UNIVERSIDADE FEDERAL DO PARANÁ

ALEJANDRO RESTREPO GONZÁLEZ

REPRODUCTION IN MAROON-BELLIED PARAKEET AND THE USE OF NEST BOXES AS A TOOL FOR CONSERVATION

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Orientador: Prof. Dr, James J. Roper

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **ALEJANDRO RESTREPO GONZALEZ** intitulada: **Reproduction in Maroon-bellied Parakeet and the use of nest-boxes as a tool for conservation**, após terem inquirido o aluno e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

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RESUMO

A família dos papagaios (Psittacidae) está entre as famílias de aves mais ameaçadas, devido ao comércio ilegal e degradação do habitat. A maior diversidade de papagaios está no Brasil, incluindo os periquitos do gênero *Pyrrhura*. Das 31 espécies do gênero, 15 estão ameaçadas, no total 17 espécies ocorrem no Brasil, 8 das quais estão ameaçadas. Apesar destas ameaças, a reprodução e as dinâmicas populacionais são desconhecidas para estas espécies. A Tiriba-de-testa-vermelha (*Pyrrhura frontalis*) é comum no sudeste brasileiro, onde utilizamos caixas-ninho para estudar a sua reprodução e o crescimento de filhotes, no município de Piraquara, Paraná. A compreensão da biologia de espécies comuns pode fornecer informações úteis para a conservação de espécies relacionadas e ameaçadas, que são difíceis de serem estudadas. Monitoramos ninhos durante três temporadas reprodutivas (2016 - 2018) para determinar o sucesso reprodutivo e como este pode ser afetado por variáveis como ano, período, tamanho da ninhada, cuidado parental e abundância de alimento. Medimos o crescimento de filhotes nas temporadas de 2016 e 2017, verificando regularmente os ninhos e medindo os filhotes (peso e comprimento de bico, tarso, asa e cauda). Utilizamos a equação do Richard para modelar as curvas de crescimento e comparar o crescimento em diferentes situações. Alguns filhotes foram parasitados por moscas (um ninho em cada temporada em 2016 e 2017), estimamos o crescimento destes filhotes para medir o efeito da miíase. Alimentamos experimentalmente os filhotes de dois ninhos em 2017 para testar o efeito da limitação de alimento. Comparamos as curvas de crescimento de filhotes controle com as dos alimentados e os parasitados. Nas três temporadas registramos 36 ninhadas de *P. frontalis*, monitoramos 191 ovos e estimamos o crescimento em 68 filhotes, descobrimos que a reprodução começa em setembro e termina em março. Os casais podem se reproduzir mais de uma vez em cada temporada e os indivíduos de um ano de idade podem se reproduzir com sucesso. Raramente, ajudantes podem ser encontrados nos ninhos (encontramos um trio criando filhotes em 2018). O crescimento foi independente do alimento suplementado, enquanto que miíase causou redução no crescimento, com maior efeito no crescimento das penas. Dois filhotes morreram pela miíase e quatro morreram acidentalmente asfixiados, aparentemente pelos irmãos mais velhos. A abundância de alimento não parece limitar o tamanho da ninhada ou o crescimento de filhotes, consequentemente, nosso estudo não fornece informações que ajudem a entender a assincronia de eclosão ou a redução da ninhada. A ampla variação no tempo de nidificação sugere que, talvez em algum nível, alimento pode afetar o tempo de reprodução, porém outros estudos serão necessários para resolver esse problema. As abelhas também tentam aninhar nas caixas-ninho, evitá-las ou eliminá-las será uma parte importante do uso de caixas-ninho para conservação. Não registramos predação de ninhos durante o estudo, e assim o uso de ninhos artificiais pode ser uma ferramenta eficaz no estudo e conservação em *Pyrrhura.*

Palavras-chave: *Pyrrhura frontalis.* Sucesso reprodutivo. Curvas de crescimento. Parasitismo de moscas. Ninhos artificiais.

ABSTRACT

The parrot family (Psittacidae) is among the most threatened of bird families due to illegal trade and habitat loss. The greatest diversity of parrots is found in Brazil and includes the parakeet genus *Pyrrhura*. Of the 31 species in the genus, 15 are threatened, and of those, 17 species are found in Brazil, eight of which are threatened. Despite these threats, reproduction and population dynamics are unknown for this and most species of *Pyrrhura*. The Maroon-bellied Parakeet (*Pyrrhura frontalis)* is common in southern Brazil where we used nest-boxes to study breeding and nestling growth, in the municipality of Piraquara, Paraná. Understanding biology of common species can provide useful information for conservation of closely-related but threatened species that are themselves difficult to study. We monitored nests during three breeding seasons (2016 – 2018) to determine reproductive success and how it may be influenced by variables such as year, timing, clutch size, parental effort, and food abundance. We measured nestling growth in the 2016 and 2017 seasons, by regularly checking nests and measuring nestlings (bill, tarsus, wing and tail lengths, and weight). We use the Richards' equation to model growth curves and to compare growth in different situations. Several nestlings suffered myiasis due to flesh-fly larvae (in one nest box each in 2016 and 2017) and we estimated growth in these nestlings to measure the effects of myiasis. We experimentally fed nestlings in two nests in 2017 to test the effect of food limitation. We compared growth curves between control nestlings and those with supplemented food and those with myiasis. We registered 36 broods of *P. frontalis* in the three seasons. We monitored 191 eggs and estimating growth in 68 nestlings, we found that the breeding season of this species began in September and ended in March. Pairs may breed more than once each season and individuals can successfully breed at one year of age. Rarely, apparently helpers may be found at nests (we found one threesome rearing young in 2018). Growth was independent of food supplementation while myiasis caused reduced growth, with the effect being greatest on feather growth. Two nestlings died due to myiasis and four young died from apparent accidental asphyxiation by their larger sibling. Food abundance does not seem to limit either clutch size or nestling growth and as a consequence, our study does not provide information that will help understand hatching asynchrony and brood reduction. The wide variation in timing of nesting suggests that perhaps on some level, food may influence that timing, but other studies will be required to address that issue. Honey bees also find the boxes and often try to nest in them and avoiding or eliminating bees will be an important part of using nest boxes for conservation. Nest predation was non-existent during this study, and so the use of artificial nests can be a very effective tool in studying and conservation of *Pyrrhura*.

Keywords: *Pyrrhura frontalis*. Reproductive success. Growth curves. Fly parasitism. Artificial nests.

