



RESEARCH ARTICLE

Post-fledging parental care in the pale-breasted thrush, *Turdus leucomelas* (Passeriformes: Turdidae)

Renan N. Medeiros Haddad¹, Augusto F. Batisteli¹, Juan D. Ibañez-Álamo², Marco A. Pizo¹

¹Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista “Júlio de Mesquita Filho”. Avenida 24A 1515, 13506-900 Rio Claro, SP, Brazil.

²Department of Zoology, Faculty of Sciences, University of Granada. Avenida de Fuente Nueva, E-18071, Granada, Spain. Corresponding author: Augusto Florisvaldo Batisteli (augustofb@gmail.com)

<https://zoobank.org/2E4F343C-325F-43A9-A8F3-F90B4AEB6DA2>

ABSTRACT. Parental division of offspring care in the post-fledging stage of passerines is scarcely studied, especially for neotropical species. We describe the division of parental care in the post-fledging stage of the pale-breasted thrush, *Turdus leucomelas* Vieillot, 1818, focusing on the food provisioning rate, its effects on fledgling vocalization and foraging, as well as the way parents divide their brood for care. We made direct observations on 13 fledglings from eight families (mean \pm standard deviation: 1.88 \pm 0.83 fledglings per family) for 70.2 hours. We found no differences in food provisioning rate between adult males and females, nor was it affected by brood age or size. Food provisioning rate was not associated with the frequency of foraging and vocalization by fledglings; foraging was the only behavior 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: male-only care (while females incubated a new clutch), brood division between the two parents, female-only care (in the absence of a new nesting attempt), and biparental care (both adults take care of the same fledgling). The mode of parental care (uniparental or biparental) did not affect the rate of food provisioning to fledglings. The diversity in modes of brood division between parents was greater than expected, which calls for further studies to uncover the underlying reasons for such variation.

KEY WORDS. breeding behavior, brood division, fledglings, parental provisioning, urban bird.

INTRODUCTION

Birds have a wide array of mating systems, including polyandry, polygyny, and lekking, but social monogamy is the most common type of breeding arrangement in this group (Kempnaers 2022). The sexual division of parental tasks is a remarkable life history trait that, though more evident in polygamous species, can vary broadly even in socially monogamous birds, in which one can find from male or female exclusive attendance to biparental care (Cockburn 2006). These different strategies arise primarily from sexual and parental-offspring conflicts mediated, among a number of other factors, by sexual dimorphism (Møller 2003, Cockburn 2006, Valcu et al. 2023).

Social monogamy is especially interesting in monomorphic species, where there are less obvious sources of

sexual conflict related to ornamentation that affect parental investment (Møller 2003). Indeed, equitable care between parents is the most common tactic adopted by monomorphic monogamous species (Wilkin et al. 2009, Gill and Haggerty 2012, Sánchez et al. 2018). Nevertheless, sexual asymmetry of parental tasks is fairly common even in such species, in which females and males usually perform exclusive tasks but both parents provide food to their offspring to some extent (Auer et al. 2007). The level of symmetry in biparental care, despite being well studied during the nestling stage, is rarely studied in the post-fledging stage worldwide. The reason for this lies in the methodological difficulty of studying parent-offspring interactions of moving birds compared to birds stationed on nests (the most widely studied stage for parental investment in birds – Ogden and Stutchbury 1997,

Green and Cockburn 2001). The post-fledgling stage may be especially costly for southern hemisphere and tropical species, as it is usually longer than in northern hemisphere species, and because parental protection is needed due to the higher mortality risk during the first weeks after the young leave the nest (Russell et al. 2004, Tarwater and Brawn 2010). Thus, understanding parental investment during this later reproductive stage is important to fully comprehend parent-offspring interactions in birds.

One of the basic aspects to know about parental investment in the post-fledging period in socially monogamous species is if and which scheme parents adopt to divide care among fledglings (Tarwater and Brawn 2010). In these species, there are three basic patterns of division of fledgling care between parents (Russell 2000, Rivera et al. 2000): (1) equal care, in which both parents equally care for all fledglings (Rivera et al. 2000); (2) uniparental care, when a single parent cares for the whole brood while the other is engaged in another nesting attempt (Rivera et al. 2000); and (3) brood division, in which each parent cares for a portion of the offspring. Occasionally, parents will only care for certain fledglings without shuffling fledglings with their partner (Russell 2000, Rivera et al. 2000, Bonnevie 2004). Brood division supposedly enhances parent foraging efficiency and reduces the predation risk of the whole brood by promoting fledgling dispersion, which increases the survival of fledglings (Anthonisen et al. 1997, Russell 2000, Martin et al. 2018, Jones et al. 2020). In multi-brood species, the potential advantages of brood division are constrained by the need males to assume provisioning for the entire brood while females incubate a new clutch (Edwards 1985, Weatherhead and McRae 1990, Rivera et al. 2000). Despite the importance of the topic to understand the biology of birds, we still lack information about the post-fledging parental care behavior of many bird species, particularly in tropical areas, where the duration of fledgling dependence is extended and fledgling survival is higher (Russell et al. 2004, Tarwater and Brawn 2010, Lloyd and Martin 2016).

The post-fledging dependency period, when fledglings are provisioned and protected by their parents, represents a point of parental-offspring conflict because, although increased parental effort promotes higher offspring survival, it compromises their future breeding attempts (López-Idiáquez et al. 2018). Optimal rates of parental feeding should reduce the need for risky activities that potentially attract predators, such as begging and contact calls, increasing both offspring and parental fitness (Naef-Danzer et al. 2001, Evans et al. 2020). As fledglings get older, their vocalization frequency

tends to decrease because begging for food and contact calls could become increasingly unanswered as they approach to independence (Schaefer et al. 2004), while the foraging skills of fledglings slowly enhance. Therefore, parental food provisioning is expected to be negatively correlated with foraging frequency by fledglings and fledgling age in passerines (Middleton et al. 2007, Thompson et al. 2013).

