incubação pelas fêmeas. Também verifiquei que a estabilidade dos casais está diretamente relacionada ao desempenho reprodutivo, e que o sucesso da ninhada aumenta a chance da reutilização imediata dos ninhos. Ainda, a ocupação dos edifícios como local de nidificação esteve associada a fêmeas com uma personalidade distinta, menos neofóbica.

Os resultados do capítulo 1 não dão suporte à ideia de que os edifícios como locais de nidificação seriam escolhas sub-ótimas à reprodução do ponto de vista de sobrevivência da prole. Pelo contrário, a chance de um ovo se desenvolver até o momento de abandonar o ninho é maior, sobretudo devido à diferença de sobrevivência dos ovos entre ninhos em edifícios e em árvores. Essa maior chance de sobrevivência deve aumentar a probabilidade de que ninhos em edifícios tenham sucesso aparente (i.e., que ao menos um filhote sobreviva até deixar o ninho). De acordo com os resultados do capítulo 3, esse fator levaria as fêmeas a reutilizar mais frequentemente estes ninhos do que os localizados em árvores. Além disso, os ninhos em edifícios, apesar de serem eventualmente removidos por interferência humana, são geralmente protegidos das intempéries climáticas, permanecendo íntegros de um ano a outro, o que pode influenciar as chances de sua reutilização.

As vantagens da utilização de edifícios vão além da sobrevivência da prole, como demonstrado no capítulo 2. Os ninhos em edifícios apresentam temperaturas internas ligeiramente maiores. Isso implica em menor custo termorregulatório à prole e aos parentais, o que pode resultar em filhotes com melhor desenvolvimento corporal e maior expectativa de vida (Nord & Nilsson 2016, Mueller *et al.* 2019). Embora não tenha acessado diretamente o gasto energético das fêmeas em incubação durante esse estudo, é provável que aquelas dos ninhos em edifícios tenham um balanço energético mais positivo, pois: 1) elas passam menos tempo incubando seus ovos, podendo dedicar mais tempo ao forrageio; 2) os recessos de incubação são compensados pelo efeito do micro-habitat do ninho, que mantém a temperatura interna do mesmo mais alta; 3) ao retornarem aos ninhos, as fêmeas devem gastar menos energia para reaquecer os ovos até o patamar ideal. Além disso, é possível que o menor tempo gasto pelas fêmeas no ninho tenha relação com o menor risco de predação durante a incubação comparando ninhos em edifícios e em árvores (Morosinotto *et al.* 2013), como mostrado no capítulo 1. A despeito das prováveis causas dessa diferença de comportamento, a energia obtida ou poupada pode ser investida na ninhada atual ou nas tentativas de reprodução futuras (Ardia *et al.* 2009, Vafidis *et al.* 2018).

De acordo com os resultados do capítulo 1, determinadas fêmeas são mais inclinadas a utilizarem os edifícios como suportes do que outras. No capítulo 4, verificamos que essas fêmeas possuem uma personalidade distinta das demais, sendo menos neofóbicas. As preferências pelo local de nidificação, além de possuírem um certo grau de herdabilidade genética, podem também ser transmitidas dos pais à prole por *imprinting* (Slagsvold *et al.* 2013). Por isso, independentemente do mecanismo de transmissão desse comportamento, é esperado que os filhotes criados em ninhos em edifícios também os utilizem como local para reprodução, favorecendo a seleção de uma linhagem adaptada a nidificar nesses locais. Assim, os benefícios desses substratos artificiais devem concentrar-se em indivíduos específicos e pré-determinados da população, garantindo-lhes um sucesso reprodutivo maior. Portanto, os resultados obtidos nesse estudo sugerem que o uso de substratos antrópicos pode contribuir efetivamente com a evolução de linhagens adaptadas ao ambiente urbano.

A ocupação do meio urbano pelas aves geralmente está relacionada a alterações nos padrões comportamentais das espécies (Evans *et al.* 2010, Audet *et al.* 2015), especialmente com relação ao comportamento reprodutivo (Yeh *et al.* 2007, Lomáscolo *et al.* 2010, Kunca & Yosef 2016). A utilização de edifícios ou outros elementos antrópicos como local de nidificação parece ter um papel particularmente importante no processo da conquista do ambiente urbano pelas aves (Møller 2010). Esse é um ponto comum na trajetória de algumas espécies que passaram de evitadoras a exploradoras do ambiente urbano. Por exemplo, o melro-preto (*Turdus merula*) era considerado uma ave restrita a florestas no século XIX, mas atualmente encontra-se plenamente adaptada ao ambiente urbano (Evans *et al.* 2009). Esse processo também foi acompanhado durante a colonização do ambiente urbano pelo rapinante açor (*Accipiter gentilis*) na Alemanha (Rutz 2008). No entanto, as prováveis vantagens de ocupar os edifícios e outros substratos antropogênicos como local de nidificação devem estar restritas a algumas espécies, já que as características funcionais de determinadas espécies podem impedir a ocorrência e limitar o sucesso das mesmas em territórios urbanos (Kark *et al.* 2007, Croci *et al.* 2008).

Então, é provável que a utilização de edifícios favoreça a colonização do ambiente urbano a um subconjunto de espécies de aves que sejam capazes de explorar esse recurso.

Ao longo do estudo, 20 espécies de aves foram registradas utilizando elementos antropogênicos como local de nidificação, as quais possuem ampla variação quanto aos tamanhos corporais e tipos de ninhos (Anexos I, II e IV). Isso sugere que uma parte considerável das espécies que ocorrem no ambiente urbano pode, ao menos eventualmente, beneficiar-se desses locais alternativos de nidificação. No entanto, a nidificação em edifícios parece ser um comportamento muito mais disseminado entre algumas espécies (Anexo IV), a exemplo da utilização de outros recursos antropogênicos, como materiais para construção do ninho (Anexo III). Embora não tenha sido possível acompanhar a performance reprodutiva de todas as espécies que nidificaram em edifícios, houve uma frequente reutilização dos ninhos em edifícios por diversos ciclos reprodutivos consecutivos para espécies como a avoante (*Zenaida auriculata*) e o pombão (*Patagioenas picazuro*). Essas duas espécies expandiram sua área de ocorrência e aumentaram suas abundâncias no estado de São Paulo nos últimos 50 anos (Willis & Oniki 1987, Ranvaud & Bucher 2006), sendo atualmente extremamente abundante em ambientes urbanos dessa e de outras regiões (Leveau & Leveau 2005, Fontoura *et al.* 2014, Lessi *et al.* 2016). É provável que a ocupação de edifícios como locais para nidificação esteja contribuindo para o estabelecimento dessas populações em áreas urbanas. Em diversos casos, um mesmo local de nidificação foi ocupado por diferentes espécies em diferentes épocas (i.e., *Z. auriculata*, *P. picazuro*, *T. leucomelas* e *T. amaurochalinus*), indicando que deve haver competição interespecífica por este recurso.

A evolução de linhagens urbanas com comportamento distinto das populações selvagens tem sido reportada em diversos grupos animais, como em mariposas (Altermatt e Ebert 2016). As populações de alguns grupos animais estão estruturadas geneticamente de forma a sugerir que populações urbanas sejam mais semelhantes entre si, independente da proximidade com populações em áreas naturais. Isso indica que o isolamento reprodutivo entre as linhagens urbanas e aquelas de áreas naturais pode ocorrer independentemente do isolamento geográfico entre elas. No entanto, estudos com o melro-preto (*Turdus merula*) suportam uma teoria alternativa, de que a colonização do ambiento urbano acontece independentemente em diversos locais (Partecke *et al.* 2006, Evans *et al.* 2009).

Os potenciais benefícios dos recursos antropogênicos sobre uma porção específica das populações de aves favorecem o domínio de determinadas personalidades, o que pode representar uma preocupação do ponto de vista da conservação do comportamento natural das espécies (Berger-Tal *et al.* 2011, Cordero-Rivera 2017). Nos congêneres melros-pretos, por exemplo, populações urbanas estabelecidas nos últimos dois séculos apresentam mudanças profundas na personalidade, na história de vida e no hábito migratório (Ibáñez-Álamo & Soler 2010, Miranda *et al.* 2013, Møller *et al.* 2014), evidenciando uma microevolução de linhagens urbanóides. Processo semelhante pode estar se iniciando com o sabiá-barranco e outras espécies que se aproveitam de substratos antropogênicos para a construção do ninho, como as listadas no Anexo IV, incluindo o migratório Sabiá-poca *Turdus amaurochalinus* (Anexo II).

Em aves, diversos aspectos podem diferir entre as populações urbanas e seus coespecíficos em áreas naturais, incluindo hábitos comportamentais, a fisiologia e a história de vida (Partecke *et al.* 2004, Partecke & Gwinner 2007, Ibáñez-Álamo & Soler 2010, Ibáñez-Álamo *et al.* 2018). Então, a possível diferenciação entre as linhagens urbanas e não-urbanas desperta a preocupação sobre os possíveis impactos antrópicos do ponto de vista da conservação da morfologia e do comportamento das espécies. Assim, futuros estudos sobre a fisiologia, a citogenética e o comportamento das aves que ocupam elementos antropogênicos como local de nidificação podem ajudar a compreender a extensão dos impactos antrópicos sobre a conservação das espécies em busca do convívio equilibrado entre os humanos e a fauna urbana.

REFERÊNCIAS

Altermatt, F., Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology Letters*, 12(4), 20160111.

Ardia, D. R., Pérez, J. H., Chad, E. K., Voss, M. A., & Clotfelter, E. D. (2009). Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. *Journal of Animal Ecology*, 78(1), 4-13.

Audet, J. N., Ducatez, S., & Lefebvre, L. (2015). The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, 27(2), 637-644.

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. P., & Saltz, D. (2011). Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*, 22(2), 236-239.

Cordero-Rivera, A. (2017). Behavioral diversity (ethodiversity): a neglected level in the study of biodiversity. *Frontiers in Ecology and Evolution*, 5, 7.

Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits. *The Condor*, 110(2), 223-240.

Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, 116(7), 588-595.

Evans, K. L., Gaston, K. J., Frantz, A. C., Simeoni, M., Sharp, S. P., McGowan, A., ... & Hatchwell, B. J. (2009). Independent colonization of multiple urban centres by a formerly forest specialist bird species. Proc*eedings of the Royal Society B: Biological Sciences*, 276(1666), 2403-2410.

Fontoura, P. M. (2014). Dominance of the Eared Dove (*Zenaida auriculata*) in a columbid assemblage in Northern Paraná, Southern Brazil. *Bioikos*, 27(1), 33-39.

Ibáñez-Álamo, J. D., & Soler, M. (2010). Does urbanization affect selective pressures and life-history strategies in the common blackbird (*Turdus merula* L.)?. *Biological Journal of the Linnean Society*, 101(4), 759-766.

Ibáñez-Álamo, J. D., Pineda-Pampliega, J., Thomson, R. L., Aguirre, J. I., Díez-Fernández, A., Faivre, B., ... & Verhulst, S. (2018). Urban blackbirds have shorter telomeres. *Biology Letters*, 14(3), 20180083.

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: can anyone become an ‘urban exploiter'? *Journal of Biogeography*, 34(4), 638-651.

Kunca, T., & Yosef, R. (2016). Differential nest-defense to perceived danger in urban and rural areas by female Eurasian sparrowhawk (*Accipiter nisus*). *PeerJ*, 4, e2070.

Lessi, B. F., Pires, J. S. R., Batisteli, A. F., & MacGregor-Fors, I. (2016). Vegetation, urbanization, and bird richness in a Brazilian periurban area. *Ornitología Neotropical*, 27, 203-210.

Leveau, C. M., & Leveau, L. M. (2005). Avian community response to urbanization in the Pampean region, Argentina. *Ornitologia Neotropical*, 16, 503-510.

Lomáscolo, S. B., Monmany, A. C., Malizia, A., & Martin, T. E. (2010). Flexibility in nest-site choice and nesting success of *Turdus rufiventris* (Turdidae) in a montane forest in northwestern Argentina. *The Wilson Journal of Ornithology*, 122(4), 674-680.

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*, 19(9), 2634-2644.

Møller, A. P. (2010). The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behavioral Ecology*, 21(5), 913-918.

Møller, A. P., Jokimäki, J., Skorka, P., & Tryjanowski, P. (2014). Loss of migration and urbanization in birds: a case study of the blackbird (*Turdus merula*). *Oecologia*, 175(3), 1019-1027.

Morosinotto, C., Thomson, R. L., Korpimäki, E. (2013). Plasticity in incubation behavior under experimentally prolonged vulnerability to nest predation. *Behaviour*, 150, 1767-1786.

Mueller, A. J., Miller, K. D., & Bowers, E. K. (2019). Nest microclimate during incubation affects posthatching development and parental care in wild birds. *Scientific Reports*, 9(1), 1-11.

Nord, A., & Nilsson, J. Å. (2016). Long-term consequences of high incubation temperature in a wild bird population. *Biology Letters*, 12(4), 20160087.

Partecke, J., & Gwinner, E. (2007). Increased sedentariness in European blackbirds following urbanization: a consequence of local adaptation? *Ecology*, 88(4), 882-890.

Partecke, J., Gwinner, E., & Bensch, S. (2006). Is urbanisation of European blackbirds (*Turdus merula*) associated with genetic differentiation? *Journal of Ornithology*, 147(4), 549-552.

Partecke, J., Van't Hof, T., & Gwinner, E. (2004). Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1552), 1995-2001.

Ranvaud, R. D., & Bucher, E. H. (2006). Explosions of the eared dove: the unique case in southeast Brazil. *Acta Zoologica Sinica*, 52, 568-569.

Rutz, C. (2008). The establishment of an urban bird population. *Journal of Animal Ecology*, 77(5), 1008-1019.

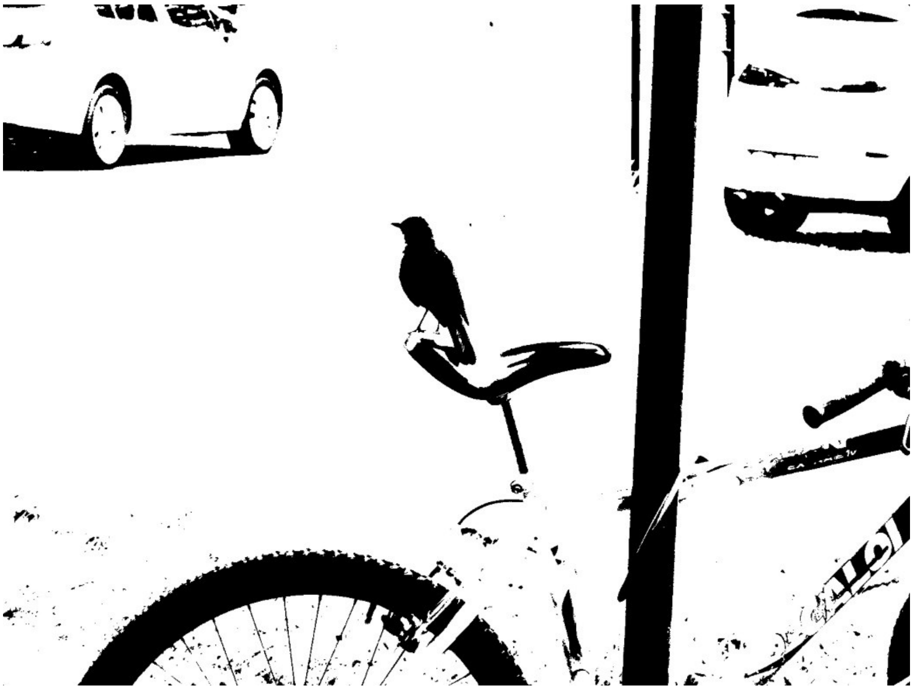
Slagsvold, T., Kleiven, K. W., Eriksen, A., & Johannessen, L. E. (2013). Vertical and horizontal transmission of nest site preferences in titmice. *Animal Behaviour*, 85(2), 323-328.

Vafidis, J. O., Facey, R. J., Leech, D., & Thomas, R. J. (2018). Supplemental food alters nest defence and incubation behaviour of an open-nesting wetland songbird. *Journal of Avian Biology*, 49(8), e01672.

Willis, E. O., & Oniki, Y. (1987). Invasion of deforested regions of Sao Paulo state by the picazuro pigeon, *Columba picazuro* Temminck, 1813. *Ciência & Cultura*, 39(11), 1064-1065.

Yeh, P. J., Hauber, M. E., & Price, T. D. (2007). Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos*, 116(9), 1473-1480.

CONCLUSÃO



CONCLUSÃO

A nidificação em edifícios favoreceu a sobrevivência da prole no sabiá-barranco, estando associada também a um menor tempo de permanência da fêmea no ninho e a fêmeas menos neofóbicas. Juntos, esses resultados sugerem múltiplas vantagens do uso de substratos antropogênicos, os quais podem contribuir para a evolução do comportamento reprodutivo dessa espécie no ambiente urbano.

No Capítulo 1, concluímos que a nidificação em edifícios aumenta a sobrevivência da prole devido a um efeito pronunciado na fase de ovos. Essa diferença sugere que, durante a incubação, as construções devem reduzir a chance de detecção dos ninhos pelos predadores. Ainda, certas fêmeas foram mais propensas a nidificar em edifícios, o que as torna mais sujeitas às prováveis vantagens desses substratos de nidificação alternativos.

No Capítulo 2, verificamos que os ninhos em edifícios exibiram maiores temperaturas internas se comparados aos ninhos em árvores. Essa diferença é tal que, durante o dia, mesmo com os eventuais recessos de incubação realizados pela fêmea, a temperatura interna dos ninhos em edifícios se mantém a níveis comparáveis à presença ininterrupta das fêmeas (período da noite) nos ninhos em árvores. As fêmeas de ninhos em edifícios também apresentaram menor constância de incubação do que aquelas em árvore, provavelmente devido ao efeito dos edifícios na temperatura interna dos ninhos.

No Capítulo 3, concluímos que a formação de novos pares no sabiá-barranco é mais comum entre uma temporada reprodutiva e outra. Pares que permanecem juntos tem maior tendência a reutilizar ninhos e produzem mais filhotes do que pares recém-formados. A reutilização de ninhos, por sua vez, é mais comum após o sucesso de uma ninhada do que após uma ninhada fracassada (diferença restrita a ninhadas em um mesmo ano), proporciona ninhadas iniciadas mais rapidamente no início da estação reprodutiva, e diminui a chance de parasitismo da ninhada pelo chupim.

