
**PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
ZOOLOGIA**

**Divisão Parental do Cuidado à Prole no Sabiá-barranco
(*Turdus leucomelas*)**

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DIVISÃO PARENTAL DO CUIDADO À PROLE NO SABIÁ-BARRANCO
(*Turdus leucomelas*)

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RESUMO

Aves tropicais apresentam estratégias reprodutivas particulares em comparação às espécies da região temperada do hemisfério norte, como a menor prole, maior investimento em cada filhote, estágio de ninhego mais curto e estágio pós-ninho extenso. No entanto, estudos sobre o cuidado parental entre as aves da região tropical são escassos em relação às aves do hemisfério norte temperado especialmente quando se considera a diversidade de aves tropicais. Portanto, são necessários mais estudos para compreender as diferenças, diversidade das espécies e padrões comportamentais da região. Nesta dissertação descrevemos a divisão do cuidado parental entre os sexos do sabiá-barranco (*Turdus leucomelas*), espécie de passeriforme socialmente monogâmico e monomórfico. Abordamos os dois estágios do ciclo reprodutivo das aves altriciais que são considerados os mais custosos em relação ao gasto energético parental, o estágio de ninhego e o estágio pós-ninho, isto é, após os filhotes terem deixado o ninho. O estudo foi feito no campus da Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP) em Rio Claro, São Paulo. Usando câmeras instaladas junto aos ninhos, obtivemos 153,5 h de gravações do estágio de ninhego em 33 ninhos e 24 casais diferentes entre 2015 e 2017. Com observações diretas, fizemos 84,8 h de observação efetiva do estágio de pós-ninho em oito famílias e 13 filhotes diferentes em 2018. No estágio de ninhego ambos os sexos forneceram alimento e realizaram limpeza do ninho. No entanto, machos alimentaram os filhotes de proles grandes mais frequentemente do que fêmeas. Apenas fêmeas realizaram a termorregulação dos filhotes, e o tempo desta atividade diminuiu com a idade dos filhotes. Não houve diferença na limpeza do ninho entre os sexos. No estágio pós-ninho, não houve diferença no fornecimento de alimento aos filhotes entre os sexos, que também não variou com o tamanho da ninhada e sua idade. A taxa de fornecimento de alimento também não alterou a frequência dos comportamentos de solicitação de alimento ou de forrageio pelos filhotes, mas este último se tornou mais frequente ao longo do desenvolvimento. Observamos a divisão do cuidado parental no cuidado à prole, segundo quatro padrões: divisão da prole, cuidado único do macho, cuidado único da fêmea, e cuidado biparental de proles de um único filhote. Filhotes que receberam fornecimento de alimento biparental foram mais frequentemente alimentados, do que aqueles que receberam uniparental. Portanto, o investimento parental é distinto entre o macho e a fêmea durante o cuidado dos ninhegos, especialmente em proles maiores, no entanto, durante o cuidado pós-

ninho a provisão de alimento é similar entre os sexos, e a diferença é existe na divisão da prole, e em quantos filhotes cada indivíduo do casal cuida durante este período.

Palavras chave: Cuidado parental, fornecimento de alimento, limpeza do ninho, conflito sexual, estágio de ninhego, ninhego, estágio pós-ninho, filhote, sabiá-barranco, *Turdus leucomelas*.

ABSTRACT

Tropical birds have particular reproductive strategies in comparison to north temperate species, such as smaller clutch size, higher investment per individual chick, shorter nesting stages and extended post-fledging stages. However, studies regarding parental care of birds in the tropical region are scarce in comparison to the temperate northern hemisphere, especially when you consider the bird diversity of the tropics. Therefore, more studies are necessary to a better understanding of the differences, unique diversity, and behavioural patterns of the region. In this dissertation we describe the division of parental care between the sexes of the Pale-breasted Thrush (*Turdus leucomelas*), a socially monogamous and monomorphic passerine. We studied the two stages considered more energetically expensive for altricial birds, the nesting and post-fledging stages. The study was conducted in the campus of the Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP) located in Rio Claro, São Paulo. Using cameras positioned close to the nests, we recorded 153.5 h of the nesting stage care from 33 nests and 24 different reproductive pairs between 2015 and 2017. With direct observations, we carried out 84.8 h of effective observation of post-fledging care in eight families and 13 different fledglings in 2018. In the nesting stage, both sexes provisioned food for the nestlings and performed nest sanitation. However, males fed more frequently larger broods than females did. Only females brooded nestlings and the time spent on this activity reduced as the brood aged. There was no difference in nest sanitation between sexes. In the post-fledging stage, there was no difference in food provisioning rates between sexes, neither brood age nor brood size affected rates of food provisioning. Food provisioning rates did not affect frequency of fledgling behaviour of foraging and fledgling vocalization, but foraging became more frequent as fledglings aged. There was brood division in parental care of the brood, of which there was four patterns: brood division, male-only care, female-only care, and biparental care of broods with a single fledgling. Fledglings that received biparental food provisioning were more frequently fed than those that received uniparental feeding. Therefore, parental investment was similar between males and females during the nestling stage, especially in larger broods, however, during the post-fledging stage there is no apparent difference between food provisioning between sexes, only differing in regards to brood division, and how many fledglings each parent cares for.

Keywords: Parental care, food provisioning, nest sanitation, sexual conflict, nesting stage, nestling, post-fledging stage, fledgling, Pale-breasted Thrush, *Turdus leucomelas*.

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1.1 INTRODUÇÃO

Reprodução no ciclo de vida de um organismo é sempre um fator importante, de fato, além da própria sobrevivência, o derradeiro objetivo de qualquer indivíduo é o sucesso reprodutivo. Em muitas espécies o sucesso reprodutivo é garantido através do cuidado parental. Cuidado parental é qualquer estratégia, que aumenta o sucesso reprodutivo por meio da promoção da sobrevivência e crescimento da prole, frequentemente à custa da própria sobrevivência e futuras chances reprodutivas dos pais (Trivers 1972, Clutton-Brock 1991, Smiseth et al. 2012). Isto significa que o cuidado parental em termos gerais pode envolver tanto o fornecimento de vitelo ao ovo até um comportamento mais complexo como o progenitor ensinando a progênie a forragear (Clutton-Brock 1991, Smiseth et al. 2012).

Cuidado parental é intrinsecamente uma estratégia que realiza uma troca entre o bem-estar físico do adulto pelo aumento da chance de sobrevivência da prole atual, estabelecendo assim uma demanda conflitante (*trade-off*) (Trivers 1972). O cuidado parental tem como propósito maximizar o *fitness* do indivíduo, equilibrando ao mesmo tempo os custos relacionados à redução da saúde dos pais, menor taxa de sobrevivência, aumento no risco de predação, e expectativas futuras de acasalamento com o aumento das chances de sucesso reprodutivo presente (Gross e Sargent 1985, Trivers 1972). Estes são alguns dos principais limitadores do investimento parental, isto é, qualquer tipo de investimento (de energia e tempo) feito pelos pais que promova a sobrevivência da prole referida, ao custo da habilidade dos pais em investir em outras proles concomitantes ou futuras (Trivers 1972, Clutton-Brock 1991). O conflito sexual entre os pais existe quando ambos os sexos se beneficiam a partir do investimento parental um do outro, mas pagam apenas pelo próprio investimento, e pelo fato de que uma característica ou comportamento de um dos pais que tem como propósito maximizar seu *fitness* pode não beneficiar o *fitness* de seu parceiro (Trivers 1972, Lessels 2012).

Aves são uns dos táxons com maior diversidade de padrões de cuidado parental (Cockburn 2006, Balshine 2012). São poucas as espécies de aves que não fornecem cuidado parental, entre estas estão as espécies parasitas que ovipõem em ninhos de outras espécies, deixando o cuidado parental a ser realizado pelos hospedeiros que adotam os parasitas, e as espécies da família Megapodidae, cujos filhotes precociais nascem independentes e incubados em aterros nos quais o ovos são cobertos (Silver et al. 1985, Cockburn 2006). Na maior parte

das espécies de aves o cuidado parental ocorre e pode se manifestar de diferentes maneiras. A prole pode ser cuidada por apenas um sexo, isto é, cuidado uniparental do macho ou da fêmea; por ambos os sexos ou cuidado biparental; ou por mais de dois indivíduos além do par, em cuidado cooperativo, no qual membros de um mesmo grupo familiar oferecem cuidados (Cockburn 2006). Cuidado biparental é o mais comum nas aves ocorrendo em 80,8% das espécies, seguido de cuidado cooperativo com 9,0%, cuidado uniparental da fêmea com 8,2%, e por fim cuidado uniparental do macho em apenas 1% das espécies (Cockburn 2006).

Outro fator determinante do ciclo reprodutivo das aves são os dois modos de desenvolvimento da prole, estes são os desenvolvimentos precocial e altricial. Passeriformes, por exemplo, são aves altriciais, isto é, a prole não tem mobilidade ao nascer, sendo dependentes do cuidado dos pais e da estrutura do ninho (Silver et al. 1985). As aves precociais têm mobilidade e não são atreladas ao ninho por possuírem capacidades básicas de mobilidade, forrageio e termorregulatórias logo ao nascer (Buntin 1996). O que difere estas estratégias é o período do ciclo reprodutivo em que a maior parte do investimento energético é feito. Aves precociais necessitam investir mais recursos para que seus ovos possam conceber filhotes bem desenvolvidos, enquanto aves altriciais necessitam investir menos energia na produção dos ovos, mas em compensação investem mais após o nascimento da prole. No entanto, todas as aves altriciais são dependentes dos pais para fornecer abrigo, comida, zelar por sua saúde, regular sua temperatura corporal, e defendê-los, logo, o custo aos pais posterior ao nascimento é maior para aves altriciais (Lack 1947, Silver et al. 1985). Por isso, cada filhote adicionado a uma prole altricial é um custo adicional aos pais. O investimento parental necessário para se obter uma prole maior de igual qualidade é multiplicado pelo número de filhotes. No entanto, este aumento em investimento parental é frequentemente não linear, levando a um *tradeoff* entre tamanho da prole e sua qualidade (Stutchbury e Morton 2001, Martin 2015).

Em geral, o ciclo reprodutivo dos Passeriformes pode ser dividido em quatro estágios, apesar de haver exceções nas espécies parasitas e de cuidado cooperativo. A primeira é composta pela corte entre casal, acasalamento e a construção do ninho. O segundo é o estágio de ovoposição, em que é realizada a incubação dos ovos (que pode ser realizado pela fêmea ou ambos os sexos), a proteção destes, e a alimentação da fêmea pelo macho que ocorre em algumas espécies. A terceira é o estágio de ninhego (*nesting stage*), em que a prole nasce e começa a receber cuidados dos pais exclusivamente dentro do ninho. Este estágio dura desde o nascimento até o momento em que os filhotes estão suficientemente desenvolvidos a ponto

de terem capacidade de voo suficiente para deixar o ninho. O estágio de ninhego é um dos mais bem estudados do ciclo reprodutivo dos pássaros, justamente porque todo o cuidado ocorre em um ponto estático, o ninho (Gowaty 1996). Muitos dos estudos que envolvem cuidado parental nas aves tratam do fornecimento de alimento dos pais aos filhotes, que é um ótimo meio para se tentar quantificar o investimento parental, pois é frequentemente considerado a atividade mais energeticamente custosa aos pais e também porque é comumente realizado por ambos os sexos. No entanto, atividades como a limpeza e defesa do ninho, e termorregulação dos filhotes são também importantes aspectos que podem ajudar a avaliar este investimento.

Por fim, o último estágio reprodutivo ocorre quando os filhotes saem do ninho, mas ainda são dependentes dos pais e deles recebem proteção e alimentação. Os filhotes neste estágio (*fledglings*) podem passar desde duas semanas até meses sob cuidado dos pais dependendo da espécie. Por conta da baixa mobilidade dos filhotes, durante os primeiros dias ao saírem do ninho sua taxa de mortalidade é mais alta (Russell 2000, Rivera 2000). Por conta disto, após a saída do ninho os filhotes permanecem entre a vegetação densa nos arredores dos ninhos, como arbustos e árvores baixas, provavelmente como uma estratégia para diminuir as chances de serem predados (Naef-Danzer et al. 2001, Bonnevie 2004, Tarwater 2010, Cox et al. 2014, Vernasco et al. 2017). Durante o período de pós-ninho, a prole permanece dentro do território dos pais, sendo alimentada e protegida, enquanto os filhotes continuam a desenvolver suas capacidades locomotoras, de forrageio, e sensoriais. Em certo momento do desenvolvimento, que dependerá da espécie, os pais diminuem o atendimento aos pedidos de alimento dos filhotes e, eventualmente os expulsam de seu território, levando-os a atingirem sua independência. Todos estes comportamentos de cuidado parental durante estes estágios estão sujeitos a fatores externos (e.g. latitude e região, clima, disponibilidade de comida, predação) e internos (e.g. tamanho da prole, conflito sexual e conflito pais-filhotes, plasticidade comportamental e personalidade) (Stutchbury e Morton 2001).