We investigated post-fledging parental care in a socially monogamous, monomorphic, and widespread neotropical thrush species, the pale-breasted thrush, *Turdus leucomelas* Vieillot, 1818, with a special focus on the different roles played by male and female parents. Considering that this species has biparental care during the nestling stage (Haddad et al. 2024), no differences were expected between males and females in the rate of food provisioning to fledglings. We expected to find rare occurrences of brood division as the pale-breasted thrush is a multi-brooded species, and the male usually needs to assume the care of all fledglings when the female starts incubating a new clutch. We also recorded fledgling foraging and vocalization behaviors and hypothesized that both food provisioning rate by parents and fledgling vocalization frequency would decrease with fledgling age, due to an increase in fledgling foraging frequency as fledglings get older.

MATERIAL AND METHODS

Study area and species

Our study was conducted on 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, southeast Brazil. The 111.46 ha area of the campus has fragments of native vegetation with plant species from Cerrado and semideciduous Atlantic Forest, mixed with buildings, streets, and gardens in a typical suburban area. The study site has a tropical climate with average monthly temperatures ranging from 16.5 to 23.0 °C (Alvares et al. 2013) and 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).

The pale-breasted thrush occurs in Brazil (except the westernmost states of Acre and Rondônia), Paraguay, the north of Argentina, Guyana, French Guyana, and the south of Colombia and Venezuela (Haverschmidt 1959, Sick 1997). It is a monomorphic monogamous species, with an omnivore diet, preying on invertebrates and eating fruits (Sick 1997). It inhabits savannahs, forest borders, clearings, and gallery forests, also occurring in rural and urban environments (Sick

1997). In the study region, its breeding season goes from September to January (Davanço et al. 2013).

Observations on families

From September to December 2018, we actively searched for nests and monitored them every two to three days (every two days near the expected fledging date) to gather information on egg laying, hatching, and fledging days. We color-banded nestlings when they were 8–10 days old to avoid their premature fledging after manipulation, as they usually fledge around 15–16 days old. Many of the thrushes of the area were already color-banded as part of a long-term monitoring study (e.g., Batisteli et al. 2021). Thus, for all investigated nests, at least one of the parents from the families (i.e., parents and fledglings from the same nest) was also color-banded to enable the visual identification of the sex. Sex identification of marked birds was done by UNIGEN São Paulo, an outsourced laboratory, using blood samples (licenses SISBIO 45434-5, CEMAVE 3362). The Polymerase Chain Reaction (PCR) amplification of DNA was done to identify genetic material with DNA sex markers.

After nestlings fledged, we followed the families, locating the fledglings by using cues such as the activity of parents, the vocalizations of fledglings and parents, and searching in usual resting spots. We started our observations the day after the first fledgling left the nest. Because all nestlings of a single nest fledged usually in the same or consecutive days, we assumed the age of fledglings from the same family as equal with a maximum error of one day. The first day out of the nest was considered the age zero of the fledglings. Families were followed until fledglings were not found in the company of parents or cared for by them after two consecutive days of observation attempts.

Observations were carried out with binoculars in 2-hour sessions in the morning (05:30–10:30 a.m.) and in the afternoon (02:30–07:00 p.m.) on sunny days. For each family, a single fledgling (“target fledgling”, usually the first we found) was observed for a given observation session. Because parents might feed preferentially one of the fledglings, which could harm our inferences about parental provisioning in function of fledgling age, we actively avoided following the same fledgling in consecutive observation sessions on families with more than one fledgling, aiming for a better representation of the whole brood. The parent and the target fledgling were identified in each provisioning event. Gaps in the observation when the target fledgling was out of sight were discarded from the analyses, and the remaining time intervals with useful data were named ‘effective observation time’. During

each observation session, we recorded the number of food provisioning events for the target fledgling. When opportunistically witnessed, feeding events directed to the non-target fledgling of the same family group were also recorded but used exclusively to support our classification of the family groups as uniparental or biparental care. In only one family, a male observed feeding the non-target fledgling, which allowed us to classify this family as having biparental care, while other 78 feeding events of the non-target fledgling in two other families supported the classification based on the target fledglings.

The behavior of the target fledgling was recorded every five minutes (observation scan) across observation sessions. The behaviors considered were (1) foraging, either as an individual (i.e., when fledglings were picking apart or rustling through their surroundings) or social foraging (parent-offspring interaction in which fledglings follow and observe foraging adults, are fed by them, and forage accompanied by them), and (2) vocalization (probably mostly to maintain contact with the family and indicate hunger). These behaviors were treated as binary variables: foraging (yes/no) and vocalization (yes/no).

Statistical analyses

We built Generalized Linear Mixed-Effects Models (GLMMs) with Poisson distribution to analyze parental food provisioning to fledglings. Seven out of the sessions with no feeding events of the target fledgling were retained for assessing potential differences regarding modes of brood division and calculating the number of provisioning events per hour, but discarded from the comparisons between males and females in families with biparental care to avoid artificially inflating the similarity between sexes given our modest sample size. First, we tested if the frequency of food provisioning to the target fledgling differed as a function of the parental division mode (uniparental or biparental care) using brood size (i.e., the number of nestlings that fledged from the nest of that family) and brood age as covariates, and the effective duration of each observation session as an offset variable (i.e., an explanatory variable with a coefficient fixed at 1). To test whether males and females differed in their contribution to fledgling provisioning, we used the frequency of food provisioning to the target fledgling as a response variable, with sex as a fixed factor, brood size and brood age as a covariate, and the effective duration of the observation session as an offset variable. The identity of each family group was set as a random effect in both models.