Por fim, no Capítulo 4, concluímos que a ocupação dos edifícios como local de nidificação pelas fêmeas de sabiá-barranco tem relação com a personalidade das mesmas. Fêmeas que nidificaram em edifícios mostraram-se menos neofóbicas que aquelas que nidificaram em árvores.

Os resultados desse estudo indicam que o uso de suportes antropogênicos favorece o desempenho reprodutivo do sabiá-barranco, promovendo maior sobrevivência da prole com um menor investimento parental. Esse estudo sugere que a espécie é capaz de explorar recursos alternativos presentes no ambiente urbano, podendo ser beneficiada especialmente pela oferta de edifícios como local de construção do ninho.

ANEXO I

JOURNAL OF NATURAL HISTORY
2019, VOL. 53, NOS. 39–40, 2397–2412
https://doi.org/10.1080/00222933.2019.1704462

Taylor & Francis
Taylor & Francis Group

Check for updates

Breeding biology of the Sayaca Tanager (*Thraupis sayaca*) in southeast Brazil

A. F. Batisteli[a], E. N. da Silva Neto[a], T. P. Soares[b], M. A. Pizo[c] and H. Sarmento[d]

[a]Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, Brazil; [b]Centro de Ciências Biológicas e da Saúde, Universidade Federal de São Carlos, São Carlos, Brazil; [c]Instituto de Biociências, Universidade Estadual Paulista Júlio de Mesquita Filho, Rio Claro, Brazil; [d]Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, Brazil

ABSTRACT

Thraupis is a genus of the American endemic Thraupidae (subfamily Thraupinae), comprising seven species that inhabit tropical forests to urban centres. The Sayaca Tanager (*Thraupis sayaca*) is a disturbance-tolerant species of high representativeness in plant-frugivore networks, but information on its breeding biology is scarce and often restricted to non-systematic surveys. We studied the breeding biology of the *T. sayaca*, following 39 active nests in a periurban area of southeast Brazil during two breeding seasons (2017/2018, 2018/2019). The breeding season ranged from early September to middle December, and the nests were placed in native and exotic plants and human buildings (nest height above ground: 3.35 ± 1.73 m, mean ± SD). Only females incubated and brooded, but both adults built the nests, fed the nestlings, and removed their faecal sacs. Clutch size was 2.86 ± 0.38 eggs and nest attentiveness was 71.2%. The incubation and nestling periods were, respectively, 13.4 and 17.4 days. Males and females did not differ on nestling provisioning and nest sanitation rates. Nestling provisioning (13.35 ± 6.25 trips/hour) increased with nestling age, while mean brooding time was 37.2% and decreased with nestling age. Apparent nest success was 38.7%, and nest survival according to the Mayfield method was 27.2%. Five nests (20.8%) were parasitised by the Shiny cowbird (*Molothrus bonariensis*), and we recorded five events of nest-site reuse. We concluded that the most remarkable breeding traits of *T. sayaca* in comparison with close-related tanagers are the use of anthropogenic nest sites, the higher clutch size and number of feeding trips, and the longer nestling period.

ARTICLE HISTORY
Received 15 July 2019
Accepted 10 December 2019

KEYWORDS
Neotropical; nesting behaviour; parental care; Thraupidae; urban bird

Introduction

The knowledge on the natural history of species is crucial to understand evolutive and biogeographical patterns of biodiversity (Ricklefs 1980; Conway and Martin 2000). Reproduction is a particularly important moment of life cycle due to the high energetic investment and its direct link with individual fitness. In birds, for instance, breeding traits such as clutch size, the duration of nest phases, and the investment on parental care are mutually connected and related to breeding success in complex ways (Tieleman et al.

CONTACT A. F. Batisteli augustofb@gmail.com

2004; Martin et al. 2017). The Neotropical avifauna has a highly representative portion of the world bird diversity in species richness and endemism (Stotz et al. 1996). The increasing efforts applied to explore the breeding biology of Neotropical birds have revealed the variety and complexity of their breeding traits (Auer et al. 2007; Marini et al. 2012; Marques-Santos et al. 2015), and their potential contributions as modelling species to the study of behavioural ecology (Dias et al. 2009; Marques-Santos et al. 2018). Nevertheless, basic aspects of the natural history of most Neotropical bird species are still poorly known.

Thraupidae (Passeriformes) is a speciose family of songbirds comprising *ca* 408 species in 105 genera endemic to Americas (Hilty and Bonan 2019). The breeding biology of several Thraupidae species has been recently described with special attention to finches (e.g. Gressler and Marini 2011; Chiarani and Fontana 2015) and seedeaters (e.g. Franz and Fontana 2013; Vizentin-Bugoni et al. 2013; Repenning and Fontana 2016; Ferreira and Lopes 2017; Rosoni et al. 2019). Although these efforts have considerably improved the knowledge of natural history of Thraupidae, the breeding biology of other representative groups of this diverse passerine family remains understudied.

The genus *Thraupis* and five close-related genera (*Ixothraupis, Chalcothraupis, Poecilostreptus, Stilpnia* and *Tangara*) compose a speciose monophyletic clade within subfamily Thraupinae with 65 species (Burns et al. 2016; Hilty and Bonan 2019). The Sayaca Tanager (*Thraupis sayaca*), one among seven *Thraupis* species, is widely distributed in South America, occurring in most of the Brazilian territory except in Amazonian Forest, Bolivia, Paraguay, Uruguay and northern Argentina (Sick 2001; Remsen et al. 2019). This species inhabits a variety of habitats, including riparian forests, savannas, plantations, and anthropic fields with isolated trees (Sick 2001; Pizo and dos Santos 2011). *Thraupis sayaca* is classified as a disturbance-tolerant species, being common in urban areas and one of the first to settle in restoration sites during early vegetation development (Athiê and Dias 2010; Batisteli et al. 2018). Due to this wide habitat distribution and tolerance, *T. sayaca* is amongst the main dispersers of a number of zoochoric plants, being especially relevant for plant-frugivore networks in disturbed landscapes (Pizo 2004; Pizo and dos Santos 2011).

To date, systematic studies focused on the breeding biology of *Thraupis* spp. or close-related genera cited above are still rare in the scientific literature (e.g. Gómez et al. 2000; Eisermann et al. 2011; Sheldon et al. 2014). The most complete available data on *T. sayaca* breeding provides the characterisation of nests, eggs, and nest placement, clutch size, the length of reproductive season, incubation and nestling periods, instances of nest-site reuse, and the sexual division of parental tasks (Di Giácomo 2005). Hayes (2014) reported breeding phenology and clutch size for 17 nests in Paraguay. Further information is scattered and from few (two to six) nests each study (Borges and Marini 2010; Marini et al. 2012; Marques-Santos et al. 2015; de la Peña and Salvador 2016). Furthermore, quantitative data on *T. sayaca* incubation rhythm and nestling care is lacking in the scientific literature.

Here, we describe the breeding biology of *T. sayaca* from a systematic nest searching and monitoring study in southeast Brazil. We report nesting phenology, nest site, nest and eggs characteristics, the duration of incubation and nestling periods, estimates of nest survival, nest site and nest reuse, brood parasitism by the Shiny cowbird (*Molothrus bonariensis*), and the first detailed information on parental behaviour (the time parents spent incubating eggs and brooding nestlings, and the rates of nestling provisioning and nest sanitation). We also tested if males differ from females in the number of feeding trips to the nest, and the frequency of nest sanitation, and whether the feeding rate, the time spent brooding the young, and the proportion of faecal sacs ingested by parents vary with nestling age.

Materials and methods

Study area

This study took place at the campus of the Universidade Federal de São Carlos (21º59′02″S, 42º52′58″W), São Carlos municipality, southeast Brazil. The climate is classified as subtropical with two well-marked seasons, with mean monthly temperatures varying from 16.2ºC to 22.4ºC, and annual rainfall of 1435 mm, concentrated from September to Abril (Alvares et al. 2013). The study site is in the southern region of the Cerrado (Brazilian savanna) domain, but the original vegetation is highly converted in agriculture, mainly pastures and sugar cane plantations. The campus is a periurban area, and its urbanised portion where the study was conducted has well-spaced buildings surrounded by gardens with native and exotic shrubs and trees (Lessi et al. 2017).

Fieldwork

We captured adult birds with mist nets and marked them with unique combinations of coloured leg bands. We searched nests from August to February 2017/2018 and 2018/2019 by inspecting all the likely nesting sites (shrubs, trees and buildings) and following behavioural cues of adults. Nests were monitored using a mirror attached to a pole every 2–3 days to determine nest fate. We also checked the nests daily near expected dates of hatching and fledging to register the duration of incubation and nestling periods. We made 1-h duration sessions of focal observation using binoculars 8 × 40 mm and 10 × 42 mm at a minimum distance of 10 m from the nests at places of wide pedestrian flow to avoid observer effect. Observation sessions were carried out between sunrise and 10:00 h of non-rainy days. Nests were observed from 1 to 6 h each during incubation (mean ± standard deviation: 2.58 ± 1.62 h per nest) and from 1 to 14 h each during nestling period (4.09 ± 3.86 h per nest). During observations, we quantified the per cent time spent incubating the eggs (i.e. nest attentiveness) or brooding the nestlings, the frequency of nestling provisioning as the number of feeding trips to the nest, and nest sanitation as the number of faecal sacs swallowed or carried away by parents. In four nests where at least one adult was banded, nestling provisioning and nest sanitation was quantified for each adult. In these four nests, only one adult was seen incubating the eggs and brooding the nestlings, which we assumed to be the female. Therefore, we assumed that individuals that were incubating or brooding were females in all the nests, as already reported for species belonging to close-related genus (Arcos-Torres and Solano-Ugalde 2007; Freeman and Greeney 2009).

To estimate clutch size, we considered only nests found during the construction or laying phases. Eggs were measured to the nearest 0.1 mm using a manual caliper and weighed using a digital scale (± 0.1 g). We measured the nests (internal diameter, external diameter, internal height, and external height) using a rule to the nearest 0.1 cm. Nest height above ground and the height of supporting plant were measured with a graduated pole to the nearest 0.1 m. Plant supports were identified at the lowest taxonomic level possible based on morphology.

Statistical analyses

To test whether nestling provisioning and nest sanitation rates differed between parents, we created generalised linear mixed-effects models (GLMMs) with the Poisson distribution. The number of feeding trips to the nests or the number of faecal sacs removed by each parent were set as dependent variables, with parent sex as a factor, and breeding pair ID as a random factor in both models. We also tested if nestling age (as a continuous dependent variable) affects (a) the nestling feeding rate using a GLMM with Poisson distribution, and (b) the percentage of time spent brooding (arcsine transformed) using a linear mixed-effects model, setting nest ID as a random variable in both tests. We used a log link function for the feeding rate model assuming that feeding trip frequency is constrained by energetic limitations in parental effort (Moreno 1987), and we set a negative exponential link function for the brooding model since parents are expected to completely cease nestling brooding some days before they fledge (Skutch 1954). We created a GLMM to test whether the proportion of faecal sacs carried away instead swallowed vary with nestling age. We calculated apparent nest success as a simple ratio between successful nests (i.e. nests that produced at least one fledgling) and the number of total nests. Since apparent nest success do not account for nests that failed before they could be found, we also estimated nest survival according to the Mayfield protocol (1961), which provides a more reliable estimate of nesting success based on nest exposure time. This method provides a daily survival rate (DSR) considering the number of nest failures in an interval of *n* nest exposure days (i.e. two nests exposed during 5 days correspond to 10 nest exposure days), through the equation DSR = 1 – [nest failures/exposure days]. We estimated separately the DSRs for incubation and nestling phases and compared them following Hensler and Nichols (1981). This comparison consisted in confronting the critical z-value at a given α to the z-value obtained from

$$z = \frac{|\mathrm{DSR}_{\mathrm{egg}} - \mathrm{S}^2_{\mathrm{egg}}|}{\sqrt{\mathrm{DSR}_{\mathrm{nestling}} - \mathrm{S}^2_{\mathrm{nestling}}}}$$

where S^2 is the variance of DSR in each nest phase. This variance, in turn, is expressed by

$$\mathrm{S}^2 = \frac{\mathrm{DSR} \times (1 - \mathrm{DSR})}{\mathrm{exposuredays}}$$

To obtain the estimated Mayfield survival across the entire nest cycle duration, we considered that incubation and nestling periods last 14 and 17 days, respectively (see Results). All analyses were made in the software R (R Core Team 2019) using the package 'lme4' (Bates et al. 2015), with α = 0.05. Values are reported in the text as mean ± standard deviation.

Results

We found 39 nests (eight in 2017, and 31 in 2018) between early September to middle December, with a first peak in late September, a second in late October, produced by the cumulative effect of nests in different phases, and a third peak of new nesting attempts in middle November (Figure 1). Mean nest height above ground was 3.35 ± 1.73 m (n = 39, range 1.4–10.1 m). The height of plants used as nesting support was 6.18 ± 3.32 m (n = 27, range 2.7–5.0 m), and most of the nests were placed on exotic plants (Table 1) (Figure 2(a)). Twelve nesting attempts (30.8%) occurred in nests placed in anthropogenic supports. Both adults participated in the nest construction performing 16.5 ± 13.5 trips per hour (n = 4 h of observation in four nests). Male and female brought the material to the nest usually in synchronous trips, when each of them deposited the material and shaped the nest. The nest was a thick-walled open cup attached to the support by the bottom and laterals. Nests were internally coated with vegetal fibres and externally lined with dry leaves, seed down, rachises of compound leaves, and anthropogenic debris, such as plastic twines, pieces of sewing threads, and hygienic paper (Figure 2(b,c)). Some nests were externally covered by seed down, which conferred them a general whitish appearance. The main components of nest walls were vegetal fibres, pieces of dry grass, grass inflorescences, petioles and roots. Nest measurements (n = 5) were: internal diameter 6.90 ± 0.54 cm, external diameter 11.50 ± 1.36 cm, internal depth 4.40 ± 0.30 cm and external height 7.98 ± 2.38 cm.

Clutch size was 2.86 ± 0.38 eggs (n = 7), and eggs measured 23.3 ± 2.1 mm in length (range 20.2–29.7 mm), 17.1 ± 0.7 mm in width (range 1.56–1.81 mm) and weighed 3.42 ± 0.32 g (range 2.8–3.9 g) (n = 16 eggs from six nests). Eggs had a whitish background,

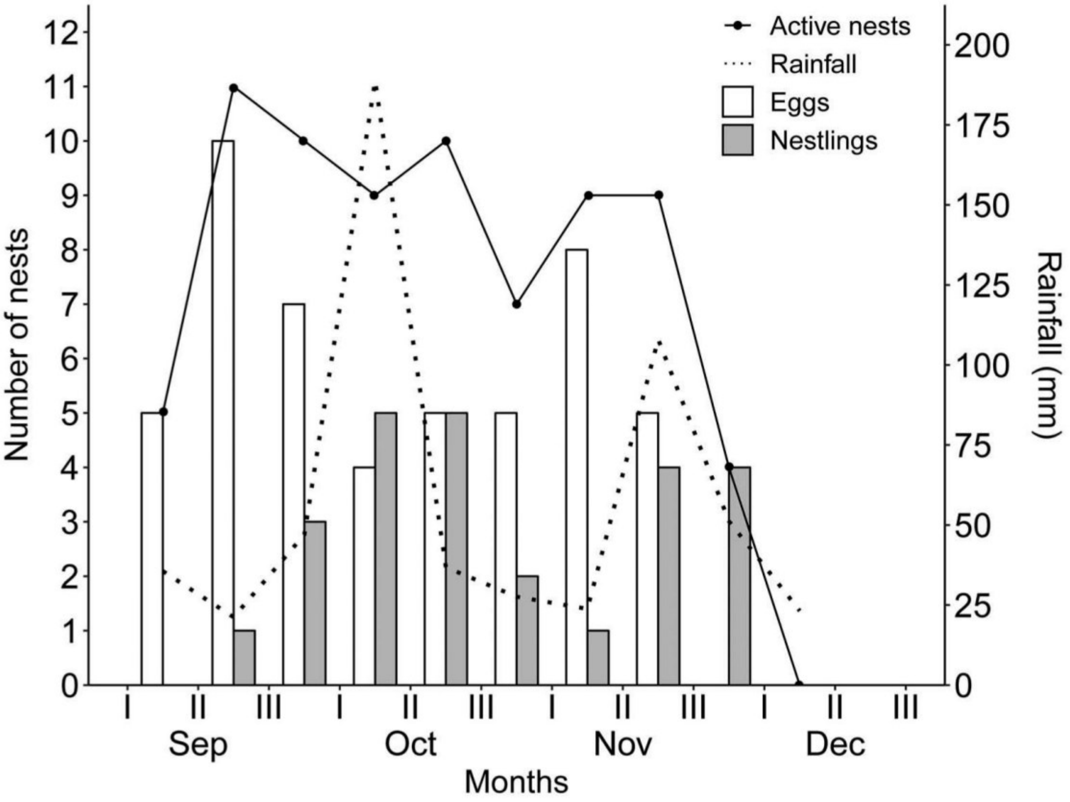


Figure 1. Number of active nests (solid line) of the Sayaca Tanager (*Thraupis sayaca*), number of nests with eggs (white bars) and nestlings (grey bars), and rainfall (dotted line) across months of the breeding season (subdivided in ten-day intervals).

Table 1. Plants used as nesting support by the Sayaca Tanager (*Thraupis sayaca*) in a periurban area of southeast Brazil, their botanical family, and the frequency of nests in each species. Asterisks indicate exotic species.

Family	Plant species	Frequency
Arecaceae	*Caryota mitis**	1
	*Phoenix roebelenii**	5
Asparagaceae	*Dracaena fragrans**	2
	*Yucca gigantea**	1
Asteraceae	*Gymnanthemum amygdalinum**	3
Bignoniaceae	*Handroanthus impetiginosus*	1
	Tabebuia roseoalba	1
Fabaceae	*Bauhinia variegata**	1
	*Delonix regia**	1
	Hymenaea courbaril	1
Lauraceae	*Nectandra megapotamica*	2
Melastomataceae	*Tibouchina granulosa*	1
Moraceae	*Morus nigra**	1
Oleaceae	*Ligustrum lucidum**	2
Podocarpaceae	*Podocarpus macrophyllus**	1
Rosaceae	*Eriobotrya japonica**	1
	*Pyrus communis**	1
Rutaceae	*Murraya paniculata**	1

abundant brown spots in patterns that varied mainly between nests, from concentrated in the blunt pole to uniformly distributed, and black marks that sometimes resembled punctures (Figure 2(d,e)). Eggs were laid in consecutive days (n = 20 eggs from seven nests), and the incubation started when the second egg was laid. Females spent 71.2 ± 17.2% of the time incubating the eggs (range 18.2–98.7%), and incubation recesses took 6.16 ± 3.05 min, ranging from 20 s to 15:22 min (n = 32 h in 12 nests). Males were never seen feeding females on the nest. The incubation period lasted 13.4 ± 0.5 days (n = 5 nests) and hatching may be synchronous or asynchronous, with two hatchings in a day and one in the subsequent day. Hatchlings had purplish dark skin, white commissures, intense pink mouth, and a dense grey down in the back, upwings and head.