A região tropical e temperada do hemisfério sul é caracterizada por um período mais curto de cuidado no estágio de ninhego, supostamente uma resposta evolutiva à alta predação dos ninhos nestas regiões (Martin 2015). Em compensação, as aves destas regiões tendem a apresentar um estágio pós-ninho mais extenso (Russell 2000, Martin 2015, Remeš and Matysiovská 2016). O tamanho da prole também costuma ser reduzida, devido à menor abundância de alimento numa região de sazonalidade menos pronunciada e pela alta chance de predação (Stutchbury and Morton 2001, Martin 2015). No entanto, foram poucos os

estudos sobre os ciclos reprodutivos e cuidados parental de aves na nossa região em comparação ao norte temperado, o que é especialmente grave considerando a grande diversidade de aves existente aqui.

Buscamos aqui adicionar aos trabalhos da região um estudo sobre o cuidado parental no sabiá-barranco (*Turdus leucomelas*), um Passeriforme tropical, monogâmico e sem dimorfismo sexual, com ênfase na divisão de investimento e diferenças de comportamentos entre os pais. Descrevemos e quantificamos comportamentos de cuidado parental do estágio de ninhego e pós-ninho, determinando em que fases e atividades existem diferenças ou similaridades entre os pais. No estágio de ninhego, registramos e comparamos os comportamentos de fornecimento de alimento, limpeza do ninho, permanência no ninho e termorregulação da prole. No estágio pós-ninho, registramos e comparamos o comportamento de fornecimento de alimento aos filhotes por machos e fêmeas, e buscamos relações entre as taxas de alimentação dos filhotes com o comportamento de forrageamento e a vocalização destes.



Figura 1. 1: Sábíá-barranco (*Turdus leucomelas*) adulto no câmpus da UNESP de Rio Claro.

CAPÍTULO 1

DIVISION OF NESTLING PARENTAL CARE IN THE PALE-BREASTED THRUSH (TURDUS LEUCOMELAS)

ABSTRACT

Studies of parental care in the tropical region are generally scarce and even fewer are done with the accuracy and sample size necessary to identify patterns. In addition, these studies only focus on food provisioning rates. Herein, we studied the division of care between the sexes of the tropical monomorphic, socially monogamous passerine, Pale-breasted Thrush (*Turdus leucomelas*). We recorded food provisioning, nest sanitation, nest attendance and brooding. Throughout the breeding seasons of 2015 to 2017 in a suburban area of Southeast Brazil, we recorded 153.5 h of nestling care in 33 nesting attempts by 24 different pairs. Considering of the region and species characteristics, we expected a similar parental investment in care. We found that males had higher food provisioning rates for larger broods, while female's total food provisioning rate remained constant regardless of brood size. Brood age positively affected of food provisioning rates for both sexes. Nest sanitation rate was similar for both sexes and varied solely with brood size. Interestingly, the predominant method of fecal sac removal was ingestion throughout the nesting stage, despite literature predicting a drop in ingestion frequency with brood age. Nest attendance was done predominantly by females (34 ± 27 % of observation time on the nest), being closely linked to brooding behaviour, a female-only task, while males remained away from the nest for most of the time (4 ± 4 % of observation time on the nest). Parental investment between sexes is very similar and met our expectations; however their tasks differed and complemented each other.

2.1 INTRODUCTION

Parental care is described as any strategy or behaviour adopted by an adult to promote the survival of its offspring (Trivers 1972). It encompasses a variety of aspects, from energy provision for gametes to food provisioning and protection of offspring (Clutton-Brock 1991). Although the investment of an individual on its offspring improves its current reproductive success, it may compromise its ability to produce future offspring (Clutton-Brock 1991). Therefore, parental investment is a balancing game, as an individual's total investment in current offspring will influence its own fitness, survival and prospects for future reproduction (Trivers, 1972; Gross and Sargent, 1985). The strategies and patterns of parental investment are deeply ingrained in a species' reproductive cycle is inevitably crucial for its life reproductive performance, aiding us to understand evolutionary and ecological drivers of reproductive behaviour (Clutton-Brock 1991, Martin 2015). Certain reproductive strategies and parental care patterns predominate in birds, although great variety may be found (Silver et al. 1985, Cockburn 2006).

Social monogamy with biparental care is the most common reproductive strategy in birds (Cockburn 2006). Parents in monomorphic and monogamous species parents commonly have similar reproduction investment in activities like food provisioning, nest sanitation, and brooding (Greenberg and Gradwohl 1983, Breitwisch 1986, Alatalo 1988, Carere and Alleva 1998, Wilkin 2009, Gill and Haggerty 2012, Sánchez et al 2018). However, there are monomorphic and socially monogamous species in which energy investment and the role performed by each sex differ considerably, with each sex performing nest activities much more frequently or exclusively in comparison to their counterpart (Gowaty 1996, Stutchbury and Morton 2001, Kokko and Jennions 2008).

Another aspect that heavily influences the dynamic of parental care in birds is whether the species is altricial or precocial (Silver et al. 1985). Altricial birds invest less energy into eggs than precocial birds, but in turn their offspring are born less developed completely reliant on their parents for food, with no locomotor or thermoregulatory capacity upon birth (Buntin 1996). These factors lead the parental investment costs associated with the increase in brood size and age to scale rapidly in altricial species (Lack 1947, Skutch 1949). Parental investment needed to care for a smaller brood is multiplied with each additional chick. This investment increase is often non linear, as bigger broods usually receive less total food

provisioning, leading to a tradeoff between brood size and offspring quality (Stutchbury and Morton 2001, Martin 2015). There are, however, asymmetric investments between parents even in more equitable arrangements due to anisogamy, physiological and behavioural differences between sexes (Lessels 2012). Even if parental investment in monogamous monomorphic birds are more equitable in comparison to dimorphic species, higher reproductive costs associated with parental care normally rests upon the female (Gowaty 1996). Females bear the burden of egg laying costs, frequently brooding eggs and nestlings on their own, and provisioning food more frequently than males in some monogamous species (Carere and Alleva 1998, Bowers et al. 2014). Meanwhile, males are frequently assigned tasks of territorial and nest defence, through vigilance, vocalization and physical aggression, and some food provisioning (Gowaty 1996, Winkler 2016). Therefore, differences in parental investment and division of tasks are expected to be found to some degree in monogamous monomorphic birds, even if not as distinctively as in other reproductive systems (Carere and Alleva 1998, Espíndola-Hernández 2017, Sánchez et al. 2018).

Though biparental care can have equitable relationships between the reproductive pair, competition remains constant between males and females as a means to maximize their own fitness (Clutton-Brock 1991, Gowaty 1996). It is of the interest of both sexes to invest as little energy as possible in reproduction, conserving their own health for future reproductive prospects while aiming for maximum attainable reproductive success. As a consequence, mates might react to each other's behaviour, total care effort, and individual quality and fitness, either by making up for shortcomings of their partner, reducing their own care or even abandoning their partner and nest (Markman 1994, Wilkin 2009, Gow and Wlebe 2014, Bebbington and Hatchwell 2015, Bolopo et al. 2015). The priority of the parents on their own reproductive success and continued survival are also showcased by how uniquely they react to different environmental and in-nest stimuli, such as lower or higher food availability, intensity of brood begging and predation risk (Hinde et al. 2010, Low et al. 2011). Hence, even in situations where a more equitable care is expected, sexual conflict is present and can lead to differences in reproductive effort between sexes.

Geographic differences also affect patterns in parental care, changing the dynamics of reproductive cycles. For example, the trend in life-history traits of tropical and southern temperate regions includes higher adult survival, smaller clutches, shorter nesting stage and extended post-fledging care in comparison with their northern temperate counterparts (Russell et al. 2004, Gill and Haggerty 2012, Martin 2015). In the nesting stage, tropical species

usually provide increased care for individual nestlings, which is explained by the need to increase fledgling survival through faster development in response to higher nest predation rates and lower food availability (Skutch 1949, Greenberg and Gradwohl 1983, Gill and Haggerty 2012, Martin 2015, Remeš and Matysiovská 2016).

One of the most frequent forms of care utilized to quantify parental effort in the nesting stage is provisioning of food to the nestlings. The time and energy required to provision food escalates quickly with brood size and age, as the offspring demands increase (Silver et al. 1985, Bowers et al. 2014). Therefore, food provisioning in altricial birds has been used as an easily quantifiable way to study sexual and parent-offspring conflicts, as well as to elucidate their breeding strategies (Greenberg and Gradwohl 1983, Low et al. 2011, Gill and Haggerty 2012, MacLeod and Brouwer 2018). Nest attendance and nestling brooding (thermo regulation of nestlings) are also important for the comprehension of sex asymmetry in energy investment, as they can occupy a large part of the daily activities of parents (Carere and Alleva 1988, Hill et al. 1999, Evans and Stutchbury 2012). Lastly, nest sanitation, which is an understudied topic in the nesting stage (Ibañez-Álamo et al. 2017), is usually studied in the context of testing its importance as a means to reduce nestling infections, and attraction of ectoparasites and predators, but rarely in the context of accessing parental expenditure (Lang et al. 2002, McKay 2009, Ibañez-Álamo et al. 2016, 2017).

Nest sanitation can be a costly activity for parents just as food provisioning, as it frequently requires parents visiting the nest to take away or ingest nestlings' excrements (Blair and Tucker 1941, Hurd et al. 1991, Ibañez-Álamo et al. 2017) in order to avoid potential negative effects of these excrements soiling the nest structure (Ibañez-Álamo 2014, 2016). In many altricial bird species nestling excrements are enclosed in a mucous covering, which are called fecal sacs (Ibañez-Álamo et al. 2013). The research focus on nest sanitation has been usually concentrated on the study of its importance to assure the good health of parents and offspring in the nest either by removing a potentially dangerous product or to obtain direct benefits (i.e. nutrients or water) (Morton 1979, Hurd 1991, Ibañez-Álamo 2016, 2017). Potentially, the higher ingestion of fecal sacs by a specific sex (favouring recycling of water and nutrients) could serve as an indication of higher effort in that sex, helping us to compare energy expenditure between parents (Hurd et al. 1991, McKay 2009). However, there are few studies that integrate nest sanitation in the framework of sexual differences in parental care. Nonetheless, there are cases of female-dominant, male-dominant, and equitable nest sanitation between the sexes, even if the toll or benefit to the parents is not clear (Carere

and Alleva 1998, Markman 1994, McKay 2009, Bolopo et al. 2015). Finally, when investigating parental care behaviours during the nestling stage, such as those we describe previously, it seems important to control for additional factors like brood size and brood age (Martin 2010, 2015).

The topic of sexual conflict has traditionally attracted a lot of attention from the scientific community, but gaps in our knowledge do remain for many of the monomorphic monogamous species of birds, especially from the tropics (Stutchbury and Morton 2001). In our study, we focused on three forms of parental care (i.e. food provisioning, nest attendance and brooding, and nest sanitation) during the nestling stage to evaluate parental division of tasks in the Pale-breasted Thrush (*Turdus leucomelas*), a monomorphic monogamous tropical passerine for which such behaviours are not known (Sick 1997, Collar 2005).

We hypothesized that the Pale-breasted Thrush would show indistinguishable food provisioning rates between sexes irrespective of brood size and age, but nest attendance and brooding would be carried out by females, mirroring other species of the genus (Howell 1942, Snow 1958, Hill et al. 1999, Sánchez et al. 2018, Batisteli et al. 2020). Nest sanitation is a broad topic, so we focused on the most commonly study aspect of fecal sac removal. This behaviour through ingestion could be viewed as a toll or as food resource to the parents, depending if it is used a way to recycle nutrients or as a more efficient method of removal (McGowan 1995, McKay 2009). If nest sanitation is mainly a costly activity, it would possibly be performed by the sex with the least energetic burden; if nest sanitation is a source of resources by ingestion of nestling fecal sacs, then it would be performed by the most energetically constrained sex. Therefore, in case that higher consumption of fecal sacs is a sign of energetic constraint by a given sex, fecal sac removal rates through ingestion might be an indicator in an asymmetry between the sexes energy expenditure during the nesting stage.

2.2 METHODS

2.2.1 Study Area

The study was conducted in the campus of the Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP) (22°23'45.7"S 47°32'38.3"W) at Rio Claro, Brazil. The campus (111.46 ha) consists of a mix of manmade gardens and small forest patches with native vegetation. Of the 196 flowering plant species recorded in the campus, 37.7% are exotic (Potascheff 2007). The regional climate has two well defined seasons, a dry season from April to September (180-200 mm rainfall) and a wet season from October to March (~1200 mm) (Troppmair 1978). Rio Claro is at the transition between the semideciduous Atlantic Forest and the Cerrado biomes, though heavily impacted by anthropic land uses as sugarcane farmland, pasture and *Eucalyptus* plantations (Matias 1989).

2.2.2 Study Species

The Pale-breasted Thrush has a widespread distribution in South America, from the Guyanas, south of Colombia and Venezuela, almost every state in Brazil (except Acre and Rondônia), Paraguay and north Argentina (Haverschmidt 1959, Sick 1997). Pale-breasted Thrushes have no sexual dimorphism (Figure 2.1) (Sick 1997, Collar 2005). It is an omnivore species, feeding on invertebrates (mainly arthropods) and fruits, with occasional small vertebrates (Sazima and Angelo 2011). They occur in forest borders, clearings, savannahs, and gallery forests, rural and urban areas (Sick 1997, Collar 2005)



Figure 2. 1: Due to the absence of apparent dimorphism between males (e.g. left) and females (e.g. right) in the Pale-breasted Thrush (*Turdus leucomelas*), marking individuals with unique combinations of coloured rings were necessary for visual identification.

