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**AMANDA MURCIA SANCHES**

**Fecundidade anual e parasitismo de ninho em uma população do Curutié  
*Certhiaxis cinnamomeus* (Aves:Furnariidae) no Sudeste Brasileiro**

Sorocaba– SP

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*Certhiaxis cinnamomeus* (Aves: Furnariidae) no sudesde Brasileiro**

Dissertação apresentada ao Programa de Pós-Graduação em Conservação da Fauna da Universidade Federal de São Carlos para obtenção do título de mestra profissional em Conservação da Fauna.

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*It's a dangerous business, Frodo, going out your door. You step onto the road, and if you don't keep your feet, there's no knowing where you might be swept off to."*

-J. R. R. Tolkien, Lord of the Rings

## RESUMO

O curutié (*Certhiaxis cinnamomeus*) é um furnarídeo, que como muitas outras espécies neotropicais, tem poucos aspectos de sua biologia elucidados. A espécie é sabidamente hospedeira do Saci (*Tapera naevia*), no entanto, nenhum estudo acerca desse sistema hospedeiro-parasita foi conduzido. O presente estudo foi conduzido numa área de brejo em Santa Bárbara d'oeste, nas temporadas reprodutivas de 2017/2018 e 2018/2019. Através de captura e marcação e busca ativa por ninhos levantamos dados sobre a biologia reprodutiva da espécie e sobre as taxas de parasitismo por Saci (*Tapera naevia*).

O primeiro capítulo trata dos aspectos reprodutivos da espécie. A temporada reprodutiva da espécie na área estudada vai do fim de Setembro a Fevereiro do ano seguinte. A fecundidade anual da população estudada é de 0,33 *C. cinnamomeus* e 0,66 *T. naevia* por fêmea, mostrando que parasitismo é a maior causa de perda de prole por *C. cinnamomeus*. O período de incubação é de 17 dias, e o de permanência no ninho é de 18 dias. Pares reprodutivos construíram de 1 a 4 ninhos durante a temporada (2,8 em média).

O segundo capítulo trata do parasitismo de ninho por *T. naevia*. Através de GLM, testamos a hipótese de que a entrada tubular pode ser uma barreira para o parasita. Nossos dados não corroboram essa hipótese, assim como nem um outro aspecto da arquitetura do ninho tem influência na probabilidade de um ninho ser parasitado por *T. naevia*. O único aspecto que mostrou uma correlação negativa com parasitismo foi a cobertura vegetal acima do ninho, sugerindo que *T. naevia* utiliza pistas visuais para a localização dos ninhos, e que ninhos mais escondidos podem ter uma maior chance de não serem parasitados.

Esse estudo é o primeiro a tratar especificamente da biologia reprodutiva de *C. cinnamomeus* e a tratar desse sistema hospedeiro-parasita.

**Palavras chave:** João do brejo, parasitismo de ninho, Matin pererê

## ABSTRACT

The yellow-chinned spinetail is a Furnariid that, as many other neotropical species, has few aspects of its biology fully studied. It's been a known host for the striped cuckoo (*Tapera naevia*) for years. However, this particular host-parasite system has never been studied.

The present study was conducted in a marsh area in the municipality of Santa Bárbara d'Oeste, state of São Paulo, in the reproductive seasons of 2017/2018 and 2018/2018. Through capture and marking of individuals and active search for nests, we built a database about the reproductive biology of this species and the parasitism by *T. naevia* rates.

The first chapter is about the reproductive aspects of the species. The reproductive season lasted from late September to February; The annual fecundity of this population was 0,33 *C. cinamomeus* and 0.66 *T. naevia* per female, showing that brood parasitism is the main constrain to the reproduction of *C. cinnamomeus* in this population. The incubation period was 17 days, and fledging period of 18 days. Reproductive breeding pairs built from 1 to 4 nests during the reproductive season (average of 2.8).

The second chapter is about the brood parasitism by *T. naevia*. Using GLM analysis we tested the hypothesis that the tubular nest entrance might be a constrain to the parasite. Our data didn't corroborate this hypotheses. Further, no other aspect of nest architecture seems to influence the likelihood of parasitism. The only aspect that showed a negative correlation with the likelihood of a nest being parasitized by *T. naevia* was vegetation coverage above the nest. This indicates that *T. naevia* might use visual cues to locate host's nests, and vegetation coverage might conceal host activity, making more concealed nests less likely of being parasitized. This study is the first to address specifically the reproductive biology of *C. cinnamomeus* and this particular parasite-host system.

**Key words:** Yellow-throated spinetail, brood parasitism, Stripped cuckoo

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## 1. APRESENTAÇÃO

Espécies neotropicais são frequentemente pouco estudadas. Furnarídeos, apesar de terem ampla distribuição nas américas, possuem, em geral, poucos aspectos de sua biologia estudados. A presente dissertação visa contribuir com o entendimento sobre a biologia reprodutiva de uma espécie de ave Neotropical pouco estudada, o curutié (*Certhiaxis cinnamomeus*), e a interação de parasitismo com um cuculídeo Neotropical. O estudo foi desenvolvido através do acompanhamento de 30 ninhos ativos distribuídos em 2 temporadas reprodutivas.

Assim sendo, esta dissertação está dividida em três partes para melhor compreensão. Inicialmente, apresento um escopo teórico – o que se sabe sobre as espécies, e uma base teórica sobre parasitismo de ninho em aves. Seguem-se então dois capítulos. O primeiro trata da biologia reprodutiva da espécie na área de estudo, endereçando períodos de incubação, permanência no ninho, número de ovos por postura, postura por temporada, divórcios e output reprodutivo. Observamos um output reprodutivo baixo, em grande parte pelas altas taxas de parasitismo de ninho na área, apesar de todos os pares marcados tentarem fazer 2 ninhos ou mais por temporada.

O segundo capítulo trata do parasitismo de ninho por Sacis (*Tapera naevia*) em ninhos de curutié, discutindo as taxas de parasitismo e testando quais fatores, tanto da arquitetura do ninho quanto do seu entorno, podem influenciar na probabilidade deste ser parasitado. Observamos que o comprimento do tubo de entrada do ninho, ou a sua abertura, não influenciam na probabilidade de um ninho ser parasitado, assim como nenhum outro fator da arquitetura do ninho. Porém a cobertura vegetal acima do ninho é relacionada com a probabilidade de um ninho ser parasitado. Nosso estudo foi o primeiro a explorar a relação

de parasitismo entre as duas espécies, e gerou diversas novas perguntas como o efeito das taxas de parasitismo na população de *C. cinnamomeus* a longo prazo, e o porquê de uma espécie aparentemente não apresentar mecanismos de defesa contra um parasita que acarreta perdas tão pesadas para a espécie hospedeira.

## 2. FUNDAMENTAÇÃO TEÓRICA

### 2.1 PARASITISMO DE NINHO

Parasitas de ninho obrigatórios são aqueles que não constroem ninhos, ou alimentam e cuidam de sua prole. São espécies que põem seus ovos em ninhos de outras espécies (hospedeiros) para que estas arquem com os custos de se criar a prole (FIORINI et al. 2019). Parasitismo de ninho é bem documentado em aves, insetos, peixes e mais recentemente em anuros (PAYNE 1977, SATO 1986, WISENDEN 1999, BARBERO et al. 2009, BROWN et al. 2009, SPOTTISWOODE et al. 2012), mas é melhor documentado em aves, onde ocorre em cerca de 1% das espécies (cerca de 100 espécies), em quatro ordens diferentes, implicando em pelo menos sete origens diferentes para essa estratégia (SORENSEN & PAYNE 2005).

Para ecólogos comportamentais e ornitólogos interessados em coevolução, parasitas de ninho obrigatórios são um excelente sistema de estudo (FIORINI et al. 2019). O sistema de reprodução dessas espécies lhes impõe desafios permanentes para a reprodução bem sucedida, ao mesmo tempo em que coloca os hospedeiros sob forte pressão de seleção para reduzir os custos associados ao parasitismo como destruição de ovos pelas fêmeas parasitas e os potenciais custos de se criar ninhos de outras espécies. Essas pressões de seleção podem resultar em parasitas e hospedeiros entrando em uma corrida armamentista coevolutiva, onde uma série de adaptações e contra-adaptações podem surgir (FIORINI et al. 2019). Para citar alguns exemplos, as fêmeas da maior parte das espécies de parasitas de ninho apresentam postura rápida de ovos e podem destruir ovos do hospedeiro quando visitam o ninho (SEALY et al. 1995; SOLER & MARTINEZ 2000; FIORINI et al. 2014). Em contra-partida, hospedeiros desenvolveram a habilidade de reconhecer e atacar parasitas adultos (FEENEY et al. 2012). Parasitas normalmente têm rápido desenvolvimento, com ovos que eclodem antes que os ovos do hospedeiro e reduzem a sobrevivência dos outros ninhos (REBOREDA et al. 2013), enquanto diversas espécies de hospedeiros desenvolveram reconhecimento e

rejeição de ovos estranhos, o que por sua vez pressiona por ovos miméticos (BROOKE & DAVIES 1988, GIBBS et al. 2000). Estes são apenas alguns exemplos de adaptações e contra-adaptações que tem recebido atenção de estudos recentes (para revisões sobre o assunto, ver Davies 2011, Feeney et al. 2012 e SOLER 2017).