During the nestling phase, females spent 37.2 ± 19.7% of the time brooding the young, and on-bouts duration decreased with nestling age (linear mixed model, $t = 4.505$, $p < 0.001$) (Figure 3(a)), so that females did not brood the nestlings in 12 of 15 h of observation when they were older than 8 days. Both parents fed the young at a rate of 13.35 ± 6.25 feeding trips per hour (n = 45 h in 11 nests), which corresponds to 5.65 ± 2.85 feeding trips per nestling/hour. The frequency of feeding trips increased with nestling age (GLMM, $z = 5.072$, $p < 0.001$) (Figure 3(b)). The frequency of nestling provisioning did not differ between parental sexes (GLMM, $z = 0.900$, $p = 0.366$; males 6.37 ± 3.08 trips per hour; females 7.74 ± 3.81 trips per hour; n = 27 h in four nests). Food items delivered to nestlings were small fruits, bites of fruit pulp (i.e. mango and avocado), and small arthropods. Both male and female were engaged on nest sanitation, usually swallowing faecal sacs (85.4% of all nest sanitation events) which the nestlings excreted immediately after being fed, and the frequency of nest sanitation did not differ between parental sexes (GLMM, $z = -0.328$, $p = 0.743$). The proportion of faecal sacs carried away instead swallowed increased with nestling age (GLMM, $z = 2.015$, $p = 0.044$). The nestling period lasted 17.4 ± 0.5 days (n = 7 nests), and siblings left the nest invariably at the same day. The fledgling plumage

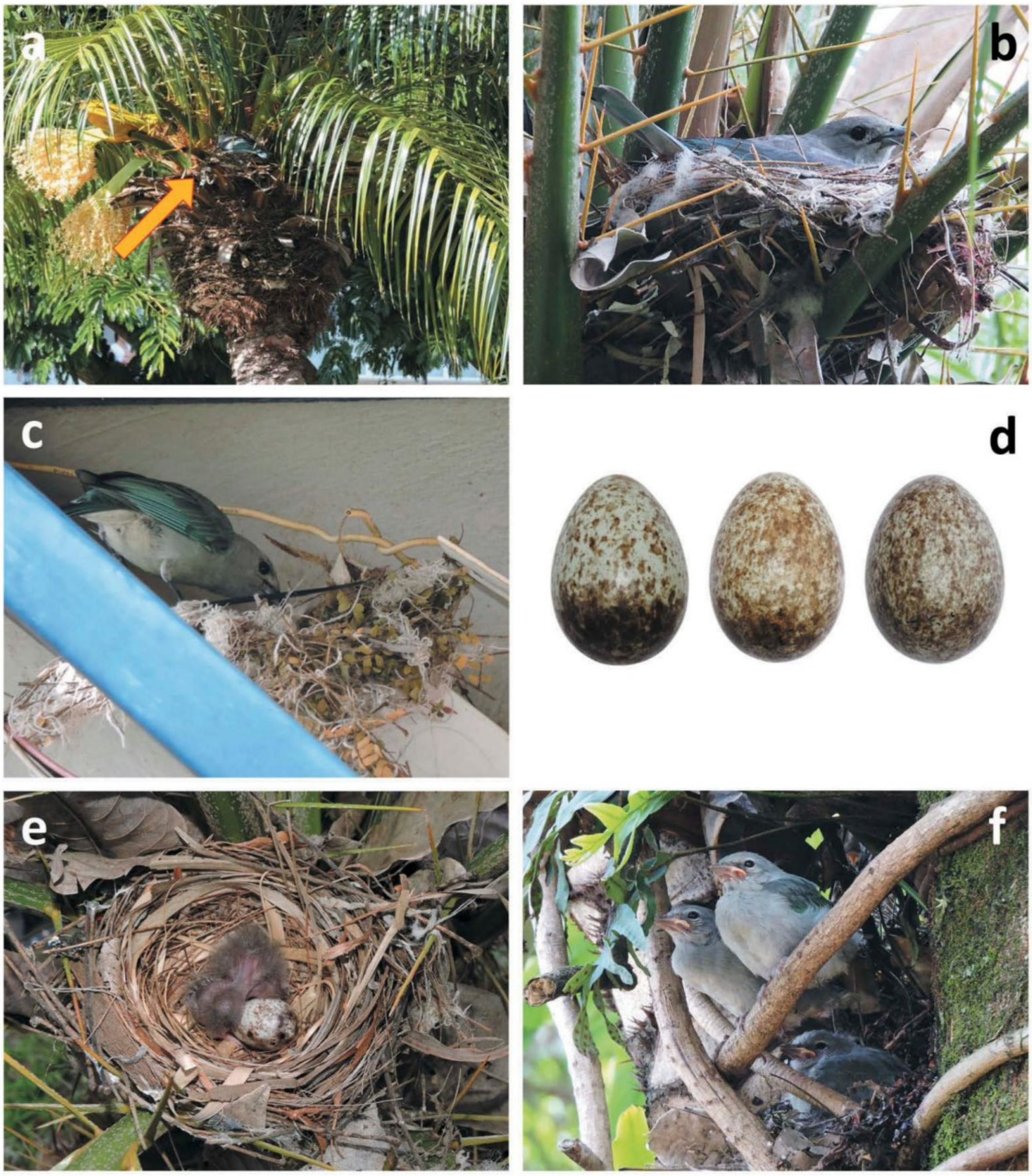


Figure 2. Nest site, nest, eggs, hatchings and fledglings of the Sayaca Tanager (*Tangara sayaca*). A nesting site under the leaves of a Phoenix palm (a), an incubating female (b), a nest externally coated with compound leaves and sewing threads in a human building structure (c), patterns of egg shell colouration (d), 1-day-old hatchling and one egg (e), and newly 17-day-old fledglings (f).

colouration was quite similar to that of adults, but without the same brightly bluish tonality in the primary wing feathers (Figure 2(f)).

Apparent nest success was 38.7% (12 successful nests in 31 monitored nesting attempts). The DSR estimated according to the Mayfield protocol did not differ between nest phases ($Z = 0.966$, $p = 0.334$), being 0.949 ± 0.132 during the egg phase ($n = 235$ exposure days in 26 nests), and 0.964 ± 0.013 during the nestling phase ($n = 195$ exposure days in 17 nests). The survival according Mayfield during the egg phase was 50.6%, and during the nestling phase 53.7%, resulting in a nest survival of 27.2% during the whole

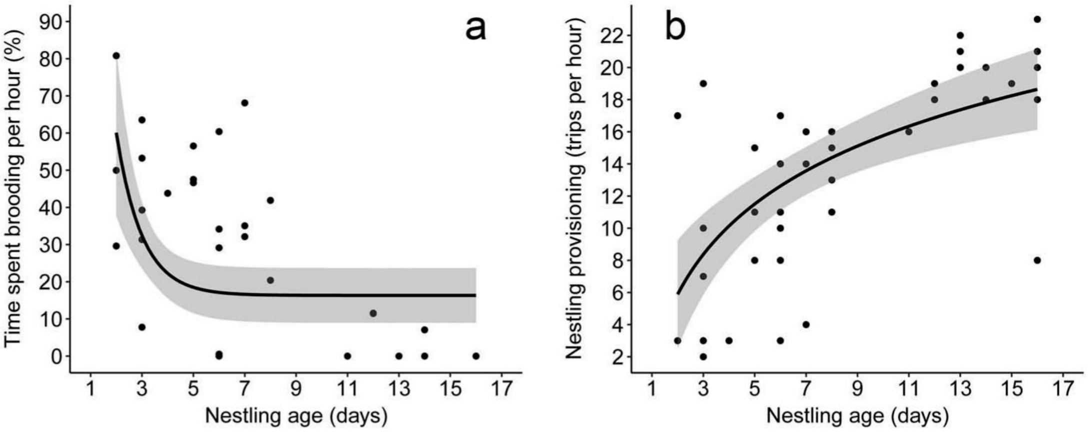


Figure 3. Percent time spent brooding the nestlings per hour (a), and the number of feeding trips per hour (b) in relation to nestling age in the Sayaca Tanager (*Thraupis sayaca*).

nesting cycle. The only nest abandonment occurred during incubation. We observed no partial brood loss during the nestling phase. Brood parasitism by *M. bonariensis* occurred in five of 24 nests (20.8%) when the nest content could be checked, and all of them contained a single cowbird egg. In the only predation event we witnessed, a Toco Toucan (*Ramphastos toco*) depredated two 8-d old nestlings of a nest placed in a *Morus nigra* tree.

We observed five events of nest-site reuse among the 39 breeding attempts. Four nesting sites (two anthropogenic and two natural supports) used in 2017 were reused in 2018, and one nest was occupied in two consecutive broods in 2018 (both successful and separated by 25 days between the fledging day of the first and the laying of the second clutch). In the four between-seasons instances of nest site reuse, birds built new nests over the old ones or in the very same place of an old, dismantled nest, while the nest used two times in 2018 was just lined between the first and the second brood. A male was seen feeding fledglings while her female incubated a new clutch. In this case, the young fledged in October 27 and the laying of a second clutch in a new nest started at November 7. These two nests of the same pair (the first an indoor nest, and the second placed in a tree) was *ca* 20 m apart from each other.

Discussion

The breeding season of tanagers is widely variable among regions and species, following local climate and its effect on food availability (Greeney and Nunnery 2006, 2006; Duca and Marini 2011; Sheldon et al. 2014). The breeding season of *T. sayaca* we recorded (early to middle rainy season) matches most tanagers in Paraguay, central, south and southeast Brazil (Andrade 1996; Willis and Oniki 2003; dos Santos and Marini 2010; Gussoni and Develey 2011; Marini et al. 2012; Hayes 2014; Veloso et al. 2018; Zima et al. 2019), although it can extend over January in south Brazil and Argentina (Di Giácomo 2005; Marques-Santos et al. 2015; de la Peña and Salvador 2016). The phenology of breeding attempts showed three peaks of active nests. Although we did not find more than two nesting attempts by the same breeding pair each breeding season, several other Neotropical passerines can make up to three or four nesting attempts per breeding season when at least one of the first have failed (Repenning and Fontana 2016; Ferreira and Lopes 2017; Morais et al. 2019).

The mean height above ground of *T. sayaca* nests in our study was lower than in Argentina (mean 5.58 m, de la Peña and Salvador 2016) and central Brazil (mean 3.83 m, Marini et al. 2012). It was also lower than the Palm Tanager *Thraupis palmarum* (Andrade 1996) and the Burnished-buff Tanager *Stilpnia cayana* (Willis and Oniki 2003). The few robust samples of tanager nests available in the literature report a mean nest height above ground of 3.7 m for the White-rumped Tanager *Cypsnagra hirundinacea* (dos Santos and Marini 2010), 14.9 m for the Flame-faced Tanager *Tangara parzudakii* (Sheldon et al. 2014), 21 m for the Azure-rumped Tanager *Poecilostreptus cabanisi* (Eisermann et al. 2011), and less than 1 m for the grassland White-banded Tanager *Neothraupis fasciata* (Alves and Cavalcanti 1990). We found no nests <1 m height from the ground, corroborating that such nests are rare among tanagers, with exception of some grassland tanagers and some nests of the Silver-beaked Tanager *Ramphocelus carbo* (Alves and Cavalcanti 1990; Sick 2001; Batisteli and Fieker 2011).

Thraupis sayaca was largely flexible about nesting support choice, using mainly exotic plants, and being one of the few tanagers to nesting in human buildings as reported by Di Giácomo (2005), as well as for *T. parzudakii* and the Blue Tanager (*Thraupis episcopus*) (Gómez et al. 2000; Sick 2001; Sheldon et al. 2014). Exotic plants as nesting supports are punctually reported for this and several close-related species, such as the Blue-and-yellow Tanager *Thraupis bonariensis* (Di Giácomo 2005; de la Peña and Salvador 2016), *T. palmarum* (Andrade 1996), *T. episcopus* (Skutch 1954), *Tangara* spp. such as the Brassy-breasted Tanager *T. desmaresti* (Gonzaga and Castiglioni 2006), the Gilt-edged Tanager *T. cyanoventris* (Gussoni and Develey 2011), and *T. cabanisi* (Eisermann et al. 2011), and the Scrub Tanager *Stilpnia vitriolina* (Freile 2015). The use of exotic plants and anthropogenic structures as nesting supports may enhance the settlement of bird species in human-modified areas (Møller 2010; Reynolds et al. 2019). However, studies on the effect of these nesting supports on the breeding performance of adults report controversial findings, so that these alternative nesting sites may sometimes act as ecological traps (Borgmann and Rodewald 2004; Rodewald et al. 2010; Mainwaring 2015).

Information available on nest measurements for *Thraupis* and close-related tanagers are often limited to a few nests per species. The nest measurements we found matched (although around 10% deeper) those of Azure-shouldered Tanager *Thraupis cyanoptera* in Brazilian Atlantic Forest (Zima et al. 2019), *T. sayaca*, and *T. bonariensis* in Argentina (de la Peña and Salvador 2016). However, the nests we measured were in general larger than reported for the Black-capped Tanager *S. heinei* (Arcos-Torres and Solano-Ugalde 2007; Greeney et al. 2008) and five *Tangara* spp. (Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007; Sheldon and Greeney 2007; Greeney et al. 2011), with exception of *T. parzudakii* nests and a nest of the Green-and-gold Tanager *T. schrankii*, which were slightly deeper (Van Houtan and Alvarez-Loayza 2006; Sheldon et al. 2014). In comparison with two other tanagers of similar clutch size, the nests of *T. sayaca* were larger but slightly shallower than those of White-rumped Tanager *Cypsnagra hirundinaceae* (dos Santos and Marini 2010), and smaller than those of White-banded Tanager *Neothraupis fasciata* in all dimensions but external height (Alves and Cavalcanti 1990).

Thraupis sayaca nests look similar to those of congeneric species, being a relatively robust open cup firmly attached to the substrate (Sick 2001), although with some differences regarding nest composition compared to close-related species. Several *Tangara* spp., for instance, employ lichens and moss either in nest structure or lining (Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007; Sheldon and Greeney 2007; Greeney et al. 2008, 2011; Gussoni and Develey 2011; Sheldon et al. 2014), which we not observed in *T. sayaca* nests. The vegetal materials we recorded in *T. sayaca* nests are also found in nests of *Stilpnia* spp. and *Tangara* spp. (Willis and Oniki 2003; Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007; Greeney et al. 2008; Gussoni and Develey 2011; Freile 2015). Anthropogenic materials, including cloth and plastic were previously reported only in nests of *T. sayaca* and *S. vitriolina* (Almeida et al. 2012; Freile 2015), and we firstly reported the use of hygienic paper among the studies cited above. The frequent use of anthropogenic nesting material suggests that these items may resemble natural nesting materials (Batisteli et al. 2019). The pieces of sewing threads, for instance, are likely substitutes to plumose seeds regard to their white colour and malleability. The presence of anthropogenic debris on bird nests is thought to be maladaptive, since it may reduce nest survival due to increased visibility to predators and cause the death of adults and juveniles by entanglement (Borges and Marini 2010; Townsend and Barker 2014; Canal et al. 2016). Although we had not recorded any case of entanglement, we do not discard that debris had contributed to reduce nest survival in our study by increasing nest predation.

Unlikely suggested by Di Giácomo (2005), males of *T. sayaca* contribute effectively for nest construction, gathering material and modelling the nest, as in the congeneric Golden-chevroned Tanager *Thraupis ornata*, Yellow-winged Tanager *Thraupis abbas, T. cyanoptera, T. palmarum*, and *T. episcopus* (Skutch 1954; Kirwan 2009; Zima et al. 2019), besides *T. parzudakii* (Arcos-Torres and Solano-Ugalde 2007) and *S. vitriolina* (Freile 2015). In other tanagers, however, both members of the pair gather nesting material, but only the females shape the nest (reviewed in Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007), or the females solely build the nest (Greeney et al. 2008; dos Santos and Marini 2010; Sheldon et al. 2014). Males were never seen feeding incubating females, unlike in some *Tangara* and *Stilpnia* species (Van Houtan and Alvarez-Loayza 2006; Arcos-Torres and Solano-Ugalde 2007; Freeman and Greeney 2009; Freile 2015). In summary, the sexual division of further breeding duties in *T. sayaca* resembles such close-related species in which females are exclusively responsible for incubation and nestling brooding, and both sexes account for nestling provisioning (Arcos-Torres and Solano-Ugalde 2007; Freeman and Greeney 2009). This pattern also occurs in other Thraupidae, such as seedeaters and finches (Franz and Fontana 2013; Vizentin-Bugoni et al. 2013; Ferreira and Lopes 2017; Rosoni et al. 2019).

Egg-laying in consecutive days as we recorded was previously reported for *T. sayaca* (Di Giácomo 2005), but is not a rule among tanagers (consecutive days: Skutch 1954; Van Houtan and Alvarez-Loayza 2006, 48 h interval: Greeney et al. 2008; Freile 2015). The eggshell background colour and spotting patterns we observed is similar to previous descriptions (Di Giácomo 2005; de la Peña and Salvador 2016). *Thraupis sayaca* eggs in our study site were larger than in Argentina (Di Giácomo 2005) and those of *S. heinei* (Greeney and Nunnery 2006; Greeney et al. 2008), *S. vitriolina* (Freile 2015), *T. parzudakii* (Sheldon et al. 2014), and Blue-and-black Tanager *Tangara vassorii*

(Greeney et al. 2011), but smaller and less elliptical than eggs of the congeneric *T. cyanoptera* (Zima et al. 2019) and *T. bonariensis* (de la Peña and Salvador 2016). Mean clutch size of *T. sayaca* in our study is higher than in Paraguay (Hayes 2014), than *T. episcopus* (Gómez et al. 2000), other *Tangara* spp. and *Stilpnia* spp. (Skutch 1954; Greeney et al. 2008; Sheldon et al. 2014), and three other syntopic tanagers in central Brazil (Alves and Cavalcanti 1990; dos Santos and Marini 2010; Veloso et al. 2018), but virtually the same mean clutch size of southern American traupids (Yom-Tov et al. 1994). The hatchlings of *T. sayaca* differ from those of the congeneric *T. cyanoptera* and *T. episcopus, S. heinei*, and *S. vitriolina* due to their purplish instead of pinkish skin (Skutch 1954; Arcos-Torres and Solano-Ugalde 2007; Freile 2015; Zima et al. 2019), and from those of *T. schrankii* due to their grey instead of white down feathers (Van Houtan and Alvarez-Loayza 2006).