The breeding season of the Pale-breasted Thrush at the study region spans from September to January (Davanço 2014). A nesting cycle has an average duration of two months from egg laying and incubation (12-13 days), nestling (14-16 days) to post-fledging stages (30-40 days) (Davanço 2014). At the campus the species prefers open areas with sparse to dense trees and shrubs, nesting in buildings and on the vegetation, mainly on forks of large

tree trunks. One to four eggs are laid (usually two to three) in a cup shaped nest built by the female from roots, vegetation and mud (Ridgely and Tudor 1989, Davanço 2014). Up to two successful clutches are laid in a breeding season, with a replacement clutch occurring if one of the previous clutches was unsuccessful (Davanço 2014).

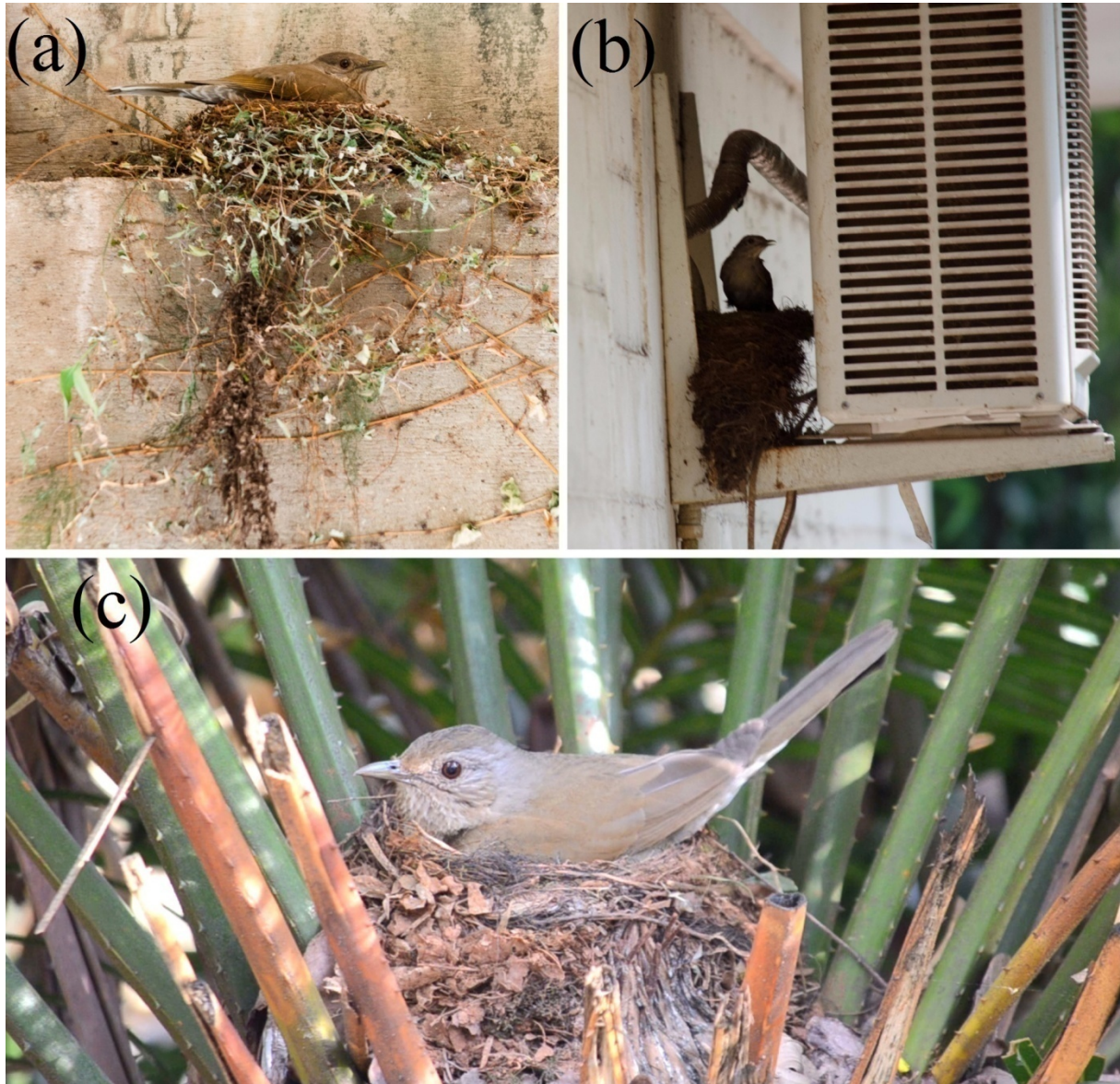


Figure 2. 2: The variety of nest location of Pale-breasted Thrush (*Turdus leucomelas*) in the study area. (a) Nest 15 meters above ground on in the interior of a tall and thick concrete building. (b) Nest behind an air-conditioner two meters above the ground. (c) A nest placed on the top of a Cycadaceae just one meter above the ground with limited cover.



Figure 2. 3: Eggs and nestlings of Pale-breasted Thrush (*Turdus leucomelas*). (a) eggs; (b) newborn chicks and two parasitic eggs of the Shiny Cowbird (*Molothrus bonariensis*), (c) 4-6 days old nestlings; (d) 15 days old nestlings and an adult female.

2.2.3 Field procedures

Adult thrushes were captured with mist nets and marked both with a coded metal ring and coloured rings throughout each year. Sex identification was done by an outsourced laboratory (UNIGEN, São Paulo) with blood samples analyzed with Polymerase Chain Reaction (PCR) amplification of genetic material for sex identification using DNA sex markers. Families selected for our study had at least one of the parents colour-ringed to enable identification from a distance, without the necessity of recapture, of which sex provided care. Unidentified individuals within a couple were assumed to be of the opposite sex to the identified individual.



Figure 2. 4: Pale-breasted Thrush (*Turdus leucomelas*) (a) before ringing and (b) after ringing with a metal identification ring and a unique combination of coloured rings.

Nests were found by active nest searching in the study area. We regularly monitored nests from September to December of 2015-2017 with the aid of a wood pole with an attached

mirror. By monitoring nests (every 2 to 3 days), we recorded the number of eggs (clutch size) in each nest and the day that eggs hatched. The activity of parents in the nests was recorded using a similar protocol followed with other Turdidae (Ibañez-Álamo et al. 2012). We used GoPro Hero 2 cameras positioned near the nest at distances that allowed for quality recordings and minimum interference with parental behaviour (0.5 to 1.0 m from nests). Recordings began the following day all eggs hatched for nests found with eggs ($n = 24$), or immediately when found for nests detected already with nestlings ($n = 9$). Recording sessions on a given nest were done with an interval of two days in the morning (07:00-12:30 h) or afternoon (14:00-18:00 h), aiming for a filming session duration of 1.5 h. We only filmed in good weather conditions. Recordings were ceased when nestlings were 14-16 days old to avoid their premature departure from the nest upon our approximation.



Figure 2. 5: Image from one of our camera recordings (with a GoPro Hero 2 camera) showcasing a female Pale-breasted Thrush during brooding of nestlings.

Videos were carefully watched to record the food provisioning rate (i.e. feeding visits per hour), food quantity rate (i.e. number of food items brought per hour), and food load (i.e. number of food items per food provision), following protocols in previous studies (Biermann and Sealy 1982, Gill and Haggerty 2012). Nest sanitation visits (i.e. visits in which there was

fecal sac removal), fecal sac removal rate (i.e number of fecal sacs removed per hour) and method of removal, either (1) physical removal by carrying the fecal sac away from the nest in their beaks or (2) ingestion of fecal sacs at the nest (Ibañez-Álamo et al. 2013). In addition, we quantified parents' attendance to the nest, and time spent brooding the nestlings. Because, brood parasitism can modify parental care behaviour and sometimes sexual conflict (Hoover and Reetz 2006, Požgayová et al. 2015), we removed from the analyses nests parasitized by the Shiny Cowbird (*Molothrus bonariensis*). We also removed the exceptional case of a couple that laid two broods with four nestlings consecutively, given the fact that brood size can influence the studied parental care behaviours and we did not have enough sample size for this case (see above).



Figure 2. 6 (a) Nestling provisioning by a Pale-breasted Thrush (*Turdus leucomelas*) female and (b) nest sanitation by a male.

2.2.4 Statistical Analysis

We used General Linear Mixed-Models (GLMMs) to investigate whether there were sex differences in parental care behaviour during the nestling stage. We ran different models for each response variable (food provisioning, food quantity, food load, nest sanitation, and fecal sac removal). The feeding and nest sanitation behaviours responsible variables were weighted by brood size. In these models we included parental sex (male-female), brood size (1-3), and the interaction between sex x brood size as fixed factors, and brood age as a covariate. Nest identification and its specific brood code (made up of nest identification and year) were used as random factors. We ran Tukey pairwise post-hoc tests to evaluate male and female differences in case the interaction term was significant, or to identify the differences in parental care behaviours according to brood size when this factor was significant. For nest attendance we built Linear Mixed-Effects Model (LMM) using the proportion of time spent on the nest by each sex in relation to the observation period as the response variable; sex, brood size, and the interaction between sex and brood size, were set as fixed factors, brood age as a covariate. Herein, nest identification and its brood code were used as random factors. We used a backward stepwise procedure to select significant factors in the models. We used the Akaike Information Criterion (AIC) to confirm the results and best model, and the most relevant factors from our previous procedure. We visually checked whether the residuals of each model comply with the assumptions of normality of the residuals of each model was checked visually. All analyses were done with R Statistical Software version 3.6.2 (R Development Core Team), and the packages ‘car’ (Fox et al. 2016), ‘emmeans’ (Lenth et al. 2018), ‘ggplot2’ (Wickham 2011), ‘lme4’ (Bates et al. 2007), ‘lmerTest’ (Kunzetsova et al. 2020), ‘nlme’ (Pinheiro et al. 2018).

Table 2. 1: List of response variables included in the GLMMs (feeding behaviours and nest sanitation behaviours) and the response variable of the LMM (nest attendance) and its descriptions.

Response variable
<i>Food provisioning</i>
Number of trips to the nest in which feeding behaviour was realized.
<i>Food quantity</i>
Number of food items that were brought to the nest.
<i>Food load</i>
Average load of food items carried by the individual to the nest in each feeding trip.
<i>Nest sanitation</i>
Number of trips to the nest in which fecal sac removal behaviour was realized.
<i>Fecal sac removal</i>
Total number of fecal sacs removed from the nest.
<i>Nest attendance</i>
Proportion of the observation time that the individual spent inside the nest.

2.3 RESULTS

We recorded 33 nesting attempts by 25 unique Pale-breasted Thrush pair combinations throughout the breeding seasons of 2015 to 2017. Videos averaged 1.5 ± 0.2 h, ranging from 0.9-2.0 h. In total we filmed for 153.5 h. Each nest was filmed on average 3.2 ± 1.4 times (range 1-6 times).

2.3.1 Feeding behaviour

The mean food provisioning rate was 1.61 ± 1.13 visits/h and the food quantity rate 2.08 ± 1.66 food items/h. Both sexes fed the nestlings, with males having a higher average rate of food provisioning (males = 1.76 ± 1.12 food provisioning rate/hour/nestling, females = 1.45 ± 1.12 food provisioning rate/hour/nestling) and food items (males = 2.33 ± 1.64 food items/hour/nestling, females = 1.80 ± 1.64 food items/h/nestling). Mean female food provisioning rate for different brood sizes was 2.23 ± 1.51 , 2.45 ± 1.43 , 2.70 ± 1.24 visits/h for broods with one, two and three nestlings, respectively. Male food provisioning rate for different brood sizes was 2.42 ± 1.42 , 3.35 ± 2.21 , 4.28 ± 1.96 visits/h for broods with one, two and three nestlings, respectively.

Through stepwise regression, the best model for food provisioning included all factors initially considered (Table 2.1). Sex of the parent did not affect food provisioning rate, but there was a significant interaction between sex and brood size. Post-hoc tests revealed that males showed higher food provisioning rates than females in broods with three nestlings (Tukey: $z = 2.954$, $p = 0.037$), but not in broods with one or two nestlings (Tukey: $z = 0.657$, $p = 0.986$; $z = 1.798$, $p = 0.467$, respectively). Post-hoc tests also revealed that food provisioning by males did not differ between broods with one or two (Tukey: $z = -1.570$, $p = 0.619$), two or three (Tukey: $z = -0.938$, $p = 0.937$), and one or three nestlings (Tukey: $z = -2.339$, $p = 0.178$). Food provisioning by females, in contrast, decreased from broods with one to three nestlings (Tukey: $z = -4.098$, $p < 0.001$), but there were no differences between broods of one or two (Tukey: $z = -2.514$, $p = 0.120$), and two or three nestlings (Tukey: $z = -2.081$, $p = 0.297$). Food provisioning rate was affected by brood age (Figure 2.7 b). Brood

size was also a significant factor in food provisioning rates (Table 2.1, Figure 2.7 a). Post-hoc tests revealed that broods with one nestling had higher food provisioning rates than broods with two (Tukey: $z = -2.423$, $p = 0.041$) and three nestlings (Tukey: $z = -3.983$, $p < 0.001$), but broods with two or three nestlings did not differ from each other (Tukey: $z = -1.986$, $p = 0.115$).