SUMMARY

CHAPTER I: BREEDING BIOLOGY OF *PYRRHURA FRONTALIS* IN SOUTHERN BRAZIL

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ABSTRACT

About half the species of parakeets in the genus *Pyrrhura* are threatened or endangered (15 of 31 species). More than half the species are found in Brazil (17 of 31), eight of which are endangered due to the illegal pet trade and habitat loss. Five of these species are endemic to Brazil and whose habitat is currently very fragmented. Yet, breeding biology and population dynamics are poorly known for all species in the genus. Here we used nest-boxes to study reproduction in the Maroon-bellied Parakeet (*Pyrrhura frontalis*) as a model species to begin filling the gap about the natural history of the genus and to make recommendations for conservation. We used nest-boxes that we built during three years in the municipality of Piraquara, state of Paraná, southern Brazil. With regular nest checks (weekly in 2016, otherwise every other day), we determined dates of laying, hatching and fledging, along with clutch size and hatching success. We numbered, measured (once) and weighed (at each check) eggs, beginning on or near (< 24 h) lay date. Nestlings were uniquely marked, measured and weighed at each check. We used these dates and measurements to test whether box of origin, lay date, laying sequence, clutch size and egg size were associated with nest success or size of offspring at time of fledging. Breeding begins in September and ends in March, for a total of about 160 days. With a total of 191 eggs the modal clutch size was six eggs (range 2 – 8). Around 71% of the eggs hatched and 92% of the nestlings fledged (mode of 3 per box, range 1 - 7). In 36 nesting attempts during three years, nest success and quality of fledglings were independent of all variables. Flesh-flies (genus *Philornis*) infested several nestlings, but because we removed these larvae, only two young died in 2016. An additional seven nestlings died, not due to siblicide or starvation, but rather four died apparently due to accidental asphyxiation or for unknown reasons. Parakeets can breed during their first year after birth, and pairs may breed more than once within any given breeding season. Cooperative breeding, with one helper, was observed in one nest box in 2018. The eggs success was dependent on the laying order and independent of the clutch size and the breeding season. If all species in the genus have commonalities with the

Maroon-bellied Parakeet, then they have potential for rapid recovery, especially with the use of nest boxes, which prove to be very useful tools for research and conservation.

Keywords: Conservation. Nest-box. Parakeets. Reproductive success.

INTRODUCTION

Parakeets in the genus *Pyrrhura* comprise 31 Neotropical species, over half of which (17) are found in Brazil, where eight are threatened or endangered (HBW and BirdLife International 2018, ICMBio 2016). The principal threats are wildlife traffic and habitat loss due to agricultural development (BirdLife International 2018). Despite these threats, little is known about the natural history in the wild of these species. Five of the endangered species (*P. cruentata*, *P. griseipectus*, *P. lepida*, *P. leucotis*, and *P. pfrimeri*) are endemic to Brazil. Because their populations tend to be small, they are potentially subject to rapid population decline, especially in their severely fragmented ranges in which degradation and habitat loss continue (BirdLife International 2018). Only two have been studied in some detail. *Pyrrhura griseipectus* is under study and is subject to *ex situ* conservation (captive breeding) and their status was recently changed from Critically Endangered to Endangered (BirdLife International 2018). *Pyrrhura cruentata*, whose entire range is in protected areas, continues to suffer rapid population decline (BirdLife International 2018).

Deforestation for agriculture and the pet trade are both a constant threat for Neotropical parrots and so some populations tend to be more threatened than others, with uncertain consequences for metapopulation dyanamics of these species (Berkunsky et al., 2017). Because few species have been studied in the wild, understanding the life history of *Pyrrhura* in general should be the first step to informing management plans (Jones, 2004). Breeding biology especially must be studied to understand population dynamics and to inform conservation measures. Studying these details in endangered populations can be problematic, and so information about closely related species can be useful and informative (Green, 2004; Ortiz-catedral, Hauber, & Brunton, 2013).

The Maroon-bellied Parakeet (*P. frontalis*) is found in southeastern Brazil and adjacent regions in Paraguay, Uruguay and Argentina (Juniper and Parr 1998, Guix, Martín, & Mañosa, 1999). This parakeet is the most abundant species of *Pyrrhura* and thus provide an opportunity to better understand the natural history of the genus. We used nest boxes to study the breeding biology of *P. frontalis* during three breeding seasons, to the aim of describing the clutch size, the hatching and fledging success and the factors that can affect this success (laying order, clutch size, initial date of the nest, or eggs size). We use our results to provide important information for understanding reproduction in the genus *Pyrrhura* to offer suggestions for the conservation of threatened congeners.

METHODS

We built and placed nest boxes in a rural area in the municipality of Piraquara, state of Paraná (Brazil, 25º 31'18'' S, 49º5'33'' W), beginning in 2010. Here, we describe three breeding seasons when birds were studied more systematically (2016, 2017 and 2018). Ten boxes were available in 2016 with six boxes added in 2017. Boxes were built with pine on all sides and a plastic roof that provided an overhang on all sides of about 10 cm, with a bit more (20 cm) over the perch in front. We found that this roof protected the wood and boxes last longer. A sliding door in the back of the boxes was used for nest monitoring. Inside the box, we lined the nest chamber with another layer of pine cut to fit, which provided adults and nestlings with material to gnaw. We found in previous years that the parakeets often gnawed their way through the boxes, which we then had to repair. Within the nest chamber we added 5 - 8 cm depth of wood shavings (commercially made for lining cages of small mammals). We added a 5 – 8 cm long foyer to the entrance of the box to also reduce predation likelihood (Figure 1A, B).

We used a pulley system to hang the boxes, usually between two trees that provided the support of the pulleys and the line from which the box was suspended. The line was tied to a tree at the appropriate height (3 – 5 m), then passed through a ring at the top of the box. On the next tree the pulley was tied and the line was fed through the pulley and then back to the ground. A nail or cleat was attached to the tree at the base to tie the line once the box was raised to hold it in place

(Figure 1C). The way the line went through the ring at the top of the box prevented the box from rotating.

We monitored boxes prior to the breeding seasons when we checked for signs of nesting in boxes where we observed visiting, we continued monitoring boxes when we found one or more eggs, weekly in 2016 and every other day during 2017 and 2018 until the last nestling fledged. We checked boxes until there were no further signs of reproduction and thus established dates of the end of the breeding season. Checking the boxes every other day we determined laying and hatching order in 2017 and 2018.

All eggs were numbered and weighed (digital balance with 0.01 g precision) at every visit. All eggs were photographed at least once and then were measured using the program ImageJ (Version 1.50i, Wayne Rasband, National Institute of Health) and the egg measuring tool (Troscianko, 2014). We determined egg viability by candling (Lokemoen & Koford, 1996) after the first week of laying.

We monitored nestlings until just before fledging in 2017 to determine their age at fledging. In 2017 nestlings were measured every other day, beginning two days after hatching to around 38 - 50 days after hatching. Upon hatching, each nestling within a box was uniquely marked by trimming a nail for measuring growth rates (in 2017). At that time, nestlings were weighed and photographed for later measuring on the computer using Image J. Birds were photographed in standardized positions with rulers parallel to the plane of the structure (bill, tarsus, wing and tail lengths) to be measured. Standardizing photographs with the ruler allowed us to process each nest much more rapidly than if we had measured each nestling at the nest. Also, precision of measurement was increased by measuring individuals in photos. We also captured, color-banded, measured (photographically) and weighed seven adult pairs breeding in 2017. During nest box visits we often observed adults, nearby, leaving or arriving at nest boxes; we then observed those individuals to identify them and the box they used.

From these data, we estimated the incubation and nestling intervals, and the beginning and end of the nesting season (breeding season length). We then tested whether there were relationships between laying date, clutch size, egg measurements, nesting period and nest box and eventual nesting success using regressions and anovas (Analysis of variance). Duration of laying and incubation intervals were only calculated with nests at which we observed the interval from start to finish, with a precision of ± 1 day. We tested whether clutch size or year influence fledging success and whether laying order influences nestling survival. We also tested for a correlation between egg volume and nestling size at fledging. We compared offspring size at fledging with adult size to determine whether offspring already reached asymptote or if further growth was required to read adult size. Statistical analyses were carried out in R (version 3.5.1, R Core Team 2018).