Among the 29 Thraupidae species victims of brood parasitism by *M. bonariensis*, only 12 are effective hosts (i.e. successfully raise parasitic nestlings, Lowther 2018). Five victims belong to *Thraupis*, and only *T. palmarum, T. bonariensis* and *T. sayaca* are hosts for *M. bonariensis* (Lowther 2018). Brood parasitism among studied nests was low compared to other potential hosts in the study area, such as the Rufous-collared Sparrow (*Zonotrichia capensis*) and the Pale-breasted Thrush (*Turdus leucomelas*), which have >90% of their nests parasitised (Batisteli, unpublished data). In areas where *M. bonariensis* is common, such as our study site (Lessi et al. 2016), egg puncture may be an important cause of clutch reduction even in unparasitized nests (Massoni and Reboreda 2002). The scarcity of partial clutch loss during incubation suggests that *T. sayaca* nests in our study site are actually barely visited and explored by cowbirds, probably because of the predominance of certain parasitic female lineages that prefer the hosts mentioned above (Mahler et al. 2007).

Nest attentiveness by *T. sayaca* females during incubation was close to reported for the congeneric *T. episcopus* in Costa Rica (Skutch 1954), and high compared to other tanagers, such as *S. heinei* and *S. vitrolina* in Ecuador (Freeman and Greeney 2009; Freile 2015), *C. hyrundinacea* and the Swallow Tanager *Tersina viridis* in central Brazil (dos Santos and Marini 2010; Veloso et al. 2018), and several other neotropical passerines in Argentina (Auer et al. 2007), but close to other tropical tanagers (reviewed in Chalfoun and Martin 2007). However, the nest attentiveness we observed is lower than reported for other predominantly granivorous Thraupidae in southeast Brazil, such as the Double-collared Seedeater (*Sporophila caerulescens*, Francisco 2006), and the Lined Seedeater (*Sporophila lineola*, de Oliveira et al. 2010).

The incubation period of *T. sayaca* eggs we observed is close to the 14 days reported for Argentinean populations (Di Giácomo 2005; de la Peña and Salvador 2016) and relatively short compared to *Stilpnia* spp. (14–15 days, Greeney et al. 2008; Freile 2015), *Tangara schrankii* (15–17 days, Van Houtan and Alvarez-Loayza 2006), and other tanagers (15–17 days: Alves and Cavalcanti 1990; dos Santos and Marini 2010; Valdez-Juarez and Londoño 2016; 17–19 days: Veloso et al. 2018). On the other hand, the duration of nestling period we reported is longest than in *Tangara* species, which range from 13 to 17 days (Skutch 1954; Eisermann et al. 2011) and other tanagers (Alves and Cavalcanti 1990; Duca 2007; dos Santos and Marini 2010; Valdez-Juarez and Londoño 2016) with exception of the secondary cavity-nester *T. viridis* (22–24 days, Veloso et al. 2018). A long nestling period after a relatively short incubation period seems to be a remarkable difference on the life-history traits of *T. sayaca* and the congeneric *T. episcopus* (Skutch 1954; Gómez et al. 2000) in relation to close-related species.

The rate of feeding trips per nestling we observed was higher than in most of the tanagers (Gonzaga and Castiglioni 2006; dos Santos and Marini 2010; Sheldon et al. 2014; Veloso et al. 2018), albeit lower than reported for *S. heinei* (Freeman and Greeney 2009) and Beryl-spangled Tanager *T. nigroviridis* (Sheldon and Greeney 2007). The increase in the rate of feeding trips with nestling age indicates that parents are not able to adjust completely the amount of food delivered at each feeding event to attend the growing energetic demand of nestlings. This increasingly parental activity has been reported in other Neotropical passerines (Francisco 2006; Franz and Fontana 2013; Sheldon et al. 2014; Arslan and Martin 2019), and it is expected to enhance nest detectability for visually oriented predators, reducing nest survival as predicted by Skutch (1949). Nestling brooding declined until completely ceasing in most of our observations after nestlings were 8-d old, as in *T. nigroviridis* and *T. parzudakii* (Sheldon and Greeney 2007; Sheldon et al. 2014, but see Freeman and Greeney 2009).

Our data revealed an equivalent rate of feeding trips and nest sanitation between males and females. Such inter-sexual comparisons of participation in breeding duties are rare among tanagers because sexes is often undistinguishable, but other studies reported that both members of the pair-fed the young in a quick succession, suggesting an equivalent participation of both adults (Sheldon and Greeney 2007; Freeman and Greeney 2009; Sheldon et al. 2014). In some tanagers, however, females surpass males in nest attendance, making more feeding trips or removing more faecal sacs (Van Houtan and Alvarez-Loayza 2006; Freeman and Greeney 2009; Freile 2015). Nest sanitation behaviour differed from *T. nigroviridis* and *T. parzudakii* (Sheldon and Greeney 2007; Sheldon et al. 2014), which carry away instead ingest most of faecal sacs regardless of nestling age. Although nest helpers are known for some tanager species (Alves and Cavalcanti 1990; Gelis et al. 2006; dos Santos and Marini 2010), we did not observe more than two adults attending the nests.

Nest success was higher than in other tanagers that make open-cup nests (Greeney et al. 2008; dos Santos and Marini 2010; Eisermann et al. 2011), but lower than reported for other open-cup Thraupidae (i.e. seedeaters and finches) in southeastern Brazil (Francisco 2006; de Oliveira et al. 2010; Freitas and Francisco 2012; Ferreira and Lopes 2017). The longer nest cycle including an extended nestling period in *T. sayaca* may have contributed to this relatively lower nesting success compared to finches and seedeaters. We observed five events of nest-site reuse (12.8% of all nesting attempts), of which four occurred from one breeding season to the next. Nest reuse, although rare among open-cup nesters, is known to occur in *T. schrankii* (Van Houtan and Alvarez-Loayza 2006), while nest site fidelity between consecutive breeding seasons is reported for *T. sayaca* (Di Giácomo 2005), *T. palmarum* (Andrade 1996) and *P. cabanisi* (Eisermann et al. 2011). The reasons underlying nest and nest site reuse in *T. sayaca* and other tanagers require further studies.

Our study provides a complete assessment of the breeding biology of the Sayaca Tanager, being one of the first systematic nesting biology study on this genus and one of the few on tanagers in general. We highlighted the participation of males on nest construction, the use of anthropogenic nest sites and nesting materials, the high clutch size and number of feeding trips, and the relatively long nestling period when compared to other Thraupidae.

Acknowledgements

We are grateful to Raquel Boschi and Ana C. B. Marcondelli for helping with plant identification, and the Brazilian bird banding agency (ICMBio-CEMAVE) for providing the metallic bands. This study was supported in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. MAP receives a research grant from the Brazilian Research Council (CNPq). HS has a CNPq productivity grant (process 309514/2017-7).

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The authors received no funding for this work.

ORCID

A. F. Batisteli http://orcid.org/0000-0003-4866-487X
M. A. Pizo http://orcid.org/0000-0002-3103-0371
H. Sarmento http://orcid.org/0000-0001-5220-7992

References

Almeida SM, Evangelista MM, Silva EJA. 2012. Biologia da nidificação de aves no município de Porto Esperidião, Mato Grosso. Atualidades Ornitológicas. 167:51–56.

Alvares CA, Stape JL, Sentelhas PC, de Moraes G, Leonardo J, Sparovek G. 2013. Köppen's climate classification map for Brazil. Meteorol Z. 22(6):711–728. doi:10.1127/0941-2948/2013/0507.

Alves MDS, Cavalcanti RB. 1990. Ninhos, ovos e crescimento de filhotes de *Neothraupis fasciata*. Ararajuba. 1:91–94.

Andrade MA. 1996. Observações sobre ninhos e ovos de algumas aves em Minas Gerais. Atualidades Ornitológicas. 74:13.

Arcos-Torres A, Solano-Ugalde A. 2007. Notas sobre la anidación de tres especies del género *Tangara* (Thraupidae: Aves) en el noroccidente de Ecuador. Bol Soc Antioqueña Orn. 17:133–137.

Arslan NŞ, Martin TE. 2019. Reproductive biology of Grey-breasted Wood-Wren (*Henicorhina leucophrys*): A comparative study of tropical and temperate wrens. Wilson J Ornithol. 131(1):1–11.

Athiê S, Dias MM. 2010. Avian community composition in an urban park in central São Paulo state, southeastern Brazil. Revista Brasileira de Zoociências. 12(1):67–73.

Auer SK, Bassar RD, Fontaine JJ, Martin TE. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. Condor. 109(2):321–333. doi:10.1093/condor/109.2.321.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4: linear mixed-effects models using Eigen and S4. J Stat Softw. 67(1):1–48. doi:10.18637/jss.v067.i01.

Batisteli A, Tanaka M, Souza A. 2018. Bird functional traits respond to forest structure in riparian areas undergoing active restoration. Diversity. 10(3):90. doi:10.3390/d10030090.

Batisteli AF, Fieker CZ. 2011. Nidoparasitismo por várias fêmeas de vira-bosta (*Molothrus bonariensis*) (Passeriformes: Icteridae) em ninho de pipira-vermelha (*Ramphocelus carbo*) (Passeriformes: Thraupidae) em São Carlos, São Paulo, Brasil. Atualidades Ornitológicas. 162:14–15.

Batisteli AF, Guilhermo-Ferreira R, Sarmento H. 2019. Abundance and prevalence of plastic twine in nests of Neotropical farmland birds. Wilson J Ornithol. 131:201–205.

Borges FJA, Marini MÂ. 2010. Birds nesting survival in disturbed and protected Neotropical savannas. Biodivers Conserv. 19(1):223–236. doi:10.1007/s10531-009-9718-z.

Borgmann KL, Rodewald AD. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecol Appl. 14(6):1757–1765. doi:10.1890/03-5129.

Burns KJ, Unitt PHILI, Mason NA. 2016. A genus-level classification of the family Thraupidae (Class Aves: Order Passeriformes). Zootaxa. 4088(3):329–354. doi:10.11646/zootaxa.4088.3.

Canal D, Mulero-Pazmany M, Negro JJ, Sergio F. 2016. Decoration increases the conspicuousness of raptor nests. PLoS One. 11(7):e0157440. doi:10.1371/journal.pone.0157440.

Chalfoun AD, Martin TE. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. Anim Behav. 73(4):579–585. doi:10.1016/j.anbehav.2006.09.010.

Chiarani E, Fontana CS. 2015. Breeding biology of the Lesser Grass-Finch (*Emberizoides ypiranganus*) in southern Brazilian upland grasslands. Wilson J Ornithol. 127(3):441–456. doi:10.1676/14-137.1.

Conway CJ, Martin TE. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution. 54(2):670–685. doi:10.1111/evo.2000.54.issue-2.

de la Peña MR, Salvador S. 2016. Aves argentinas: descripción, comportamiento, reproducción y distribución. Mimidae a Passeridae. Comunicaciones del Museo Provincial de Ciencias Naturales "Florentino Ameghino": Nueva Serie. 21(2):1–564.

de Oliveira LS, Sousa L, Davanco PV, Francisco MR. 2010. Breeding behaviour of the Lined Seedeater (*Sporophila lineola*) in southeastern Brazil. Ornitol Neotrop. 21(2):251–261.

Di Giácomo AG. 2005. Aves de la Reserva el Bagual. Temas de Naturaleza y Conservación. 4:201–465.

Dias RI, Santos ES, Macedo RH. 2009. Mating system and sexual conflict in the Blue-black Grassquit (*Volatinia jacarina*, Aves: Emberizidae): extra-pair mating. Oecologia Brasiliensis. 13(1):183–191. doi:10.4257/oeco.2009.1301.14.

dos Santos LR, Marini MÂ. 2010. Breeding biology of White-rumped Tanagers in central Brazil. J Field Ornithol. 81(3):252–258. doi:10.1111/jofo.2010.81.issue-3.

Duca C. 2007. Biologia e conservação de *Neothraupis fasciata* (Aves: Thraupidae) no Cerrado do Brasil central [Doctoral thesis]. Brasılia: Universidade de Brasılia.

Duca C, Marini MÂ. 2011. Variation in breeding of the Shrike-like Tanager in central Brazil. Wilson J Ornithol. 123(2):259–265. doi:10.1676/10-116.1.

Eisermann K, Arbeiter S, López G, Avendaño C, de León Lux J, Burge A, … Buchan E. 2011. Nesting ecology of the endangered Azure-rumped Tanager (*Tangara cabanisi*) in Guatemala. Ornitol Neotrop. 22:39–57.

Ferreira DDF, Lopes LE. 2017. Natural history of the Lined Seedeater *Sporophila lineola* (Aves: Thraupidae) in southeastern Brazil. J Nat Hist. 51(23–24):1425–1435. doi:10.1080/00222933.2017.1319518.

Francisco MR. 2006. Breeding biology of the Double-collared Seedeater (*Sporophila caerulescens*). Wilson J Ornithol. 118(1):85–91. doi:10.1676/1559-4491(2006)118[0085:BBOTDS]2.0.CO;2.

Franz I, Fontana CS. 2013. Breeding biology of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) in southern Brazilian upland grasslands. Wilson J Ornithol. 125(2):280–292. doi:10.1676/12-059.1.

Freeman BG, Greeney HF. 2009. Parental care of the Black-capped Tanager (*Tangara heinei*) in northeastern Ecuador. Bol Soc Antioqueña Ornitol. 19:32–37.

Freile JF. 2015. Nesting of the scrub tanager (*Tangara vitriolina*) in Andean Ecuador. Ornitol Neotrop. 26(1):51–58.

Freitas MS, Francisco MR. 2012. Nesting behavior of the Grassland Yellow-Finch (*Sicalis luteola*) in southeastern Brazil. Ornitol Neotrop. 23(3):341–348.

Gelis RA, Greeney HF, Dingle C. 2006. Cooperative breeding and first nest description for Golden Tanager *Tangara arthus*. Cotinga. 26:79–81.

Gómez J, Monrós JS, Gil-Delgado JA. 2000. Notas sobre la biologia reproductora de la Tangara Azuleja *Thraupis episcopus* em Santa Clara (Costa Rica). Ardeola. 42(2):265–267.

Gonzaga LP, Castiglioni G. 2006. Description of the nest and notes on the breeding behaviour of Brassy-breasted Tanager *Tangara desmaresti*. Cotinga. 25:69–73.

Greeney HF, Freeman B, Sheldon KS, Dobbs RC, Gelis RA. 2008. Notes on the nest architecture and nesting biology of Black-capped Tanager (*Tangara heinei*) in northeastern Ecuador. Bol Soc Antioqueña Ornitol. 18:10–15.

Pizo MA, dos Santos BT. 2011. Frugivory, post-feeding flights of frugivorous birds and the movement of seeds in a Brazilian fragmented landscape. Biotropica. 43(3):335–342. doi:10.1111/j.1744-7429.2010.00695.x.

R Core Team. 2019. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Remsen JV Jr., Areta JI, Cadena CD, Claramunt S, Jaramillo A, Pacheco JF, Robbins MB, Stiles FG, Stotz DF, Zimmer KJ. 2019. A classification of the bird species of South America. American Ornithological Society. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm.

Repenning M, Fontana CS. 2016. Breeding biology of the Tropeiro Seedeater (*Sporophila beltoni*). Auk. 133(3):484–496. doi:10.1642/AUK-15-226.1.

Reynolds SJ, Ibáñez-Álamo JD, Sumasgutner P, Mainwaring MC. 2019. Urbanisation and nest building in birds: a review of threats and opportunities. J Ornithol. 160(3):841–860. doi:10.1007/s10336-019-01657-8.

Ricklefs RE. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk. 97(1):38–49.

Rodewald AD, Shustack DP, Hitchcock LE. 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. Biol Invasions. 12(1):33–39. doi:10.1007/s10530-009-9426-3.

Rosoni JRR, Krügel MM, Fontana CS, Behr ER. 2019. Breeding biology of Rusty-collared Seedeater (*Sporophila collaris*) in the grasslands in southern Brazil. Wilson J Ornithol. 131(2):296–309. doi:10.1676/18-3.

Sheldon KS, Greeney HF. 2007. Nest and parental care of the Beryl-spangled Tanager (*Tangara nigroviridis*) in northeastern Ecuador. Ornitol Neotrop. 18(4):603–606.

Sheldon KS, Greeney HF, Dobbs RC. 2014. Nesting biology of the Flame-faced Tanager (*Tangara parzudakii*) in northeastern Ecuador. Ornitol Neotrop. 25(4):397–406.

Sick H. 2001. Ornitologia Brasileira. 3a ed. Rio de Janeiro (Brasil): Ed. Nova Fronteira.

Skutch AF. 1949. Do tropical birds rear as many young as they can nourish? Ibis. 91(3):430–455. doi:10.1111/j.1474-919X.1949.tb02293.x.

Skutch AF. 1954. Life histories of Central American birds. Vol. 2. California (CA): Cooper Ornithological Society.

Stotz DF, Fitzpatrick JW, Parker TA III, Moskovits DK. 1996. Neotropical birds: ecology and conservation. Chicago (IL): University of Chicago Press.

Tieleman BI, Williams JB, Ricklefs RE. 2004. Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds. Funct Ecol. 18(4):571–577. doi:10.1111/fec.2004.18.issue-4.

Townsend AK, Barker CM. 2014. Plastic and the nest entanglement of urban and agricultural crows. PLoS One. 9(1):e88006.

Valdez-Juarez SO, Londoño GA. 2016. Nesting biology of Carmiol's Tanager (*Chlorothraupis carmioli frenata*) in Southeastern Peru. Wilson J Ornithol. 128(4):794–803. doi:10.1676/15-058.1.

Van Houtan KS, Alvarez-Loayza P. 2006. Diet of nestling green-and-gold tanagers (Tangara schrankii), with notes on nesting behavior and seed dispersal. Ornitol Neotrop. 17(2):307–312.