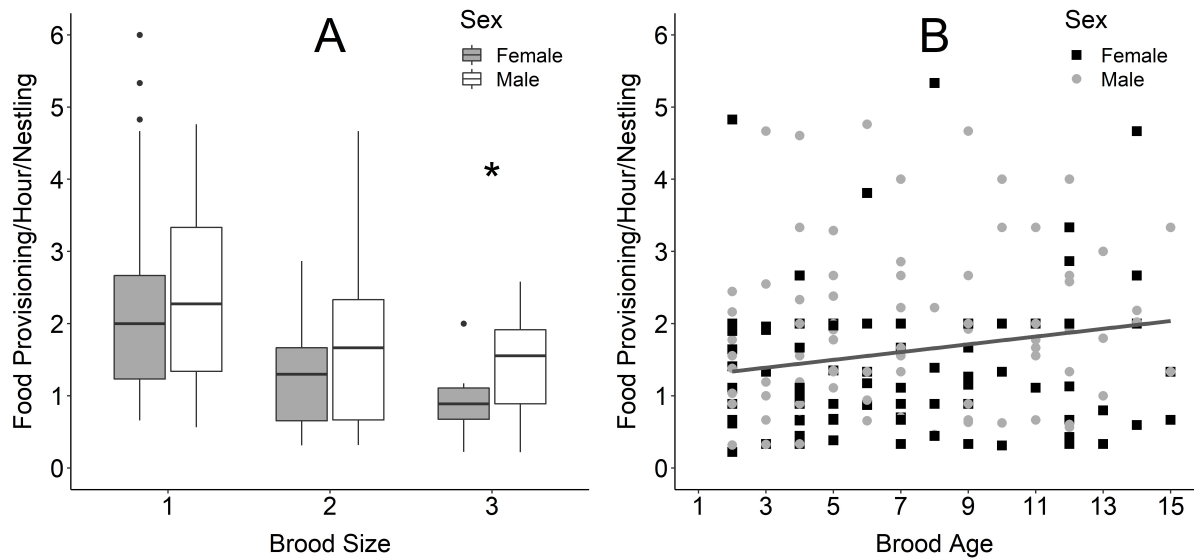


Figure 2. 7: Food provisioning rate (feeding trips/h/nestling) of males and females according to brood size (a) and brood age (b) ranges. In the box-plot (a) horizontal lines represent the median, the whiskers represent minimum and maximum values in the range, dots represent outliers, and the asterisk pinpoints a significant difference between sexes.

Table 2. 2: Results of the General Linear Mixed-Effects Models testing the effect of sex, brood size, sex $\times$ brood size (fixed factors) and brood age (covariate) on feeding behaviour response variables (food provisioning, food quantity, and food load) by the Pale-breasted Thrush (*Turdus leucomelas*). Statistical significance at $\alpha = 0.05$ (*).

<i>Food provisioning</i>	Chisq	Df	<i>P</i>
Sex	0.474	151.630	0.491
Brood Size	22.483	25.690	<0.001*
Brood Age	5.192	150.760	0.023*
Sex $\times$ Brood Size	6.214	150.460	0.045*
Rejected Terms			

Random Factors	Variance
Nest Number	0.325
Clutch Code: Nest Number	0.001

<i>Food quantity</i>	Chisq	Df	<i>P</i>
Sex	0.408	148.448	0.523
Brood Size	16.382	17.003	<0.001*
Sex $\times$ Brood Size	8.725	147.464	0.013*
Rejected Terms			

Brood Age	2.182	149.470	0.140
Random Factors	Variance		
Nest Number		0.222	
Clutch Code: Nest Number		0.003	

<i>Food load</i>	Chisq	Df	<i>P</i>
Sex	12.093	721.260	<0.001*
Brood Size	10.320	29.860	0.006*
Rejected Terms			
Brood Age	1.428	367.060	0.232
Sex $\times$ Brood Size	2.419	744.820	0.298

Random Factors	Variance
Nest Number	0.007
Clutch Code: Nest Number	0.007

Table 2. 3: Model selection results from the feeding and nest sanitation behaviour models (General Linear Mixed-Effects Models), and nest attendance models (Linear Mixed-Effects Models). The models are ranked from the most supported to the least supported. The ΔAIC represents the difference between the referred model of that line and the model with the lowest AIC.

Model	AIC	ΔAIC
<i>Food provisioning</i>		
Brood size + Brood age + Sex $\times$ Brood size + Sex	434.5	0.0
<i>Food quantity</i>		
Brood size + Sex $\times$ Brood size + Sex	539.1	0.0
Brood size + Brood age + Sex $\times$ Brood size + Sex	538.9	0.2
<i>Food load</i>		
Brood size + Sex	982.9	0.0
Brood size + Brood age + Sex	983.5	0.6
Brood size + Brood age + Sex $\times$ Brood size + Sex	985.1	2.1
<i>Nest Sanitation</i>		
Brood size + Sex $\times$ Brood size + Sex	7.6	0.0
Brood size + Brood age + Sex $\times$ Brood size + Sex	8.3	0.7
<i>Fecal Sac Removal</i>		
Brood size + Sex $\times$ Brood size + Sex	26.3	0.0
Brood size + Brood age + Sex $\times$ Brood size + Sex	27.4	1.1
<i>Nest Attendance</i>		
Brood age + Sex $\times$ Brood size + Sex	-36.2	0.0
Brood size + Brood age + Sex $\times$ Brood size + Sex	-33.1	3.1

Sex was not significant regarding food quantity, but the interaction between sex and brood size did, as well as brood size on its own. Food quantity, in contrast to food provisioning, was not affected by either brood age. Sex of the parent and brood size affected food load. Food load was neither related to brood age, nor to the interaction between sex and brood size (Figure 2.8, Table 2.1).

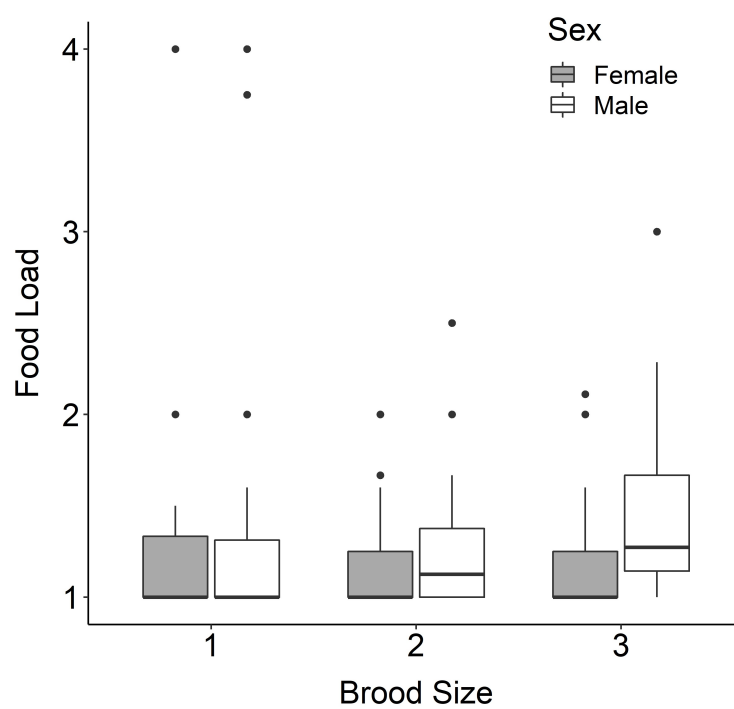


Figure 2. 8: Food load (food items/food provisioning visit) of males and females per brood size category. In the box-plot horizontal lines represent the median, the whiskers represent minimum and maximum values in the range, and the dots represent outliers.

2.3.2 Nest Sanitation

Both sexes participated in nest sanitation, with males presenting a higher average nest sanitation rate than females (males = 0.71 ± 0.59 nest sanitation/h/nestling, females = 0.59 ± 0.73). Of all nest sanitation visits, 91.55% had a single fecal sac removed from the nest. Therefore, we did not analyze the proportion of fecal sacs removed per nest sanitation event. In 377 events of nest sanitation 418 fecal sacs were removed by either ingesting or carrying fecal sacs away. Females ingested 153 fecal sacs (90.53% of their total fecal sac removal) and males ingested 214 fecal sacs (86.29%). Females carried away 16 fecal sacs and males carried away 34 fecal sacs. A female fed 1 fecal sac to a nestling. There were no fecal sacs that were not removed from the nest, and most of them were removed as soon as a nestling defecated, as nestlings frequently synchronized defecation with food provisioning.

The best model for nest sanitation included solely brood size, sex, and the interaction between these two factors. Sex of the parent was not significant for nest sanitation rate. Nest sanitation rates were not affected by brood age, but were affected by brood size, as well as the interaction of sex and brood size (Figure 2.9). Post-hoc tests revealed that there were no differences between males and females in nest sanitation rate in broods with one, two or three nestlings ($z = -1.663$, $p = 0.556$; $z = 2.324$, $p = 0.184$; $z = 1.553$, $p = 0.629$; respectively). The interaction between sex and brood size was significant for nest sanitation (Table 2.4).

Table 2. 4: Results of the General Linear Mixed-Effects Models assessing the effect of sex, brood size, sex $\times$ brood size (fixed factors) and brood age (covariate) on nest sanitation by the Pale-breasted Thrush (*Turdus leucomelas*). Statistical significance at $\alpha = 0.05$ (*).

<i>Nest Sanitation</i>	Chisq	Df	<i>P</i>
Sex	2.668	137.136	0.102
Brood Size	25.808	31.935	<0.001*
Sex $\times$ Brood Size	8.882	136.886	0.012*
Rejected Terms			
Brood Age	1.285	113.479	0.257
Random Factors		Variance	
Nest Number		0.002	
Clutch Code: Nest Number		0.003	

<i>Fecal Sac Removal</i>	Chisq	Df	<i>P</i>
Sex	2.694	137.136	0.101
Brood Size	16.772	31.935	<0.001*
Sex $\times$ Brood Size	7.863	136.886	0.020*
Rejected Terms			
Brood Age	0.961	113.479	0.327
Random Factors		Variance	
Nest Number		0.023	
Clutch Code: Nest Number		0.024	

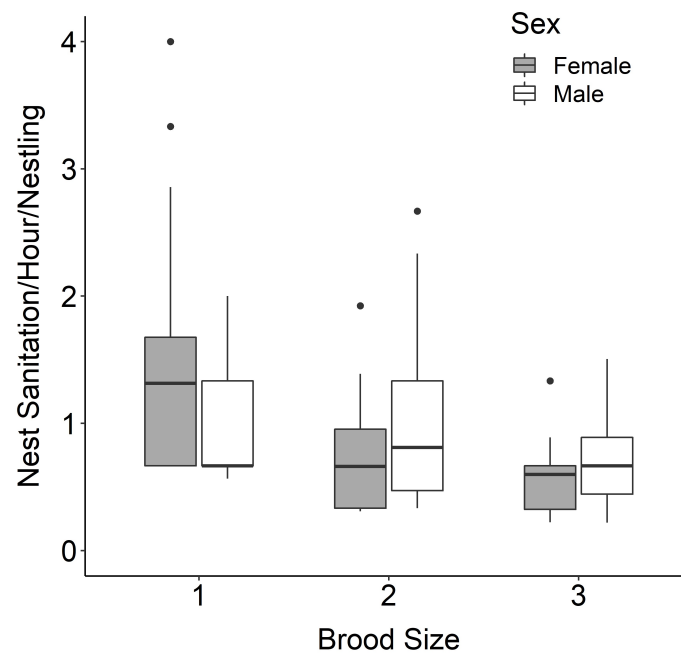


Figure 2. 9: Nest sanitation rates (nest sanitation/h/nestling) of males and females over the brood size range. In the box-plot horizontal lines represent the median, vertical lines are the whiskers of the boxplot, and the dots represent outliers.

2.3.3 Nest Attendance

Each nest visit lasted on average 7.05 ± 8.45 min for females and 0.82 ± 1.7 for males. Females spent on average 34 ± 27 % of observation time on the nest and 24 ± 26 % of observation time brooding nestlings. Males spent 4 ± 4 % of observed time on the nest and did not exhibit any brooding behaviour toward nestlings.

The best model for nest attendance included all factors, except for brood size. Nest attendance was not influenced by brood size, but it decreased with brood age (Figure 2.4). The interaction between sex and brood age was significant, females decreased their attendance to nests as nestling grow, while male nest attendance remained constant and low (Figure 2.4, Table 2.5).