Nos últimos 50 anos, diversos estudos sobre parasitismo de ninho em aves tem contriuiuído para uma boa compreensão das interações entre parasitas e hospedeiros, mas infelizmente pouco desse trabalho se foca em sistemas do novo mundo. Nos neotrópicos, oito espécies de parasitas de ninho foram descritas em três diferentes famílias: Icteridae (quatro chupins *Molothrus* sp.), Cuculidae (três espécies de cucos Neomorphinae, em dois gêneros, *Tapera* e *Dromococcyx*), e Anatidae (Marreca-de-cabeça-preta, *Heteronetta atricapilla*, os únicos parasitas de ninho precociais) (FIORINI et al. 2019). Sistemas de parasitismo de ninho em aves neotropicais refletem um amplo espectro de estratégias, de especializações a parasitas que são generalistas extremos, com diferentes níveis de custos evolutivos aos hospedeiros e a maioria desses sistemas é pouco estudado (DAVIES 2011, FIORINI et al. 2019).

O sistema parasita-hospedeiro, retratado neste estudo, entre *Tapera naevia* (Cuculidae, parasita) e *Certhiaxis cinnamomeus* (Furnariidae, hospedeiro) é conhecido há muitos anos (HARVERSHMIDT 1955, HARVERSHMIDT 1962, De la PEÑA 2013, BODRATI & SALVADOR 2015, LOWTHER 2013, FIORINI et al 2019). Apesar disso, não existem estudos que foquem na relação de coevolução entre as duas espécies.

## 2.2 ESPÉCIES

### 2.2.1. O Curutié *Certhiaxis cinnamomeus*

O curutié, ou João-do-brejo, é uma ave da ordem Passeriformes, família Furnariidae. Mede 16 cm de comprimento, e pesa de 13 a 17g. Possui coloração marrom avermelhada no dorso e na cabeça, face acinzentada e ventre creme. As asas são marrom avermelhadas e o

bico é preto. Não há dimorfismo sexual (REMSEM e de JUANA, 2019) com uma mancha amarelada logo abaixo do bico.

Habita brejos de água doce e bordas de mangue, sendo encontrado numa variedade de áreas alagadas com uma mistura de gramíneas, arbustos e vegetação emergente e flutuante. Se distribui por toda a porção leste da América do sul, da Colômbia e Guianas à Bolívia, Argentina, Paraguai e Uruguai e em todo o Brasil. Ao longo de sua distribuição, 8 subespécies são reconhecidas (REMSEM e de JUANA, 2019): *Certhiaxis cinnamomeus fusifrons* (Mararász, 1913), no norte da Colômbia; *C.c. marabinus* (Phelps Sr. e Phelps Jr, 1946), no nordeste da Colômbia e Noroeste da Venezuela; *C.c.valencianus* (Zimmer e Phelps Jr, 1944) no Centro oeste venezuelano; *C.c. orenocensis* (Zimmer, 1935), no baixo vale do rio Orinoco na Venezuela; *C.c. cinnamomeus* (Gmelin, 1788), no nordeste venezuelano, guianas e no norte e nordeste brasileiro (Do Pará ao Maranhão); *C.c.pallidus* (Zimmer, 1935) no sudeste da Colômbia e Amazonia brasileira; *C.c. cearenses* (Cory, 1916), no nordeste brasileiro (sul do Maranhão, Ceará, Piauí, Pernambuco e Bahia) e *C.c. russeolus* (Viellot, 1817), no leste boliviano e Centro oeste, sul e sudeste brasileiro (Sul da Bahia, Mato Grosso até o Rio Grande do Sul), Paraguai, norte da Argentina e Uruguai (REMSEM & de JUANA, 2019).

Apesar de existirem poucos estudos acerca da espécie, sabe-se que é insetívora, generalista, se alimentando de coleópteros, larvas de lepidóptera, hemípteros, ortópteros e himenópteros (ORDANO et al., 1999; ALESSIO et al. 2005; de la PEÑA & SALVADOR, 2016). Além de insetos, existem registros da espécie se alimentando de gramíneas, peixes e girinos (anfíbios) (HEREDIA et al. 2010; SALVADOR & BODRATI, 2013; de la PEÑA & SALVADOR, 2016).

A espécie é monogâmica social, formando pares estáveis durante a estação reprodutiva, assim como outras espécies de Furnariidae. Não existem dados sobre a época de nidificação da espécie no sudeste brasileiro, mas sabe-se que na Argentina, nidifica de

outubro a fevereiro (de la PEÑA & SALVADOR, 2016). O ninho é globular, com uma entrada tubular, usualmente curvada para cima. O ninho todo é construído com gravetos, juncos, folhas e esterco, com o interior frequentemente forrado com material vegetal macio. O ninho é grande (de 20 a 40 cm de comprimento e 20 a 30 cm de altura) e frequentemente exposto, (de la PEÑA & SALVADOR 2016, REMSEM & de JUANA 2019), geralmente fixado em arbustos ou mesmo na grama, próximo ou sobre a água, geralmente em uma altura de 0,2 a 1,5m, raramente mais alto. Tanto o macho quanto a fêmea se envolvem na construção do ninho, buscando materiais a no máximo 40 metros do ninho e demorando bastante para acomodá-los (5 minutos ou mais) e o casal se comunica cantando durante o processo (de la PEÑA & SALVADOR 2016). A fêmea põe de 3 a 5 ovos verdes pálidos a branco esverdeados por ninhada (de la PEÑA & SALVADOR 2016; REMSEM & de JUANA 2019). O número alto de ovos é pouco usual para o tamanho da espécie e para outros Furnariidae. O período de incubação é de cerca de 17 dias (de la PEÑA & SALVADOR 2016) e os filhotes deixam o ninho em cerca de 17 dias (CONTRERAS 1990; de la PEÑA & SALVADOR 2016). Existem registros de parasitismo de ninho por chupim (*Molothrus bonarensis*) (FRIEDMANN 1963) e saci (*Tapera naevia*) (DI GIACOMO, 2005; de la PEÑA. 2013).

A maior parte das informações sobre a espécie vem de estudos conduzidos na Argentina, e está contida em literatura de difícil acesso. Atualmente, é considerada não ameaçada na lista da IUCN (2018), mas brejos e áreas alagadas são constantemente submetidos a ameaças como drenagens, dragagens, aterros e poluição, o que faz a espécie suscetível aos problemas de conservação que frequentemente afligem espécies de áreas alagadas (REMSEM e de JUANA, 2019).

### 2.2.2. O Saci *Tapera naevia*

O saci, também conhecido popularmente como martim-pererê, martimpererê, matinta-



pereira, matintaperera, matitaperê, dentre outros é um cuculidae neotropical que mede de 26 a 30 cm e pesa de 40 a 59g. Adultos possuem a testa, a coroa e a curta crista com coloração marrom (variando de marrom avermelhado a castanho) com listras pretas (uma tarja central sobre cada pena), com uma mancha esbranquiçada estreita com uma nítida faixa escura sobre os olhos e a faixa malar é escura. A garganta é cor de areia e o peito cinzento. Dorso e escapulários com listras enegrecidas, uropígio e penas supracaudais com as raias do eixo pretas e estreitas. As bochechas são castanhas com listras escuras. Possuem rêmiges acinzentadas com faixas largas pálidas na ponta. A álula é longo, proeminente e preta. O ventre é mais claro, esbranquiçado e o crisso de coloração camurça. A cauda é longa, um pouco graduada e marrom com as bordas castanhas. O bico é curto e levemente curvado e os tarsos e pés são cinza azulados. Não existe dimorfismo sexual. A alula longa é exibida na corte (PAYNE & SORENSEN 2005). Esse cuco ocorre em habitats abertos como pastos, campos e cerrados, do sul do México ao norte da Argentina. É uma espécie solitária e pouco conspícua, que utiliza o canto e duetos na reprodução e defesa de territórios. Indivíduos são frequentemente ouvidos cantando mas são difíceis de se visualizar. Forrageiam entre a vegetação ou próximos do chão e se alimentam primariamente de insetos (HOWELL & WEBB 1955). Parasita apenas passeriformes que constroem ninhos fechados, especialmente furnarídeos. É generalista com 26 espécies conhecidas de hospedeiros, das quais 20 são furnarídeos (LOWTHER 2013). A biologia reprodutiva dessa espécie é pouco conhecida (PAYNE & SORENSON 2005; Mark 2013).

Normalmente deposita um ovo no ninho do hospedeiro, algumas vezes dois. Os ovos variam de verde-azulado a branco, dependendo da localização geográfica (PAYNE & SORENSEN 2005). Na América central, os ovos são azuis, miméticos aos seus hospedeiros locais (MARK 2013), enquanto na América do Sul os ovos são brancos, como os ovos dos hospedeiros furnariidae. Existe uma área onde esses dois grupos de hospedeiros se sobrepõem

e os sacis apresentam ovos polimórficos. As outras espécies de cucos dentro do clado do *T. naevia* botam ovos brancos. Logo, essa provavelmente é a condição ancestral e ovos azuis seriam uma contra-adaptação a rejeição de ovos pelo hospedeiro (PAYNE & SORENSEN 2005). No entanto, essa e outras adaptações e contra-adaptações de sistemas de parasita-hospedeiro envolvendo *T. naevia* foram pouco estudadas (MARK 2013, FIORINI et al 2019).

Ninhegos de saci matam os ninhegos do hospedeiro no ninho utilizando um gancho afiado na ponta do bico e demonstram comportamento agressivo assim que nascem (MORTON & FARABAUGH 1979). São então criados sozinhos pelos hospedeiros e perdem o gancho do bico conforme crescem (MORTON & FARABAUGH 1979).

O período de incubação do *T. naevia* varia de 15 a 16 dias (De la PEÑA 2006), e juvenis deixam o ninho entre 16 e 18 dias (De la PEÑA 2006) e permanecem incapazes de voar por cerca de uma semana, podendo ser cuidados pelos pais hospedeiros até um mês de idade (PAYNE & SORENSEN 2005).