For vocalization and foraging behaviors of fledglings, we built GLMMs with the presence or absence of each

behavior at a given observation scan set as a binomial response variable, and the provisioning rate at that observation session and fledgling age as covariates. In both GLMMs, fledgling identity within family group identity was set as a nested random effect. All analyses were done with R Statistical Software version 3.6.2 (R Core Team 2022) using the packages “lme4” (Bates et al. 2015) and “lmerTest” (Kuznetsova et al. 2017). Values are reported as mean ± standard deviation.

RESULTS

We made 49 observation sessions on 13 fledglings from eight thrush families, but two observation sessions were discarded due to the short effective observation time (i.e., 5 and 25 min). Therefore, we retained data from 47 observation sessions, resulting in 70.2 hours of total effective observation time (mean effective observation time per session: 89.6 ± 23.9 min, range: 35–130 minutes). The mean number of sessions per family group was 5.9 ± 5.6 , ranging from 1 to 19. The brood size of families was one ($n = 3$), two (3), or three (2), averaging 1.88 ± 0.83 fledglings per family. Fledglings were observed between 0 and 30-days after fledging (i.e., between 16 and 48 days after hatching), and the mean age of observed fledglings was 12.4 ± 8.2 days old.

Fledglings spent the first three days after leaving the nest in the surroundings of the nesting site (e.g. around 10 m from the nest but sometimes farther away in the case of nests made on buildings), amidst the dense vegetation of bushes and shrubs. After that, fledglings were found in specific spots, often less than 30 m away from the nest, and continued to select areas with denser vegetation.

Parents caring for fledglings alternated between staying near them while at a high vantage point and leaving to forage. Social foraging occasionally occurred in this early period. Later in their development, fledglings became capable of flying longer distances to follow their parents (up to ~75 m from the usual fledgling resting spot and back again).

The overall provisioning rate was 4.74 ± 3.05 feeding trips/h, ranging between 0 and 12 feeding trips/h. Seven out of 344 feeding events were performed by an unidentified sex and were excluded from further analyses. Both parents (together or separately) fed the fledglings in at least one observation session in four of the eight families followed, which were then classified as biparental feeding. In the other four families classified as uniparental feeding, fledglings were fed exclusively by males ($n = 2$ families) or females ($n = 2$) during the observation sessions (Fig. 1).

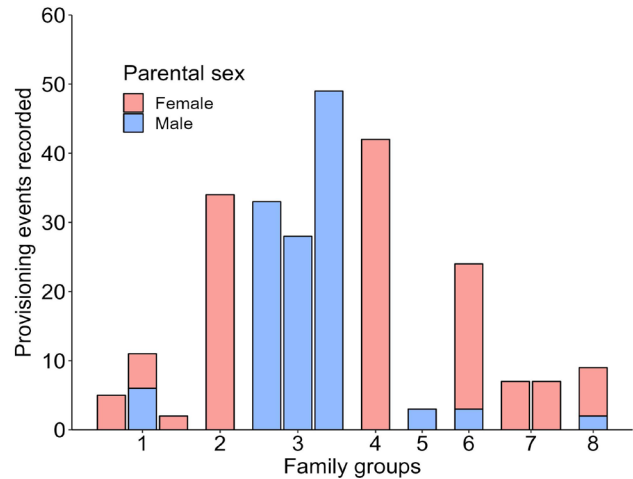


Figure 1. Total number of food provisioning events to fledglings of the Pale-breasted Thrush *Turdus leucomelas* by each parental sex. Grouped bars refer to fledglings from the same family group (1 to 8) and reflect clutch size, with exception of families 5 and 6 (two fledglings each, one of them non assessed during focal observations). Families 1 and 6 to 8 were assigned as biparental care; in family 7, biparental care was assigned because the male was observed feeding one non focal nestling.

Uniparental vs. biparental food provisioning

When examining all the families, there was no effect of fledgling age on food provisioning rate to the target fledgling of each observation session (Table 1, Fig. 2), which also did

Table 1. Factors affecting the rate of food provisioning to fledglings in the pale-breasted thrush, *Turdus leucomelas*. Generalized linear mixed-effects models addressing the effect of fledgling age, mode of parental care (uniparental/biparental feeding), parental sex, and brood size on food provisioning considering all observed families ($n = 8$, 70.2 of observation) and families with biparental food provisioning ($n = 4$, 24.5 hours of observation).

Model structure	Estimate	Std. error	z	p
All families				
Intercept	-2.210	0.416	-5.309	< 0.001*
Fledgling age	-0.011	0.008	-1.270	0.204
Parental care mode	-0.029	0.171	-0.102	0.919
Brood size	-0.184	0.084	-1.085	0.278
Families with biparental care				
Intercept	-3.337	0.699	-4.776	< 0.001*
Fledgling age	0.011	0.025	0.431	0.666
Parental sex	-0.403	0.339	-1.189	0.234
Brood size	0.223	0.157	1.428	0.153

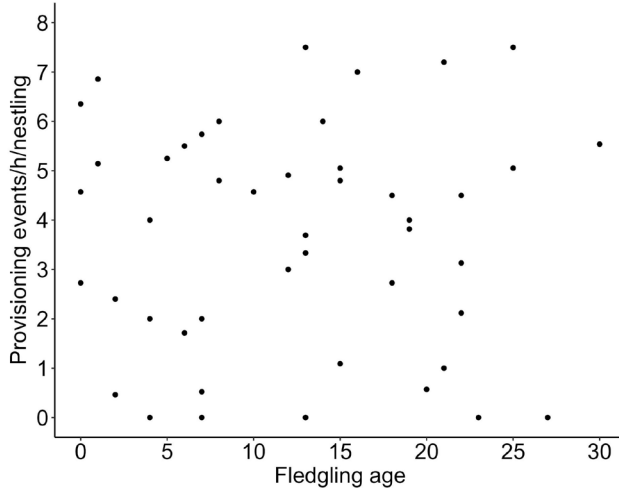


Figure 2. Food provisioning rate (events per fledgling per hour) in the Pale-breasted Thrush *Turdus leucomelas* in relation to fledgling age expressed as days from fledging.