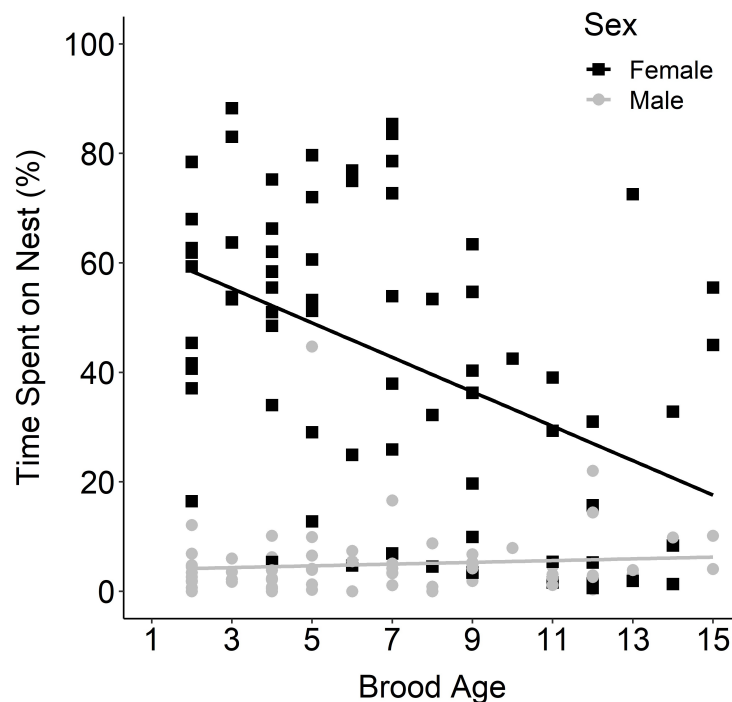


Figure 2. 10: Percentage of the observation time spent on the nest (time spent on nest/observation period) by males and females across brood ages.

Table 2. 5: Results from the Linear Mixed-Effects Models assessing the effect of sex, brood size, sex $\times$ brood age (fixed factors) and brood age (covariate) on provisioning and nest sanitation of the Pale-breasted Thrush (*Turdus leucomelas*). Statistical significance at $\alpha = 0.05$ (*).

<i>Nest attendance</i>	Chisq	Df	<i>P</i>
Sex	234.605	116.110	<0.001*
Brood Age	17.017	127.120	<0.001*
Sex $\times$ Brood Age	24.976	116.440	<0.001*
Rejected Terms			
Brood Size	1.065	22.447	0.587
Random Factors		Variance	
Nest Number		0.383	
Clutch Code: Nest Number		0.001	

2.4 DISCUSSION

We found that both males and females of the Pale-breasted Thrush engaged in food provisioning, nest sanitation and nest attendance, but there are differences in their specific roles depending on the behaviour considered. Interestingly, for all response variables we found a significant effect of the interaction between sex and brood size which clearly suggest that the initial breeding investment (number of nestlings) greatly influences male and female roles. In some cases, we detected a significant effect of brood age, which indicates the relevance of nestling requirements that greatly change over the chick period. More specifically, both sexes took part in food provisioning, but males outpaced females as brood size increased. This is probably due to a greater reduction in food provisioning by females rather than an increase by males. Similarly, both sexes perform nest sanitation behaviour although their differences according to brood size show a less clear pattern. Finally, nest attendance showed the greater sex differences in our model species, with the females as the only sex brooding nestlings. Nonetheless, the extensive nest attendance by females decreased rapidly as nestlings aged.

2.4.1 Food provisioning

Parental sex may deeply affect provisioning rates, which is markedly different in dimorphic and polygamous species (Low et al. 2011, Požgayová et al. 2015). We expected similar provisioning rates between males and females of the Pale-breasted Thrush, but these provisioning rates were dissimilar in a specific case. Males modulated their provisioning rates to brood size, and so sex differences in provisioning were only found for larger broods. Some of the other most widely known factors affecting food provisioning rates in birds are brood size and age (Silver et al. 1985, Gill and Haggerty 2012, Bowers et al. 2014). As both increase so does the food demands of the offspring (Clutton-Brock 1991, Whittingham 1988). Our results supported that both brood size and age affected food provisioning in our model species. Moreover, we found that larger or older broods meant an increase in total food

provisioning, which was accomplished by an increase in food provisioning rate rather than food load.

Even though the total quantity of food items increased with brood size, larger broods experienced a lower per capita provisioning in comparison with single nestling broods. Aging of nestlings also increased the rate of food provisioning rate, while the total quantity of food items was not affected, suggesting that parents adjust the demand to offspring growth by increasing provisioning rate rather than food load. Thus, for total food items to remain constant, despite the increase in food provisioning rates, food load likely decreased. It is possible that as nestlings age, food loads have smaller quantity but larger food items.

Larger broods of altricial birds require greater parental effort for growth and maintenance (Silver et al. 1985), which means additional investment from parents to assure offspring survival (Lack 1947, Skutch 1949). Maintaining the per capita food provisioning would demand that the quality of the does not fall drastically (Stutchbury and Morton 2001, Martin 2015). According to our results, males modulate their total food provisioning, and is the sex to keep the per capita food provisioning from decreasing heavily as brood size increases. Meanwhile, female per capita provisioning rates decreases in larger broods, meaning that their total food provisioning effort is probably constant. These differences became clear in broods with three nestlings, in which males had clearly higher per capita food provisioning rate. A similar case of only males modulating food provisioning rates in relation to brood size was found in the Common Swift (*Apus apus*) (Carere and Alleva 1998).

Birds are not able to increase the size of their clutches above a certain threshold as parents are constrained to maintain their own fitness, prospects of future copulations and offspring. Thus, their maximum energy expenditure on current nesting attempts is limited (Skutch 1949, Trivers 1972). In general, tropical birds have higher adult survival rates and higher nest predation rates than temperate counterparts (Martin 2015). This leads to the tropical tendency of having smaller clutches and shorter nesting periods, as their strategy seems to favour higher parental investment per nestling, as a means to enhance fledgling survival (Martin et al. 2000, Tieleman 2007, Martin 2015). Consequently, males might be essential to maintain a high enough food provisioning rate to improve nestling survival past the nesting stage in our study species. Since broods of three nestlings are common in the Pale-breasted Thrush, the food provisioning rates we recorded were likely enough to guarantee fledgling survival, even though individual quality of nestlings from large broods might drop in relation to smaller broods.

Since larger clutches represent a higher energetic cost than smaller clutches for females (Visser and Lessells 2001), their tendency to maintain total food provisioning rates constant might be due to fitness constraints due to laying a large clutch. Nevertheless, if that was the case, the total food provisioning would have been expected to be higher in smaller clutches and not constant. A conservation of body condition and prospects of successful future nesting attempt might be more beneficial for females than a potential higher quality of the current brood given the higher nest predation risk in tropical environments (see above). In this case, males may compensate females' constraints on energy requirement in larger broods (Whittingham 1988, Markman 1994, Low 2011). Thus, while males do increase their food provisioning efforts for larger broods, they alone are not able to keep the same food provisioning rates as in smaller broods. This means that the combined per capita food provisioning will be inevitably reduced for large broods, which may impact nestling quality (i.e. body mass and/or nestling development) and survival in the post-fledging stage (Styrsky 2005, Gill and Haggerty 2012, Bowers et al. 2014, Sofaer et al. 2018, Evans et al. 2019). Thus, a trade-off could be at play, as the higher survival chance of a small clutch might be balanced against a larger clutch with lower survival probability (Smith 1989). However, there is some contention on the claim that clutch size directly influences fledgling survival (Bowers et al. 2014, Gow and Wiebe 2014, Remeš and Matysiovská 2016). Given that clutches of three eggs are common in our model species, we assume that despite the possibility of lower post-fledging survival of a larger brood, producing a higher number of fledglings remains advantageous for the Pale-breasted thrushes.

The amount of investment provided by males of the Pale-breasted Thrush was unexpected, as there are few cases of higher male food provisioning in biparental care in passerines (Hill et al. 1999, Reed, 2007). For this to happen, a higher brood size needs to be worth investing and do not compromise future copulation prospects. In a more equal sexual selection scenario, both sexes will seek and attempt to maintain high quality partners. With this in mind, it might be that males consider the ability to lay clutches of three eggs as a trait that indicates a high quality female (Burley 1986, Gill and Stutchbury 2005, Mahr 2012, Jelinek 2016, Peralta-Sánchez et al. 2020), as the investment in reproduction of an individual has been shown to influence the other (Gori 1988, Bebbington, 2015). Possibly, males might also be contributing to avoid extreme losses in female condition, which could enhance the chance of a second nesting attempt. If couples last through multiple nesting attempts and years, the advantages of great investment in a current partnership increase, as securing high

quality and experienced partners is advantageous for reproductive success (Peralta-Sánchez et al. 2020).

In our study population, while body masses do not differ between sexes in non-breeding seasons, the breeding season leads to a reduction in male, but not female, body mass (Pizo unpublished data). Therefore, we could assume that male care of nestlings together with their other reproductive tasks (e.g. territory defence, nest sanitation, fledgling care) might take a more severe toll on their fitness than for females.

2.4.2 Nest sanitation

Both males and females took part in nest sanitation by removing fecal sacs. As opposed to food provisioning rates, nest sanitation and fecal sac removal rates did not differ between sexes. The decrease in per capita fecal sac removal in larger broods may be explained by two reasons, which are connected to the reduction of per capita food provisioning. As larger broods were provisioned with less food per capita, it probably reduced the output of fecal sacs. Additionally, as defecation is synchronized with feeding as in other species (Quan et al. 2015), the per capita nest sanitation rate might have been reduced along with the frequency of feeding visits of parents to the nest. This seems initially contradictory, as this synchronization of provisioning and nest sanitation events led us to expect higher nest sanitation rates for males in larger broods. This might simply be explained by the short time that some males spend in the nest for food provisioning, possibly leaving the nest before nestlings defecate. As females spent much more time in the nest, they might have removed these “delayed” fecal sacs. Anyway, explaining in-depth how these mechanisms work is out of the scope of this study. Additionally, removal of fecal sacs did not increase in relation to brood age, which suggests that the size of the fecal sacs rather than the number of fecal sacs produced increases with nestling age.

As mentioned previously, the ingestion of fecal sacs might imply both an energetic strain or possibly reveal something about the sexual conflict at hand. A few hypotheses explaining the putative benefits of fecal sac ingestion are: (1) Parental-Nutrition Hypothesis, which predicts that recycling nutrients from fecal sacs is beneficial, increasing with energetic stress and thus with brood size (McGowan 1995, McKay 2009). (2) The Economic Disposal

Hypothesis (Hurt et al. 1991) says that the time saved by ingestion of fecal sacs is beneficial to invest time in other activities. Finally, the (3) The Nest Predation Hypothesis predicts that ingestion is beneficial by reducing parental movement in and out of the nest, therefore reducing risk of nest predation and enabling higher nest attendance. Additionally, in this hypothesis, frequency of fecal sac ingestion increases with larger brood sizes (Ibañez-Álamo et al. 2013). The first two hypotheses predict higher frequency of ingestion from the most stressed sex, which usually is the female. However, in our study males seem to invest a great deal into provisioning and as mentioned previously, males' body condition suffer a greater reduction along the breeding season than females. Males and females ingested similar proportions of fecal sac, suggesting a similar energetic demand, which is nonetheless contradicted by the reduced male body condition. Nevertheless, the lower body condition of males during breeding season suggests otherwise.

2.4.3 Nest attendance and brooding

Early in nestling development, females spent most of their time in the nest, mainly dedicated to brood the nestlings. Female presence in the nest is quickly reduced as nestlings developed enough to thermo-regulate by themselves as has been described in other altricial birds (Carere and Alleva 1998, Hill et al. 2010). Apparently, time spent on the nest by males was restricted to the time necessary to provision food to the nestlings and also to perform nest sanitation tasks, though there were rare cases of extended male presence in the nest due to unknown causes, possibly a defence of the nest against predators or brood parasites. Nonetheless, we were not able to record attendance at the immediate vicinity of the nest, so we cannot evaluate male participation on nest defence. It might be that males attend the nest surroundings to guard it, as is the case for other Turdidae species, as the Wood Thrush (*Hylocichla mustelina*) (Evans and Stutchbury 2012). Brooding of nestlings was only carried out by females, thus following what seems to be a pattern for the genus (Howell 1942, Hill et al. 1999, Batisteli et al. 2020).

2.4.4 Conclusion

Several of our initial expectations for the division of task between the sexes in the Pale-breasted Thrush were met, as their parental investment seems to be similar in most situations, just as expected for a monomorphic monogamous altricial species. We have come to the conclusion that males increase their effort in food provisioning depending on brood size, while it seems that a higher demand from offspring development is also supplied with an increase in food provisioning rather than in food load. Parents did not differ in nest sanitation rates as fecal sac removal seems to be closely linked with food provisioning events, which are reduced per capita in larger broods. Interestingly their preferential method of removal was ingestion throughout the whole stage. Finally, overall nest attendance is reduced as females down-regulated their brooding efforts as nestling develop. Considering the nesting stage, sexes are complementary in parental expenditure, differing in their tasks, which are brooding and nest attendance by females, and higher food provisioning by males in the case of large broods.