RESULTS

BREEDING BIOLOGY

Our sample includes 36 broods with a total of 196 eggs in the 2016, 2017 and 2018 breeding seasons (Table 1). Six nests were abandoned and 126 eggs hatched (71% of incubated eggs) and 116 nestlings fledged. The likelihood of fledging was independent of year (χ^2 = 3.39, df = 2, p = 0.184) and clutch size (χ^2 = 4.84, df = 4, p = 0.304). However, being the last egg in larger clutches was associated with accidental mortality and was dependent on laying order (χ^2 = 16.03, df = 7, p = 0.025), the last eggs laid were less likely to hatch and fledging (the sixth, seventh and eighth eggs laid). A total of 51 eggs did not hatched, which 47 were infertile and the remaining four had dead, but developed, embryos. The mode of clutch size was 6 eggs (range 2 – 8). The smallest clutch size in our study was two eggs (only one brood) and, for unknown reasons, this nest was abandoned just after the first egg hatched (and was excluded from analyses). Therefore, the smallest clutch size was four eggs in three nests of 2016 and one nest in 2017 and 2018, just two nests had eight eggs (one in 2016, one in 2018, Figure 2A).

Eggs tended to be laid every other day. In 2017 and 2018 (122 eggs in 21 successful broods, of which 101 allow calculating intervals), 81 eggs (80%) had 2-day intervals in laying between them, three eggs (3%) had 3-day intervals, 16 (16%) eggs followed the previous egg after four days, and one egg had 5-day intervals.

Eggs hatched within ≤ 24h in seven broods, and all were the first two eggs laid, the others eggs hatched in the same sequence as they were laid. However, because of 36 eggs did not hatch, the effective interval between siblings was often more than two days. The age interval between siblings, therefore, was three days for six nestlings, four days for 16 nestlings and six days for one nestling.

Incubation lasted 20 - 25 days, with a mode of 23 days (N = 88, Figure 2B). Because of unhatched eggs, broods had a mode of four nestlings (range 1 – 8, Figure 2C). We estimated the interval from hatching to fledging more precisely in 2017 and on average was 44 days (SE = 0.52 d, min 39 d, max 52 d, $N = 31$, Figura 2D). Due to mortality, the number of fledged young had a mode of three (1 – 7, Figure 2E).

Nine nestlings died, three of which were in two nests in 2016 season, one in 2017 and five in 2018. One mortality was in a three-egg clutch, two were the first to hatch in two clutches of four, four were the last in clutches of six (1), seven (2), and eight (1), and two were due to myiasis (the first and the last nestling). The four that were the last to hatch in clutches of 6, 7 and 8, died due unknown reasons, but not starvation as their crops were full. We observed nestlings huddled very closely together when the temperature was cool, with the smallest nestling in the middle of, or beneath, the huddle and we suspect they were inadvertently asphyxiated by their larger siblings. Only one, in a clutch of three, may have died due to starvation (crops were empty when they were found dead). The other deaths were of unknown causes, but not due to sibling interactions because they were not the smallest nestlings.

We registered the behavioral and determined the sex considering that females stay in the nest during the laying and hatching periods and that males visiting constantly the nest to fed the females. Three color-banded individuals removed their bands after laying eggs. The other seven of 10 color-banded birds remained banded and were observed nesting in 2017 and 2018. Three pairs (with color-banded females) nested twice during the same breeding season. Two of those pairs used different boxes in 2017, the first brood of one of them began 29 September 2017 and had five eggs. All eggs were infertile and we removed them 24 days after the last egg was laid. That pair nested in a different box on 15 November and again laid five eggs, two of which were infertile. Another pair began the first brood on 19 September 2017 and laid six eggs, the last three of which were infertile. Eighteen days after those three young fledged (15 December), this pair started their second brood with four eggs in another box, all of which survived to fledging. One female (colored-banded) had two clutches in 2018 in the same box, the first began on 13 September and had six nestlings. The second brood began on 14 December (approximately 20 days after finishing the first brood) but was abandoned with four eggs due to bees invasion on the end of December.

One female of 2018 season laid seven eggs (beginning on 13 September), and only the first egg hatched (6 October). We removed the others eggs after they were determined to be infertile or dead and 13 days later the female began laying again, with the first nestling still in the nest. This second clutch was of six eggs, four eggs hatched, three of which fledged. The first nestling at hatching of the second brood died due to unknown causes, one egg was cracked and the embryo died, and one egg was infertile.

Three nesting pairs included at least one individual that was born the previous breeding season (color-banded as a nestling). In 2017 two pairs included males born in 2016 (females were unbanded). One of those pairs abandoned their nest after fighting with a pair that occupied a nearby box, while the other successfully reared four offspring. In 2018, one box was occupied by three individuals (two of which were banded in 2017) that apparently shared in nest care. The laying eggs began on 3 October and complete a clutch of seven eggs, from which six young fledged. The three individuals were observed searching a box to nesting, after choosing the box, we observed they coming and going from the box throughout the duration of the nesting, from incubation through fledging.

Three pairs used the same boxes in 2017 and 2018. We observed that these three pairs nesting at the end of the season of 2017 and approximately seven months later, at the beginning of the 2018 season, they again nested. One pair had two successful broods in 2017 (using different boxes and raised three and four nestlings respectively), the second brood completely left the nest around 25 February 2018. The same pair initiated a new nest in the same box on 17 September 2018, which had seven eggs and resulted in five nestlings. Another pair also nested twice in 2017, but the first was of five infertile eggs. The second nest ended 7 February 2018 (three nestlings). This pair nested again in the same box 17 September 2018 and successfully reared three young. Finally, the latest nesting pair (of 2017) finished on 11 March 2018 (two nestlings). They initiated a nest 27 September 2018 (six nestlings).

BREEDING SEASON

Breeding season length as measured from the date of the first egg laid to that of the last fledging, was 164 days in 2016 (20 September 2016 – 3 March 2017), 182 days in 2017 (15 September 2017 – 16 March 2018), and 126 days in 2018 (9 September 2018 - 13 January 2019). More eggs were laid between 9 September and 18 October. The latest date of egg laying was between 3 November and 30 December (Figure 3). The mean nest interval, as the interval between the laying of the first egg and fledging of the youngest nestling, was 74 days. The minimum interval was 66 days in a nest with only one nestling, and the longest interval, 84 days, was in a nest with three nestlings that had myiasis, perhaps causing a delayed fledging. The longest interval for nests without myiasis was 79 days for a nest with six nestlings. In the pair that had two broods in 2017, the first lasted 69 days (3 nestlings) and the second 72 (4 nestlings). With an 18 day interval between fledging and laying, this pair spent 159 in breeding activity and had a total success of seven young. Nesting interval was not simply a linear relationship such that it was a fixed number of days, plus 2 days for each egg laid (generating a regression slope of 2), but rather the per-nestling-interval declined as the number of nestlings increased (for nestlings that fledged: interval = 68.5 + 1.455 * individuals, $F_{1, 27} = 13.1$, $r^2 = 0.301$, $p = 0.001$, for number of nestlings that hatched: interval = 69.0 + 1.250 * individuals, $F_{1, 27} = 10.7$, $r^2 = 0.257$, $p = 0.003$, and original clutch size: interval = 67.6 + 1.164 * individuals, $F_{1, 27} = 3.61$, $r^2 = 0.085$, $p = 0.068$).