not differ between families with uniparental or biparental feeding (Table 1). In families with uniparental care, this rate was 3.52 ± 2.33 feeding trips/h (range: 0–7.5 trips/h), under an effective observation time of 52.2 h distributed in 32 observation sessions (97.8 ± 19.0 min per session, range: 60–130 min). In families with biparental care, the provisioning rate

for the target fledgling was 2.33 ± 2.39 feeding trips/h (range: 0–7.00 trips/h), under an effective observation time of 24.5 h distributed in 15 observation sessions (70.0 ± 24.2 min per session, range: 35–110 min). We also did not observe a significant effect of brood size on food provisioning rates for the target fledgling (Fig. 3A, Table 1), which were 4.66 ± 2.41 (n = 9 sessions in three families), 2.95 ± 2.27 (n = 13 sessions in three families), and 3.30 ± 2.44 (n = 24 sessions in two families) for broods with one, two, and three fledglings, respectively.

Male vs. female in biparental food provisioning

In the 13 out of 15 sessions from families with biparental food provisioning when at least one feeding event was recorded, fledglings were fed solely by females in eight sessions, while males fed the fledglings alone in one session. Males and females were recorded provisioning fledglings together in three of the sessions, but they fed the same fledgling in only two of those observation sessions. Regarding brood division, our results were restricted to two families that met the prerequisites for assessing brood division between parents (i.e., with biparental food provisioning and more than one fledgling). We found little evidence of this due to the overall low participation of males in these particular cases. For instance, in one of these families, the male fed only one of the two fledglings a single time, while

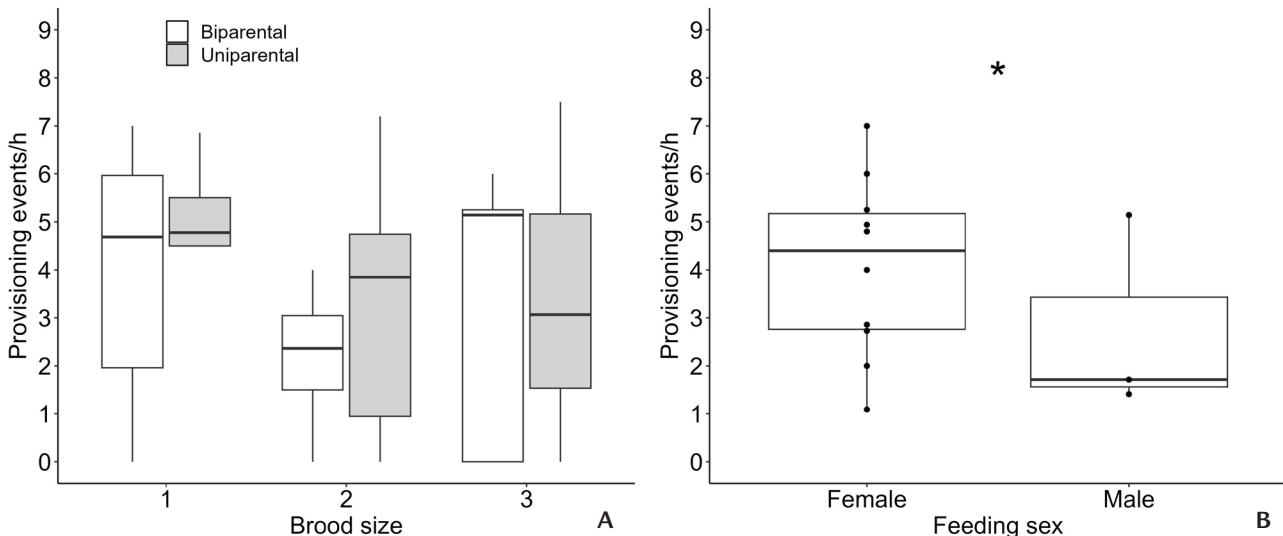


Figure 3. Food provisioning rate (events per fledgling per hour) in the Pale-breasted Thrush *Turdus leucomelas*. A) effect of brood size and mode of parental care division (uniparental/biparental), and B) by females and males in family groups with biparental food provisioning. Points in B represent the values comprised in the boxplots, in which the box delimit interquartile ranges, the vertical lines indicate minimum and maximum and the horizontal line denotes medians.

the female performed 18 feeding events in total. In the other family with three fledglings, the male fed only one of them seven times.

In families with biparental feeding, females and males did not differ about food provisioning rate (females: 4.06 ± 1.86 feeding trips/h; males: 2.75 ± 2.07 feeding trips/h; Fig. 3B) (Table 1). Provisioning rates also did not vary in relation to brood sizes or fledgling age in these families (Table 1).

Vocalization and foraging behavior of fledglings

The average number of scan samples per family was 81.8 ± 15.1 scans (range: 17–446 scans), which were distributed in 63.5 h of effective observation time during 41 observation sessions. We failed to detect fledgling behavior in 187 of the total 974 scan samples. The earliest foraging behaviors were observed on the same day fledglings were out of the nest, which were instances of social foraging, and at the sixth day after fledging occurred the first instances of sole fledgling foraging. Vocalizations were recorded for all fledgling ages in all but one (a fledgling with 27 days) observation session. Foraging frequency increased with fledgling age but was not related to the provisioning rate of food by parents (Fig. 4A, Table 2), while vocalization did not vary with fledgling age or the rate of food provisioning by parents (Fig. 4B, Table 2).

Table 2. Fledgling behavior changes in the pale-breasted thrush, *Turdus leucomelas*. Results of generalized linear mixed-effects models addressing the effect of fledgling age and the frequency of food provisioning by parents on the foraging and vocalization of fledglings (as binomial response variables).