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CAPÍTULO 2

PARENTAL CARE DURING THE POST-FLEDGING STAGE IN THE PALE-BREASTED THRUSH (*Turdus leucomelas*)

ABSTRACT

The post-fledging stage of passerines is scarcely studied, especially for Neotropical species. As a consequence, different forms of parental care in this stage are poorly understood. We describe the division between parents of parental care in the post-fledging stage of the Pale-breasted Thrush (*Turdus leucomelas*) focusing on food provisioning rate, its effects on fledgling behaviour, as well as the way parents divide their brood for care. We made direct observations of eight families and 13 fledglings for 84.8 h. We found no differences between males and females in food provisioning rates, a factor that was not affected either by brood age or size. Food provisioning rate had also no significant effect on the overall frequency of foraging and vocalization by fledglings; foraging was the only behaviour that varied with brood age, increasing in frequency. Although there was no difference between parents in food provisioning, Pale-breasted thrushes presented four different arrangements of fledgling care between parents: male-only care (during simultaneous nesting attempts), brood division (brood divided between the two adults), female-only care (in the absence of simultaneous nesting attempts), and biparental care (both adults take care the same fledgling). Parental investment in the form of feeding behaviour did not differ with parental sex; however, fledglings that were provisioned by both parents more frequently fed than those that only received care from a single parent. The diversity in modes of care in brood division between parents were more diverse than initially expected, and as such, further studies on post-fledgling brood division would be necessary to uncover underlying reasons for such variation.

3.1 INTRODUCTION

Parental care encompasses a variety of aspects ranging from the provision of resources to gametes to the post-birth care of the offspring, all of them with the ultimate objective of improving their offspring chances of survival and reproduction (Trivers 1972, Clutton-Brock 1991). However, parental investment (i.e. the time and energy to provide care) involves important costs as it bears a negative relationship with future reproduction prospects and survival of adults (Lessels 2012). Reducing their own investment is one of the priorities of the parents, as it may benefit their body condition and thus the possibility for future reproduction. However, attempts of reduced investment may be counter-balanced by the negative reaction of the pair mate which may have present chance of reproductive success reduced (Wilkin 2009, Bebbington and Hatchwell 2015, Bolopo et al. 2015). While the parents will seek to alleviate their own burden, individuals may react differently and may be affected by external and internal factors such as the stimulus from nestlings, intensity of begging from the offspring, food availability, and predation risk (Hinde et al. 2010, Low et al. 2011). Thus, regional differences can be seen within and between species closely related, due to variations in latitude and altitude, as these factors shift the selective pressures that influence parental investment (Gill and Haggerty 2012, Martin 2015). Therefore, it is a dynamic and complex aspect of the life of reproductive adults that requires a balance between maximizing investment on the current offspring, and ensuring their own fitness (Gross and Sargent 1985, Trivers 1972).

Parental investment throughout a reproductive cycle is not constant, as there are differing costs to copulation, egg-laying, and caring for the young. Simultaneously, the total expenditure of energy by the parents accumulates throughout a reproductive cycle (Trivers 1972). This leads to advanced stages of the breeding cycle becoming more worthwhile of investments, as the energy and time spent are higher and as these stages have the offspring nearer to independence (a better proxy for reproductive success) (Trivers 1972, Balshine 2001). Therefore, as the final stage parental care before independence of the offspring, the post-fledging is the culmination of all that effort and spent energy, and thus, considered a critical period for the survival and reproductive success of the offspring (Tarwater 2010).

Avian parental care is probably among the most well understood, due to their habits and conspicuous nature. The most well-known stage of bird reproductive cycle is the nesting stage, when the nest-dependent offspring is bound to its limits and cared for by the parents in the nest. The fixed position of the brood at the nests facilitates its study and hence the parental care associated with it. In contrast, the post-fledging stage is the least studied of reproductive cycle of altricial birds, due to the difficulty in accompanying mobile offspring and family units (Tarwater 2010, Vernasco 2017). As this stage advances, the families increasingly move away from the nest, the fledglings become more capable fliers, and the vegetation strata they can dwell increases. Therefore, accompanying and locating a highly mobile, small, airborne group of fledglings is challenging for an observer (Ogden and Stutchbury 1996).

The post-fledging stage is expected to be costlier for parents than the nesting stage, as it is usually twice as long, the energetic demands of fledglings are higher, and more protection is needed due to a more hazardous environment (Tarwater 2010). Indeed, food provisioning rates were reported to increase around 1.5 times in some bird species from the nestling to the post-fledging stage (With 1990, Ogden and Stutchbury 1996). There are three basic patterns of division of care between parents in the post-fledging stage (Russell 2000, Rivera 2000): (1) Equal care, in which both parents equally care for all fledglings (Rivera 2000). (2) Brood division care, in which each parent cares for a portion of the offspring. This could be extreme when the same parent always takes care of the same fledgling (Russell 2000, Rivera 2000, Bonnevie 2004). Brood division supposedly enhances parent foraging efficacy and reduces predation risk of the whole brood by promoting fledgling dispersion (Anthonisen et al. 1997, Russell 2000). Alternatively, (3) a uniparental care would imply that a single parent cares for the whole brood, if the other is engaged in another reproductive attempt (Rivera 2000).

The general expectation is that parental care is intensive and demanding in the post-fledging stage, especially in tropical birds as they are reported to have extended post-fledging care (Tarwater 2010, Remeš and Matysiovoká 2016). In this stage, fledglings are still cared for by their parents, being for the most part dependent on them for food provisioning and protection. As the fledglings grow older they become more skilled in flight, foraging, and self-preservation as the parents provide less care over time, eventually leading to offspring independence (Remeš and Matysiovoká 2016). However, there are few works comparing the temporal trend of food provisioning in the post-fledging stage, due to the difficulties of observing this feeding behaviour (Ogden and Stutchbury 1996, Green and Cockburn 2001).

Certain fledgling behaviours may be connected to the parental behaviours (i.e. food provisioning). Fledgling vocalization, for instance, may depend on parental food provisioning rate as higher feeding rate should reduce the need of a risky activity such as begging and contact vocalization (Naef-Danzer et al. 2001, Evans et al. 2019). Therefore, we expect a reduction in vocalization frequency as fledglings get older because begging for food and contact calls could be increasingly unanswered as fledglings reach independence (Schaefer 2004). Similarly, as fledglings get older, their foraging skills are augmented as it is crucial for juvenile survival (ref.). Therefore, we hypothesized that parental food provisioning would be negatively correlated with foraging frequency by fledglings and fledgling age.

We investigated the poorly known post-fledging parental care in a widespread tropical thrush species from South America, the Pale-breasted Thrush (*Turdus leucomelas*), with a special focus on the different roles of males and females. Considering that equitable care between sexes is the most common option among monomorphic monogamous species (Wilkin 2009, Gill and Haggerty 2012, Sánchez et al 2018), we hypothesized no differences between males and females in food provisioning during this stage. However, we expect that food provisioning rate will increase in relation to fledglings' age due to an expected increase in their body's energetic expenditure as they develop and grow. We also recorded fledgling behaviour during this critical life-cycle stage, particularly their foraging strategies and general vocalization behaviour. Finally, we evaluated parent-offspring interactions by checking for the association between food provision and fledgling behaviour. We hypothesized that parent food provisioning rate will affect fledglings foraging and vocalization behaviours. Higher provisioning rates would increase foraging by fledglings, but decrease vocalization behaviours. As fledgling foraging is a costly activity supposedly with low efficiency, high access to resources would increase its frequency; meanwhile fledgling vocalization would be reduced, as for a well fed fledgling it would represent an unnecessary risk that could increase predator attraction.

3.2 METHODS

3.2.1 Study Area

Our study was conducted in the campus of the Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP) (22°23’45.7”S 47°32’38.3”W) at Rio Claro, Brazil. The 111.46 ha area of the campus has fragments of native vegetation with plant species from the Cerrado and semideciduous Atlantic forest, mixed with buildings, streets and man-made gardens in a typical suburban area (Matias 1989, Potascheff 2007). There are two well defined seasons, a wet season lasting from October to March (~1200 mm rainfall), and a dry season from April to September (180-200 mm rainfall) (Troppmair 1978).

3.2.2 Study Species

The Pale-breasted Thrush occurs in Brazil (except the westernmost states of Acre and Rondônia), Paraguay, north of Argentina, Guyanas, and south of Colombia and Venezuela (Sick, 1997; Haverschmidt, 1959). It is a monomorphic monogamous species, with an omnivore diet, preying on invertebrates and small vertebrates, as well as eating fruits (Sick 1997, Sazima and Angelo). Their habitat is comprised of savannahs, forest borders, clearings and gallery forests, also occurring in rural and urban environments (Sick 1997). Its breeding season encompasses from September to January (Davanço 2014)

Observed individuals were marked with a metal ring and unique combination of coloured rings (Figure 3.1). Sex identification was done by UNIGEN São Paulo, an outsourced laboratory, using blood samples from the ringed individuals, and said blood was collected from the cut vascularised claw. Polymerase Chain Reaction (PCR) amplification of DNA was done to identify genetic material with DNA sex markers. At least one of the parents from the families included in our study was colour-ringed to enable the visual identification of the sex by the observer. We actively searched for nests and regularly monitored them every

two to three days to collect information on egg laying, hatching days, and mark the nestlings with rings just before leaving the nest (8 to 10 days old).



Figure 3. 1: A 16 day old fledgling (approximately one day after fledging) of the Pale-breasted Thrush (*Turdus leucomelas*). Fledglings have low mobility and are not particularly reactive in the first few days after leaving the nest, enabling capture for ringing with bare hands.

3.2.3 Post-fledging stage

After nestlings fledged, we accompanied the Pale-breasted Thrush families (parents and fledglings derived from a nest). These families did not usually leave the boundaries of the male's territory (which we had a rough idea of its extension from yearly observations). Fledglings were then found using cues such as parental activity, usual resting spots in the area and fledgling and parents' vocalizations (Figures 3.2 and 3.3). We started fledgling observations the following day brood left the nest, (all nestlings fledged within a short span of time). Families were followed until fledglings were not found in the company of parents or

cared by them after two consecutive observation attempts. If after two attempts fledglings were not found, depending on brood age we assumed either independence (> 25 days of age) or death (< 25 days of age).

For each family, a single fledgling ('target fledgling') was observed for a given observation session, a predetermined period of observation to register behaviours. The target fledgling was usually the first we found, but we actively avoided following the same fledgling in consecutive observations on families with more than one fledgling, aiming for a better representation of the whole brood. Observations sessions lasted for two hours, but gaps in the observation when the target fledgling was out of sight were discarded from analysis leading us to calculate the effective observation time. During each observation session, we recorded the number of food provisioning events and food items brought to the target fledgling through direct observation aided by binoculars (Figure 3.4 a). Food items were identified individually in the beak. We calculated the food provisioning rate as the number of food provisioning events divided by the effective observation time. Food load was calculated by the number of food items brought per food provisioning event. The parent and the target fledgling were identified in each provisioning event (Figure 3.4 b).

The behaviour of the target fledgling was recorded with scan samples of the instant taken every 5 min. Behaviours considered were (1) foraging (attempt at or successful foraging, i.e. fledglings picking apart or rustling through their surroundings), (2) fledgling vocalization (which probably were mostly to maintain contact with the family and indicate hunger), and (3) social foraging (parent-offspring interaction in which fledglings follow foraging adults, are fed by them or forage accompanied by them). For the purpose of this study, however, we combined these behaviours into two binary variables: foraging (yes/no) and vocalization (yes/no).



Figure 3. 2: A 20 day old Pale-breasted Thrush (*Turdus leucomelas*) fledgling resting on the ground under dense vegetation.



Figure 3. 3: A 27 day old Pale-breasted Thrush (*Turdus leucomelas*) fledgling perched on the branches of a shrub.



Figure 3. 4: (a) Pale-breasted Thrush (*Turdus leucomelas*) fledgling being fed a cicada nymph by its father. (b) Fledgling begged to its father after being fed. The three fledglings from this brood were cared by the male only, while the female incubated the eggs of a simultaneous nesting attempt.

3.2.4 Statistical Analysis

We built General Linear Mixed-Effects Models (GLMMs) to analyze parental food provisioning to fledglings. We used provisioning rates and food load as response variables with sex, brood size (number of nestlings that fledged from the nest of that family), and the interaction between these terms as fixed factors (this seemed like an important factor in the nestling stage; see chapter 2), brood age as a covariate, and the identity of the target fledgling and or with the brood code (family/nest identification) as random factor (as we had several observation sessions for each individual fledgling). We tested if food provisioning rates for each fledgling differed among the three categories of parental assistance we detected (i.e. whether fed by male only, female only or both parents) using brood size as a fixed factor, brood age as a covariate, and the identity of the target fledgling as random factor. For fledgling vocalization and foraging behaviour of fledglings, we built Linear Mixed-Effects Models (LMMs) using the relative frequency of each behaviour at each observation day as continuous response variables (arc-sin transformed), provisioning rate and brood size as fixed factors, brood age as a covariate, and the target fledgling as a random factor. We ran Tukey pairwise post-hoc tests when the brood size, parental assistance, or interactions between sex and brood size were significant. We used a backward stepwise procedure based on the Akaike Information Criterion (AIC) to select the best model explaining our variance. We checked the assumptions of normality in each model by visually inspecting residuals. All analyses were done with R Statistical Software version 3.6.2 (R Development Core Team), and particularly with the following packages: ‘car’ (Fox et al. 2016), ‘emmeans’ (Lenth et al. 2018), ‘ggplot2’ (Wickham 2011), ‘lme4’ (Bates et al. 2007), ‘lmerTest’ (Kunzetsova et al. 2020), ‘nlme’ (Pinheiro et al. 2018).