EGG AND NESTLING MEASUREMENTS

Average egg weight within 24 h of laying was 6.06 g (SE = 0.07 g, range 4.88 - 7.12 g, *N* = 47). Average egg volume was 5913 mm^3 (SE = 91.8, range 4470 – 7815 mm^3). Average egg length was 26.23 mm (SE = 0.15 mm, range 23.03 - 28.37 mm) and width was 20.91 mm (SE = 0.14 mm, range 19.23 - 23.07 mm). During incubation, eggs lost an average of 1.07 g (SE = 0.06, 18% of the initial egg weight), and so final egg weight varied from 2.84 to 5.90 g (mean = 4.94 g, SE = 0.08 g, *N* = 57). Egg size (as volume) was independent of the date of laying ($r_{Spearman} = -0.125$, df = 28, $p = 0.187$).

At hatching (0-2 days old), nestling weight averaged 5.38 g (SE = 0.18, range 3.71 - 7.04 g, *N* = 26). Bill length averaged 5.2 mm (SE = 0.12, range 4.3 - 6.1, *N* = 14), and tarsus length averaged 6.4 mm (SE = 0.14, range 5.3 - 7.4, *N* = 14). Average weight at fledging (38-44 days old) was 81.68 g (SE = 0.82, range 72.34 - 92.64, *N* = 31). At fledging, bill length averaged 13.7 mm (SE = 0.13, range 12.0 – 15.2, *N* = 31), tarsus length 16.3 mm (SE = 0.03, range 16.1 – 16.6, *N* = 28), wing length 117 mm (SE = 0.93, range 105.5 – 127.9, *N* = 31) and tail length 92.2 (SE = 1.58, range 70.7 – 115.9, *N* = 31). Weight and tarsus length of nestlings at fledging was equal to that of adults (weight: $t = 1.30$, df = 43, $p = 0.100$, tarsus length: $t = 0.72$, df = 40, $p = 0.236$). Bill length was only 1.8 mm larger in adults than fledglings (15.5 mm in adults and 13.7 in nestlings, $t = 7.72$, df = 43, $p < 0.005$). Both wing and tail lengths were greater in adults, but wing length was less than

4% smaller in fledglings (5 mm shorter, 122 mm in adults and 117 mm in nestlings, $t = 2.83$, df = 43, $p < 0.005$), while tail length was 30% shorter (40.9 mm shorter, 133.1 mm in adults and 92.2 mm in nestlings, $t = 15.00$, df = 40, $p < 0.005$). Fledgling size at the time of fledging was independent of egg size (as volume, r = -0.39, df = 28, $p = 0.982$) and so larger eggs did not translate to larger offsprings.

USE OF NEST-BOXES

Parakeets nested in14 of the 16 available boxes during the three years of study (only 10 available boxes in 2016), for a total of 36 clutches (Table 1). One box with one egg and one hatchling was abandoned in 18 December 2016 (approximately 24 days after the first egg was laid). Two nests that were near each other were abandoned in 2017. At these boxes, we observed agonistic interactions, including direct body contact, between the two pairs on October 13. Two eggs were found pierced on 15 October when we removed both eggs, and subsequently, we found another egg laid on 17 October. This egg was incubated and hatched on 8 November, but the nestling was abandoned around 30 November (21 days after hatching). The other pair in that interaction laid two eggs which were abandoned on 15 October. Three nests were abandoned during laying in 2018, due to invasion of the boxes by honey bees (*Apis mellifera*), on 1 October, 20 and 28 December.

In addition to the boxes abandoned because of the bees, two additional boxes were being invaded by bees when we interceded and drove the bees away and the nests were successful. One was invaded 1 October 2018 at laying of the fifth egg, and while the female was apparently stung, she laid another egg and continued nesting. The other nest was being invaded 4 December, when six nestlings were near fledging. Another 4 boxes were occupied by the bees, which we then eliminated using a commercially available fogging insecticide. Honey bees are invasive species in Brazil and as boxes were to be used by birds, we have noted over the years that if left unchecked, all boxes would soon be occupied by honey bees.

We found some nestlings parasitized by flesh-flies in the genus *Philornis* sp. (Diptera, Muscidae). In 2016 one box had four parasitized nestlings, two of which died 2 - 4 days after hatching. The other two (the second and the third in sequence) survived, probably because we began removing larvae at every nest check over an interval of three weeks. Five nests were infested in 2017, most of which were noted at only one nest check. In one box the flies remained a problem, and we checked for larvae every other day over an interval of 18 days, during which time we removed 10 larvae in three occasions. Larval growth and development was very rapid, and often we removed very large larvae just two days after we removed all larvae that we previously found. We found very few fly larvae in two nests of 2018, comprising four nestlings in one box (9 - 16 November) and two of four nestlings in another nest (23 November), neither of which continued to have larvae after these dates.

DISCUSSION

We found that the Maroon-bellied Parakeet may often have more than one nest per year, allowing a surprisingly large potential annual fecundity with 10+ offspring, depending on clutch size. For example, a pair had two nests in 2017, the first with six eggs (three nestlings fledged) and the second with four eggs (all four fledged). Also, parakeets can begin breeding their first year after hatching. This, combined with potentially long life-spans, common among the Psittacidae, allows for a potentially very high annual productivity and should allow populations to rebound quickly after population loss. Thus, if nesting sites are limiting, nest boxes are a great tool for studying and managing reproduction in *Pyrrhura*. Predation was absent in the boxes, but honey bees and flesh-flies can be a problem in the reproduction of parakeets. The breeding season of 2018 was especially short due to the abandonment of the two last nests, which were invaded by bees during the laying period (in the moment of the invasion each female had laid four eggs).

BREEDING SEASON

Maroon-bellied Parakeets are reported to nest from October to December (90 days, Juniper and Parr 1998), yet our data suggest that they may begin in September and finish nesting around 160 days later. With this much longer breeding season and multiple nesting attempts, productivity is potentially much greater (Roper et al., 2010). Pairs may have more than one successful nest each year, and nests that started much later (near fledging of the earlier nests) are likely often to have been second nests. We monitored nests through fledging and were unable to follow post-fledging survival. In some species, the period after fledging can be the most vulnerable for the survival of nestlings and this have an important consequence in the growth of the population (Robinet and Salas, 1999; Masello & Quillfeldt, 2002).

We observed helpers at the nest for the first time in this species, in one nest with three adults, that apparently cared for six nestlings. This behavior may indicate that nest boxes were limiting and other nesting opportunities were unavailable, and so this third individual (perhaps offspring from one of the other adults) gained inclusive fitness. But another reasons can explain this behavior and further study will be required to determine how helping behavior may arise in this species. If so, then we might expect in conservation of other endangered species, that once all boxes are occupied, facultative helpers at nests may become common (Klauke, Segelbacher, & Schaefer, 2013; Theuerkauf, Rouys, Mériot, Gula, & Kuehn, 2009). One other species (*Pyrrhura orcesi*) in the genus has had helping behavior described, in which reproductive success of the pair was improved by the helper (Klauke, Segelbacher, & Schaefer, 2013).