Veloso SL, Pesquero MA, Rodrigues LG, Pesquero MF. 2018. Parental care of the Swallow Tanager (*Tersina viridis*) in Southern Goiás, Brazil. Wilson J Ornithol. 130(3):658–663. doi:10.1676/17-063.1.

Vizentin-Bugoni J, Areta JI, Di Giacomo AG, Di Giacomo AS, Jacobs F, Coimbra MAA, Dias RA. 2013. Breeding biology and conservation of the Marsh Seedeater *Sporophila palustris*. Bird Conserv Int. 23(2):147–158. doi:10.1017/S0959270913000221.

Willis EO, Oniki Y. 2003. Roosting and nesting of the Burnished-buff Tanager (*Tangara cayana*) in southeastern Brazil. Ornitol Neotrop. 14:279–283.

Yom-Tov Y, Christie MI, Iglesias GJ. 1994. Clutch size in passerines of southern South America. Condor. 96(1):170–177. doi:10.2307/1369074.

Zima PVQ, Perrella DF, Francisco MR. 2019. First nest description of the Azure-shouldered Tanager (*Thraupis cyanoptera*, Thraupidae). Rev Bras Ornitol. 27(2):122–125.

Greeney HF, Nunnery T. 2006. Notes on the breeding of north-west Ecuadorian birds. Bull Br Ornithol Club. 126(1):38.

Greeney HF, Simbaña JF, Gelis R. 2011. The nest and eggs of Blue-and-black Tanager *Tangara vassorii*. Cotinga. 33:82.

Gressler DT, Marini MÂ. 2011. Breeding biology of the Stripe-tailed Yellow-finch (*Sicalis citrina*) in Central Brazilian cerrado. Ornitol Neotrop. 22(3):319–327.

Gussoni COA, Develey PF. 2011. New data on the breeding biology of Gilt-edged Tanager *Tangara cyanoventris*. Cotinga. 33:81.

Hayes FE. 2014. Breeding season and clutch size of birds at Sapucái, Departamento Paraguarí, Paraguay. Boletín Del Museo Nacional de Historia Del Paraguay. 18:77–97.

Hensler GL, Nichols JD. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93:42–53.

Hilty S, Bonan A. 2019. Tanagers (Thraupidae). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, editors. Handbook of the birds of the world alive. Barcelona: Lynx Edicions; [accessed 2019 June 10]. https://www.hbw.com/node/52380.

Kirwan GM. 2009. Notes on the breeding ecology and seasonality of some Brazilian birds. Rev Bras Ornitol. 17(2):121–136.

Lessi BF, Bataghin FA, Pires JSR. 2017. Diversity and distribution of trees on the Federal University of São Carlos campus, Brazil: implications for conservation and management. Revista da Sociedade Brasileira de Arborização Urbana. 12(1):92–104. doi:10.5380/revsbau.v12i1.

Lessi BF, Pires JSR, Batisteli AF, MacGregor-Fors I. 2016. Vegetation, urbanization, and bird richness in a Brazilian periurban area. Ornitol Neotrop. 27:203–210.

Lowther PE. 2018. Lists of victims and hosts of the parasitic cowbirds (*Molothrus*). [accessed 2019 June 14]. https://www.fieldmuseum.org/sites/default/files/cowbird-hosts-05sep2018.pdf.

Mahler B, Confalonieri VA, Lovette IJ, Reboreda JC. 2007. Partial host fidelity in nest selection by the shiny cowbird (*Molothrus bonariensis)*, a highly generalist avian brood parasite. J Evol Biol. 20 (5):1918–1923. doi:10.1111/j.1420-9101.2007.01373.x.

Mainwaring MC. 2015. The use of man-made structures as nesting sites by birds: a review of the costs and benefits. J Nat Conserv. 25:17–22. doi:10.1016/j.jnc.2015.02.007.

Marini MÂ, Borges FJ, Lopes LE, Sousa NO, Gressler DT, Santos LR, … França LF. 2012. Breeding biology of birds in the Cerrado of central Brazil. Ornitol Neotrop. 23:385–405.

Marques-Santos F, Braga TV, Wischhoff U, Roper JJ. 2015. Breeding biology of passerines in the subtropical Brazilian Atlantic Forest. Ornitol Neotrop. 26(4):363–374.

Marques-Santos F, Wischhoff U, Roper JJ, Rodrigues M. 2018. Delayed plumage maturation explains differences in breeding performance of Saffron Finches. Emu-Austral Ornithol. 118(4):323–333. doi:10.1080/01584197.2018.1450637.

Martin TE, Boyce AJ, Fierro-Calderón K, Mitchell AE, Armstad CE, Mouton JC, Bin Soudi EE. 2017. Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. Funct Ecol. 31(6):1231–1240.

Massoni V, Reboreda JC. 2002. A neglected cost of brood parasitism: egg punctures by Shiny Cowbirds during inspection of potential host nests. Condor. 104(2):407–412. doi:10.1093/condor/104.2.407.

Mayfield H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

Møller AP. 2010. The fitness benefit of association with humans: elevated success of birds breeding indoors. Behav Ecol. 21(5):913–918. doi:10.1093/beheco/arq079.

Morais R, Araújo LC, Silva GR, Duca C. 2019. Multiple nesting attempts and long breeding seasons of *Mimus gilvus* (Aves: Mimidae) in southeastern Brazil. Zoologia. 36:1. doi:10.3897/zoologia.36.e25717.

Moreno J. 1987. Parental care in the wheatear *Oenanthe oenanthe*: effects of nestling age and brood size. Ornis Scand. 18:291–301. doi:10.2307/3676898.

Pizo MA. 2004. Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. Ornitol Neotrop. 15:117–126.

ANEXO II

STUDIES ON NEOTROPICAL FAUNA AND ENVIRONMENT
https://doi.org/10.1080/01650521.2020.1728032

Taylor & Francis
Taylor & Francis Group

ORIGINAL ARTICLE

Breeding biology of the Creamy-bellied Thrush (*Turdus amaurochalinus*) in southeast Brazil

Augusto Florisvaldo Batisteli[a], Mariana Yamamoto Costiuc[b], Isadora Zavan Santieff[c], Rosane Oliveira Costa[c], Hugo Sarmento[c] and Marco Aurélio Pizo[b]

[a]Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, Brazil; [b]Instituto de Biociências, Universidade Estadual Paulista Júlio de Mesquita Filho, Rio Claro, Brazil; [c]Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, Brazil

ABSTRACT

The description of life-history traits is a prerequisite to understand the complex patterns of bird biodiversity. However, most of the highly diverse Neotropical avifauna still lack basic information on their reproductive behavior. Here, we describe the breeding biology of the Creamy-bellied Thrush (*Turdus amaurochalinus*) in a periurban area of southeast Brazil. We found 67 nests between early September and December in 2017 and 2018. Nests were 3.8 ± 1.9 m (mean ± SD) above ground, in native plants (43.3%), exotic plants (43.3%), and anthropogenic structures (13.4%). Clutch size was 2.9 ± 0.3 eggs, which were incubated exclusively by females during 75.6 ± 18.1% of the time. Both sexes reared the nestlings, but females performed more feeding trips and removed more fecal sacs than males. Incubation and nestling periods lasted, respectively, 13.0 ± 0.6 and 13.2 ± 1.5 days. Overall nesting success according to Mayfield method was 31.6%, and predation was the major cause of nest failure (52.8%). We concluded that this species had higher nest attentiveness, shorter nestling period, and higher nest survival compared to other Neotropical thrushes. The use of exotic plants and anthropogenic structures as nesting substrate may enhance the settlement of this migratory thrush in human-modified areas.

ARTICLE HISTORY
Received 12 July 2019
Accepted 29 January 2020

KEYWORDS
Neotropical; nesting behavior; Turdidae; songbird; urban bird

Introduction

Life-history traits are key to study evolutive adaptations of species to the environmental contexts they inhabit (Shaw & Cresswell 2014; Martin et al. 2015). Descriptive information on bird breeding, for instance, can be integrated to understand the geographic patterns of bird biodiversity (Ghalambor & Martin 2001; Martin et al. 2017). The Neotropical region holds a great part of the world bird richness (c.a. 4 000 species, Stotz et al. 1996), but systematic studies on the breeding biology of Neotropical birds intensified only recently (e.g. Francisco 2006; Perrella et al. 2017; Veloso et al. 2018). Most of the Neotropical birds, including common species, still lack basic information on their reproductive traits, such as the description of nests, eggs, nesting phenology, and parental behavior.

Turdus (Turdidae) is a widely distributed genus, with species native to Europe, Asia, Africa, and America (Collar 2019). The breeding biology of most north temperate *Turdus* species is fairly studied, and they have been frequently used as model species for studies on the evolution of bird life-history traits and behavioral ecology (Ibáñez-Álamo & Soler 2010; Kryštofková et al. 2011; Croston & Hauber 2015). In contrast, only a few of the Neotropical thrushes had their breeding biology formally described (e.g. Auer et al. 2007; Halupka & Greeney 2009; Davanço et al. 2013; Ruiz et al. 2017), which limits the comprehension of the geographical variation in the reproductive traits of this group. The Creamy-bellied Thrush (*Turdus amaurochalinus*) is one of the 26 *Turdus* spp. in South America, occurring from northeastern Brazil to Bolivia and Argentina (Sick 2001). This species is considered an austral migrant (Stotz et al. 1996; Capllonch et al. 2008), and inhabits a variety of ecosystems, from riparian forests and Brazilian savanna to urban areas (Willis 2004; Gasperin & Pizo 2009).

To date, formal studies focused on the breeding biology of *T. amaurochalinus* are restricted to a temperate site in Argentina (Astié & Reboreda 2005, 2006, 2009; Astié & Luchesi 2012), with additional data for other Argentinean localities (Mason 1985; De la Peña 2013), central, southeast, and southern Brazil (Marini et al. 2007, 2012; Borges

CONTACT Augusto Florisvaldo Batisteli augustofb@gmail.com

Supplementary material for this article can be accessed here.

& Marini 2010; Marques-Santos et al. 2015). Despite the relevant information contained in these sources, details on the parental care of *T. amaurochalinus* are not available in the scientific literature. In this study, we describe the breeding biology of *T. amaurochalinus* in southeast Brazil, and provide for the first time a quantitative assessment of parental care tasks and their sexual division. We report the nesting phenology, nest placement characteristics, nest and egg measurements, the length of incubation and nestling periods, nest success estimates, and provide the first detailed information on parental behavior (i.e. sexual roles, nest attentiveness, and the rates of nestling provisioning and nest sanitation performed by parents).

Materials and methods

Study area

This study was carried out in the campus of the Universidade Federal de São Carlos (21°59′02″S, 47°52′58″W, 848 m a.s.l.), in São Carlos municipality, southeast Brazil. The study area was inserted in a landscape of cerrado (Brazilian savanna) originally, today highly impacted by sugarcane monoculture and pastures. The regional climate is subtropical, with average monthly temperatures of 19.9°C (range: 16.2–22.4°C), and an annual rainfall of 1435 mm (Alvares et al. 2013). The campus (645 ha) is a periurban area composed by patches of native vegetation (mainly Brazilian savanna and riparian forests), stands of *Eucalyptus* and *Pinus* with regenerating native understory. Our nest search effort was concentrated in the urbanized portion of the campus (c.a. 100 ha), which is composed by sparse buildings surrounded by lawns and gardens with high tree species richness (mainly Fabaceae) (Lessi et al. 2017).

Field procedures

Two researchers actively searched for nests from August, when males start to sing and defend territories, to the end of January. Nests were located by direct inspection of every plant or man-made structures and by following adults carrying nesting material or food to the nestlings. Once located, the nests were checked every 1–3 days using a pole with a mirror until nestlings fledged or the nest was depredated. Concomitantly with nest searching, adult thrushes were caught with mist nests and received a metallic ring and a unique combination of colored leg bands.

We assessed parental behavior during 1-h focal observation sessions conducted between sunrise and 10:00 h of non-rainy days. Observations were carried out at a minimum distance of 10 m from the nests with the aid of 8 × 40 mm binoculars. During incubation, we quantified nest attentiveness (the time spent incubating by females) and male nest guarding (the time a given male spent perched on nest rim) as percent time of each observation hour. During the nestling period, we estimated the time females spent brooding the nestlings (percent time of each observation hour), and the frequency of nestling provisioning (number of feeding trips to the nest) and nest sanitation by sex, discriminating when fecal sacs were swallowed or carried away by each adult. In nests attended by two unbanded parents, sex differentiation was based on differences of bill coloration between individuals and supported by behavioral cues (i.e. when the male sang near the nest). Male bill was often more intensely yellow-colored than in females (Sick 2001). Nests in which parents could not be securely individualized were excluded from intersexual comparisons. Nest measurements (inner diameter, outer diameter, inner height, and outer height) were taken using a rule to the nearest 0.1 cm. Eggs were measured with a manual caliper (±0.1 mm) and weighed at a maximum of 3 days after they were laid to the nearest 0.1 g with a digital scale. Nest height above ground and the height of plant supports were estimated to the nearest 0.1 m with a graduated pole. Estimates of a clutch size considered only nests found during the construction or laying stages.

We defined incubation period as the interval between the first incubation day (usually with the second egg) and the first hatching, whereas the nestling period is the interval between the first hatching and the day the first young left the nest. We considered the hatchday as age 0 days of the offspring, and hatch asynchrony when siblings hatched in different days. To estimate the temporal distribution of first-egg laying dates, we used nests for known laying dates and nests with known approximate hatching dates (±1 day) by backdating14 days (i.e. incubation starts after the second egg and took 13 days). We adopted 1 September as a reference for reporting nesting phenology.

Statistical analyses

To test whether nestling provisioning and nest sanitation rates performed by parents differed between males and females, we created generalized linear mixed models (GLMMs) with Poisson distribution, with the frequency of feeding trips to the nests and the number of fecal sacs removed as dependent variables, adult sex as a categorical explanatory variable, and breeding pair ID as a random factor. We estimated apparent nest success

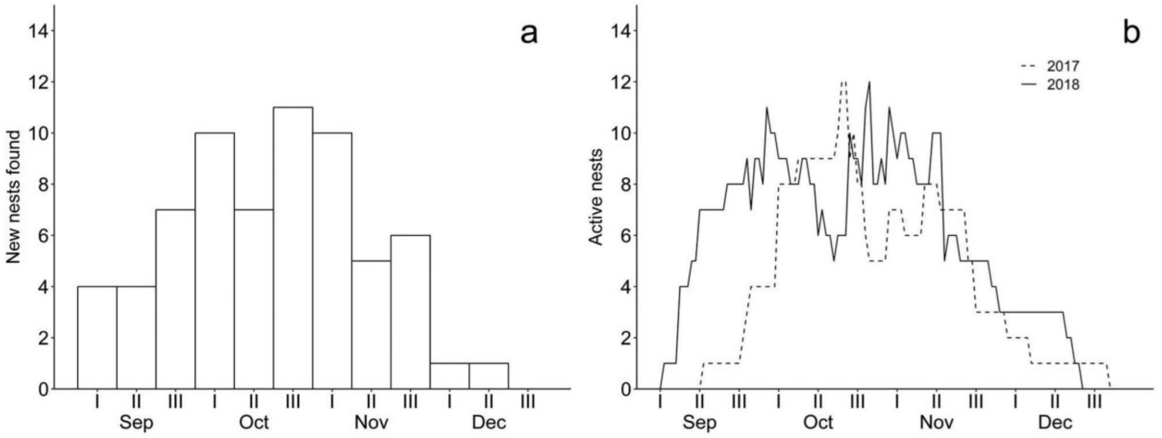


Figure 1. Nesting phenology of the Creamy-bellied Thrush (*Turdus amaurochalinus*) in a periurban area of southeast Brazil, with the number of new nests found (A) and active nests (B) across the breeding season divided into 10-day intervals.

by a simple ratio between the number of successful nests (when at least one nestling survived until fledging) and the total number of monitored nests. We also calculated the nest survival according to Mayfield (1961), comparing the daily survival rates (hereafter 'DSR') of the nests between incubation and nestling phases following Hensler and Nichols (1981). To estimate the survival according to the Mayfield method across the whole nesting cycle, we considered that egg and nestling phases last 13 days each (see Results). Values are presented as mean ± standard deviation and α = 0.05. All analyses were conducted in the software R (R Core Team 2019).

Results

We followed 67 nesting attempts, 25 in 2017 and 42 in 2018. Fifteen nests (22.4%) were found during nest construction, two (3.0%) during laying, 31 (46.3%) during incubation, 15 (22.3%) during nestling phase, and four (6.0%) had uncertain status. Active nests were found mostly between early October and early November, with a bimodal distribution peaking first between early and late October and second between late October and middle November (Figure 1). The earliest egg was laid on 7 September and the latest egg was laid on 3 December (first-egg laying dates averaged 41.5 ± 25.3 days after 1 September, n = 23). During nest searching and monitoring activities, AFB opportunistically witnessed three copulations, all occurred on the ground, when males mounted females two to three times consecutively in less than 1 min.

The nest was a dense-walled cup attached to the support by the base and sides. The predominant nesting materials were roots, petioles, and rachises of compound leaves, which were used on either nest structure or internal lining. Nest walls also contained pieces of dry grass, compound leaves, and eventually human hair, and some nests were externally lined with paper and plastic pieces. Most nests (86.6%) were placed on plants, which belong to 28 species of 20 families (Table S1, Supplementary material), while the others were built on concrete and metallic structures in buildings. Nest height above ground was 3.8 ± 1.9 m (range: 1.1–11.2 m), and the height of plant supports was 7.0 ± 2.6 m (range: 2.3–15.0 m). Nest construction took 3–11 days (n = 3) and was exclusively performed by females, which made from 12 to 37 trips per hour (n = 3 h in three nests). Nests were 8.0 ± 0.4 cm in inner diameter (range: 7.2–8.5 cm), 13.0 ± 0.7 cm (range: 11.9–13.7 cm) in outer diameter, 5.1 ± 0.7 cm (range: 4.5–6.5 cm) in inner height, and 9.2 ± 1.6 cm (range: 7.5–12.0 cm) in outer height (n = 7).