Além dos óbvios custos associados a perda total da prole do hospedeiro e o tempo e energia gastos em criar um parasita, muitas vezes maior que os hospedeiros, outros custos menos óbvios foram demonstrados na literatura. Parasitismo por *T. naevia* pode gerar mudanças no comportamento de *Thryophilus rufalbus* (Aves: Troglodytidae) hospedeiros, porque juvenis de *T. naevia* deixando o ninho se deslocam para longe do centro do território em direção as bordas de florestas e áreas abertas que não são utilizadas pelo hospedeiro (MARK & GAMEZ-RUGAMA 2015). Além disso, os custos fisiológicos de serem parasitados são carregados para tentativas subsequentes de nidificação, como sugerido pela correlação entre parasitismo e a latência entre tentativas de nidificação (MARK & RUBENSTEIN 2013).

Pouco se sabe sobre o comportamento após deixar o ninho, especialmente em uma espécie pouco conspícua. Mark e Gamez-Rugama (2015) utilizaram radio colares em juvenis

de Saci deixando o ninho e descobriram que estes podem se associar com conspecíficos adultos, em interações geralmente iniciadas pelos adultos, resultando em pares de adultos e juvenis que se deslocam e forrageiam juntos e até cantam em duetos.

### 3. OBJETIVOS

#### 3.1 OBJETIVO GERAL

Através de observações de campo, elucidar aspectos da biologia reprodutiva do Curutié *C. Cinnamomeus* (Aves: Furnariidae) em uma área de brejo em Santa Bárbara d'Oeste, São Paulo, Brasil, e elucidar os fatores que influenciam nas taxas de parasitismo por *T. naevia* nesta população.

#### 3.2 OBJETIVOS ESPECÍFICOS

##### Capítulo 1:

Elucidar aspectos da biologia reprodutiva de *Certhiaxis cinnamomeus* tais quais como descrição do ninho, períodos de incubação e permanência dos filhotes nos ninhos, tamanho de prole, número de nidificações por temporada reprodutiva e produtividade anual.

##### Capítulo 2:

Investigar a influência do tamanho do tubo de entrada do ninho nas taxas de parasitismo por *T. naevia*, bem como a influência de outras variáveis ambientais.

#### **4. CAPÍTULO 1: Annual fecundity in a population of the Yellow-Chinned Spinetail *Certhiaxis cinnamomeus* (Aves, Furnariidae) in Southern Brazil**

##### 4.1 INTRODUCTION

Avian annual fecundity is a key parameter for the understanding of population dynamics, viability, and life history adaptations (PEASE & GRYBOSKY 1995). It is defined as the number of offspring produced per female per reproductive season, and results from a combination of factors, including clutch sizes, nest survival, and number of nesting attempts in a season. Although clutch size and nest survival information are available for many taxa and locations, renesting data are scarce due to the difficulty to mark and follow females throughout an entire breeding season. For this reason, annual fecundity has been often estimated by algorithms, which however, were proved to be highly dependent on precise renesting data (GRZYBOWSKY & PEASE 2005). Further, the lack of information impedes the proper interpretation of important theories, some of which classical, such as the prediction that Neotropical birds have more nesting attempts due to longer reproductive seasons. However, data are highly biased towards northern hemisphere taxa, making empirical observations on nesting attempts and renesting rates still of scientific interest.

Here we addressed annual fecundity in the neotropical yellow-chinned Spinetail, *Certhiaxis cinnamomeus* (Furnariidae). Specifically, we combined reproductive phenology, nesting attempts, and nest survival data to estimate the number of offspring produced per female based on nine marked pairs that could be observed during an entire breeding season. We also provide further basic reproductive information for this poorly studied species.

##### 4.2 MATERIALS AND METHODS

###### **4.2.1 Study species**

Furnariidae are an exclusively Neotropical Family containing more than 280 species

(REMSEN, 2019). However, like many neotropical taxa, they have been poorly studied, and little is known about their phylogeny, ecology, behaviour and reproductive biology (SHELDON and WINKLER, 1999). When it comes to reproductive biology, even less is known. Most genera build closed nests, made of twigs or mud, while some nest in natural or man-made cavities. Many species are territorial and monogamous, being easy to spot in pairs (SKUTCH, 1996).

This is the case of the yellow-chinned spintail. This bird inhabits freshwater marshes and mangroves, along all the east portion of South America (REMSEN & de JUANA, 2019), with 8 described subspecies. The species measures around 16 cm, weighting from 13 to 17 grams. Their back and wings are reddish brown, with grey face and cream colouring venter. Below the black beak there is a small yellow spot. Throughout its distribution, there are 8 different subspecies (REMSEM and de JUANA, 2019): *Certhiaxis cinnamomeus fusifrons*(Mararasz, 1913) in north of Colombia; *C.c. marabinus* (Phelps sr. and Phelps jr. 1946) in northeast of Colombia and northwest of Venezuela; *C.c. valencianus* (Zimmer and Phelps Jr. 1944) in the centre-west of Venezuela; *C.c. orenocensis* (Zimmer 1935) in the low Orinoco Valley in Venezuela; *C.c. cinnamomeus* (Gmelin, 1788) in the northeast of Venezuela, Guianas and north and northeast of Brazil; *C.c. pallidus* (Zimmer 1935) in the southesat of Colombia and Brazilian Amazon; *C.ccearenses* (Cory, 1916), in the northeast of Brazil and *C.c. russeolus* (Viellot, 1817), in east Bolivia and Centre-west, south and southeast of Brazil, Argentina and Uruguay (REMSEN and de JUANA 2019).

According to de la Peña and Salvador (2016), the species forms stable pairs during the reproductive season, like other furnariids. Reproductive season in Argentina is from October to February (de la PEÑA & SALVADOR 2016), but there are no data about reproductive season in Southern Brazil. The nest is a globular mass (20 to 40 cm of width,

20 to 20 of height), built with twigs, thorns, leaves and manure, with a tube shaped entrance with soft plant material lining the interior of the incubatory chamber (de La PEÑA & SALVADOR 2016, REMSEN & de JUANA 2019). It is frequently quite exposed, fixed in shrubs or even on grass, near or over water, from 0.2 to 1.5m height, rarely higher. Both male and female get participate in nest building, picking up materials and taking a long time to accommodate them in the nest, with the couple communicating throughout the process.

Although the species forms stable pairs throughout the reproductive season, it is not known if these pairs remain the same from one season to another, or if the couples maintain their territories. Some aspects of the reproductive biology of this species have been described for Argentina (de la PEÑA & SALVADOR, 2016), like nest size and shape, and number of eggs per brood, but nothing like that has been done for Brazilian populations.

There are reports of brood parasitism by *Tapera naevia* (e.g. Harvershmidt 1955, Harvershmidt 1962, Lowther 2013, Fiorini et al 2019), although this host-parasite system has not been addressed in any other research to our knowledge.

The objective of this study was to address aspects of phenology, reproductive biology, nesting attempts and nest parasitism in yellow-chinned spinetail nests to infer fecundity rates, and provide more reproductive data on this poorly studied species.

#### **4.2.2 Study site**

The study site is located in the municipality of Santa Barbara in the state of São Paulo, Brazil. It consists in a three perennial lakes and surrounding marshes system. The lakes are 6, 14 and 45ha, and are 300 to 800 meters apart. They are around 1 meter deep, and present abundance of vegetation of the genera *Rhynchosporae* and *Cyperus*. Around the lakes the

vegetation is constituted by a reforestation forest consisting in a mix of native species. Around every lake there is a belt of wetland, with only grass and small shrubs. The whole complex is located inside a private sugarcane farm, and isolated, since it is surrounded by sugarcane monoculture.

The climate is mesothermic and the rainy season is from October to March, with average temperatures of 22°C and precipitation around 1100mm. Dry season is from April to September, average temperature below 18°C and precipitation around 300mm.

#### **4.2.3. Nest and reproductive data search**

We conducted field work in two different reproductive seasons, the first from December 2017 to February 2018, and the second from October 2018 to February 2019. The nest search was conducted by following the adults which showed evidence of reproductive activity, like carrying nest material or food, and systematically inspecting the vegetation. We visited the nests at intervals of 3-4 days, increasing visits to every other day during expected laying, hatching or fledging periods. The incubation period was measured from the first day of incubation until the day before hatching. Nesting period was from hatching day to a day before they left the nest. To determine the beginning of the incubation period we performed focal observations of the nests.

In every nest visited we carefully opened a small gap in the twigs to be able to look inside, and recorded status (active, inactive) and content (eggs, nestlings, parasite nestlings or empty) for every visit. If a nest was found empty before the expected fledging date, we searched for evidence of predation or disturbance. If signs were found, this nest was considered to be predated.

We recorded external measurements for every nest: height, nest globe length, nest globe width, tube length, tube opening external and internal diameters, as well as position of the tube insertion in the globe, presence or absence of a tube curve and angle of the tube



insertion on the globe. Measurements taken can be seen in Figure 1 and Figure 2.

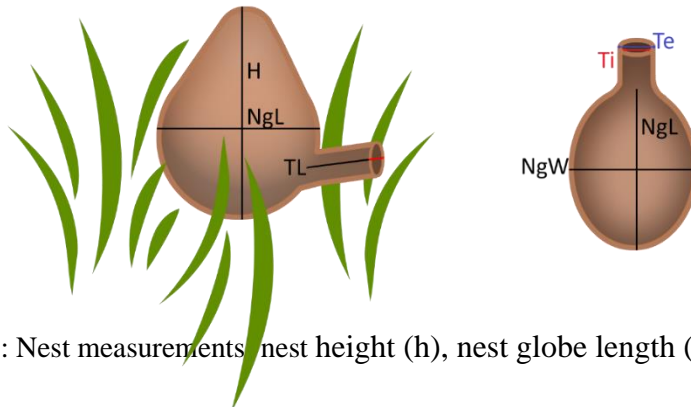


Figure 1: Nest measurements: nest height (h), nest globe length (ngL), nest globe width (ngW), tube length, tube opening external and internal diameters (TE and TI).