Model structure	Estimate	Std. error	z	p
Foraging				
Intercept	-5.169	0.753	-6.864	< 0.001*
Fledgling age	0.084	0.018	4.662	< 0.001*
Food provisioning	0.001	0.041	0.031	0.975
Vocalization				
Intercept	-1.601	0.501	-3.192	0.001*
Fledgling age	0.022	0.013	1.694	0.090
Food provisioning	0.038	0.033	1.128	0.259

The number of food items delivered to fledglings was one in 92.1% of the 344 provisioning events, ranging from 1 to 5. Food items were identified in 45.9% of the provisioning events, being classified as “invertebrates” (e.g., earthworms, cicadas, winged termites, caterpillars, and other insects), “fruits”, and “others” (e.g., dog food, pieces of bread) (Fig. 5). As the fledglings became older, the proportion of unidentified food items decreased while the proportion of invertebrates increased (Fig. 6).

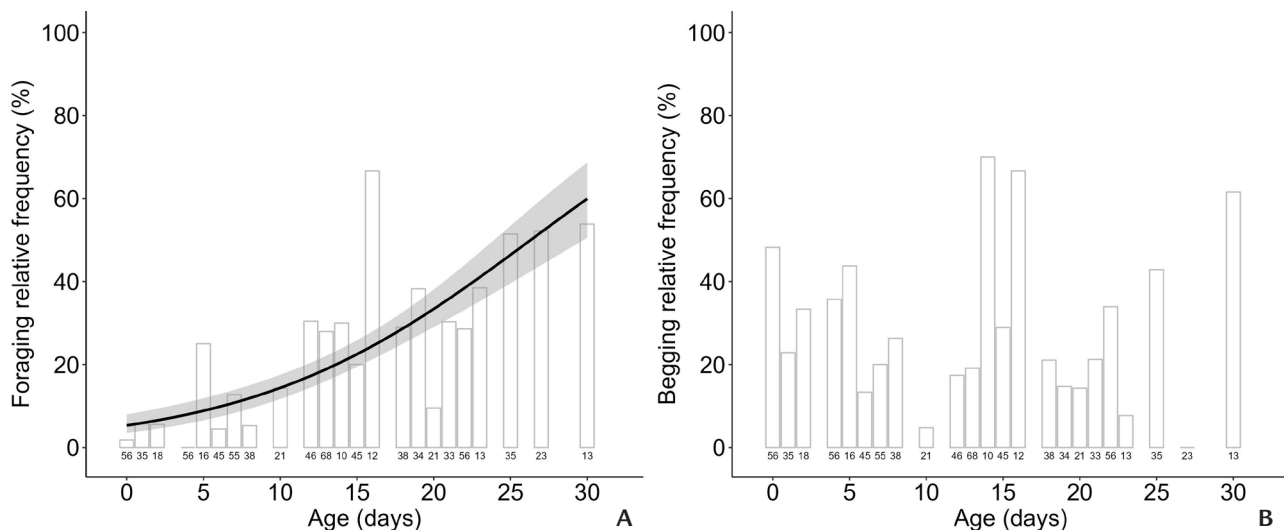


Figure 4. Age-related variation in the frequency of foraging and vocalization behaviors in fledglings of *Turdus leucomelas*. The curve in the panel A represents a significant logistic relationship between the variables, and its 95% confidence interval denoted by the shaded area. Bars in both panels represent the relative frequency of the behaviors followed by the number of scans (below bars) within 1-day age intervals ($n = 787$ in total), with fledgling age corresponding to the number of days after fledging.



Figure 5. Food provisioning to fledglings of the Pale-breasted Thrush *Turdus leucomelas*: (A) fledgling (front) swallowing a fruit delivered by the adult; (B) the fledgling (right) receives a piece of an arthropod.

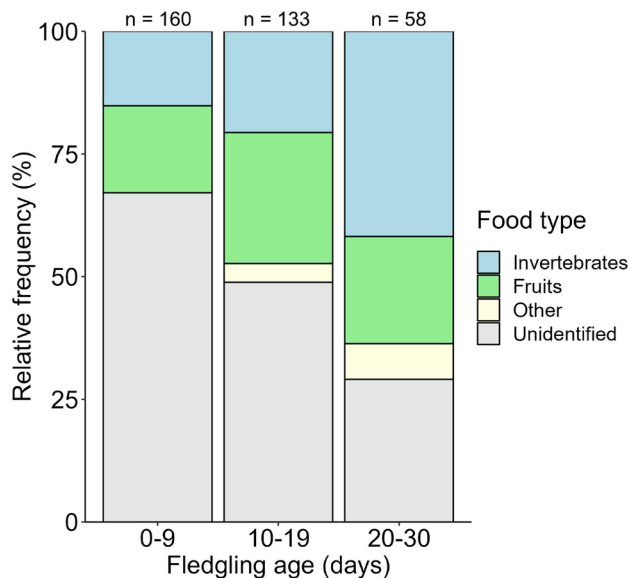


Figure 6. Relative frequency of food items delivered to *Turdus leucomelas* fledglings in relation to their age (days after fledging). Sample sizes are indicated above bars. “Other” refers to food items like dog food and pieces of bread.

DISCUSSION

Our study provides novel information regarding the largely unknown fledgling stage of passerines. We found similar food provisioning rates between families with uniparental and biparental food provisioning. Our expectation of an equitable parental investment between sexes in families where both parents fed the fledglings was then confirmed, as in other studies (e.g., Weatherhead and McRae 1990, Wilkin

et al. 2009, Gill and Haggerty 2012, Sánchez et al. 2018). In contrast, we unexpectedly found that food provisioning rates did not vary with brood size or age. Previous studies suggest that the parental effort to supply the energy demand of young is limited by different factors (Martin et al. 2000, Tinbergen and Verhulst 2000) and therefore we expected that the per capita food provisioning rate would be lower in large broods than in small broods. One potential explanation could be that this species has a small brood size variation (1–3 nestlings; Batisteli et al. 2021) compared to other species that can produce more fledglings per breeding attempt (e.g., Marques-Santos et al. 2015). With few fledglings, adult thrushes could easily adjust their food provisioning efforts.