NEST SUCCESS

Parakeet nesting success was very good in these nest boxes and essentially all nests in which young hatched were successful. However, hatching success was relatively low, with only 71% of eggs being viable and 83% of the nests had one or more unhatched eggs (9 nests with one egg, 9 nests with two eggs, 3 nests with three eggs, 1 nest with all five unhatched eggs and other nest with 6 unhatched eggs). In the Burrowing Parrot (*Cyanoliseus patagonus*) hatching success was 90% and only 25% of the nests had eggs that failed to hatch (Masello & Quillfeldt, 2002), while nestling survival was similar to this study (around 92%). On the other hand, there was no predation, demonstrating one of the benefits of nesting in boxes that were built and suspended as in this study. Nesting density was greater than 10 pairs per hectare. Apparently, nest sites are limiting in the region, so when many boxes are available, and due to the social nature of the parakeets (that forage in larger groups), many pairs find them and soon occupy them. In *Ara macao*, reproduction is similar in both natural and artificial nests, and so nest boxes provide additional nest opportunities where natural cavities are limiting (Olah, Vigo, Heinsohn, & Brightsmith, 2014).

The relative synchrony of egg laying and the somewhat larger percentage of infertile eggs (29%) offer some tools for conservation. When nests are checked regularly, infertile eggs can be discovered within a few days. Moving fertile eggs from nests with larger clutches to nests with more infertile eggs could distribute the likelihood of mortality of the smallest offspring or reduce the likelihood of losing a whole clutch to predation. Six infertile eggs were in one clutch (and thus by one female), five in another clutch (different female) and two other females each had 3 in 6 infertile eggs (one clutch each). Thus, these females had more than half of their broods as failed eggs. Thus, apparently a few pairs may either have difficulties in fertilization, or some eggs can be affected due to climate conditions, without intervention, would incubate the infertile eggs much longer than a normal incubation period (pers. obs.). By intervening and bringing eggs from nests with larger clutch sizes (nest synchrony permitting), these females could rear young that might otherwise have died.

USE OF NEST-BOXES

Most of our boxes were used, and the breeding density was around ten pairs per hectare. Prior to making nest boxes available, parakeet nests were never seen and birds were only seldom observed in the study area (JJR pers. obs. From 2001 to 2010) and today, they are seen at all times and they often roost in boxes at night. Thus, we suggest that natural cavities in this rural area can be limiting. In conversation with other residents, we have both seen evidence and heard stories of parakeets nesting in roofs of houses, often with complaints because they chew through just about anything. Thus, in a rural area with very few mature trees providing cavities, parakeets apparently find and use nest boxes as they are available, suggesting that boxes are limiting, similar to that in *Forpus passerinus* in Venezuela, where 58 nest attempts were in nest boxes (Beissinger & Waltman, 1991). We placed our boxes in a variety of locations with more and less visibility at a distance, which also may have contributed to their use (White, Gordon Brown, & Collazo, 2006). Conservation implications include placing many boxes in areas that are sometimes visited by the species of interest and they will do the rest.

While we never observed predation, in other regions other predators may be a problem. For example, smaller mouse opossums may easily traverse the line used to suspend the nest box (Roper, 1992). We recommend monitoring regularly to determine whether boxes are visited by other animals, and if so, cones used to keep squirrels away from bird feeders can be strategically placed above and below where lines are connected to the trees to reduce the possibility of predation. Also, it may be unlikely that smaller mammals prey on parakeet nests. Because nest predation is often the greatest cause of nest failure, if these boxes simply reduce predation risk then reproductive success should increase accordingly (Reuleaux et al., 2014).

Temperature might be an important component of successful use of nest boxes, especially in hotter regions. We suggest this through behavioral observations of nestlings. When the temperature was relatively cool, all nestlings huddled in tight groups to keep warm (which we suggest inadvertently caused the suffocation of the smallest nestlings). However, when temperatures were hotter (above 27ºC), the nestlings were all as far from one another as possible when we checked the nest, clearly trying to remain cool. While we did not systematically test this, we recommend choosing nest-box locations well so that they have shade during the hottest parts of the day.

Agonistic interactions may occur between pairs in adjacent nest boxes or for other reasons. In 2017 we observed agonistic behavior that seemed to cause the abandonment of one of the two nests. In 2018 we observed a agonistic behavior, but because birds were not color-banded we cannot speculate on the cause or consequence. While nesting close together may cause agonistic interactions, at the same time these interactions occurred, other nests were equally close to one another with no agonistic interactions. Indeed, birds seem to vocalize as they prepare to leave the nest which seems to alert bird nesting nearby that they are going foraging. As they leave the box we have observed that several join each other and forage together. Thus, we think that placing boxes close together is not an issue, but careful observations will determine whether it might be in other species or locations.

Honey bees are likely to be the most important problem with nest box use. We actively eliminated bees as they began to use a box. This was possible because one of us lives at the study location. In other situations, only regular nest-box checks can determine whether bees become an issue. At our study area, if bees were not removed, it is likely that they would have occupied all nest boxes available. Thus, it will become essential to control bees, because honey bees are apparently ubiquitous in the Americas and competition for nests is likely to be very common, with the bees always winning (Downs, 2005; Oldroyr, Lawler, & Crozier, 1994). Both owls and parakeets have lost nests in the study area due to sudden invasion of nest boxes by bees (killing two owl nestlings, and causing abandonment of at least three parakeets nests during laying) that went unnoticed for one day (JJR, pers. obs.). Other bees and wasps were never problems in these larger nest boxes.

Fly larvae were occasionally problems for nestling growth, principally that of feathers (Restrepo-González and Roper unpublished data). However, while potentially causing fatalities, the numbers of boxes infested was always low. And, the flies may not be exclusive to parakeets and enclosed nest-boxes (Löwenberg-Neto, 2008), because we observed woodcreepers in smaller boxes (*Lepidocolaptes falcinellus*), flycatchers (*Myiophobus fasciatus*) and thrushes (*Turdus rufiventris*) with flesh-fly larvae (pers. obs.). To clearly identify larvae requires larvae and adults, so we do not know if all these flies were the same species. But, because of the potential problems with flies and parakeet nestling survival and growth, we recommend further study. Also, we recommend that once found, larvae are always removed from the nestlings, and they should completely recover. Flies also seemed to become issues only after the earliest nests were near fledging (and in other species, were not issues with earlier nests as well, unpubl. data). Only with further study will it be possible to understand how climate interacts with fly biology to influence when flies may be a problem (Antoniazzi et al., 2011).

Bird behavior can be influenced by research schedules, as we found when during each breeding season, a different number of days passed between nest checks. In 2017, when we checked nests most often (every other day), nestlings became accustomed to handling and were much more cooperative when being manipulated. In 2016 and 2017, when we checked much less often, nestlings vocalized loudly and often bit while being manipulated, making work much more difficult. Studies with *Aratinga auricapilla* had similar results (Lima & Santos, 2005). Thus, and perhaps surprisingly, we recommend that for endangered and threatened species, nests should be checked often so the young accept handling as well as to insure fly larvae are removed quickly.

CONCLUSIONS

Low nest predation rates, long breeding seasons, repeated nesting attempts and early breeding together suggest that *Pyrrhura* parakeets have potentially rapid population growth rates when nesting in boxes. The ease with which boxes can be used and maintained also suggests an excellent conservation strategy for other species. Negative consequences of boxes may be invasion by exotic honey bees and parasitism by flesh flies. However, the negative side is easily controlled and may not always be an issue in all places. Also, nests may be more easily poached, and so boxes will need to be placed in safe locations or constantly monitored to avoid theft of nestlings.