Figure 2: Nest pictures with measurements. A – Top view, B – Tube entrance, C- lateral view, D – Construction process, showing the interior of the nest globe.

#### 4.2.4. Capture and marking of individuals

Once found the territories and nests, we used mist nets to capture the individuals

(Figure 3) and mark them with colourful plastic rings to assign individuals to their pairs and nests. Once marked, we observed the individuals during incubation and parental care.



Figure 3: *Certhiaxis cinnamomeus* individuals being captured and marked.

### 4.3. RESULTS

#### 4.3.1. Reproductive biology

During the 2017/2018 breeding season, we monitored 10 active nests of yellow-chinned spinetail, and during the 2018/2019 breeding season, 20 active nests were monitored.

This discrepancy is due partially to the fact that we were able to start conducting field work earlier in the second season, and partially because we were already familiarized with the area and territories.

Nests were built using thick long twigs and thorns, pieces of plastic or other materials, and in one nest snake or other reptile skin sheds were used. The incubatory chamber lied inside the nest globe, lined with lichen and moss. Out of 30 nests, we measured 29, because one nest was destroyed overnight before we took its measurements. Average nest measurements were  $224.00 \pm 37.39$  mm for nest globe length,  $184.46 \pm 23.44$  mm for nest globe width,  $228.93 \pm 43.23$ mm for nest height. Average nest tube measurements were  $48.02 \pm 8.94$ mm for tube external opening,  $38.36 \pm 8.29$ mm for internal opening and  $92.36 \pm 27.55$ mm for tube length.

Tube insertion position in the nest also varied, between nests with tubes arising from the base, from the middle and even from the top of the nests. because one nest was destroyed overnight before we took its measurements. 23 of the 29 (79.31%) of the nests had tubes arising from the base of the nest, while 5 had tubes arising from the mid-section of the nest globe (17.24%) and only 1 (3.45%) had the tube arising from the top. Out of the 29 measured nests, 17 (58.62%) presented a curved entrance tube, and most tubes (62.06%) were angled upwards more than  $45^\circ$ , while one was parallel to the floor (3.44%) and the others were angled upwards but less than  $45^\circ$  (34.49%) (Table 1).

Of the 30 active nests found, 15 (50%) were built in *Rhynchospora* sp. 8 (26.67%) on *Typha* sp., 3 on (10%) on *Andropogon bicornis* sp., 1 (3.33) in an old tree trunk, 1 (3.33%) in *Eleocharis* sp., 1 (3.33%) in *Brachiaria* sp. and 1 (3.33%) in an unidentified short shrub. Nests were built on an average distance of the water or floor of  $228.93 \pm 43.23$ mm. In the first season, 9 of the 10 nests were built over the water. In the second season, only 8 of the 20 nests were built over water, probably because it was a much drier season, making most shrubs

exposed.

Table 1: nest measurements with means and range values.

<b>Variable</b>	<b>Mean</b>	<b>SD</b>	<b>Min</b>	<b>Max</b>
External tube opening (mm)	48,60	8,6368	35.0	65.3
Internal tube opening (mm)	38,84	8,9463	26.0	57.6
Tube length (mm)	94,69	29,3603	65.0	183.0
Globelength (mm)	222,58	37,8532	150.0	291.0
Globewidth (mm)	185,75	24,0981	130.0	245.0
Height (mm)	236,50	45,9442	160.0	329.0
Distance from water or floor (mm)	351,04	203,735	0.0	782.0
Waterdepth (mm)	205,62	238,8041	0.0	803.0

In the 2018/2019 breeding season we were able to infer the beginning of the breeding season by the first nests we found on October 1<sup>st</sup> (N=3). The nests were already active, with eggs being incubated, and by regression it is possible to infer that reproductive season started on late September, and the last active nest for this season was recorded on February 13<sup>th</sup>, with the fledging of a parasitic striped cuckoo (*Tapera naevia*). Nest parasitism rates for this species were incredibly high. From the 24 nests that we were able to identify the nestlings, 18 were parasitized by the striped cuckoo (66,67%).

Mean clutch size for nests that bred only yellow-chinned spinetail chicks was  $2.67 \pm 0,47$  eggs (N=6). All nests with 4 eggs with known outcomes hatched Stripped cuckoos, so we further considered nests with 4 eggs to be parasitized. Figure 4 shows yellow-chinned spinetail and striped cuckoo chicks in nest.

The incubation period recorded for this species in this area was 17 days (N=2 nests). Only females incubate, but males remain in the territory guarding. When females left the nest to forage, the couple communicated repeatedly through singing. Focal observations (N=2 pairs, 3 hours) showed that parental care was given by both male and female, alternating



guarding and foraging between male and female most of the time. The couple often communicated through singing and calls.



Figure 4: *C. cinnamomeus*(above) and *T. naevia* (botton) chicks inside the nest.

Fledging period for chicks was 18 days (N=1). It was difficult to collect more data from different nests because these nests were heavily parasitized by Stripped cuckoos (*Tapera naevia*), making the total number of nests that raised yellow-chinned spinetails low. The three chicks which left the nest were captured, marked and had blood samples collected for sexing and paternity analysis. They remained in the parents' territory for at least 2 months, being fed and cared for.

After fledging either Stripped cuckoos or yellow-chinned spinetails, nests were dismantled and the material was used to build a new nest in a close location, or another nest was built on top of the first one (N=5). We even found one nest with 3 different incubatory chambers, from previous attempts.

We also observed a nest being reutilized. After the fledging of a *T. naevia* chick, the nest tube was fixed and the nest was reutilized, raising another *T. naevia* chick. We believe that this was due to the fact that this particular territory had no other shrubs big enough to support a *C. cinnamomeus* nest.

#### **4.3.2. Mate fidelity**

We were able to correctly mark and identify 6 pairs in the first season, and 9 in the second breeding season. Although we have not monitored the territories during the whole first season, all of the couples had more than one nesting attempt (see results bellow), and within-breeding season divorces were not observed in none of the years. Of the six couples marked in the first season, one disappeared. Of the five remaining couples, one remained together across seasons, and the individuals changed partners. It is worth noting that one member of each pair formed in 2017/2018 season constructed nests very close to the nest-sites of the previous year.

#### **4.3.3. Nesting attempts and reproductive output**

Of all 30 active nests, 4 were depredated during incubation stage, 8 were depredated during nestling stage, 1 was lost due to flooding, 2 were destroyed by passing animals, and fate is unknown for 2 nests. Of the 13 successful nests, 3 fledged *C. cinnamomeus*, and 10 fledged *T. naevia* youngs.

For the second season, we observed that couples could initiate the construction of 1-4 nests ( $2.89 \pm 0.93$ ), they completed the construction of 0-3 nests ( $2.11 \pm 1.05$ ), and they

produced 0-3 clutches ( $2.11 \pm 1.05$ ) ( $n =$  nine marked pairs) (Table 2). Of the 19 clutch initiations, only one resulted in yellow-chinned Spinetail fledging successfully (three young), and 6 resulted in one Stripped cuckoo fledgling each.

Table 2: Identified pairs, nest attempts and outcomes.

<b>Pair ID</b>	Construction initiations	Constructed nests	Clutch initiations	<i>C. cinnamomeus</i> fledgings	<i>T. naevia</i> fledgings
Pair 2	3	3	3	0	2
Pair 3	4	3	3	0	0
Pair 7	3	2	2	0	1
Pair n9	4	3	3	0	0
Pair n10	3	3	3	0	1
Pair n11*	1	1	2	0	2
Pair n12	2	2	2	0	0
Pair 13	3	2	1	1	0
Pair n14	3	0	0	0	0

\*Nest reutilized by the pair.

Therefore, in 2018/2019 breeding season, reproductive output was 0.33 *C. cinnamomeus* and 0.66 *T. naevia* per breeding pair (Table 2). The maximum number of successful broods produced per pair was two, and in all of the cases ( $n = 2$ ) only Stripped cuckoos were produced.

#### 4.4. DISCUSSION

Our data seems to corroborate the data previously collected in Argentina in many aspects. Nests matched the ones described by de la Peña and Salvador (2016). Incubation period was the same as reported by di Giacomo (2005). De la Peña (2013) reports a shorter incubation period (15 to 16 days). Permanence periods reported in literature varied from 16 to 19 days (CONTRERAS 1990, di GIACOMO 2005, De la PEÑA 2013) and our data reports

18 days (n=1). The low sample number is due to the fact that most nests were parasitized, and many others were predated in egg stage or before we could differentiate the chicks. Focal observations corroborate what other authors had reported about nest building and offspring care (Di GIACOMO 2005, de La PEÑA 2013) being made by both parents.

Clutch size was smaller in our study than what is previously reported in literature. De la PEÑA and SALVADOR (2016) report 3 to 5 eggs. In our study site, clutch size was  $2.67 \pm 0.47$ . We did observe a number (n=10) of nests with 4 eggs, but they all hatched striped cuckoo chicks.