We also found that the food provisioning rate by parents was constant across fledgling ages, rejecting our hypothesis. The food load for each feeding trip was usually a single food item. If there are adjustments to the energetic demand of growing fledglings by the parents, it does not seem to be done through increased feeding trip rates or food load. We suggest two potential explanations for this: 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. Although we have not assessed the size of food items delivered to fledglings, the variation in the size of food items might be a mechanism in the adjustment of parental food provisioning during the fledgling stage akin to what happens in other species (Carey 1990, Wiebe and Slagsvold 2014). Accordingly, we suppose that the inverse trends in the proportion of unidentified items and invertebrates as the fledglings aged (Fig. 6) are biased by our limitations in recognizing the smaller food items delivered in the early fledgling stage. Second,

fledglings might have supplied their increasing food demand by foraging themselves, which becomes more frequent and effective throughout the post-fledging stage (Weathers and Sullivan 2011). Despite the constant parental food provisioning, fledglings become more skilled and efficient in foraging and would be able to support any temporary increase in their own additional energetic demands, which should stabilize when they complete body and feather development. Considering that the development of foraging skills may vary among siblings, observing each fledgling with more detail across the entire fledgling period could also reveal different trends in parental food provisioning among the brood towards fledgling independence, which is beyond the focus of this study. Based on our data, we can state that fledglings are still being fed by their parents as long as we can observe them. Whether they are in fact dependent on parental provisioning (i.e., unable to supply themselves) during this whole period or if the food provided by parents merely supplements their energetic needs, especially as they get older, is an open question.

Although we did not find an increase in provisioning rate during the post-fledging stage with brood age, our data indicates that it did occur in the transition from the nesting to the post-fledging stages. Compared to the nesting stage, mean food provisioning rates in the post-fledging period for biparental feeding were 1.56 and 2.8 times higher for males and females, respectively (Haddad et al. 2024). This increase is within the range reported for other passerine species (With and Balda 1990, Ogden and Stutchbury 1997) and may reflect a higher food provisioning demand by fledglings compared to nestlings. Moreover, parental activity in the nest may be constrained by the risk of brood predation, as higher provisioning rates to nestlings are known to increase the cues of nest location for visually-oriented predators (Stutchbury and Morton 2001, Eggers et al. 2008, Martin et al. 2011, Ghalambor et al. 2013, Trillmich et al. 2016). Alternatively, fledglings may have greater value than nestlings, considering the accumulated energy expenditure by parents during the breeding cycle. This would induce parents to invest more by, in this case, performing higher food delivery rates in the post-fledging stage than in the nestling stage, as predicted by the parental investment theory (Redmond et al. 2009).

Brood division

Interestingly, we found a large variation in parental care arrangements (four arrangements in eight families), some with unknown underlying reasons for their occurrence. Male-only care and biparental care are in line with what was found in other Turdidae species, in which parental care ar-

rangements depend on the presence of simultaneous nesting events. For instance, when there are simultaneous nesting attempts, usually only males care for the fledglings, either for the majority or the whole post-fledging stage, while females lay and incubate a new clutch, as in European blackbirds, *Turdus merula* (see Edwards 1985), American robins, *Turdus migratorius* Linnaeus, 1766 (see Weatherhead and McRae 1990), and wood thrushes, *Hylocichla mustelina* (Gmelin, 1789) (see Rivera et al. 2000). When there is not a simultaneous nesting attempt, fledgling care would be divided between male and female (Rivera et al. 2000). Due to our modest sample size, we cannot discard that the low male participation in biparental care is a matter of individual characteristics.

In 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). It is thus uncertain if, in these cases, there was uniparental care directed to the missing fledgling. In addition, in one family for which we assumed to have female-only care in a brood of two fledglings, we observed the male caring for the non-target fledgling. Nevertheless, this episode was likely an exception since this male was not recorded delivering food to his fledglings during systematic observations, and therefore "female-only care" fits better the real proportion of male and female participation in this family. We cannot discard, however, that the same might have occurred in other families classified as male- or female-only care, so this terminology should be taken with caution and denotes, at least, the predominance of one sex over the other regarding post-fledging food provisioning.

Some of the cases of broods with multiple fledglings had a fledgling fed exclusively by one of their parents during observations (Fig. 1), a pattern found in other species (Rivera et al. 2000, Green and Cockburn 2001). Broods of a single fledgling were expected to be cared for 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 the variation in parental care strategy and our low sample size prevent us from completely discarding this possibility.

Final remarks

This study provides novel and valuable information on the difficult-to-investigate fledgling stage of a passerine

species. We found that parental food provisioning to fledglings was overall comparable between males and females as well as among families with uniparental and biparental fledgling care. Interestingly, parental investment in food provisioning did not influence the frequency of fledgling foraging, which increased as fledglings age towards nutritional independence. Future studies should identify if there is a pattern for parental choice of cared fledgling and investigate potential causes of food provisioning variation (e.g., geographic variation).

ACKNOWLEDGMENTS

We are grateful to everyone that helped on nest searching and monitoring. We thank Kristina Cockle and an anonymous reviewer for their valuable suggestions and the editors Claudia Hermes, Sionei R. Bonatto and Ricardo M.M. Rocha for the careful handling of our manuscript. AFB receives a postdoctoral grant #2020/12211-0, São Paulo Research Foundation (FAPESP) and MAP receives a research fellowship from the Brazilian Research Council (CNPq #304742/2019-8).