Clearly individually-marked birds provide useful information for ecology and conservation and only with marked birds were we able to determine that they breed during the first year, and that three birds cared for one nest. Nestling tarsi are about adult size at less than half the interval they will remain in the nest, so they may be color-banded when young and they will accept the bands. Nest boxes also makes it possible to capture adults, that may be done at night, when they will remain in the nest box if lowered (for example). Other ways may be determined to capture adults in boxes.

We recommend applying these ideas for other species of *Pyrrhura* to determine how general reproductive biology is among the species. Especially for threatened species, many nest boxes should be made available where they may be monitored frequently and protected from those that might take the nestlings for the pet trade.

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Author contributions: Both James J. Roper and Alejandro Restrepo-González conceived the idea, carried the research and analyses, and participated in writing the manuscript.

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TABLE 1

Table 1. Summary of studied nest-boxes of *Pyrrhura frontalis* in southern Brazil on 2016 - 2018.

Season	Nests	Abandoned nests	Eggs	Hatched	Fledged	Died
2016	10	1	52	40	37	3
2017	12	2	58	33	31	2
2018	14	3	81	55	50	5
Total	36	6	191	128	118	10

FIGURE LEGENDS

Figure 1. Diagram of the nest-boxes used by *Pyrrhura frontalis* during the breeding season of 2016 - 2018. A) Dimensions of the biggest nest used, we also use other nests that were 30 X 25 X 50 cm. B) Dimensions of the tunnel at the entrance of the nest to prevent their predation (the branches were variable in the length). C) Representation of the nest hanged between two trees using a pulley system, the ring above the box permits that the box slides on, which keep the box from rotating, the string should be a strong nylon line and should be checked regularly to make sure it's not wearing out. The pulley should be one with ball-bearings if possible and made so that the line can't jump out of the groove.

Figure 2. Size of broods of *Pyrrhura frontalis* in nest boxes during 2016 - 2018 in southern Brazil. A) The number of eggs laid by each female. B) Duration of the incubation period (gray 2017, black 2018). C) The number of nestlings reared by each female. D) Age of nestlings at fledging (in 2017). E) The number of nestlings that fledged. The color bars represent the seasons of 2016 (white), 2017 (gray) and 2018 (black).

Figure 3. Duration of the breeding season of *Pyrrhura frontalis* in southern Brazil. The week 36 of the year correspond approximately with 9 September, and the week 14 with early of April. The continuous line represents the laying period of the eggs, the dashed line represents the period in that eggs hatched and the dot-dash line represents the period in that nestlings fledged.