3.3 RESULTS

We studied eight families and 13 different fledglings with ages ranging from 15 to 46 days throughout the 2018 breeding season. The total observation time was 109.1 h and effective observation time was 84.8 h. Each family was observed on average 6.4 ± 5.5 times. Observation time averaged 1.98 ± 0.08 h per observation session, while effective observation time in which the target fledgling was visible averaged 1.54 ± 0.44 hours per session.

After the brood fledged, they spent their first days in the surroundings of the nest (around 10 meters from the nest, but could be farther away in the case of fledglings originating from nests on buildings), amidst the dense vegetation of bushes and shrubs. After the first few days (around 3 days) parents guided fledglings towards specific spots, normally with denser vegetation, which were the usual spots where we found the thrushes families.

Parents caring for the fledglings alternated between staying in close proximity to them while in a high vantage point and leaving to forage. Social foraging occasionally occurred ($n = 68$), (i.e. situations in which parents foraged accompanied by a single or all their fledglings, which were sometimes fed but also foraged on their own). Later in their development, fledglings became capable of flying longer distances to follow their parents (up to approximately 75 meters from the fledglings usual resting spot and back again).

3.3.2 Food provisioning

None of the factors we investigated were related to parental food provisioning rates, and the final model contained none of them. Food provisioning rate was not associated with brood age (Figure 3.5) or brood size. Both sexes provisioned their fledglings, with females having a slightly higher feeding frequency (females = 4.20 ± 1.81 food provisioning rate/hour, males = 3.34 ± 2.16 food provisioning rate/hour), but food provisioning rates did not significantly differ between sexes. The interaction between sex and brood size was not significant for food provisioning rate (Table 3.1). Food load was on average 1.7 ± 0.7 items for males and 1.2 ± 0.3 items for females, with a 92% of provisioning events with a single food item. Food load was not affected by brood age, or by brood size. However, there were

significant differences between the sexes in food load. The interaction of sex with brood size was not significant (Table 3.1).

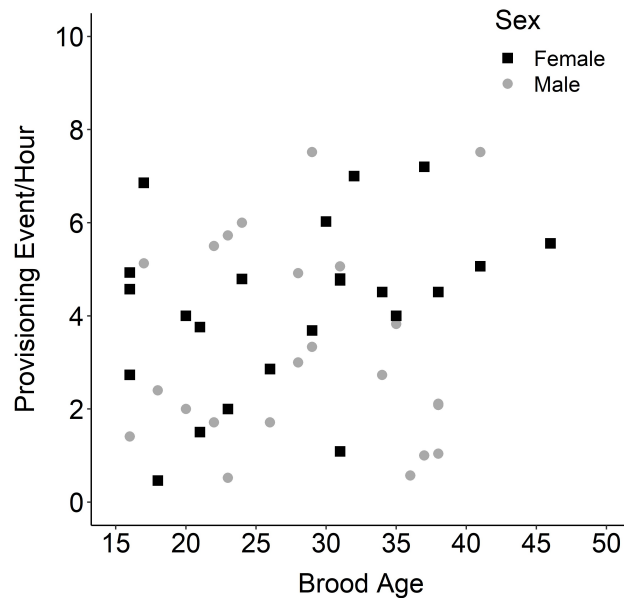


Figure 3. 5: Food provisioning rates of males and females over the brood age range.

Table 3. 1: Results from the General Linear Mixed-Effects Models assessing the effect of sex, brood size, sex $\times$ brood size (fixed factors) and brood age (covariate) on parental feeding behaviour of the Pale-breasted Thrush (*Turdus leucomelas*). Statistical significance at $\alpha = 0.05$ (*).

<i>Food provisioning</i>	<i>Chisq</i>	<i>Df</i>	<i>P</i>
Rejected Terms			
Sex	1.120	6.133	0.290
Brood Size	1.696	10.984	0.700
Sex $\times$ Brood Size	2.646	29.789	0.266
Brood Age	0.074	37.899	0.786
Random Factors		Variance	
Brood Sex Code		0.000	
Target Fledgling: Brood Sex Code		0.000	

<i>Food load</i>	<i>Chisq</i>	<i>Df</i>	<i>P</i>
Sex	8.169	3.026	0.004*
Rejected Terms			
Brood Size	0.142	196.540	0.707
Sex $\times$ Brood Size	1.096	197.553	0.578
Brood Age	0.047	213.340	0.829
Random Factors		Variance	
Brood Sex Code		0.000	
Target Fledgling: Brood Sex Code		0.000	

Table 3. 2: Model selection results from the food provisioning and provisioning pattern models (General Linear Mixed-Effects Models), and foraging and vocalization models (Linear Mixed-Effects Models). The models are ranked from the most supported to the least supported. Δ AIC represents the difference between the referred model of that line and the model with the lowest AIC.

Model	AIC	Δ AIC
<i>Food provisioning</i>		
Intercept	200.2	0.0
Sex	201.1	0.9
Brood size + Sex	204.4	4.2
Brood size + Sex $\times$ Brood size + Sex	204.7	4.5
Brood size + Brood age + Sex $\times$ Brood size + Sex	206.6	6.4
<i>Food load</i>		
Brood size	870.6	0.0
Brood size + Sex	872.3	1.7
Brood size + Sex $\times$ Brood size + Sex	873.6	3.0
Brood size + Brood age + Sex $\times$ Brood size + Sex	875.5	4.9
<i>Foraging</i>		
Brood Age	-10.2	0.0
Provisioning + Brood Age	-7.0	3.2
Provisioning + Brood Size + Brood Age	-5.0	5.2
<i>Vocalization</i>		
Intercept	-59.9	0.0
Brood Age	-58.0	1.9
Provisioning + Brood Age	-54.4	5.5
Provisioning + Brood Size + Brood Age	-77.6	17.8
<i>Parental assistance</i>		
Parental assistance	55.8	0.0
Parental assistance + Brood Size	58.7	2.9

3.3.3 Fledgling behaviour

Foraging made up to 12.1% of all scan samples ($n = 800$), increasing significantly with brood age (Figure 3.6). However, neither food provisioning rate by parents nor brood size affected the frequency of fledgling foraging behaviour (Table 3.3). Thus, only brood age composed the final model of foraging frequency (Table 3.2). Fledgling vocalization occurred in 29.8% of all scans, and it was not related to food provisioning rate, brood age or brood size (Table 3.3). Therefore, none of the factors included in the initial model of vocalization were significant (Table 3.2).

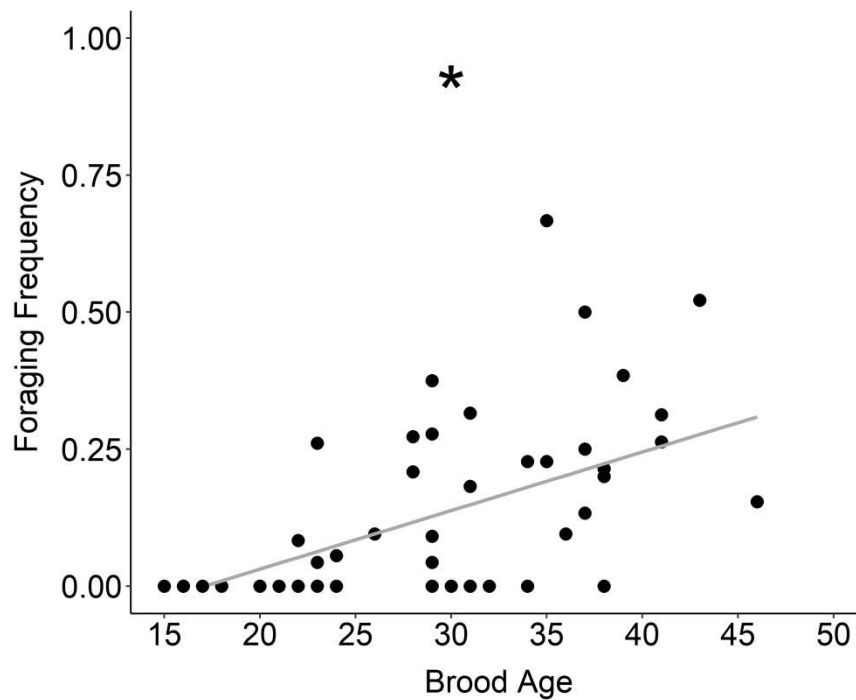


Figure 3. 6: Frequency of foraging by fledglings of the Pale-breasted Thrush (*Turdus leucomelas*) over the brood age range. Proportions were calculated in relation to the total behaviours recorded in scan samples ($n = 800$) taken every 5 min.

Table 3. 3: Results from the Linear Mixed-Effects Models assessing the effect of food provisioning by the adults, brood size (fixed factors) and brood age (covariate) on fledgling Pale-breasted Thrush (*Turdus leucomelas*) behaviour (foraging and vocalization). Statistical significance at $\alpha = 0.05$ (*).

Foraging	F	Df	P
Brood Age	67.937	249.990	<0.001*
Rejected Terms			
Food provisioning	0.423	244.590	0.516
Brood Size	0.503	4.352	0.636
Random Factors		Variance	
Target Fledgling: Brood Sex Code		0.012	

Vocalization	F	Df	P
Rejected Terms			
Brood Age	1.189	236.720	0.277
Brood Size	0.157	8.739	0.857
Food provisioning	0.000	237.821	0.988
Random Factors		Variance	
Target Fledgling: Brood Sex Code		0.011	

3.3.4 Brood division

We recorded four different parental care arrangements: Male-only care with its mate caring for a simultaneous nesting attempt (one family), brood division (four families), female-only care (one family) and single-fledgling biparental care (two families). A simultaneous nesting attempt occurred in a family, in which we recorded male-only care of fledglings, while the female stayed within the nest laying and incubating. Of the 13 fledglings observed, ten were provisioned by a single parent (six by female and four by male), and three were fed by both parents. The average rate of uniparental provision to the target fledgling was 3.4 ± 1.28 for females, and 3.3 ± 0.8 for the males, while biparental food provisioning rate to the target fledgling was 7.7 ± 3.0 . The pattern of parental food provisioning (uniparental and biparental) was consistent across all observation sessions for all fledglings, except for one fledgling which received uniparental and biparental provisioning on different sessions.

Food provisioning rate in uniparental significantly differed from biparental care (Figure 3.7, Table 3.4). Post-hoc tests revealed that food provisioning rate provided by either females or males only was different from food provisioning provided by both parents ($z = -3.470$, $p = 0.001$; $z = -3.053$, $p = 0.006$; respectively). There was no sex difference in food provisioning rate in uniparental care ($z = -0.108$, $p = 0.994$). Food provisioning rate was not affected by brood size ($p = 0.561$). Therefore, in our final model, food provisioning was solely affected by the pattern of provisioning (whether biparental or uniparental) (Table 3.2). Two of the cases of biparental provisioning involved single-fledgling broods, while in one case, a fledgling was fed by both parents despite being in a brood of three fledglings.

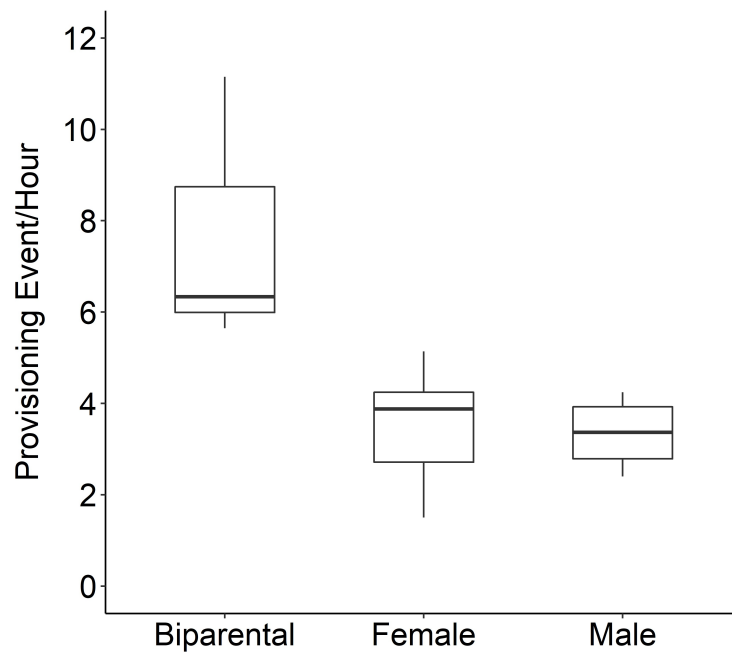


Figure 3. 7: Food provisioning rates to Pale-breasted Thrush (*Turdus leucomelas*) fledglings fed by both parents, only female, and only male. In the box-plot horizontal lines represent the median and the whiskers represent minimum and maximum values in the range.