LITERATURE CITED

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JDM, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22(6): 711–728. <http://doi.org/10.1127/0941-2948/2013/0507>
- Anthonisen K, Krokene C, Lifjeld JT (1997) Brood Division is Associated with Fledgling Dispersion in the Blue-throat (*Luscinia s. svecica*). *The Auk* 114(4): 553–561. <https://doi.org/10.2307/4089274>
- Auer SK, Bassar RD, Fontaine JJ, Martin TE (2007) Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *The Condor* 109(2): 321–333. [https://doi.org/10.1650/0010-5422\(2007\)109\[321:BBO-PIA\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2007)109[321:BBO-PIA]2.0.CO;2)
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Batisteli AF, Sarmiento H, Pizo MA (2021) Nest reuse by Pale-breasted Thrushes reduces the chance of cowbird parasitism and allows earlier initiation of breeding. *Journal of Field Ornithology* 92(2): 105–114. <https://doi.org/10.1111/jofo.12363>
- Bonnevie BT (2004) Song and breeding observations of suburban Olive Thrushes (*Turdus olivaceus olivaceus*) in Grahamstown, South Africa. *Ostrich-Journal of African Ornithology* 75(3): 110–117. <https://doi.org/10.2989/00306520409485422>
- Carey M (1990) Effects of brood size and nestling age on parental care by male field sparrows (*Spizella pusilla*). *The Auk* 107(3): 580–586. <https://www.jstor.org/stable/4087922>
- Cockburn A (2006) Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences* 273(1592): 1375–1383. <https://doi.org/10.1098/rspb.2005.3458>
- Davanço PV, Oliveira LS, Sousa LM, Francisco MR (2013) Breeding life-history traits of the Pale-Breasted Thrush (*Turdus leucomelas*) in Southeastern Brazil. *Ornitologia Neotropical* 24: 401–411. [https://sora.unm.edu/sites/default/files/ON%2024\(4\)%20401-411.pdf](https://sora.unm.edu/sites/default/files/ON%2024(4)%20401-411.pdf)
- Edwards PJ (1985) Brood division and transition to independence in Blackbirds *Turdus merula*. *Ibis* 127(1): 42–59. <https://doi.org/10.1111/j.1474-919X.1985.tb05036.x>
- Eggers S, Griesser M, Ekman J (2008) Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behavioral Ecology* 19(5): 1056–1062. <https://doi.org/10.1093/beheco/arn063>
- Evans DR, Hobson KA, Kusack JW, Cadman MD, Falconer CM, Mitchell GW (2020) Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a Neotropical migratory songbird. *Ibis* 162(2): 331–344. <https://doi.org/10.1111/ibi.12727>
- Ghalambor CK, Peluc SI, Martin TE (2013) Plasticity of parental care under the risk of predation: How much should parents reduce care? *Biology Letters* 9(4): 20130154. <https://doi.org/10.1098/rsbl.2013.0154>
- Gill SA, Haggerty TM (2012) A comparison of life-history and parental care in temperate and tropical wrens. *Journal of Avian Biology* 43(5): 461–471. <https://doi.org/10.1111/j.1600-048X.2012.05637.x>
- Green DJ, Cockburn A (2001) Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* 70(3): 505–514. <https://doi.org/10.1046/j.1365-2656.2001.00503.x>
- Haddad RN, Batisteli AF, Ibáñez-Álamo JD, Pizo MA (2024) Sexual division of nestling parental care in the Pale-breasted Thrush (*Turdus leucomelas*). *Journal of Ornithology* 165(1): 193–202. <https://doi.org/10.1007/s10336-023-02100-9>
- Haverschmidt F (1959) Notes on the nesting of *Turdus leucomelas* in Surinam. *Wilson Bulletin* 71(2): 175–177. <https://sora.unm.edu/sites/default/files/journals/wilson/v071n02/p0175-p0177.pdf>