Mean size was 2.9 ± 0.3 eggs (n = 9 nests), and varied between two and three eggs (one laid egg per day). Eggs had a light blue background and numerous brown spots either uniformly distributed or concentrated in the rhomb pole (Figure 2A). The eggs weighed 5.4 ± 0.8 g (range: 4.1–6.5 g), and measured 27.5 ± 2.0 mm (range: 22.3–29.9 mm) in length and 20.0 ± 0.6 mm (range: 18.8–20.9 mm) in diameter (n = 19 eggs from six nests). In 49 h of observation in 22 nests, only females were seen incubating. Nest attentiveness during incubation was 75.6 ± 18.1% (range: 37.6–100%), and incubation recesses averaged 8.84 ± 6.30 min (range: 2 sec–36 min). Some males stayed perched on the nest rim when females took incubation recesses, performing a guarding behavior during 48–462 s, but this behavior was rare (n = 5 events in three nests). The male fed the incubating female in only one nest two

Figure 2. The eggs and nest (A), a male with food in its bill and the female brooding the nestlings (B), hatchlings (C), 7-day-old and 11-day-old nestlings (D and E, respectively) and a fledgling (F) of the Creamy-bellied Thrush (*Turdus amaurochalinus*).

times in 4 h of observation. Incubation period lasted 13.0 ± 0.6 days (range: 12–14, n = 6 nests), and hatching was asynchronous in 6 of 8 nests. Hatchlings had closed eyes, pinkish skin, straw-colored down concentrated across the center of their back, and the interior of their mouths was yellow (Figure 2C).

Parents made 5.95 ± 3.29 feeding trips per hour (range: 1–14, n = 42 h), and the number of feeding trips by nestling/hour was 3.06 ± 1.71. Both members of the pair provisioned the nestlings, and females did more feeding trips than males (GLMM, z = −3.029, p = 0.002, n = 34 h in 17 nests; females: 3.47 ± 2.83 trips per hour; males: 2.03 ± 2.14) (Figure 3A). Food

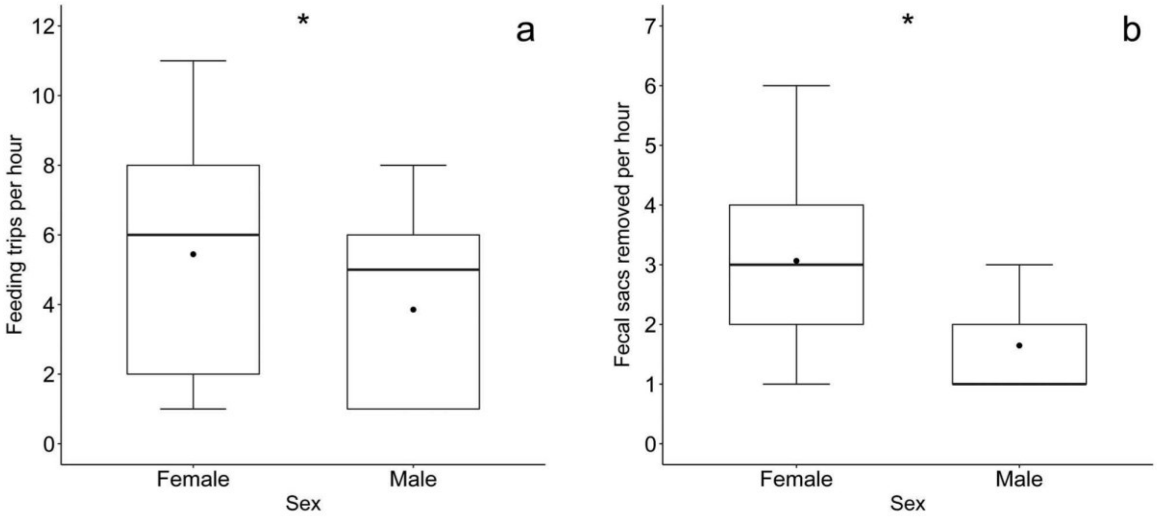


Figure 3. Rates of food provisioning to the nestlings and nest sanitation performed by females and males of the Creamy-bellied Thrush (*Turdus amaurochalinus*). Dots represent the means, and the asterisks indicate a significant difference between sexes for 34 h of observation in 17 nests (α = 0.05).

items delivered to nestlings were small fruits (e.g. blackberry and Brazilian cherry, as a whole or in pieces), bites of large fruits (e.g. avocado, mango, and papaya), Lepidoptera larvae, adult insects (e.g. cicadas), and earthworms. Both male and female engaged in nest sanitation usually by swallowing (95.1% of all nest sanitation events) fecal sacs 2.42 ± 1.90 times per hour, and females removed more fecal sacs than males (GLMM, $z = -3.583$, $p < 0.001$, $n = 34$ h in 17 nests; females: 2.06 ± 1.44; males: 0.64 ± 0.80) (Figure 3B).

Nestlings were brooded only by females during 12.0 ± 16.0% of the time (range: 0–87.6%). The nestling period lasted 13.2 ± 1.5 days (range: 11–15, n = 11 nests), and siblings left the nest usually in the same day. Two fledglings captured by hand soon after leaving the nests weighed 38.8 and 56.3 g and measured 3.10 and 3.22 mm in tarsus length. Fledglings had poor flight capacity, and remain hidden in brushes relatively close to the ground (i.e. up to 1.5 m height) in the nest vicinity for 3–5 days after fledging. Fledglings had whitish breast with dark spots, a predominantly brownish back with a longitudinal ocher trace in the center of lesser and median coverts, and short tail feathers (Figure 2F).

Brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*) occurred in nine of the 36 nests of which the nest content could be properly checked, with one (six nests) or two cowbird eggs (three nests). Apparent nest success was 45.3% (n = 53), and the major cause of nest failure was predation (52.8% of the nests). One nest was abandoned during incubation. DSR did not differ between nest phases ($z = 0.964$, $p = 0.335$), being 0.947 ± 0.012 during incubation (n = 323 exposure days in 39 nests) and 0.966 ± 0.009 during the nestling phase (n = 353 exposure days in 35 nests), which resulted in an estimated survival of 31.6% across the whole nesting cycle according to the Mayfield method. Partial clutch loss during the nestling phase occurred in four out of 26 nests. Both male and female engaged on nest defense, mainly through predator distraction using alarm vocalizations. Nest reuse occurred seven times (13.5% of all nesting attempts), all but one within the same breeding season. Three consecutive nesting attempts in reused successful nests occurred in intervals as short as 4–9 days.

Discussion

The breeding season of the Creamy-bellied Thrush coincides with great food availability in terms of fruiting trees and the emergence of seasonal insects such as cicadas (Lorenzi 2000; Aoki 2007). The start of the breeding season in early September, together with the rainy period, was similar to the reported in the cerrado of central Brazil (Marini et al. 2012), and for other thrushes in southeast Brazil, such as the Pale-breasted Thrush *T. leucomelas* and the White-necked Thrush *T. albicollis* (Marini et al. 2007). However, the beginning of breeding season in our study site occurred 1 month earlier than reported for higher latitudes for *T. amaurochalinus* and other thrushes (Auer et al. 2007; Astié & Luchesi 2012; Hayes 2014; Marques-Santos et al. 2015). The use of exotic plants and anthropogenic structures as nesting substrates indicates that this migrant thrush is able to find suitable breeding places in areas with poor native vegetation cover, which may enhance its settlement on urban sites and agricultural landscapes (Møller 2010; Astié & Luchesi 2012; Batisteli et al. 2019).

The nests had a typical thrush nest format of a low cup. Nest dimensions in our study site were in general similar to those of *T. amaurochalinus* in Argentina (Astié & Luchesi 2012), but our study nests were 17% shallower (5.1 vs. 6.1 cm) than in that temperate population. Nest measurements may vary among conspecific populations in response to latitudinal variation of climatic factors in species-specific ways (Crossman et al. 2011; Mainwaring et al. 2014). The lower nest depth we found may be a consequence of the 11° of latitudinal difference between our and the Argentinean populations. A similar reduction of 14.5% in the internal height occurs in *T. leucomelas* nests comparing populations of southeast and north Brazil (Davanço 2009; Ruiz et al. 2017).

Nest composition was somewhat different from other thrush species due to the presence of grass pieces (Marini et al. 2007; Davanço 2009). Unlike *T. amaurochalinus* nests of an Argentinean population (Astié & Reboreda 2005), our study nests had no mud. Most nests of *T. leucomelas* at our study site had a great amount of mud, suggesting that this material was locally available (Batisteli, personal observation). The use of anthropogenic materials by the Creamy-bellied thrush is reported in other disturbed areas (Borges & Marini 2010; Batisteli et al. 2019), and the presence of these materials reduces nest survival rates probably by increasing their detectability by visual predators (Borges & Marini 2010). However, those nests of *T. leucomelas* in the study area had no anthropogenic debris (Batisteli, personal observation), suggesting that *T. amaurochalinus* females are more prone to incorporate human debris in the nest.

The eggs were close in size to the eggs reported by Astié and Reboreda in Argentina (2005), but slightly lighter than in southern populations (De la Peña 2013; Marques-Santos et al. 2015) and those of larger-sized neotropical thrushes, such as *T. leucomelas* and the Rufous-bellied Thrush *T. rufiventris* (Auer et al. 2007; Marini et al. 2007). The clutch size was consistently larger than in other neotropical thrushes (Auer et al. 2007; Davanço et al. 2013; Hayes 2014; Ruiz et al. 2017), but similar to reported for *T. amaurochalinus* in Paraguay (Hayes 2014), and smaller than in Argentinean irrigated grooves (Astié & Reboreda 2006).

The sexual roles we observed are the same reported for other thrushes worldwide, with nest construction, incubation, and nestling brooding performed exclusively by females, while nestling provisioning and nest defense are performed by both adults (Auer et al. 2007; Halupka & Greeney 2009; Kryštofková et al. 2011; Mitchell et al. 2017). Mean nest attentiveness (c.a. 75%) was lower than in Argentina (83–90%, Astié & Reboreda 2005), but higher than reported for other neotropical thrushes such as *T. leucomelas* (67%, Davanço 2009), Slaty Thrush *T. nigriceps*, and *T. rufiventris* (66.2% and 71%, respectively, Auer et al. 2007), being among the highest nest attentiveness reported for neotropical passerines with uniparental incubation (Auer et al. 2007; Ricklefs & Brawn 2013). We suggest that some factor at local scale may have contributed to the higher nest attentiveness observed, since *T. leucomelas* nest attentiveness in the study area is also higher than reported by Davanço (2009) in another nearby urban site (76% Batisteli, in prep.).

The brood parasitic *M. bonariensis* is common in the study area and offers the threat of egg puncturing to *T. amaurochalinus* (Astié & Reboreda 2006; Lessi et al. 2016), which might be responsible for the high nest attentiveness observed. However, *T. amaurochalinus* breeding adults react to the presence of *M. bonariensis* mainly by reducing their latency to return to nest vicinity and visiting it more frequently instead of increasing nest attentiveness (Astié & Reboreda 2005). The higher nest attentiveness we observed may be a way to compensate for the absence of extreme aggressive behaviors against nest threats through passive nest defense.

In a number of passerine species, males and females have a symmetric contribution to nestling provisioning and nest sanitation because of the sexual conflict involved with the costs of nestling care (Schwagmeyer et al. 1999; Bebbington & Hatchwell 2015). However, in our study, females participated more than males in nestling provisioning. The opposite pattern was reported for the Wood Thrush *Hylocichla mustelina* in Pennsylvania, USA (Gow & Stutchbury 2013). In such species with parental asymmetric contribution to nestling provisioning, the relative importance of each sex on breeding tasks is driven mainly by specific life-history traits, such as sex-biased mortality, sexual selection, and mating system (Møller 2000; Liker & Székely 2005; Olson et al. 2007). In addition, the level of engagement of each sex in parental care may also vary temporarily in response to clutch size and nestling age (Gow et al. 2013).

Both incubation and nestling periods of *T. amaurochalinus* were slightly longer than in a southern population (11.5 and 12 days, respectively, Astié & Luchesi 2012), but within the range reported in central Brazil (Marini et al. 2012), and it was quite close to that reported for *T. rufiventris* (13.1 days, Auer et al. 2007) and *T. leucomelas* near our study site (12.8 days, Davanço et al. 2013). The incubation period we observed (13 days) was in general similar to reported for other Neotropical thrushes, despite small (i.e. ≤1 day) differences when compared to *T. nigriceps* (12.5, Auer et al. 2007) in Argentina, *T. leucomelas* in the north of the Atlantic Forest (12 days, Ruiz et al. 2017), and the Hauxwell's Thrush *T. leucops* in northeastern Ecuador (14 days, Halupka & Greeney 2009). On the other hand, the nestling period was consistently shorter compared to most of the other Neotropical thrushes (Auer et al. 2007; Halupka & Greeney 2009; Davanço et al. 2013; De la Peña 2013). This short nestling period may be related to adult body mass, since *T. amaurochalinus* has lower body mass than most of the other thrushes mentioned (Rodrigues et al. 2019), which would require a shorter interval to the nestlings reach a given percentage of adult weight to leave the nest.

Nest survival was higher than reported for other populations of *T. amaurochalinus* and other Neotropical thrushes (Auer et al. 2007; Borges & Marini 2010; Lomáscolo et al. 2010; Astié & Luchesi 2012; Ruiz et al. 2017, but see Davanço et al. 2013). Partial clutch loss was rare in our study population, unlike some studies that reported high rates of nestling starvation in human-modified environments (Ibáñez-Álamo & Soler 2010; Astié & Luchesi 2012). The shorter nestling period of our study species may have contributed to a higher nest survival. However, this result must be interpreted with caution, since both our study and Davanço et al. (2013) were conducted in urban areas, which likely differ from natural habitats in food availability and nest predator abundance (Jokimäki et al. 2005; Chamberlain et al. 2009).

The low incidence of brood parasitism by *M. bonariensis* in the nests of *T. amaurochalinus* was surprising, since their nests are largely parasitized (i.e. 60% of parasitism prevalence) in Argentina (Astié & Reboreda 2005). Nests of other potential hosts in our study area, such as *T. leucomelas* and the Rufous-collared Sparrow (*Zonotrichia capensis*), have a high prevalence of brood parasitism (i.e. >90%, Batisteli unpublished data). The low brood parasitism we found may be a consequence of the local predominance of parasite lineages that prefer other hosts, such as those we mentioned to be largely parasitized (Mahler et al. 2007).

Our study provides the description of the breeding biology and the first detailed information on the parental care of the Neotropical migrant thrush *T. amaurochalinus*. We concluded that females participated more than males in nestling provisioning and nest sanitation. Moreover, in comparison with other Neotropical thrushes, *T. amaurochalinus* showed higher nest attentiveness, shorter nestling period, and higher nest survival. We suggest that the use of exotic plants and buildings as nesting substrate may enhance the settlement of this migratory thrush in human-modified habitats, such as urban areas.

Acknowledgments

We are grateful to Talita P. Soares for field assistance, Raquel S. Boschi, and Ana C. B. Marcondelli for helping with plant identification, and the Brazilian bird banding agency (ICMBio - CEMAVE) for providing the metallic bands. We also thank two anonymous reviewers for their valuable comments on this manuscript. AFB thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a doctoral fellowship. MAP receives a fellowship from the Brazilian Council of Scientific and Technological Development (CNPq).

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The authors received no funding for this work.

ORCID

Augusto Florisvaldo Batisteli http://orcid.org/0000-0003-4866-487X
Rosane Oliveira Costa http://orcid.org/0000-0003-2876-8196
Hugo Sarmento http://orcid.org/0000-0001-5220-7992
Marco Aurélio Pizo http://orcid.org/0000-0002-3103-0371

References

Alvares CA, Stape JL, Sentelhas PC, de Moraes G, Leonardo J, Sparovek G. 2013. Köppen's climate classification map for Brazil. Meteorol Z. 22(6):711–728.

Aoki C. 2007. *Quesada gigas* (Olivier 1790): padrões de emergência, mortalidade e recurso para aves [master's thesis]. [Campo Grande (MS)]: Universidade Federal de Mato Grosso do Sul.

Astié A, Luchesi N. 2012. Reproductive success of the Creamy-bellied Thrush in a southern temperate Zone. Wilson J Ornithol. 124(1):133–138.

Astié AA, Reboreda JC. 2005. Creamy-bellied Thrush defenses against Shiny Cowbird brood parasitism. Condor. 107(4):788–796.

Astié AA, Reboreda JC. 2006. Costs of egg punctures and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) at Creamy-bellied Thrush (*Turdus amaurochalinus*) nests. Auk. 123(1):23–32.

Astié AA, Reboreda JC. 2009. Function of egg punctures by Shiny Cowbirds in parasitized and nonparasitized Creamy-bellied Thrush nests. J Field Ornithol. 80 (4):336–343.

Auer SK, Bassar RD, Fontaine JJ, Martin TE. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. Condor. 109(2):321–333.

Batisteli AF, Guilhermo-Ferreira R, Sarmento H. 2019. Abundance and prevalence of plastic twine in nests of

Neotropical farmland birds. Wilson J Ornithol. 131 (1):201–205.

Bebbington K, Hatchwell BJ. 2015. Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. Behav Ecol. 27(2):652–659.

Borges FJA, Marini MA. 2010. Birds nesting survival in disturbed and protected Neotropical savannas. Biodivers Conserv. 19(1):223–236.

Capllonch P, Ortiz D, Soria K. 2008. Migración del Zorzal común *Turdus amaurochalinus* (Turdidae) en Argentina. Braz J Ornithol. 16(1):12–22.

Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. 2009. Avian productivity in urban landscapes: a review and meta-analysis. Ibis. 151(1):1–18.

Collar N. 2019. Thrushes (Turdidae). In: Handbook of the birds of the world alive. Barcelona: Lynx Edicions; [cited 2019 May 23]. Available from: https://www.hbw.com/node/52318

Crossman CA, Rohwer VG, Martin PR. 2011. Variation in the structure of bird nests between northern Manitoba and southeastern Ontario. PLoS One. 6(4):e19086.

Croston R, Hauber ME. 2015. A recoverable cost of brood parasitism during the nestling stage of the American Robin (*Turdus migratorius*): implications for the evolution of egg rejection behaviors in a host of the Brown-headed Cowbird (*Molothrus ater*). Ethol Ecol Evol. 27(1):42–55.

Davanço PV. 2009. Biologia reprodutiva do Sabiá-barranco (*Turdus leucomelas*) na região sudeste do Brasil [undergraduate thesis]. [Sorocaba (SP)]: Universidade Federal de São Carlos.

Davanço PV, Oliveira LS, Sousa LM, Francisco MR. 2013. Breeding life-history traits of the Pale-breasted Thrush (*Turdus leucomelas*) in southeastern Brazil. Ornitol Neotrop. 24(4):401–411.