Table 3. 4: Results from the General Linear Mixed-Effects Models comparing the feeding behaviour during brood division of the Pale-breasted Thrush (*Turdus leucomelas*) with brood size and parental assistance as fixed factors. Parental assistance provisioning of the target fledgling in three different instances of brood division feeding behaviour (biparental feeding, uniparental female feeding, and uniparental male feeding) Statistical significance at $\alpha = 0.05$ (*).

Brood division provisioning	Chisq	Df	P
Parental assistance	17.160	3.933	<0.001*
Rejected Terms			
Brood Size	1.157	1.448	0.561
Random Factors		Variance	
Nest Number		0.000	

3.4 DISCUSSION

We found that food provisioning rate and food load delivered to fledglings by their parents was constant, regardless of brood size and brood age, and did not differ between sexes. Thus, both males and females of Pale-breasted Thrush, when engaged in caring for fledglings, provided similar amounts of parental care in the form of food provisioning. However, different parental care arrangements make investment comparison between the sexes more complicated, as there were cases of male-only, female-only and biparental care for individual fledglings, sometimes even varying within the same brood. In the case of male-only provisioning, the female was attending to a simultaneous nesting attempt, and in the female-only care of a single fledgling, the male was observed but did not care to the fledgling. Neither vocalization nor foraging behaviour of fledglings was affected by parental food provisioning rate, but self-foraging became more frequent with fledgling age.

Social foraging behaviour is more commonly described in cooperative breeding birds and species that form foraging groups (Raihani 2008, Thompson 2012, Truskanov and Latem 2015, 2017). Nonetheless, this seems analogous to the behaviour we described here, that clearly differs from food provisioning by parents or when fledglings forage by themselves. Well developed fledglings accompanying parents in food provisioning, which is a form of social foraging, was also reported for other Turdidae species (With 1990, Rivera 2000).

3.4.1 Food provisioning

Our expectation of an equitable parental investment towards fledglings was confirmed (Weatherhead and Mcrae 1990, Wilkin 2009, Gill and Haggerty 2012, Sánchez et al. 2018), since food provisioning rates by males and females did not significantly differ. Food load seemed to differ between males and females. However, food provisioning rate and food load did not vary with brood size or age, which was unexpected. As the energy demand of large broods is higher, we expected that food provisioning rate would be lower in large than in small broods. Following this rationale, as more developed and active fledglings would get

more food they would necessitate to fuel their energetic demands with a greater provisioning of food by parents.

Comparing with the data in Chapter 1, we found that mean food provisioning rates in the post-fledging period are higher than in the nesting stage by 1.9 times for males and 2.9 for females, which is in accordance with the literature for other passerine species (With and Balda 1990, Ogden and Stutchbury 1996). Therefore, although there was no increase in food provisioning rates during the post-fledging stage with brood age, it did occur in the transition from the nesting to post-fledging stages, and in the nesting stage over brood age, a pattern also found for the Hooded Warbler (*Wilsonia citrina*) (Ogden and Stutchbury, 1996). If such a transition happens from the last day on the nest to the first day after fledging, the provisioning rates in the nest may not be constrained by adult condition and food availability, but actually by the risk of nest predation, as higher provisioning rates in the nest are known to increase predation risk (Stutchbury and Morton 2001, Eggers et al. 2008 Martin et al. 2011, Ghalambor et al. 2013, Trillmich 2016).

3.4.2 Fledgling behaviour

Contrary to our expectation, parental provisioning rate and food load was constant across fledgling age. We envision two potential explanations for such finding. First, the average size of the food provided might have increased during the post-fledging stage; therefore a higher provisioning of food could happen even without increasing the number of feeding events. Second, fledglings might have supplied their increasing food demand foraging by themselves, which becomes more frequent and supposedly more effective throughout the post-fledging stage (Weathers 2011). As fledglings become more skilled and efficient in foraging, they would be able to support their own additional energetic demands, despite the constant parental food provisioning.

3.4.3 Brood division

We found much variation in parental care arrangements (four arrangements in eight families), some with unknown underlying reasons for their occurrence. Some of these patterns are in line with those found in other Turdidae species, of which there are varying arrangements depending on the nesting attempt and presence of simultaneous nesting events. In other Turdidae, when there are simultaneous nesting attempts, usually only males care for the fledglings, either for the majority or the whole post-fledging stage, as females lay another clutch or began incubation (Edwards 1985, Weatherhead and McRae 1990, Rivera 2000). During the last nesting attempt or without simultaneous nesting attempts, the fledglings would be divided between male and female, in what is called ‘brood division’ (Rivera 2000).

In our model species, for cases with no simultaneous nesting attempt, we observed ‘brood division’ in three out of four families that had more than one fledgling. However, in two of these supposed brood division instances we did not find one of the parents and one of the fledglings (in both cases there were two fledglings). For these cases, it is uncertain if the uniparental care occurred for the missing fledgling. In addition, in nest number 108, for which we would have assumed to be of female-only care in a brood of two fledglings, we observed the male caring for the non-target-fledgling. Most of the cases of broods with multiple fledglings had a fledgling fed exclusively by one of their parents, a pattern found also in other species (Rivera 2000, Green and Cockburn 2001). Broods of a single fledgling were expected to be cared by both parents, which did happen in two families. However, one family had a single fledgling being fed solely by the female, even though the male was spotted in their surroundings. We did not find a connection between biparental provisioning and preferential provisioning of a specific fledgling by a single sex, but it is hard to discard this as a possibility with our low sample size and the various patterns of care. It is possible that our sample size was insufficient considering the unexpected amount of variation in parental care arrangements found, a more in-depth and detailed study on this topic is necessary to determine the underlying causes of this variation.

3.4.4 Conclusion

We found that parental food provisioning to fledglings did not significantly differ, although we confirmed that certain circumstances (e.g., a concomitant nesting attempt) may put the burden of parental care over a single parent. The increasing ability of fledglings to forage by themselves make possible a constant food provisioning rate by parents despite the increasing food demands of developing fledglings. Parental investment in food provisioning did not influence the frequency of fledgling foraging, which increases with age. The arrangements in which fledgling are cared by parents (i.e. male-only, female-only or biparental care), with the exception of simultaneous nesting attempts, are case-specific, and difficult to pin-point the reasoning behind them. If there is a pattern for parent choice of cared fledgling, it was not made clear in this study. A larger sample size would be necessary to unveil underlying patterns of brood division and choice when to care for a given fledgling by a parent.

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4. CONCLUSÃO

Neste estudo tivemos como principal objetivo abordar as diferenças entre os sexos do sabiá-barranco (*Turdus leucomelas*) durante o cuidado parental da prole. Com este intuito, registramos comportamentos dos estágios de ninhego e de pós-ninho. Machos e fêmeas investiram similarmente no cuidado durante ambos os estágios, no entanto, os papéis de cada um diferiram, possivelmente como meio de dividir eficientemente as tarefas necessárias para o cuidado da prole. No estágio de ninhego, ambos os sexos proveram alimento aos filhotes e realizaram a limpeza do ninho. Entretanto, machos proveram alimento mais frequentemente a proles maiores, provavelmente para compensar a constância da provisão das fêmeas e o fato de apenas estas estarem encarregadas de permanecer no ninho e prover termo regulação dos filhotes (*brooding*). Não houve diferença entre os sexos quanto à limpeza do ninho. Ingestão dos sacos fecais como método de remoção predominante durante todo o estágio foi o mais surpreendente aspecto na limpeza do ninho, uma vez que na literatura é reportado que a ingestão dos sacos fecais se torna raro ao longo do desenvolvimento da prole. No estágio de pós-ninho, não houve diferença no fornecimento de alimento aos filhotes entre os pais. No entanto, houve a divisão da prole e arranjos adotados pelos pais para cuidar dos filhotes foram diversos, como o cuidado uniparental por ambos os sexos, divisão da prole, e cuidado biparental.

O tópico de cuidado parental em aves, principalmente em regiões tropicais, como grande parte da América do Sul, tem uma quantidade pequena de estudos apesar da grande diversidade de aves que deve se refletir em diferenças nos ciclos de reprodução e no cuidado parental. Conhecemos a existência de uma divergência nos padrões de cuidado parental das aves entre a região temperada e a tropical, mas estas diferenças ainda estão pobremente elucidadas, e registros básicos do cuidado parental das aves tropicais é chave para contribuir para esta compreensão. Neste estudo, muitas das diferenças esperadas entre a região temperada e os trópicos são relatadas, como alto investimento por filhote e investimento parental similar entre os sexos. No entanto, outras variações, como o alto investimento do macho em situações específicas, a remoção de sacos fecais predominantemente por ingestão, o investimento similar entre sexos na limpeza do ninho, e os fatores influenciando a divisão da prole não estão esclarecidos e há poucos estudos aprofundados sobre outras espécies da região para servir de comparação.

No futuro, recomenda-se aprofundar estudos sobre aspectos básicos de cuidado parental em outras famílias para delinear melhor a variação das estratégias e padrões na região tropical. A partir disto, poderemos usar de experimentação para determinar as razões e os mecanismos envolvidos nos padrões encontrados.

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ANEXO



Figura 5. 1: Os três filhotes de sabiá-barranco (*Turdus leucomelas*) provenientes do ninho 77 durante estágio pós-ninho seguindo o macho no forrageamento. Nesta imagem os três filhotes estão à frente e o macho está detrás do filhote do meio, há apenas um relance de sua anilha vermelha, camuflado ao fundo de folhas secas. Nesta situação o macho forrageava e alimentava os filhotes que o seguiam, os filhotes também realizavam forrageio apesar de não tão efetivo. Em uma destas situações o macho forrageava perto de um cupinzeiro seguido pelo filhote MAP149 (filhote no meio da fotografia com anilha verde em sua perna esquerda), o filhote foi alimentado pelo macho alguns minutos, e depois foi deixado sozinho pelo macho. O filhote MAP149 então continuou forrageando perto do cupinzeiro por si só.

Tabela 5. 1: Ninhos (ou famílias provenientes de ninhos), incluindo a lista de casais e suas identificações, registrados durante o estudo entre 2015 a 2017 (filmagens do período de ninhego), e 2018 (observações do período pós-ninho). O substrato descreve onde o ninho foi construído.

Ano	N° do Ninho	Ninhada	Fêmea	Macho	Substrato
2015	5	2	H111851	Sem anilha	Edificação
2015	9	3	H100506	H111888	Edificação
2015	15	1	H74173	H111877	Edificação
2015	16	1	Sem anilha	H74195	Edificação
2015	32		Sem anilha	Sem anilha	Edificação
2015	36	1	H63315	H110740	Edificação
2015	41	1	H110737	H100515	Edificação
2015	44	1	H63302	Sem anilha	Edificação
2015	47	1	H100506	metalE	Edificação
2015	53	2	H100506	Sem anilha	Edificação
2015	15	2	H111877	H74173	Edificação
2015	36	2	H63315	H110740	Edificação
2016	5	2	H111851	Sem anilha	Edificação
2016	16	1	Sem anilha	H74195	Edificação
2016	36	1	H63315	H110740	Edificação
2016	38	1	H74173	H100547	Edificação
2016	40	1	H63329	H100582	Edificação
2016	41	1	H110737	H100515	Edificação
2016	47	1	verde-branco E	?	Edificação
2016	51	1	Sem anilha	H74195	Edificação
2016	59	1	?	metalE	Edificação
2016	60	1	Sem anilha	laranja D/metalE	Edificação
2016	60	2	Sem anilha	laranja D/metalE	Edificação
2016	64	2	brancoD/amareloE	rosa E	Edificação
2016	66	1	Sem anilha	H100547	Edificação
2017	5	1	Sem anilha	H74195	Edificação
2017	9	1	H100506	H111888	Edificação
2017	23	2	H63312	H100564	Edificação
2017	42	1	H111851	H102127	Edificação
2017	53	1	H100518	H111877	Edificação
2017	60	2	H102141	laranja D/metal E	Edificação
2017	62	1	H102135	H100562	Edificação
2017	65	1	Sem anilha	H63310	Árvore
2017	69	1	MAP007	Sem anilha	Edificação
2017	77	1	H100539	vermelho E	Edificação
2017	80	1	Sem anilha	H100599	Árvore
2017	81	1	H111851	H102127	Edificação
2017	82	1	Sem anilha	H100515	Edificação
2017	84	1	?	?	Árvore
2017	85	1	H102108	H102146	Árvore
2017	87	1	Sem anilha	?	Edificação
2017	88	1	H100518	H111877	Edificação
2017	89	1	H74144	H110740	Edificação
2017	90	1	H63312	H100564	Edificação
2018	50	1	H74173	H63316?	Edificação
2018	70	2	H102108	metálica E?	Edificação
2018	77	1	Sem anilha	vermelho E	Edificação
2018	89	1	H74144	H100580	Edificação
2018	97	1	Sem anilha	?	Edificação
2018	98	2	H102141	laranja D/metal E	Edificação
2018	101	1	H63312	H100564	Árvore
2018	108	1	Sem anilha	amarelo/metal E	Edificação
2018	109	1	roxo D/metal E	H74195	Edificação