- Jones TM, Brawn JD, Ausprey IJ, Vitz AC, Rodewald AD, Raybuck DW, et al. (2020) Parental benefits and offspring costs reflect parent–offspring conflict over the age of fledging among songbirds. *Proceedings of the National Academy of Sciences* 117(48): 30539–30546. <https://doi.org/10.1073/pnas.2008955117>
- Kempnaers B (2022) Mating systems in birds. *Current Biology* 32(20): R1115–R1121. <https://doi.org/10.1016/j.cub.2022.06.066>
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82(13): 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lloyd P, Martin TE (2016) Fledgling survival increases with development time and adult survival across north and south temperate zones. *Ibis* 158(1): 135–143. <https://doi.org/10.1111/ibi.12325>
- López-Idiáquez D, Vergara P, Fargallo JA, Martínez-Padilla J (2018) Providing longer post-fledging periods increases offspring survival at the expense of future fecundity. *Plos One* 13(9): e0203152. <https://doi.org/10.1371/journal.pone.0203152>
- Marques-Santos F, Braga TV, Wischhoff U, Roper JJ (2015) Breeding biology of passerines in the subtropical Brazilian Atlantic Forest. *Ornitologia Neotropical* 26(4): 363–374. <https://pdfs.semanticscholar.org/9fca/b428c60eee9fd73770916756a63cb9c1a20.pdf>
- Martin TE, Martin PR, Olson CR, Heidinger BJ, Fontaine JJ (2000) Parental care and clutch sizes in North and South American birds. *Science* 287(5457): 1482–1485. <https://doi.org/10.1126/science.287.5457.1482>
- Martin TE, Lloyd P, Bosque C, Barton DC, Biancucci AL, Cheng YR, Ton R (2011) Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. *Evolution* 65(6): 1607–1622. <https://doi.org/10.1111/j.1558-5646.2011.01227.x>
- Martin TE, Tobalske B, Riordan MM, Case SB, Dial KP (2018) Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Science Advances* 4(6): eaar1988. <https://doi.org/10.1126/sciadv.aar1988>
- Middleton HA, Green DJ, Krebs EA (2007) Fledgling begging and parental responsiveness in American dippers (*Cinclus mexicanus*). *Behaviour* 144(5): 485–501. <https://doi.org/10.1163/156853907780713064>
- Møller AP (2003) The evolution of monogamy: mating relationships, parental care and sexual selection. In: Reichard UH, Boesch C (Eds) *Monogamy: Mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, 29–41.
- Naef-Daenzer B, Widmer F, Nuber M (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70(5): 730–738. <https://doi.org/10.1046/j.0021-8790.2001.00533.x>
- Ogden LJE, Stutchbury BJM (1997) Fledgling care and male parental effort in the Hooded Warbler (*Wilsoniactritina*). *Canadian Journal of Zoology* 75(4): 576–581. <https://doi.org/10.1139/z97-071>
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org>
- Redmond LJ, Murphy MT, Dolan AC, Sexton K (2009) Parental investment theory and nest defense by Eastern Kingbirds. *The Wilson Journal of Ornithology* 121(1): 1–11. <https://doi.org/10.1676/07-166.1>
- Rivera JHV, Haas CA, Rappole JH, McShea WJ (2000) Parental care of fledgling wood thrushes. *Wilson Bulletin* 112(2): 233–237. [https://doi.org/10.1676/0043-5643\(2000\)112\[0233:PCOFWT\]2.0.CO;2](https://doi.org/10.1676/0043-5643(2000)112[0233:PCOFWT]2.0.CO;2)
- Russell EM (2000) Avian life histories: Is extended parental care the southern secret? *Emu* 100(5): 377–399. <https://doi.org/10.1071/MU0005S>
- Russell EM, Yom-Tov Y, Geffen E (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* 15(5): 831–838. <https://doi.org/10.1093/beheco/arh088>
- Sánchez NV, Vargas-Castro LE, Barrantes G (2018) Nestling feeding, nest success, and notes of parental care in the Clay-colored Thrush (*Turdus grayi*): the role of females and males. *The Wilson Journal of Ornithology* 130(2): 437–444. <https://doi.org/10.1676/17-002.1>
- Schaefer HC, Eshiamwata GW, Munyekenye FB, Böhring-Gaese K (2004) Life-history of two African Sylvia warblers: Low annual fecundity and long post-fledging care. *Ibis* 146(3): 427–437. <https://doi.org/10.1111/j.1474-919X.2004.00276.x>
- Sick H (1997) *Ornitologia brasileira*. Nova Fronteira, Rio de Janeiro, 912 pp.
- Stutchbury JM, Morton ES (2001) *Behavioral ecology of tropical birds*. Academic Press, Cambridge, 208 pp.
- Tarwater CE, Brawn JD (2010) The post-fledging period in a tropical bird: Patterns of parental care and survival. *Journal of Avian Biology* 41(4): 479–487. <https://doi.org/10.1111/j.1600-048X.2010.05006.x>

- Thompson AM, Raihani NJ, Hockey PAR, Britton A, Finch FM, Ridley AR (2013) The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis. *Proceedings of the Royal Society B: Biological Sciences* 280(1760): 20130558. <https://doi.org/10.1098/rspb.2013.0558>
- Tinbergen JM, Verhulst S (2000) A fixed energetic ceiling to parental effort in the great tit? *Journal of Animal Ecology* 69(2): 323–334. <https://doi.org/10.1046/j.1365-2656.2000.00395.x>
- Trillmich F, Spiller I, Naguib M, Krause ET (2016) Patient parents: do offspring decide on the timing of fledging in zebra finches? *Ethology* 122(5): 411–418. <https://doi.org/10.1111/eth.12490>
- Valcu M, Valcu C, Kempenaers B (2023) Extra-pair paternity and sexual dimorphism in birds. *Journal of Evolutionary Biology* 36(5): 764–779. <https://doi.org/10.1111/jeb.14172>
- Weatherhead PJ, Mcrae SB (1990) Brood care in American robins: Implications for mixed reproductive strategies by females. *Animal Behavior* 39(6): 1179–1188. [https://doi.org/10.1016/S0003-3472\(05\)80790-0](https://doi.org/10.1016/S0003-3472(05)80790-0)
- Weathers WW, Sullivan KA (2011) Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* 59(3): 223–246. <https://doi.org/10.2307/1942600>
- Wiebe KL, Slagsvold T (2014) Prey size increases with nestling age: are provisioning parents programmed or responding to cues from offspring? *Behavioral Ecology and Sociobiology* 68: 711–719. <https://doi.org/10.1007/s00265-014-1684-0>
- Wilkin TA, King LE, Sheldon BC (2009) Habitat quality, nestling diet, and provisioning behavior in great tits *Parus major*. *Journal of Avian Biology* 40(2): 135–145. <https://doi.org/10.1111/j.1600-048X.2009.04362.x>
- With KA, Balda RP (1990) Intersexual variation and factors affecting parental care in western bluebirds: a comparison of nestling and fledgling periods. *Canadian Journal of Zoology* 68(4): 733–742. <https://doi.org/10.1139/z90-106>
-
- Submitted: June 29, 2023
Accepted: December 26, 2023
Editorial responsibility: Claudia Hermes
-
- Author Contributions**
RNMH: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. AFB: Formal Analysis, Writing – original draft, Writing – review & editing. JDIA: Conceptualization, Methodology, Supervision, Formal Analysis, Writing – original draft, Writing – review & editing. MAP: Conceptualization, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.
- Competing Interests**
The authors have declared that no competing interests exist.
- Data availability statement**
The data that support the findings of this study are available from the corresponding author, upon reasonable request.
- How to cite this article**
Haddad RNM, Batisteli AF, Ibañez-Álamo JD, Pizo MA (2024) Post-fledging parental care in the pale-breasted thrush, *Turdus leucomelas* (Passeriformes: Turdidae). *Zoologia* 41: e23035. <https://doi.org/10.1590/S1984-4689.v41.e23035>
- Published by**
Sociedade Brasileira de Zoologia at Scientific Electronic Library Online (<https://www.scielo.br/zool>)
- Copyright**
© 2024 The Authors.