Year-round territoriality and permanent pair bond is a common breeding system in tropical passerine birds (MORTON 1980, GREENBERG and GRADWOHL 1986, 1997, MORTON et al 2000). No variation has been reported within the furnariids in parental roles or social mating systems, and they are thought to be socially and genetically monogamous (REMSEN 2019, PORT and GREENEY 2015), but whether the species' monogamy is held across seasons or not was still unknown. Conducting field work activities, we were able to see couples from the previous season together until early July, but at the beginning of the new reproductive season all the couples but one had dissolved or abandoned the territory. Coincidentally, it was the only couple that managed to fledge three yellow-chinned spintail chicks, that stayed in their territory demanding care after the breeding season had ended. We can't affirm that the couple stability was a product of the reproductive success during the season, but the mechanisms that influence divorce and stability rates should be further investigated.

Nest site selection analysis could not be conducted. This type of analysis depends on nest and random sites comparisons (MARTIN and ROPER 1988). In our study area this analysis would not be straight forward since almost all nests were built within the tussocks of *Rhynchospora* sp. (Cyperaceae). These tussocks are circular, and the nests are large globular



structures, that displace the vegetation as they are being built, making them poorly comparable to tussocks without nests.

Predation was another analysis that we could not perform. Having two different types of nestlings (parasite and host) imposed a methodological restraint, reducing our numbers and making predation analysis impossible. Further research on nest placement and architecture and predation rates should be conducted.

There are very few studies that describe renesting rates, and this may be due to methodological restrictions. To correctly infer renesting rates, one must capture and mark the population using colourful bands (GRYSBOWSKI & PEASE 2005). This problematic is further complicated by the fact that some works available don't make clear whether what they consider as renesting is nest building initiation, egg laying or attempting double brooding (e.g. ROPER 2005), or present data only for double brooding rather than total nesting attempts data (e.g. HOWLETT et al. 1997), or do not present fecundity or means to calculate it using the data presented in the paper (e.g. DELHEY et al. 2010, DAVANÇO et al. 2013, DAROS et al. 2018) making comparisons even more difficult. Table 3 shows data regarding nesting attempts and fecundity of several species.

Nesting attempt rates were similar to those reported for two other passerine birds in tropical areas, *Turdus leocomelas* (DAVANÇO et al. 2013) and *Mimus gilvus* (MORAIS et al. 2019), and also similar to another Furnariidae from a temperate area *Anumbius annumbi* (DELHEY ET AL 2010). It is impossible to assume if renesting rates are a result of ecological trends or phylogeny.

Table 3: List of passerine species and data regarding reneating and fecundity rates.

Species	Family	Location	Fecundity	Renesting	N	Author
<i>Polioptila caerulea</i>	Poliopitilidae	Chile, temperate forest	2,5	1 to 3	51	Moreno et al. 2005
<i>Anumbius annumbi</i>	Furnariidae	Argentina, temperate forest	?	2.84	33	Delhey et al 2010
<i>Turdus leucomelas</i>	Turdidae	Brazil, tropical forest	?	2.17	6	Davanço et al 2013
<i>Setophaga citrina</i>	Parulidae	US, Temperate forest	4,9	at least 2	170	Howlett et al 1997
<i>Polioptila caerulea</i>	Poliopitilidae	US, Neotropical	1,19	1.9	42	Kershner et al 2001
<i>Tyrannus melancholicus</i>	Tyranidae	Brazil, tropical forest	?	1.15	12	Daros et al 2018
<i>Hylophylax naevioides</i>	Thamnophilidae	Panama, tropical forest	1.5	2 to 8	70	Styrsky & Brawn 2011
<i>Cyphorhinus phaeocephalus</i>	Troglodytidae	Panama, tropical forest	1,4	at least 2	9	Robinson et al 2000
<i>Thamnophilus atrinucha</i>	Thamnophilidae	Panama, tropical forest	1,8	at least 2	64	Tarwater 2010
<i>Mimus gilvus</i>	Mimidae	Brazil, tropical forest	?	2.6	14	Morais et al. 2019

Even with scarce data it is possible to infer that fecundity rates for this population are low, especially due to the high rates of parasitism. Of 19 nests with clutch initiations, 7 fledged either striped cuckoos or yellow-chinned spinetails (36,84% of nests were successful against predation), but only one of these nests was not parasitized, showing that the biggest constraint for this populations reproductive output was parasitism rather than predation.

Parasitism rates change from population to population, and fecundity must therefore follow this trend.

## 5. CAPÍTULO 2: Tube length is not predictive of parasitism by the Stripped Cuckoo *Tapera naevia* (Aves: Cuculidae) in nests of the Yellow-Chinned Spinetail (Aves: Furnariidae)

### 5.1 INTRODUCTION

Obligate brood parasitism has evolved independently in at least seven avian lineages (SORENSEN & PAYNE 2002). In this reproductive strategy, parasites lay their eggs in nests of other species, transferring the costs of parental care to their hosts (SOLER & SOLER 1999, MARK 2013). As hosts benefit from developing anti-parasitic defences, and parasites often respond with counteradaptations, brood-parasitism has been one of the main systems in the studies of coevolutionary processes (ROTHSTEIN 1990, SOLER & SOLER 1999). The relationships between parasitic birds and host species are complex and a wide range of strategies can be adopted by both parties in the different stages of the nesting cycle (DAVIES 2011). Parasitic female adaptations can include egg mimicry, rapid oviposition, and puncture of host eggs (DAVIES 2011), and parasitic offspring can show rapid development during incubation, and they can exhibit morphological and behavioural aspects capable to deceive parental hosts and to control their behaviours (DAVIES 2011, FEENEY et al. 2012). On the other hand, some of host adaptations are aggressiveness against parasitic birds for nest defence, recognition and ejection of foreign eggs or nestlings, nest concealment, changes in reproductive phenology, and nest construction near repulsive organisms (FEENEY et al. 2012). Further, for cavity nester species, smaller nest entrances can restrict parasite access in systems in which the parasite is substantially larger than the host (RUTILA et al. 2002, STANBACK et al. 2013), and for at least one group of birds, the weaverbirds, the construction of nest tubular entrances was evidenced to reduce parasitism (FREEMAN 1988). The function of tubular entrances as antiparasitic defences in closed-nester hosts, however, is one the less investigated aspects of brood parasitism.

African weaverbirds, for instance, build nest tubes up to 30 cm in length (CROOK

1963; DAVIES 2000; FEENEY et al. 2012), and in a cross species study it was found that nest tubes occur more frequently among species that were regularly parasitized by cuckoos (FREEMAN 1988; DAVIES 2000). Further, it was evidenced that weaverbird species that had tube entrances in their nests had reduced egg colour variability, which can indicate that tube construction is an antiparasitic defence that eliminates the need of egg recognition because it stops the parasite in a pre-incubation stage. However, it also could mean that the interior of nests with tube entrances are darker, making egg recognition impossible anyway. To our knowledge, this is the only system in which the relationship between nest tubes and parasitism was addressed.

Here we aim to test the hypothesis that nest tubular entrance can reduce parasitism by the striped cuckoo, *Tapera naevia* (Cuculidae) in a population of the neotropical yellow-chinned spinetail, *Certhiaxis cinnamomeus* (Furnariidae). The latter construct large globular nests made of sticks, with a prominent tubular entrance that is highly variable in length between nests, and it is frequently parasitized by the Stripped Cuckoo, which seems to be specialized in parasitize closed-nester hosts (LOWTHER 2013, FIORINI et. al 2019). We predict that if the parasite uses nest entrance to deposit its eggs, then nests with longer tubes would have lower parasitism probability. To achieve this purpose, we used Generalized Linear Models and we controlled to other potentially important parameters, including a set of variables related to tube and nest-body architecture, nest concealment, and temporal covariates.

## 5.2 MATERIAL AND METHODS

### 5.2.1 Study species

The yellow-chinned spinetail, also called yellow-throated Spinetail, is a small passerine bird, with about 14-14.5 cm in length and 13-17g in weight, being much smaller

than the striped cuckoo (see description below). It is widely distributed in South America, from Colombia, Venezuela, and most of Brazil, southern to Paraguay, Uruguay, and northern Argentina (RIDGELY & TUDOR 1994, REMSEN & de JUANA 2019). The species inhabits fresh water marshes, humid grassy areas, and mangroves (RIDGELY & TUDOR 1994, SICK 1997, REMSEN & de JUANA 2019), where they construct big globular nests built of twigs and thorns with a remarkable tubular entrance, often curved upwards (Fig 1). They are socially monogamous and clutch size vary from three to five white to greenish, short-oval eggs (Fig 1) (De La Peña 2016), but the larger clutch sizes can include parasitic eggs, as these authors made no distinctions between host and parasitic eggs (Di GIACOMO 2005, DE LA PEÑA 2016). Incubation period is estimated to be 15-16 days, and nestling period is also around 16 days (DE LA PEÑA 2016, DI GIACOMO 2005), and scattered information indicates that in Argentina reproduction occur from October to February (DE LA PEÑA 2016, DI GIACOMO 2005). Although the occurrence of parasitism by the Stripped cuckoo is somewhat well documented for this species (SICK 1997, De la PENA 2006, BODRATI 2015, LOWTHER 2013, FIORINI et al 2019), to our knowledge this system has never been studied.



Figure 1: Nest of *C. cinnamomeus*: A: eggs inside nest. B: lateral view of the nest.

The Stripped Cuckoo is widely distributed and relatively abundant in the Americas,

from the south of Mexico until central Argentina (PAYNE & SORENSEN 2005, de la PEÑA 2013, BODRATI 2015). It is also the most studied of the neotropical brood parasites (FRIEDMANN 1933, SICK 1953, PAYNE & SORENSEN 2005, LOWTHER 2013, BODRATI 2015).