De la Peña MR. 2013. Nidos y reproducción de las aves argentinas. Santa Fe (Argentina): Museo Provincial de Ciencias Naturales.

Francisco MR. 2006. Breeding biology of the Double-collared Seedeater (*Sporophila caerulescens*). Wilson J Ornithol. 118 (1):85–91.

Gasperin G, Pizo MA. 2009. Frugivory and habitat use by thrushes (*Turdus* spp.) in a suburban area in south Brazil. Urban Ecosyst. 12(4):425–436.

Ghalambor CK, Martin TE. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science. 292 (5516):494–497.

Gow EA, Musgrove AB, Wiebe KL. 2013. Brood age and size influence sex-specific parental provisioning patterns in a sex-role reversed species. J Ornithol. 154(2):525–535.

Gow EA, Stutchbury BJ. 2013. Understanding sex differences in parental effort in a migratory songbird: examining a sex-specific trade-off between reproduction and molt. Condor. 115(3):640–649.

Halupka K, Greeney HF. 2009. Breeding biology of Pale-eyed Thrushes (*Turdus leucops*) in the cloud forest of northeastern Ecuador. Ornitol Neotrop. 20(3):381–389.

Hayes FE. 2014. Breeding season and clutch size of birds at Sapucái, Departamento Paraguarí, Paraguay. Bol Mus Nac Hist Parag. 18:77–97.

Hensler GL, Nichols JD. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93(1):42–53.

Ibáñez-Álamo JD, Soler M. 2010. Does urbanization affect selective pressures and life-history strategies in the common blackbird (*Turdus merula* L.)?. Biol J Linn Soc. 101 (4):759–766.

Jokimäki J, Kaisanlahti-Jokimäki ML, Sorace A, Fernández-Juricic E, Rodriguez-Prieto I, Jimenez MD. 2005. Evaluation of the “safe nesting zone” hypothesis across an urban gradient: a multi-scale study. Ecography. 28 (1):59–70.

Kryštofková M, Haas M, Exnerová A. 2011. Nest defense in blackbirds Turdus merula: effect of predator distance and parental sex. Acta Ornithol. 46(1):53–61.

Lessi BF, Bataghin FA, Pires JSR. 2017. Diversity and distribution of trees on the Federal University of São Carlos campus, Brazil: implications for conservation and management. Rev Soc Bras Arborização Urbana. 12(1):92–104.

Lessi BF, Pires JSR, Batisteli AF, MacGregor-Fors I. 2016. Vegetation, urbanization, and bird richness in a Brazilian periurban area. Ornitol Neotrop. 27:203–210.

Liker A, Székely T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. Evolution. 59(4):890–897.

Lomáscolo SB, Monmany AC, Malizia A, Martin TE. 2010. Flexibility in nest-site choice and nesting success of *Turdus rufiventris* (Turdidae) in a montane forest in northwestern Argentina. Wilson J Ornithol. 122 (4):674–680.

Lorenzi H. 2000. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Nova Odessa (RJ): Ed. Plantarum.

Mahler B, Confalonieri VA, Lovette IJ, Reboreda JC. 2007. Partial host fidelity in nest selection by the shiny cowbird (*Molothrus bonariensis*), a highly generalist avian brood parasite. J Evolution Biol. 20(5):1918–1923.

Mainwaring MC, Deeming DC, Jones CI, Hartley IR. 2014. Adaptive latitudinal variation in Common Blackbird *Turdus merula* nest characteristics. Ecol Evol. 4(6):851–861.

Marini MA, Aguilar TM, Andrade RD, Leite LO, Anciães M, Carvalho CEA, Duca C, Maldonado-Coelho M, Sebaio F, Gonçalves J. 2007. Biologia da nidificação de aves do sudeste de Minas Gerais, Brasil. Braz J Ornithol. 15 (3):367–376.

Marini MA, Borges FJA, Lopes LE, Sousa NOM, Gressler DT, Santos LR, Paiva LV, Duca C, Manica LT, Rodrigues SS, et al. 2012. Breeding biology of birds in the Cerrado of central Brazil. Ornitol Neotrop. 23(3):385–405.

Marques-Santos F, Braga TV, Wischhoff U, Roper JJ. 2015. Breeding biology of passerines in the subtropical Brazilian Atlantic Forest. Ornitol Neotrop. 26(4):363–374.

Martin TE, Boyce AJ, Fierro-Calderón K, Mitchell AE, Armstad CE, Mouton JC, Bin Soudi EE. 2017. Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. Funct Ecol. 31(6):1231–1240.

Martin TE, Oteyza JC, Boyce AJ, Lloyd P, Ton R. 2015. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. Am Nat. 186(2):223–236.

Mason P. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. Ornithol Monogr. 36:954–972.

Mayfield H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

Mitchell AE, Tuh F, Martin TE. 2017. Breeding biology of an endemic Bornean turdid, the Fruithunter (*Chlamydochaera jefferyi*), and life history comparisons with Turdus species of the world. Wilson J Ornithol. 129(1):36–45.

Møller AP. 2000. Male parental care, female reproductive success, and extrapair paternity. Behav Ecol. 11 (2):161–168.

Møller AP. 2010. The fitness benefit of association with humans: elevated success of birds breeding indoors. Behav Ecol. 21(5):913–918.

Olson VA, Liker A, Freckleton RP, Szekely T. 2007. Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. Proc R Soc B-Biol Sci. 275(1632):301–307.

Perrella DF, Davanço PV, Oliveira LS, Sousa L, Francisco M. 2017. Reproductive aspects of the Purple-throated Euphonia, *Euphonia chlorotica* (Aves: Fringillidae) in southeastern Brazil, and first record of the species nesting inside a vespiary. Zoologia. 34:e19989.

R Core Team. 2019. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Ricklefs RE, Brawn J. 2013. Nest attentiveness in several Neotropical suboscine passerine birds with long incubation periods. J Ornithol. 154(1):145–154.

Rodrigues RC, Hasui É, Assis JC, Castro Pena JC, Muylaert RL, Tonetti VR, Martello F, Regolin AL, Costa TV, Pichorim M, et al. 2019. Atlantic bird traits: a dataset of bird morphological traits from the Atlantic forests of South America. Ecology. 100(6):e02647.

Ruiz NL, Araújo P, Lima J, Ferreira P, Andrade L, Pichorim M. 2017. Breeding biology of Pale-breasted Thrush *Turdus leucomelas* (Turdidae) in the north of Atlantic Forest, Brazil. Braz J Ornithol. 25(2):110–121.

Schwagmeyer PL, Clair RCS, Moodie JD, Lamey TC, Schnell GD, Moodie MN. 1999. Species differences in male parental care in birds: a reexamination of correlates with paternity. Auk. 116(2):487–503.

Shaw P, Cresswell W. 2014. Latitudinal variation in day length and working day length has a confounding effect when comparing nest attentiveness in tropical and temperate species. J Ornithol. 155(2):481–489.

Sick H. 2001. Ornitologia Brasileira. 3rd ed. Rio de Janeiro (RJ): Ed. Nova Fronteira.

Stotz DF, Fitzpatrick JW, Parker III TA, Moskovits DK. 1996. Neotropical birds: ecology and conservation. Chicago (IL): University of Chicago Press.

Veloso SL, Pesquero MA, Rodrigues LG, Pesquero MF. 2018. Parental care of the Swallow Tanager (*Tersina viridis*) in Southern Goiás, Brazil. Wilson J Ornithol. 130 (3):658–663.

Willis EO. 2004. Birds of a habitat spectrum in the Itirapina Savanna, São Paulo, Brazil (1982–2003). Braz J Biol. 64 (4):901–910.

ANEXO III

The Wilson Journal of Ornithology 131(1):201–205, 2019

Abundance and prevalence of plastic twine in nests of Neotropical farmland birds

Augusto Florisvaldo Batisteli,[1,2]* Rhainer Guilhermo-Ferreira,[2] and Hugo Sarmento[2]

ABSTRACT—The materials used for nesting have important structural and nonstructural functions in bird nests. A number of bird species incorporate anthropogenic debris in their nests, but there are few systematic studies about such use by terrestrial birds. Here, we test whether the prevalence and amount of plastic twine differs among nests of Neotropical birds in an orange orchard. We found 78 nests, of which 21 (27%) contained plastic. The nests with plastic belonged to 5 species (*Columbina talpacoti*, *Thamnophilus doliatus*, *Turdus amaurochalinus*, *Coryphospingus cucullatus*, and *Zonotrichia capensis*), which differed by both the prevalence and amount of plastic in their nests. The prevalence of plastic was higher in *T. doliatus* nests than in *Z. capensis* nests, and the amount of plastic was greater in *T. doliatus* nests than in those of *C. cucullatus* and of *Z. capensis*. Our results suggest that the use of anthropogenic material in nest construction may depend on the suitability of its properties to specific nest characteristics.

Received 7 November 2017. Accepted 18 September 2018.

Key words: anthropogenic debris, breeding behavior, garbage, monoculture, nesting material.

Abundância e prevalência de fitas de plástico em ninhos de aves Neotropicais em uma monocultura

RESUMO (Portuguese)—Os materiais utilizados na construção dos ninhos das aves têm importantes funções estruturais e não-estruturais. Diversas espécies de aves incorporam resíduos antropogênicos em seus ninhos, mas há poucos estudos sistemáticos sobre tal uso por aves terrestres. Neste estudo, testamos se a prevalência e a quantidade de fitas de plástico difere entre ninhos de aves Neotropicais em uma monocultura de laranjeiras. Encontramos 78 ninhos, dos quais 21 (27%) continham plástico. Os ninhos com plástico pertenceram a 5 espécies (*Columbina talpacoti*, *Thamnophilus doliatus*, *Turdus amaurochalinus*, *Coryphospingus cucullatus*, e *Zonotrichia capensis*), as quais diferiram quanto à prevalência e à quantidade de plástico em seus ninhos. A prevalência de plástico foi maior nos ninhos de *T. doliatus* do que nos ninhos de *Z. capensis*, e a quantidade de plástico foi maior nos ninhos de *T. doliatus* do que naqueles de *C. cucullatus* e *Z. capensis*. Nossos resultados sugerem que o uso de material antropogênico na construção do ninho pode depender da adequabilidade das suas propriedades às características de cada tipo de ninho.

Palavras-chave: comportamento reprodutivo, lixo, material de ninho, monocultura, resíduos antropogênicos.

Bird nest characteristics are directly linked to the species' life history traits (Lee and Lima 2016, Martin et al. 2016), therefore species developed divergent patterns of selection of nest site and nesting material (Brightsmith 2005, Botero-Delgadillo et al. 2017). The adaptive value of the chosen nesting material is related to structural functions (e.g., insulation; Hilton et al. 2004) and nonstructural roles, such as protection against predators and nestling parasites (Wimberger 1984, Schuetz 2005). Several marine and terrestrial bird species incorporate anthropogenic materials in their nests (Blem et al. 2002, Hartwig et al. 2007, Wang et al. 2009, Votier et al. 2011, Townsend and Barker 2014, Tavares et al. 2016), supposedly in relation to their availability at the breeding site (Igic et al. 2009, Radhamany et al. 2016, Witteveen et al. 2017). Anthropogenic materials can fulfill both structural and nonstructural functions in bird nests (Roda and Carlos 2003, Suárez-Rodriguez et al. 2013), but their use increases nest visibility for predators (Canal et al. 2016) and may cause deaths by entanglement (Blem et al. 2002, Townsend and Barker 2014).

Plastic is one of the most common anthropogenic materials found in bird nests (e.g., Cristofoli and Sander 2007, Cristofoli et al. 2008, Tomaz et al. 2009). The prevalence of plastic has been investigated mainly in seabird nests (Hartwig et al. 2007, Votier et al. 2011, Lavers et al. 2013), whereas systematic studies addressing the abundance and prevalence of plastic in nests of terrestrial birds are scarce (e.g., Wang et al. 2009, Townsend and Barker 2014, Møller 2017). In addition, few studies have investigated the response of sympatric bird species to the availability of anthropogenic nesting materials. Here, we report the use of plastic twine in nest construction by Neotropical birds in an orange orchard (*Citrus* sp.), and test whether the species that use plastic as nesting material differ in (1) the prevalence (percentage of nests containing plastic) and (2) the abundance of plastic in their nests. We hypothesized that both the prevalence and abun-

---

[1] Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, SP, Brazil

[2] Departmento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, SP, Brazil

* Corresponding author: augustofb@gmail.com

Table 1. Total number of nests and number of nests with plastic twine found in the study area and the amount of plastic (standardized score) in the nests (mean, SE) per species.

Species	Number of nests		Amount of plastic: standardized score
	Total	With plastic	
Columbidae			
Columbina talpacoti	8	5 (62.5%)	0.34 (0.17)
Apodidae			
Amazilia lactea	1	0 (0.0%)	—
Thamnophilidae			
Thamnophilus doliatus	5	5 (100.0%)	0.60 (0.06)
Furnariidae			
Synallaxis albescens	1	0 (0.0%)	—
Synallaxis frontalis	4	0 (0.0%)	—
Turdidae			
Turdus amaurochalinus	12	5 (41.7%)	0.23 (0.09)
Thraupidae			
Volatinia jacarina	2	0 (0.0%)	—
Coryphospingus cucullatus	9	2 (22.2%)	0.08 (0.06)
Sporophila caerulescens	6	0 (0.0%)	—
Emberizidae			
Zonotrichia capensis	30	4 (13.3%)	0.08 (0.05)
Total	78	21 (26.92%)	0.18 (0.04)

dance of plastic in the nests differ among species because they should select nesting material according to the suitability of its properties.

Methods

We carried out this study in an orange orchard in Ibitinga (48°54′50″W, 21°42′23″S), São Paulo state, Brazil. The climate is tropical with hot, wet summers and dry winters, with mean monthly temperatures between 17.9 °C and 24.1 °C and annual rainfall ~1,270 mm (Alvares et al. 2013). The study area (~4.0 ha) ranges from 475 to 489 m a.s.l. and had ~1,450 12-year-old orange trees planted in 7 × 4 m spacing. Birds took the plastic twine from abandoned harvest bags regularly found throughout the orchard area.

We actively searched for nests every week from November 2013 to January 2014, checking all the orange trees. We also located nests on the ground when females were accidentally flushed. For all nests, we recorded the species and plastic presence, and we estimated visually the amount of plastic from a general overview of the external and inner lining, using the scores 0 (no plastic), 1 (1–25%), 2 (26–50%), 3 (51–75%), or 4 (76–100%) (Schuetz 2005). We attributed a score of 4 to 4 nests built directly over plastic bags (see Results). For each bird species that had at least one nest with plastic, we calculated the prevalence (percentage of nests with plastic) and the mean plastic score, which was standardized between 0 and 1. The plastic score had a non-normal distribution (Shapiro–Wilk test, $P = 0.624$). Thus, we tested whether the prevalence and the amount of plastic in nest construction differed between species using pairwise comparisons of the Fisher exact test with Bonferroni correction and the Kruskal–Wallis test with pairwise comparisons, respectively. We conducted the analyses in the software SPSS Statistics 20 (IBM 2011).

Results

We registered 78 nests of 10 bird species. The nests of 5 bird species had no plastic and were excluded from statistical analyses (Table 1). We found plastic in 21 of 64 (33%) nests spread among the other 5 bird species: Ruddy Ground Dove (*Columbina talpacoti*), Barred Antshrike (*Thamnophilus doliatus*), Creamy-bellied Thrush (*Turdus amaurochalinus*), Red-crested Finch (*Coryphospingus cucullatus*), and Rufous-collared Sparrow (*Zonotrichia capensis*) (Table 1). Only one pairwise comparison of the prevalence of plastic twine in nests (*T. doliatus* vs. *Z. capensis*) was statistically significant (Table 2). The amount of plastic in the nests differed among species (Kruskal–Wallis; Wald = 13.045, df = 4, $P = 0.011$). The nests of *T. doliatus* had significantly more plastic than those of *Z. capensis* and of *C. cucullatus* (Table 2). The other pairwise comparisons about the amount of plastic were not statistically significant. Two nests of *C. talpacoti* and two of *Zonotrichia capensis* were built directly over plastic harvest bags (Fig. 1). No other anthropogenic material was found in bird nests during this study.

Discussion

We registered the use of plastic twine for nest construction by 5 Neotropical bird species in an orange orchard. Of these, plastic was previously

Table 2. Pairwise comparisons between studied species *Zonotrichia capensis* (*Z. cap*), *Coryphospingus cucullatus* (*C. cuc*), *Turdus amaurochalinus* (*T. ama*), *Columbina talpacoti* (*C. tal*), and *Thamnophilus doliatus* (*T. dol*) in relation to the prevalence and amount of plastic twine in the nests (plastic score).

	Prevalence of plastic		Plastic score				
Pairwise comparison	*P*	Adj. *P*	*P*	Adj. *P*	Test statistic	Std. error	Std. test statistic
Z. cap × *C. cuc*	0.607	1.000	0.761	1.000	−1.733	5.708	−0.304
Z. cap × *T. ama*	0.090	0.899	0.097	0.966	−8.525	5.13	−1.662
Z. cap × *C. tal*	0.010	0.101	0.095	0.948	−9.983	5.977	−1.67
Z. cap × *T. dol*	<0.001	0.003*	<0.001	0.002*	−27.433	7.255	−3.781
C. cuc × *T. ama*	0.642	1.000	0.305	1.000	−6.792	6.623	−1.025
C. cuc × *C. tal*	0.153	1.000	0.258	1.000	−8.25	7.298	−1.13
C. cuc × *T. dol*	0.021	0.209	0.002	0.022*	−25.7	8.378	−3.068
T. ama × *C. tal*	0.650	1.000	0.832	1.000	−1.458	6.856	−0.213
T. ama × *T. dol*	0.044	0.441	0.018	0.18	−18.908	7.995	−2.365
C. tal × *T. dol*	0.231	1.000	0.042	0.416	−17.45	8.563	−2.038

* Significant results after Bonferroni correction ($\alpha = 0.005$).