FIGURE 1

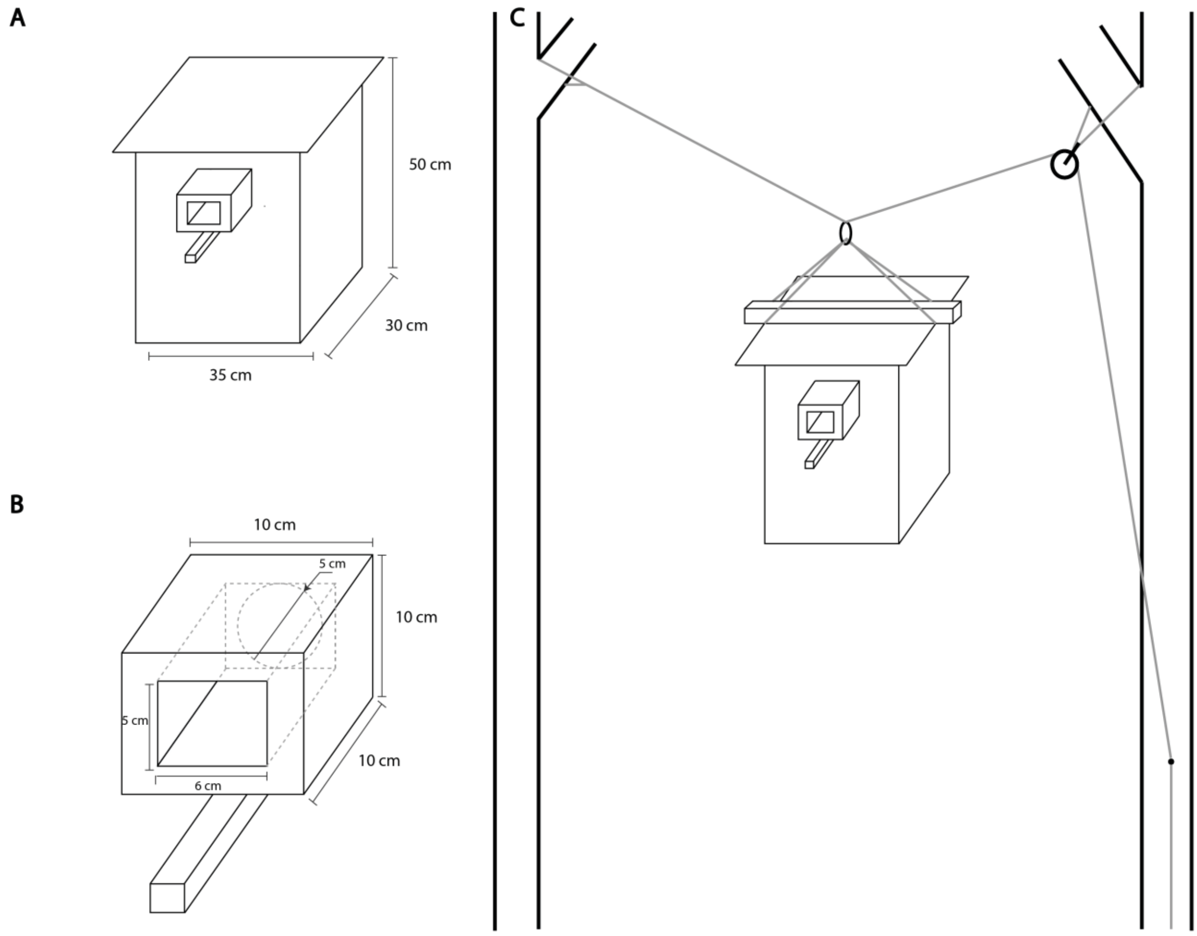


FIGURE 2

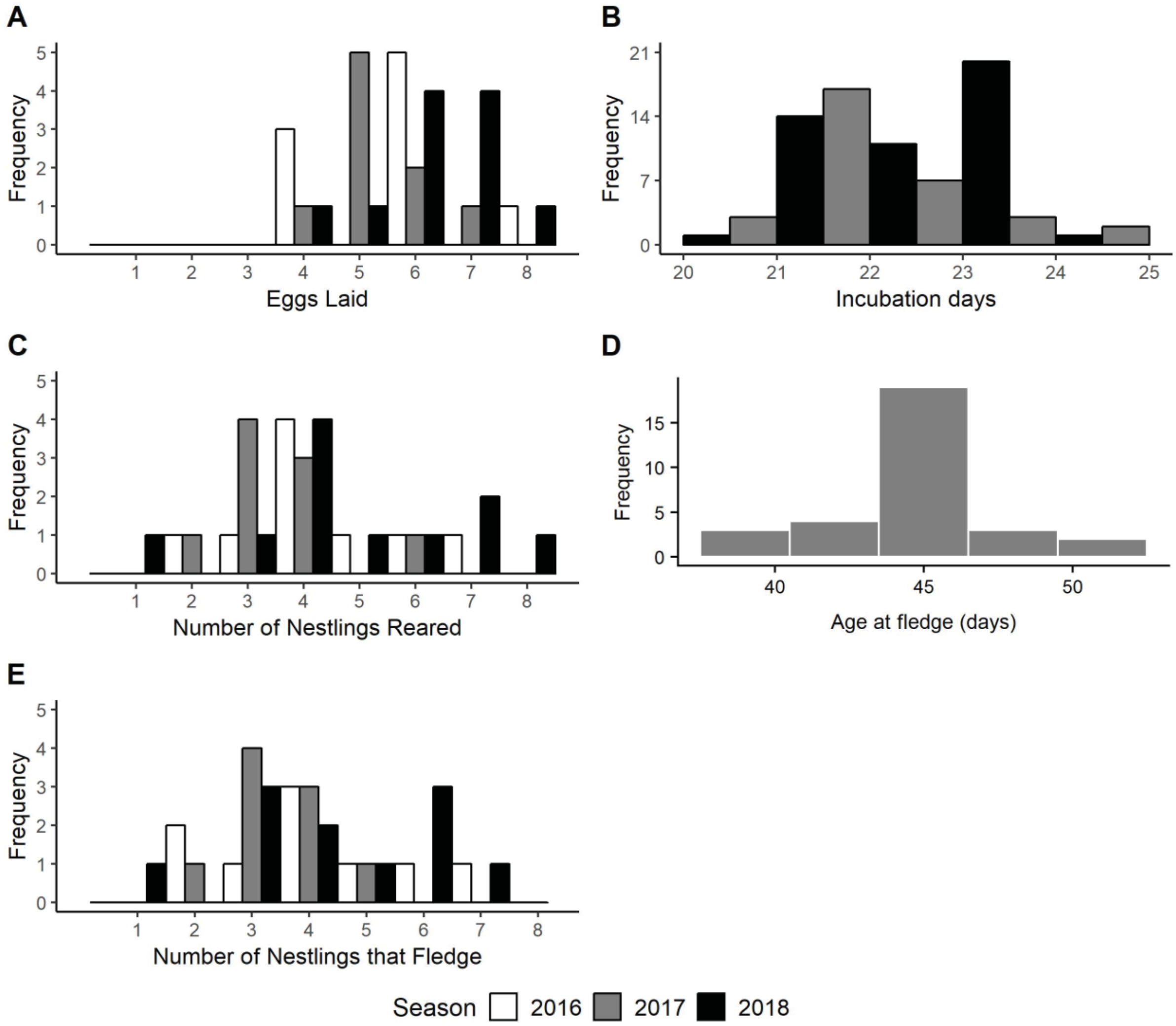
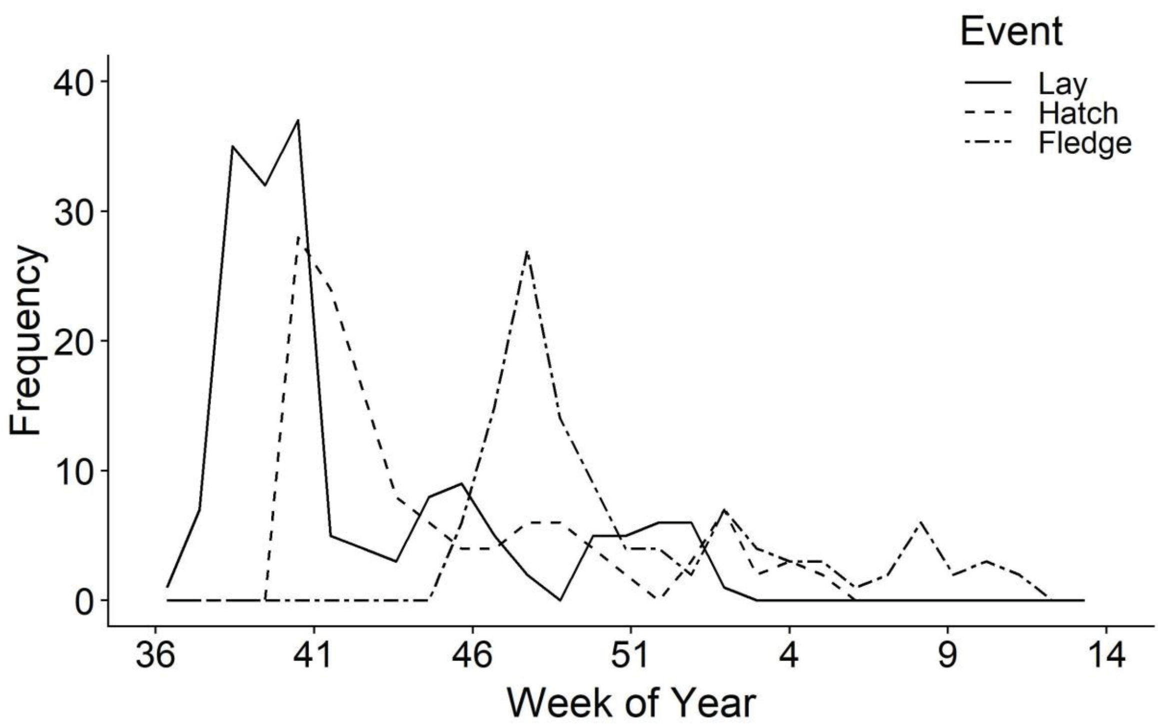

A
Frequency
Eggs Laid
B
Frequency
Incubation days
C
Frequency
Number of Nestlings Reared
D
Frequency
Age at fledge (days)
E
Frequency
Number of Nestlings that Fledge
Season 2016 2017 2018

FIGURE 3


Event
Lay
Hatch
Fledge
40
30
20
10
0
Frequency
36
41
46
51
4
9
14
Week of Year

CHAPTER II: NESTLING GROWTH IN MAROON-BELLIED PARAKEETS (*PYRRHURA FRONTALIS*) IN NEST BOXES IN SOUTHERN BRAZIL: THE INFLUENCES OF FOOD SUPPLEMENTATION AND FLY PARASITISM

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ABSTRACT

The parrot family (Psittacidae) comprises many species whose life histories are poorly studied as well as many endangered species. For example, parakeets in the genus *Pyrrhura* comprise 31 species, 15 of which are endangered (17 in Brazil, 8 endangered), yet population dynamics and reproductive biology remain poorly studied. Here, we use nest boxes to simplify nest-finding and monitoring, to ask questions about nesting biology and breeding asynchrony in the Maroon-bellied Parakeet in the Atlantic Forest, southern Brazil. Also, we use this study to provide suggestions for conservation of other species of *Pyrrhura*. During the breeding seasons of 2016 and 2017, we monitored nests to examine the importance of clutch size, laying sequence, parentage (differences among pairs), food abundance, and, fortuitously, flesh-fly parasitism on nestling growth and survival. We experimentally supplemented food to nestlings in two boxes in 2017. Using Richards' equation to model growth, we found that nestlings grew equally well in all control nest boxes and surprisingly found no evidence of an influence of clutch size, laying sequence, parentage nor of supplemented food on nestling growth rates. Hence, we also found no evidence to inform hypotheses about the causes and consequences of hatching asynchrony. Subcutaneous flesh-fly larvae (myiasis) infested several nestlings, and became problematic for nestlings in two boxes, one each breeding season. Nestlings with myiasis tended to grow more slowly, especially flight feather growth, and two nestlings died as a consequence of myiasis. We conclude that the use of nest boxes may be a very important conservation tool for *Pyrrhura* parakeets that will allow monitoring as well as care of young suffering from myiasis. Long-term studies will be required to better understand the consequences of food abundance and myiasis on population dynamics.