The Stripped Cuckoo is a Cuculidae measuring 26 to 30 cm and 40 to 59 g. It inhabits wet grasslands, second-growth scrubs, open fields with scattered trees, clearings and forest margins in tropical forests, ranging from South of Mexico to East Panama and Colombia, to the Guianas and, including Margarida island and Trinidad, throughout Brazil, West Ecuador, North of Peru, Bolivia, Paraguay, Uruguay and North of Argentina (PAYNE 2019). Adults are brown above with streaked buff and black, head with blackish stripes and rufous crest. The supercilium is white and they present a narrow black malar line, a prominent black alula extended from wing, whitish below and sides of throat and chest with black streaks. The belly is white and they have bare skin around the eye, which is yellow. The iris is brown to greenish brown, the bill is brown to orange brown, and the feet are grey.

The reproductive season reported for this species in Argentina is from October to January (BODRATI, 2015), but there are no records for this species reproductive season in the Brazilian Southeast. This species only parasites hosts that build closed nests (REMSEN 2003, FITZPATRICK 2004, KROODSMA & BREWER 2005, RISING 2011, BODRATI 2015). Furnariidae are known for building big closed and complex nests, which makes them perfect hosts for this species. There are, in total, 20 species of Furnariidae that can host the striped cuckoo (PAYNE & SORENSEN, 2005; LOWTHER 2013; BODRATI, 2015). This points to a high predilection for Furnariidae hosts, since from all the species listed as hosts for the striped cuckoo, more than 75% are Furnariidae (LOWTHER 2013, BODRATI 2015).

As other species of cuckoo, *Tapera naevia* also lays polymorphic eggs. In southern South America, the eggs are white, and so are the eggs of most of the documented hosts

(FRIEDMANN 1933, SALVADOR 1982, de LA PEÑA 1993, MARK 2013, BODRATI 2015), which indicates that matching host eggs may be one of the reproductive strategies of this cuckoo (PAYNE & SORENSEN 2005, MARK 2013). In the northern part of South America, on the other hand, this species may lay both white and greenish blue eggs, and host records show that in this case, the striped cuckoo uses multiple hosts, and colour mismatching may occur (Haverschmidt, 1955, 1961) and it is probably underestimated since hosts may reject mismatching eggs (MARK, 2013). In central America, the eggs are only bluish green, and both, color matching and mismatching have been documented (LOETSCER 1952; KIFF & WILLIAMS, 1978; MARK, 2013). There is very little data on egg matching and acceptance by hosts for new world cuckoos. Mark (2013) found evidence that in Central America, the striped cuckoo lays very mimetic eggs to its preferred host, which increases acceptance, but reduces the number of possible hosts. The trade-offs of mimetic eggs for this species are still to be studied.

Adaptations are not only seen in the egg laying phase. striped cuckoo chicks show remarkable adaptations to deceive the hosts and assure its survival. Many cuckoo species are known for ejecting their foster siblings out of the nest, but the striped cuckoo takes a different approach. The chicks are born with hook-like structures on their bills, which they use to kill the host chicks. This is similar to what is found in honeyguides (*Indicator* sp.), but the hooks are kept throughout all the nestling life. Morton and Farbaugh (1979) suggest that the hooks also serve a defence purpose rather than just infanticide, pointing that the cuckoo chicks were really aggressive, striking against any disturbance in the nest. These observations also point that the lining of the mouth of the striped cuckoo chicks is deep yellow, which matches the lining of most of the host species studied (MORTON & FARBAUGHT, 1979). Another adaptation for begging is that the cuckoo chicks only vibrate the alula when begging, instead of the whole wing, making them appear smaller (MORTON & FARBAUGHT, 1979).

### 5.2.2. Study area

The study site is located in the municipality of Santa Barbara d'Oeste (-22.857866 S, -47.488082, altitude 590-610 m), in the state of São Paulo, Brazil. It consisted of two perennial lakes and their surrounding marsh systems (Figure 2). The lakes are 14 and 45 ha and are 800 m apart. They are around 1 m deep, and present abundant emergent vegetation, mainly of the genera *Rhynchosporae* and *Cyperus*, with grassy and shrubby vegetation in the humid areas surrounding their edges. The whole marshy complex is protected by a reforestation of arboreal vegetation, in late regeneration stage. These areas are located inside a private sugarcane farm and are imbedded in a matrix of sugarcane monoculture. The climate is mesothermic and the rainy season is from October to March, with average temperatures of 22oC and precipitation around 1100mm. Dry season is from April to September, average temperature below 18oC and precipitation around 300mm.



Figure 2: Study site



### **5.2.3. Field procedures**

We conduct nest searches throughout the study area at least twice a week from September to April during two breeding seasons, 2017/2018 and 2018/2019. Nests were located by following adult yellow-chinned spintail individuals carrying nest material or delivering food to the nestlings, and also by checking the vegetation thoroughly. After found, nests were checked 1–2 times a week, and nest contents were visualized by the introduction of a portable Endoscope Inspection Camera in nest tubular entrance (Model AN97 Novadigital), with the images observed and stored in a Smartphone. Nests were considered depredated when eggs or nestlings disappeared before fledging age, and they were considered parasitized, or not, when nestlings survived to the age they could be identified as belonging to the host or parasite species (7-8 days). Nests depredated during incubation stage were considered only if they presented an excessive number of eggs. This is because all of the nests containing four eggs that survived to middle nestling stage were parasitized, indicating that the presence of a fourth egg was always derived from parasitism. As nests with two or three eggs could be parasitized, or not, they were discarded from our analyses when they were depredated in early stages.

### **5.2.4. Statistical analysis**

To test whether nest tubular-entrance length, as well as a number of concurrent covariates, were correlated to parasitism probability, we addressed a set of parameters related to nests and nesting sites. Nest parameters were: height above ground or water, water depth, nest globe length, nest globe height, nest globe width, tubular entrance length, internal tube diameter in the distal portion, and external tube diameter in the distal portion. Tube length was measured from the middle lateral portion of its insertion in nest globe to its tip, always taking its curvature into account. Tube diameters were taken by using a metal calliper

accurate to 0.01 mm, and the other measurements were taken with a measuring tape accurate to 0.1 cm. Further, tubes were classified according to three categorical variables: i) if nest contents could be observed, or not, from nest entrance as a result of tube curvature (no = 1, yes = 0), ii) tube inclination (0 to 45° upward inclination in relation to horizon, and 46° to 90° upward), and tube insertion position (tube arising from the lower portion of nest body; tube arising from the middle portion of nest body, or tube arising from the upper portion of nest body).

For nesting site variables we addressed: vegetation density in 30 cm radius, vegetation density in 3 m radius, vegetation density above nest, supporting plant height, number of tussocks in 3m radius, and the lower distance from nest to the border of the arboreal vegetation that surrounded the marsh. Vegetation density in 30 cm radius was estimated as the summation of the numbers of leaves or branches touching a 30 cm metal rod pointed from middle lateral nest body to the four cardinal directions. Vegetation density in 3 m radius was measured with a 3m metal rod subdivided into 30 intervals of 10 cm. Then, vegetation density was estimated as the total number of intervals touched by vegetation in the four cardinal directions. Vegetation density above nests were also estimated by the number of touches in 30 cm metal rod positioned upward from the central part of the top of the nest globe. Supporting plant height and distance to the border were obtained with a measuring tape. As nesting site categorical covariates we included: species of supporting plant (that could be tussocks of *Rhynchospora* sp. (Cyperaceae), *Typha* sp. (Typhaceae), and *Andropogon* sp. (Poaceae); the tree *Croton urucurana* (Euphorbiaceae), and in only one case each, the top of a highly exposed decaying trunk, and levels of water surface exposure due to the presence of aquatic vegetation in 3 m radius. Types of supporting plants (including the decaying trunk) were coded with numbers from 0 to 4 for modelling analyses (see methods below). Water surface exposure was visually classified as 0-25, 26-50, 51-75, and 76-100%, and was also coded

with numbers from 0 to 3. To address the temporal effect of across the breeding season, we estimated clutch initiation dates for each nest based on the observation of laying (most nests), or by regression based on known events (hatching or fledging) using incubation and nestling periods. Then, we adjusted the calendar to a timeline in which the earlier clutch initiation in the nesting season was day 1 (Time variable of WHITE and BURNHAM, 1999).

All of the continuous variables, and also the categorical ones that received numbers to represent more than two categories (i.e. tube insertion positions, supporting plants, and water surface) were standardized using score-z, and the corrected variables were considered as autocorrelated when they presented high Pearson correlation coefficient ( $r \geq 0.6$ ). Then, we conducted model selection analyses using Generalized Linear Models (GLMs), with binary distribution and logit link-function, with response variables coded as 0 (non-parasitized) and 1 (parasitized). To reduce computational effort the analyses were subdivided into two blocks, one considering nest architecture covariates, and another with nesting site parameters, aiming to select the most important variables for a final modelling. All of the possible models of each block and also the null model were exploited by using the dredge-function of the package MuMIn (BARTON, 2018), and the candidate models were selected using the Akaike's Information Criterion corrected to small samples (AICc) (BURNHAM & ANDERSON, 2002), as well as by the  $\Delta AICc$ , which is a measure of each model relative to the best model, and Akaike weights ( $w$ ). Relevant models were those presenting  $\Delta AICc \leq 2$  (BURNHAM; and ANDERSON, 2002), and model parameter estimates, their standard errors (SE) and 95% confidence upper and lower limits are reported to indicate the importance of each variable to the selected models. Z-tests were carried out to test the importance of each variable within the selected models. All of the statistical procedures were conducted using the software R (R CORE TEAM, 2018).