Figure 1. Nests of *Thamnophilus doliatus* (a) and *Turdus amaurochalinus* (b, c) with plastic twine and a nest of *Zonotrichia capensis* (d) over a plastic harvest bag.

documented only in *T. amaurochalinus* nests (Miller and Miller 1968, Cintra 1988, Sick 2001, Borges and Marini 2010, Zima and Francisco 2016). In accordance with our expectation, we found interspecific differences in the prevalence and abundance of plastic twine in the nests, which may be related to the suitability of this material for different nest types. Contrary to the other studied species that use grass pieces, roots, or sticks to build their nests, the natural nesting materials of *T. doliatus* in the study area are thin, flexible vegetal fibers, which are similar to plastic twine in flexibility and resistance. Similarly, some birds will use pieces of wire as nesting material instead of wooden sticks (Roda and Carlos 2003, Costa and Mäder 2011, Pereira 2011, Chaves et al. 2013) and fishing gear items rather than elongated marine vegetation (Votier et al. 2011). Thus, the use of anthropogenic nesting material in certain contexts may be purposeful instead of a selection error. This could explain the high prevalence and amount of plastic in *T. doliatus* nests at the study orchard.

The prevalence of anthropogenic material in bird nests can be used as a bioindicator of environmental pollution (Tavares et al. 2016), but our results suggest that it must be taken with caution, because species can vary in the acceptance of anthropogenic nesting materials. The use of debris in nest construction may depend on several factors beyond its abundance in nest surroundings, such as its mechanical, physical, or chemical attributes (Bailey et al. 2016). Most research to date suggests that the use of anthropogenic nesting material is maladaptive, enhancing nest detection by predators (Hartwig et al. 2007, Borges and Marini 2010) and causing deaths of juveniles and breeding adults by entanglement (Blem et al. 2002, Parker and Blomme 2007, Votier et al. 2011). Future research should focus on the spatial and temporal patterns of anthropogenic debris as nesting material (Hartwig et al. 2007, Lavers et al. 2013, Møller 2017) and its impact on individual fitness and population levels (Blem et al. 2002, Votier et al. 2011, Suárez-Rodriguez et al. 2017) to clarify the effects of environmental pollution on bird nesting behavior.

Acknowledgments

We are grateful to two anonymous reviewers and the editorial board of WJO. AFB thanks A.A. Batisteli for field assistance, C.P. Salva (in memoriam), R. Salva, M. Mazo, and A.P. Mazo for logistical support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

Literature cited

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift. 22:711–728.

Bailey IE, Morgan KV, Oschadleus HD, DeRuiter SL, Meddle SL, Healy SD. 2016. Nest-building males trade off material collection costs with territory value. Emu. 116:1–8.

Blem CR, Blem LB, Harmata PJ. 2002. Twine causes significant mortality in nestling Ospreys. Wilson Bulletin. 114:528–529.

Borges FJA, Marini MA. 2010. Birds nesting survival in disturbed and protected savannas. Biodiversity and Conservation. 19:223–236.

Botero-Delgadillo E, Orellana N, Serrano D, Poblete Y, Vásquez RA. 2017. Interpopulation variation in nest architecture in a secondary cavity nesting bird suggests site-specific strategies to cope with heat loss and humidity. Auk. 134:281–294.

Brightsmith DJ. 2005. Competition, predation, and nest niche shifts among tropical cavity nesters: Phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes). Journal of Avian Biology. 36:64–73.

Canal D, Mulero-Pázmány M, Negro JJ, Sergio F. 2016. Decoration increases the conspicuousness of raptor nests. PLoS ONE. 11(7):e0157440.

Chaves AV, Alvim RG, Lopes RAG. 2013. O uso de materiais industriais em ninhos de *Certhiaxis cinnamomeus* (Passeriformes: Furnariidae) na cidade de Cláudio, Minas Gerais, Brasil [The use of industrial materials in *Certhiaxis cinnamomeus* (Passeriformes: Furnariidae) nests in the city of Cláudio, Minas Gerais, Brazil]. Atualidades Ornitológicas. 173:6–8. Portuguese.

Cintra R. 1988. Reproductive ecology of the Ruddy Ground-Dove on the Central Plateau of Brazil. Wilson Bulletin. 100:443–457.

Costa AS, Mäder A. 2011. Utilização de metal na construção de ninho do sabiá-do-campo (*Mimus saturninus* Lichtenstein, 1823) [Use of metal in the nest construction of the Chalk-browed Mockingbird (*Mimus saturninus* Lichtenstein, 1823)]. Biodiversidade Pampeana. 9:1–2. Portuguese.

Cristofoli SI, Sander M. 2007. Composição do ninho de Corruíra: *Troglodytes musculus* Naumann, 1823 (Passeriformes: Troglodytidae) [Nest composition of the Southern House-Wren: *Troglodytes musculus* Naumann, 1823 (Passeriformes: Troglodytidae)]. Biodiversidade Pampeana. 5:6–8. Portuguese.

Cristofoli SI, Santos CR, Garcia AS, Sander M. 2008. Composição do ninho de Cambacica: *Coereba flaveola* Linnaeus 1758 (Aves: Emberizidae) [Nest composition of the Bananaquit: *Coereba flaveola* Linnaeus 1758

(Aves: Emberizidae)]. Biodiversidade Pampeana. 6:30–33. Portuguese.

Hartwig E, Clemens T, Heckroth M. 2007. Plastic debris as nesting material in a Kittiwake (*Rissa tridactyla*) colony at the Jammerbugt, Northwest Denmark. Marine Pollution Bulletin. 54:595–597.

Hilton GM, Hansell MH, Ruxton GD, Reid JM, Monaghan P. 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. Auk. 121:777–787.

IBM. 2011. IBM SPSS Statistics for Windows, ver. 20.0. Armonk (NY): IBM.

Igic B, Cassey P, Samas P, Grim T, Hauber ME. 2009. Cigarette butts form a perceptually cryptic component of Song Thrush (*Turdus philomelos*) nest. Notornis. 56:134–138.

Lavers JL, Hodgson JC, Clarke RH. 2013. Prevalence and composition of marine debris in Brown Booby (*Sula leucogaster*) nests at Ashmore Reef. Marine Pollution Bulletin. 77:320–324.

Lee JK, Lima SL. 2016. Nest building under the risk of predation: Safe nests are not always the best option. Journal of Avian Biology. 47:768–778.

Martin TE, Boyce AJ, Fierro-Calderón K, Mitchell AE, Armstad CE, et al. 2016. Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. Functional Ecology. 31:1231–1240.

Miller AH, Miller VD. 1968. The behavioral ecology and breeding biology of the Andean Sparrow, *Zonotrichia capensis*. Caldasia. 10(47):83–154.

Møller AP. 2017. Fashion and out of fashion: Appearance and disappearance of a novel nest building innovation. Avian Research. 8(1):14.

Parker GH, Blomme CG. 2007. Fish-line entanglement of nesting Mourning Dove, *Zenaida macroura*. Canadian Field-Naturalist. 121:436–437.

Pereira GA. 2011. Ninhos de *Certhiaxis cinnamomeus* (Passeriformes, Furnariidae) construídos com material metálico em Pernambuco, Brasil [Nests of *Certhiaxis cinnamomeus* (Passeriformes, Furnariidae) built with metallic material in Pernambuco, Brazil]. Atualidades Ornitológicas. 159:4–6. Portuguese.

Radhamany D, Das KSA, Azeez PA, Wen L, Sreekala LK. 2016. Usage of nest material by House Sparrow (*Passer domesticus*) along an urban to rural gradient in Coimbatore, India. Tropical Life Sciences Research. 27(2):127–134.

Roda AS, Carlos JC. 2003. On a nest of Yellow-chinned Spinetail (*Certhiaxis cinnamonmea* - Passeriformes, Furnariidae) built with bites of wire. Lundiana. 4:69–70.

Schuetz JG. 2005. Common Waxbills use carnivore scat to reduce the risk of nest predation. Behavioral Ecology. 16:133–137.

Sick H. 2001. Ornitologia Brasileira [Brazilian ornithology]. 3rd Edition. Rio de Janeiro (Brazil): Ed. Nova Fronteira. Portuguese.

Suárez-Rodríguez M, López-Rull I, Garcia CM. 2013. Incorporation of cigarette butts into nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? Biology Letters. 9(1):20120931.

Suárez-Rodríguez M, Montero-Montoya RD, Macías Garcia C. 2017. Anthropogenic nest material may increase breeding costs for urban birds. Frontiers in Ecology and Evolution. 5:4.

Tavares DC, Costa LL, Rangel DF, Moura JF, Zalmon IR, Siciliano S. 2016. Nests of the Brown Booby (*Sula leucogaster*) as a potential indicator of tropical ocean pollution by marine debris. Ecological Indicators. 70:10–14.

Tomaz VC, Fernandes VM, Alves MAS. 2009. Reprodução de *Fluvicola nengeta* (Tyrannidae) em área urbana da cidade do Rio de Janeiro, RJ, Brasil [Reproduction of *Fluvicola nengeta* (Tyrannidae) in an urban area of the city of Rio de Janeiro, RJ, Brazil]. Revista Brasileira de Ornitologia. 17:70–72. Portuguese.

Townsend AK, Barker CM. 2014. Plastic and nest entanglement of urban and agricultural crows. PLoS ONE. 9(1):e88006.

Votier SC, Archibald K, Morgan G, Morgan L. 2011. The use of plastic debris as nesting material by a colonial seabird and associated entanglement mortality. Marine Pollution Bulletin. 62:168–172.

Wang Y, Chen S, Blair RB, Jiang P, Ding P. 2009. Nest composition adjustments by Chinese Bulbuls *Pycnonotus sinensis* in an urbanized landscape of Hangzhou (E China). Acta Ornithologica. 44:185–192.

Wimberger HP. 1984. The use of green plant material in bird nests to avoid ectoparasites. Auk. 101:615–618.

Witteveen M, Brown M, Ryan PG. 2017. Anthropogenic debris in the nests of Kelp Gulls in South Africa. Marine Pollution Bulletin. 114:699–704.

Zima PVQ, Francisco MR. 2016. Reproductive behavior of the Red-crested Finch *Coryphospingus cucullatus* (Aves: Thraupidae) in southeastern Brazil. Zoologia. 33(4):1–6.

ANEXO IV

Tabela 1. Lista das espécies de aves nidificantes na área urbana do câmpus de São Carlos da Universidade Federal de São Carlos e os tipos de estruturas antropogênicas que elas ocupam. Abreviações: A = aparelhos de ar condicionado, C = Colunas metálicas, CB = Caixas-ninho de gomos de bambu, CM = Caixas-ninho de madeira, E = estruturas metálicas de coberturas, Ex = exaustores de ar, F = calhas de lâmpadas fluorescentes, J = janelas, L = luminárias, M = madeiramento de telhados, O = orifícios em blocos de concreto, P = Postes, S = sob telhados, Su = suportes de aparelho de ar-condicionado, T = telhado, Tr = trilhos de metal, Tu = tubos de PVC, V = Vigas ou colunas de concreto.

Ordem/Família/Espécie	Nome popular	Tipo de estrutura antropogênica
Cathartiformes		
Cathartidae		
Coragyps atratus	urubu	T
Charadriiformes		
Charadriidae		
Vanellus chilensis	quero-quero	
Columbiformes		
Columbidae		
Columba livia	pombo-doméstico	A, V, Tr
Columbina talpacoti	rolinha	E
Patagioenas picazuro	asa-branca	A, V, Tr
Zenaida auriculata	avoante	A, V, Tr, J
Strigiformes		
Strigidae		
Athene cunicularia	coruja-buraqueira	
Megascops choliba	corujinha-do-mato	
Apodiformes		
Apodidae		
Eupetomena macroura	beija-flor-tesoura	
Amazilia lactea	beija-flor-de-peito-azul	
Piciformes		
Picidae		
Colaptes campestris	pica-pau-do-campo	
Colaptes melanochlorus	pica-pau-verde-barrado	
Falconiformes		
Falconidae		
Falco sparverius	quiriquiri	E
Psittaciformes		
Psittacidae		
Psittacara leucophtalmus	periquitão	F
Forpus xanthopterygius	tuim	
Passeriformes		
Furnariidae		
Furnarius rufus	joão-de-barro	P
Tyranidae		
Camptostoma obsoletum	risadinha	
Elaenia flavogaster	guaracava-de-barriga-amarela	

Myarchus ferox	maria-cavaleira	CM
Pitangus sulphuratus	bem-te-vi	P
Machetornis rixosa	suiriri-cavaleiro	Tr
Myiodinastes maculatus	bem-te-vi-rajado	CM, O
Megarynchus pitangua	nei-nei	
Myiozetetes similis	bentevizinho-de-penacho-vermelho	
Tyrannus melancholicus	suiriri	
Tyrannus savana	tesourinha	
Griseotyrannus aurantioatrocristatus	peitica-de-chapéu-preto	
Empidonomus varius	peitica	
Colonia colonus	viuvinha	CB
Fluvicola nengeta	lavadeira-mascarada	
Hirundinidae		
Pygochelidon cyanoleuca	andorinha-pequena-de-casa	F, CB
Progne tapera	andorinha-do-campo	
Troglodytidae		
Troglodytes musculus	corruíra	CB, CM, O, L
Turdidae		
Turdus leucomelas	sabiá-barranco	J, E, C, V, A, Tr, F, Tu
Turdus rufiventris	sabiá-laranjeira	
Turdus amaurochalinus	sabiá-poca	V, E, Tr, Su,
Mimidae		
Mimus saturninus	sabiá-do-campo	
Passerellidae		
Zonotrichia capensis	tico-tico	
Icteridae		
Icterus pyrrhopterus	encontro	
Coerebidae		
Coereba flaveola	cambacica	
Thraupidae		
Ramphocelus carbo	pipira-vermelha	
Thraupis sayaca	sanhaço-cinzento	V, Tr, L, M, Su
Tersina viridis	saí-andorinha	O
Paroaria dominicana	cardeal-do-nordeste	
Sicalis flaveola	canário-da-terra	CB, CM, L
Volatinia jacarina	tiziu	
Sporophila lineola	bigodinho	
Sporophila caerulescens	coleirinho	
Fringillidae		
Euphonia chlorotica	fim-fim	
Passeridae		
Passer domesticus	pardal	CB

APÊNDICE I

Fig. 2 Vista lateral de prédios do câmpus da Universidade Federal de São Carlos (São Carlos–SP) com ninhos de sabiá-barranco (*Turdus leucomelas*) indicados pelas setas.

Fig. 3 Locais de nidificação do sabiá-barranco (*Turdus leucomelas*) em estruturas antropogênicas no câmpus da Universidade Federal de São Carlos (São Carlos–SP), com ninhos indicados pelas setas.

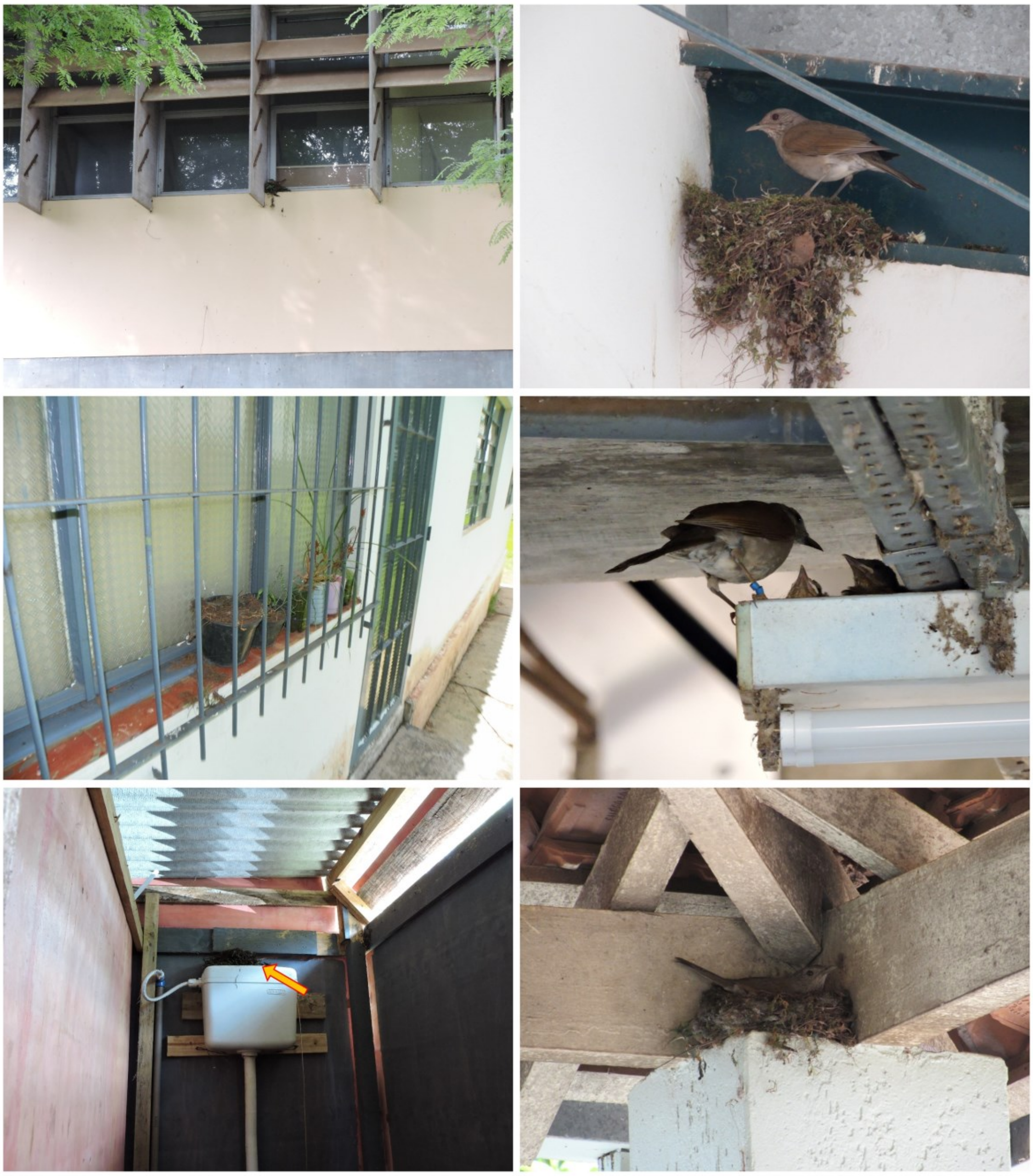


Fig. 4 Ninhos de sabiá-barranco (*Turdus leucomelas*) em estruturas antropogênicas no câmpus da Universidade Federal de São Carlos (São Carlos–SP).

Fig. 5 Ninhos de sabiá-barranco (*Turdus leucomelas*) em estruturas antropogênicas no câmpus da Universidade Federal de São Carlos (São Carlos–SP).

Fig. 6 Ninhos de sabiá-barranco (*Turdus leucomelas*) em árvores na área urbana do câmpus da Universidade Federal de São Carlos (São Carlos–SP).