### 5.3 RESULTS

In total, 30 active nests were found, 10 in the first reproductive season and 20 in the second. This discrepancy is partly due to the fact that we were able to start field work earlier in the season in the second year, and partly because we were already familiarized with territories and breeding pairs. Of the nests with known outcomes ( $n = 24$ ), 66% ( $n = 18$ ) were parasitized. Table 1 shows all nests found per season and their outcomes. Nest IDs' numbers refer to marked host pairs and letters to breeding attempt. Table 2 presents the mean values and range for nest measurements and nest site variables.

Table 1: List of nests found, outcomes and fates.

Season 2017/2018			Season 2018/2019		
Nest ID	Outcome	Fate	Nest ID	Outcome	Fate
N2A	Unknown	Predated	N2A	<i>Tapera naevia</i>	Success
N2B	<i>Certhiaxiscinnamomeus</i>	Success	N2B	<i>Tapera naevia</i>	Success
N3A	<i>Tapera naevia</i>	Success	N2C	<i>Tapera naevia</i>	Predated
N3B	Unknown	Failed	N3A	<i>Certhiaxiscinnamomeus</i>	Predated
N4A	<i>Tapera naevia</i>	Success	N3B	Unknown	Predated
N5	Unknown	Predated	N3D	<i>Tapera naevia</i>	Predated
N6	<i>Tapera naevia</i>	Success	N7A	<i>Tapera naevia</i>	Predated
N7A	<i>Tapera naevia</i>	Predated	N7B	<i>Tapera naevia</i>	Success
N7B	<i>Certhiaxiscinnamomeus</i>	Predated	N8A	<i>Certhiaxiscinnamomeus</i>	Success
N8	<i>Tapera naevia</i>	Success	N9A	Unknown	Predated
			N9B	<i>Tapera naevia</i>	Predated
			N9C	<i>Tapera naevia</i>	Unknown
			N10A	<i>Tapera naevia</i>	Predated
			N10B	<i>Tapera naevia</i>	Unknown
			N10C	<i>Tapera naevia</i>	Success
			N11A	<i>Tapera naevia</i>	Success
			N11B	<i>Tapera naevia</i>	Success
			N12A	Unknown	Failed
			N12B	<i>Certhiaxiscinnamomeus</i>	Predated
			N13A	<i>Certhiaxiscinnamomeus</i>	Success

From the 24 nests used in the analysis, 14 (58.33%) had curved tubes, while 10

(41.66%) had straight tubes. Tube insertion in the globe also varied with 21 nests (87.5%) tubes inserted in the base of the nest globe, 2 (8.33%) from the nest globe mid-section and 1 (4.17%) from the nest's top. All nests but one had tubes angled upwards (table 2)

Table 2: Nest main measurements: means, standard errors and range

<b>Variable</b>	<b>Mean</b>	<b>SE</b>	<b>Min</b>	<b>Max</b>
External tube opening (mm)	48,604	± 8,634	35.0	65.3
Internal tube opening (mm)	38,846	± 8,946	26.0	57.6
Tube length (mm)	94,692	± 29,360	65.0	183.0
Globe length (mm)	222,583	± 37,853	150.0	291.0
Globe width (mm)	185,750	± 24,098	130.0	245.0
Height (mm)	236,500	± 45,944	160.0	329.0
Distance from water or floor (mm)	351,042	± 203,73	0.0	782.0
Water depth (mm)	205,625	± 238,804	0.0	803.0
Distance from marsh edge (m)	22,725	± 5,161	4.0	100.0
Vegetation density 30cm	28,750	± 11,276	9.0	52.0
Vegetation density 3m	53,333	± 27,295	12.0	93.0
Vegetation density above the nest	3,750	± 3,011	0.0	11.0
Water surface exposure	1,833	± 1,239	1.0	4.0
Number of shrubs around the nest	4,833	± 2,615	0.0	9.0
Support shrub height (cm)	143,458	± 32,287	48.0	180.0

Nest tube was autocorrelated to nest height, and for the nest site variables, autocorrelations involved vegetation density in 30 cm radius X vegetation density in 3m radius, and Water surface exposure x water depth. Then, nest height, vegetation density in 3m radius and water surface exposure were eliminated from the analyses.

The first block of GLM analysis considering nest architecture characteristics returned five models with  $\Delta AICc \leq 2$ . Although the best model included only the tube length covariate, and this variable was also present in the second and third best models, its values were small and overlapped zero in the two best models, and probability values were never significant.

Other covariates present in the five chosen models, also always overlapped zero and their probability values were also non-significant. Then, in this block of analyses, only the null model (fourth best model) was significant, suggesting low support for the idea of tube length predicting parasitism probability (Table 3).

The block analyses that included the nest site covariates returned only two models with  $\Delta AICc \leq 2$ . Vegetation density above nest was present in both models, and it was negatively correlated to parasitism probability. The values never overlapped zero and probability values for the Z-test were significant. Although the covariate "Time" was also present in the first best model, its value overlapped zero and it was not significant, suggesting vegetation density above nests as the main variable explaining nest parasitism in the studied population.

Table 3: Model selection analysis depicting the top selected models to explain nest parasitism based on nest architecture characteristics.

Model	AICc	$\Delta AICc$	K	B	Tube length	NgLength	Tube diameter (external)	Tube Shape
Tube length	27.9	0.00	2	1.643; SE=0.719 (0.452-3.340) Z=2.286, P=0.022	1.970; SE= 1.303 (-0.026 - 4.886) Z=-1.512, P=0.131	-	-	-
Tube length + Nest globe length	28.5	0.65	3	1.542; SE=0.729 (0.390-3.323) Z=2.114, P=0.034	1.675; SE=1.423 (-0.118 - 4.997) Z=-1.178, P=0.239	0.232; SE=0.571 (-0.871 - 1.452) Z=0.406, P=0.684	-	-
External Tube, Tube length	29.0	1.16	3	1.583; SE=0.701 (0.427-3.259) Z=2.258, P=0.024	1.909; SE=1.259 (0.102 - 4.780) Z=1.516, P=0.129	-	-0.712; SE0.631 (-2.191 - 0.412) Z=-1.128, P=0.259	-
Null	29.2	1.3	1	1.099 SE=0.471 (0.229 - 2.113) Z=2.331, P=0.019				
Tube shape	29.5	1.64	2	0.405; SE=0.645 (-0.847-1.769) Z=0.628, P=0.530				1.386; SE=1.000 (-0.506 - 3.569) Z=1.386, P=0.166

Table 4: Model selection analysis depicting the top selected models to explain nest parasitism bases on nest site characteristics.

Model	AICc	$\Delta AICc$	K	w	B	Veget. Density	Time
Veget. density above nest + time	25.9	0.0	3	0.098	1.707; SE=0.743 (0.495-3.580) Z=2.99, P=0.0215	-1.667; SE= 0.790 (-3.677 - -0.402) Z=-2.111, P=0.0348	1.258; SE= 0.790 (-3.496 - 0.155) Z=-1.432, P=0.152
Veget. Density	26.2	0.3	2	0.084	1.364; SE=0.579 (0.346-2.700) Z=2.358, P=0.018	-1.220; SE=0.612 (-2.710 - -0.177) Z=-1.995, P=0.046	-

#### 5.4. DISCUSSION

The percentage of nests parasitized by the Stripped Cuckoo in our study population of the yellow-chinned Spinetail was similar to that reported by Haverschmidt (1961) for a population from Suriname (8 of 12 nests; 66.7%), yet in a population from Formosa, Argentina, the percentage was much lower (12 of 45 nests; 26.6%) (Di Giacomo 2005). The percentage of brood-parasitism by the Stripped Cuckoo on other closed-nester bird species were also lower, including a population of the Rufous-and-white Wren, *Thryophilus rufalbus*, from Nicaragua (13.8 to 33.7% across subsequent years) (Mark 2013, Mark & Rubenstein 2013); a population of the Rufous-and-white Wren from Panama (4 of 11 nests; 33.4%) (MORTON & FARABAUGH 1979), and a population of the Sooty-fronted Spinetail, *Synallaxis frontalis*, from Formosa, Argentina (8 of 34; 23.5%) (Di GIÁCOMO 2005). In our study site there are at least three other closed-nester bird species that can be potentially parasitized by striped cuckoo, for which nests were not monitored, i.e. the White-headed Marsh Tyrant *Arundinicola leucocephala*, the Spix' spinetail *Synallaxis spixii*, the Sooty-fronted spinetail *S. frontalis*, and the Masked water tyrant *Fluvicola nengeta* making difficult to infer about how dependent the Stripped cuckoo is from the yellow-chinned spinetail. On the other hand, the above comparisons suggest that the impact of the Stripped cuckoo on the yellow-chinned spinetail was relatively high. As parasitism was caused only by *T. naevia* the development of anti-parasitism defences against this specific parasitic species was expected, which makes the lack of support to the tube length hypothesis surprising.

Our sampling was affected by a number of nests (N=6) that were depredated during incubation stage, when clutch identification is unviable, and by the number of nests biased towards the parasitized category. However, we are confident that our data was enough to reject the central hypothesis that nest-tube length could be involved in the avoidance of parasitism by *T. naevia* in our study population, not only because of the modelling pointing

out other parameters as significant, but also because the six top-ranked nests based on tube length among the 30 nests we found (including two outlier nests which tubes measured 182 and 183 mm in length), were parasitized. It also precludes the need of experimental works involving tube removal for testing our main idea.

Internal tube width could be in theory another important variable, as a number of works have demonstrated that in cavity-nester species, for instance, smaller entrance diameters can avoid access by parasites (PRIBIL & PICMAN 1997, DAVIES 2000, RUTILA et al. 2002, STANBACK 2013). Despite the variations recorded for this parameter here, none of the 30 observed tubes would permit the passage of an adult Stripped cuckoo. This evidence receives support from the fact that all of the *T. naevia* young that fledged successfully have opened a hole in nest wall or have remarkably enlarged the tube to leave the nest, while we never observed tube enlargements and nest wall disturbances in parasitized nests during laying stage. Together with the fact that all of the tubes were positioned upwards (except for one that was horizontal and also was parasitized), these findings are consistent with a model in which the females may lay their eggs in the tube entrance and eggs may roll-down towards the incubatory chamber, despite tube length, curvature, and insertion position, and they are likely arranged in the incubatory chamber by the parental hosts. It also receives support from an observation of *T. naevia* parasitizing a nest of *Todirostrum* sp. (SICK 1997), a small passerine that construct tiny closed pendulous-nests in which a *T. naevia* would not fit, being oviposited from the nest entrance the only apparent option, but direct observations of such behaviour are still unavailable.

As the construction of the tubular entrances might be energetically costly and time-consuming, we see four alternative hypothesis that could account for this effort expenditure: i) sexual selection, i.e. nest characteristics could serve as cues used by females to assess male fitness (for a review see CROOK 1963, COLLIAS & VICTORIA 1978, JACOBS et al



1978), ii) tube length could vary simply as function of the vegetation density in nesting sites, in such a way that denser vegetation could constrain the construction of longer tubes, iii) avoidance of other types of parasites, or iv) predation avoidance. The first hypothesis is improbable, as the couples construct the nests together (DI GIACOMO 2005, field observations), meaning that pairing occur before nest construction. The second hypothesis predicts that vegetation density in a 30 cm radius of the nests should be negatively correlated to tube length, which was not observed in our analyses of covariates autocorrelations, eliminating any support for this theory. Regarding to the third hypothesis, the only other brood parasite in the study region is the Shiny Cowbird, *Molothrus bonariensis* (field observations). Although it has been recorded parasitizing broods of other closed-nester furnariids, such as *Furnarius rufus*, *Phacellodomus ruber*, *Anumbius anumbi*, and *Pseudoseisura cristata* (SICK 1997), which notably do not construct elongated tubular entrances, the latter were never observed raising Shiny Cowbird young. Shiny Cowbirds typically parasitize open-nester species such as the Rufous collared sparrow *Zonotrichia capensis* (KING, 1973) and the Creamy-bellied thrush *Turdus amaurocalinus* (ASTIE & REBOREDA 2005), suggesting that brood parasitism by shiny cowbirds in nests of furnariids are only occasional. Further, Shiny Cowbirds were never observed in our study marshland, which also reduces support to this hypothesis. The hypothesis of predation avoidance, on the other hand, is plausible, as it has received support from a previous study conducted with weaverbirds (CROOK 1963), as well as from studies with cavity-nester birds (LACK 1954; ALERSTAM & HÖGSTEDT 1981; MARTIN & LI 1992; see also JETZ et al. 2008). All of the depredated nests we observed presented holes above or besides the incubatory chamber, and our best supposition is that Egrets were the main predators. However, one nest monitored with camera traps (not included in our sampling) was checked by a group of Smooth billed ani *Crotophaga ani*, typical nests predators from open and semi-open Neotropical habitats

(PAYNE & KIRWAN 2019), and despite various attempts, they could not access nest interior. This is an evidence that the robust nest walls constructed of sticks, associated with the tubular entrance, can avoid at least certain types of predators. Then, nest predation modelling with increased sample sizes should be in the scope of future works.

In the northern part of its geographic distribution, the striped cuckoo presents egg colour polymorphisms that match different host species, and the most frequently parasitized birds present varying rates of foreign eggs recognition and ejection as a defence mechanism (MARK 2013). In southern South America eggs of Stripped Cuckoo are white, likely because they are more specialized in parasitize *C. cinnamomeus* and in individuals of the genera *Synalaxis*, which lay white, slightly round eggs, that are also similar in size (De La PEÑA 2013). Although we have not handled the eggs to conduct detailed morphometric analyses, we were incapable to discriminate between parasitic and host eggs based on colour, shape and sizes obtained in the snake-cam pictures. Together with the very high nest parasitism frequency, and with the fact that we have never observed clutch size reduction during laying and incubation stages that could indicate ejection, these are the first evidences that if egg ejection occurs in our study population, it must be in low frequency. This can be the result of an old coevolutionary relationship, in which the brood parasite becomes highly specialized in egg mimicry, and the host have reduced cues to discriminate and to eject the eggs of the parasite (FEENEY et al, 2012). Parasitic chick recognition has been less addressed in the literature, but it can occur in some systems (LAWES & MATHEY 2003, DAVIES 2011), and hosts can reject the foreign nestlings by abandoning the nest, by stopping feeding them, and by killing or ejecting them (see GRIM 2006). Here, of the 18 nests with confirmed *T. naevia* nestling, two we couldn't determine the fate, 6 were recognized as depredated due to partial nest destruction, and 10 fledged *T. naevia* successfully, suggesting that the capability of *T. naevia* chicks' recognition by the parental hosts is also limited.

Our modelling analysis revealed that vegetation cover above nests was the only parameter correlated to nest parasitism avoidance. Parasites may be able locate nests by observing the activity of hosts (WILEY 1988; HONZA et al. 2002), but vegetation structure around nests may conceal movements of hosts and therefore influence the probability that brood parasites will find the nest (SHARP & KUS 2006). Therefore, hosts that build their nests in more concealed areas are expected to have advantage (FIORINI et al. 2012). This is known as the nest-concealment hypothesis, that predicts that nests with lower vegetative cover (or even other types of cover) have a higher probability of being parasitized than nests that are more concealed (BURHANS 1997; CLOTFELTER 1998; LARISON et al. 1998; GRIEF & SEALY 2000; MOSKÁT & HONZA 2000; SAUNDERS et al. 2003). There is support for this prediction for Common Cuckoos (*Cuculus canorus*) and Brown-headed Cowbirds (*Molothrus ater*) (BURHANS 1997; LARISON et al. 1998; SAUNDERS et al. 2003; ANTONOV et al. 2007). Some studies have found the opposite pattern. Studies with brown-headed cowbirds showed a higher incidence of parasitism in nests with greater coverage (BRITTINGHAM & TEMPLE 1996; GRIEF & SEALY 2000; MCLAREN & SEALY 2003). One possible explanation for this pattern would be that parasites actively search for better concealed nests, as these nests may be less likely to be discovered by predators, thus, increasing survival rates (MCLAREN & SEALY 2003).

However, investigating whether the yellow-chinned spinetail has actively selected nesting sites with denser vegetation cover is not straightforward. This type of analysis relies on comparisons of vegetation parameters between nest- and random sites (MARTIN & ROPER 1988), but at least in our study area, almost all of the nests were embedded within the tussocks of Cyperacea *Rhynchospora* sp.. As the nests are large globular structures, part of the vegetation of the chosen tussock is displaced during nest construction, making the vegetation density above nests poorly comparable between nest- and random sites, or between nest- and

randomly-chosen *Rhynchospora* sp. tussocks.

Although the yellow-chinned Spinetail has been reported as a host of the brood-parasite Stripped Cuckoo many times (e.g. HARTERT & VENTURI 1909, HARVERSHMIDT 1955; HARVERSHMIDT 1962; LÓPEZ LANÚS 1997, DI GIACOMO 2005, DE LA PENÃ 2016), previous investigations about the interactions between these species were limited to report parasitism frequency. In summary, we provide the first evidences that Stripped Cuckoos are capable to have their eggs deposited in the incubatory chamber despite the wide tube length variations encountered in yellow-Chinned Spinetail nests, rejecting the hypothesis that there could be a coevolutionary race based on the selection of longer tubes, at least in this study population. It suggests that the interactions between the Chinned Spinetail and the Stripped Cuckoo can be more complex, and our findings evidenced that this is another interesting brood-parasitic system that deserves to be further investigated.

## 6. CONSIDERAÇÕES FINAIS

Dados a respeito da biologia de aves neotropicais ainda são escassos. Estudos de biologia reprodutiva acerca de taxas de divórcio, tentativas de nidificação e fecundidade ainda mais, pois dependem de procedimentos dispendiosos como captura e marcação de indivíduos, e acompanhamento regular da população estudada. Quando se trata de tentativas de reprodução, complica-se ainda mais, pois existe uma certa confusão quanto a terminologia, com alguns estudos considerando a iniciação da construção de ninho, postura e outros apenas novas tentativas após uma bem-sucedida. A dificuldade em se encontrar dados para comparar essas taxas aponta não somente uma carência no número de estudos acerca desses aspectos, como a necessidade de uma melhor padronização dessas nomenclaturas.

Embora os dados de fecundidade anual para espécies neotropicais sejam escassos, é possível inferir que a alta taxa de parasitismo na população estudada afeta e muito a fecundidade anual da mesma.

A aparente falta de mecanismos de defesa em *C. cinnamomeus* contra o parasitismo de ninho por *T. naevia* gera questionamentos sobre a manutenção dessa população a longo prazo e sobre a dinâmica de parasitismo nesse sistema parasita-hospedeiro em particular. Taxas de parasitismo variam de população para população, o que afeta também as taxas de fecundidade. Com isso em mente, perguntas acerca da dinâmica inter-populações (como possíveis sistemas fonte-sumidouro entre populações mais e menos parasitadas, ou sistemas de defesa anti-parasitismo em outras populações) são inevitáveis e enfatizam a necessidade de mais estudos acerca do assunto.

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