Key words: *Pyrrhura frontalis*, growth rates, Richards' growth curves, food limitation, fly parasitism, nesting success

INTRODUCTION

Often, ecological questions are also important conservation questions, such as those about factors that influence reproduction and reproductive success that are key to understanding and predicting population growth and persistence (Reuleaux et al. 2014, Marsden and Royle 2015). For many species of birds, failure during reproduction accounts for most mortality (Ricklefs 1969, Martin 1996, Brightsmith 2005, Britt et al. 2014). Offspring can also vary in quality, and thus their likelihood of long-term survival also varies, due to limitations during the nestling stage (Murphy 1985, Sullivan and Weathers 1992, Adams et al. 1994, Bradbury et al. 2003, Brzęk and Konarzewski 2004, Pérez et al. 2008, Jones et al. 2017). Also, theoretical questions, such as evolutionary explanations for hatching asynchrony, are also important for understanding population dynamics (Beissinger and Stoleson 1997, Laaksonen 2004, Beissinger 2008, Konarzewski 2008, Maddox and Weatherhead 2008, Stenning 2008, Banda and Blanco 2008).

Nesting success has been studied in a variety of species but the ease with which it is studied often depends on the nest type. Open nests are commonly studied because they are easier to find and monitor than cavity nests (Martin and Li 1992, Martin 1993a, 1993b, Martin and Geupel 1993). To resolve the difficulty of studying reproduction in cavity nesting birds, nest boxes are often used for many species (Slagsvold et al. 1995, Purcell et al. 1997), including those in the parrot family (Psittacidae, (Downs 2005, Klauke et al. 2013, Olah et al. 2014).

Parrots are among the most endangered families of birds, with around 30% of species being endangered due to the pet trade and habitat loss (Masello and Quillfeldt 2002, Brightsmith 2005, Velásquez et al. 2009, Marsden and Royle 2015, Berkunsky et al. 2017). Nonetheless, few parrot species are well-studied and little information is available about reproductive biology for most (Masello and Quillfeldt 2002, Velásquez et al. 2009, Berkunsky et al. 2017). Also, endangered and threatened species are especially difficult and risky to study due to small population sizes. Finally, parrots tend to have large clutches with asynchronous hatching, the evolutionary reasons for which remain largely unresolved (Beissinger and Waltman 1991, Stoleson and Beissinger 1997, 2001, Siegel and Beissinger 1999, Beissinger 2008, Budden and Beissinger 2009).

More species (72) of parrots are found in Brazil than any other country, including the genus *Pyrrhura* (17 of 31 species are found in Brazil), of which eight (of 15 endangered *Pyrrhura*) are threatened or endangered due to deforestation, habitat degradation and capture for illegal pet trade (Olmos et al. 2005, Botero-Delgadillo et al. 2013, Klauke et al. 2013, Collar et al. 2018, BirdLife International 2019). When species are threatened, studies of their not-threatened congeners can provide useful information about their nesting behaviors and causes and consequences of nest failure that can then be applied to their more threatened sister species (Ortiz-Catedral et al. 2013). Thus, additional information about breeding biology is clearly important and may only be effectively gathered by studies of more common species (Kristosch et al. 2001, Masello and Quillfeldt 2002, Girão et al. 2010, Berkunsky et al. 2014).

The Maroon-bellied Parakeet (*P. frontalis*) is common in the Atlantic Rainforest of southeastern Brazil and neighboring countries (Guix et al. 1999). Even though they are common, Maroon-bellied parakeets are probably affected by habitat loss and other anthropogenic issues that also affect other species of parakeet (Juniper and Parr 1998). Also, their natural history is surprisingly poorly known (Kristosch et al. 2001, Berkunsky et al. 2017) and, as the more-common congener of some threatened species, understanding their natural history should provide useful information for conservation for their sister species.

We followed nesting in the Maroon-bellied Parakeet during two breeding seasons using nest boxes to measure natural variation in clutch size, hatching and nesting success and their influences on nestling growth rates. We also tested, using natural and manipulative experiments, the consequences of hatching asynchrony. Specifically, we wished to compare pairs with respect to variation in date of nesting, clutch size, growth rates of nestlings and nesting success to examine consequences for fitness. By experimentally supplemented nestlings with food, we tested the importance of food limitation on growth. We predicted that food-supplemented nestlings would all grow well (at maximal rates) and faster than nestlings only fed by their parents. Control nestling growth rates should also be influenced by clutch size, such that larger clutches have some or all nestlings with slower growth. Previous observations showed that nestlings can be infested with subcutaneous flesh-fly larvae (myiasis, genus *Philornis,* Diptera, Muscidae). We compared growth and size at the time of fledging between infested with uninfested nestlings. With these data we increase understanding of this species as well as offer suggestions for the conservation of other species in the genus *Pyrrhura*.

METHODS

Nest boxes used by *P. frontalis* have been available since 2010 in a rural area near Piraquara in the state of Paraná, Brazil (25º 31’18’’ S, 49º5’33’’ W), where we studied breeding and nestling growth during the 2016 and 2017 breeding seasons. During this study, 15 boxes were available, some of which had been used in previous years. Boxes were mounted using a pulley system so that they could be easily lowered and raised for monitoring.

Boxes were monitored prior to the breeding seasons when we checked for signs of nesting if birds were observed visiting. Upon finding eggs in most nests, they were numbered, weighed and photographed every other day until egg laying ceased. At hatching, we again checked nests, weighed eggs and hatchlings and uniquely marked hatchlings by trimming a toenail. Eggs and nestlings were weighed using a digital scale with 0.01 g precision. We were able to calculate the incubation interval within ± 24 h error in most nests.

Boxes with nestlings were examined weekly during the 2016 breeding season and every other day during 2017. To reduce the time at each box check, instead of measuring nestlings at the box, we photographed each using standardized positions with a ruler to measure later using the program ImageJ (Version 1.50i, Wayne Rasband, National Institute of Health). We measured typical variables used in birds, including bill length, wing length, tail length and tarso-metatarsus length. Using ImageJ we were able to measure with more precision than is usually possible using a caliper, and so we maintained the number of decimal places provided by the program during analysis but rounded measurements to 0.1 mm in the results.

FOOD SUPPLEMENTATION

To test whether food abundance influenced nestling growth and the peak demand hypothesis (Stoleson and Beissinger, 1997), we supplemented food in two nest boxes during the 2017 breeding season (four nestlings in one nest and three in another). Commercially available food for young parrots (Alcon Club brand), as a powder, was mixed with warm water to a firm, thick, porridge-like, consistency just prior to the first feeding. The food was kept warm while feeding (nestlings refuse cold food). We fed nestlings two times each day of feeding (every other day) with the first feeding between 08:00 – 10:00 h and the second 15:00 – 17:00 h. At each feeding, nestlings were fed until they no longer accepted food and each was weighed before and after. We began feeding nestlings on the day that all eggs hatched. We fed all nestlings until the oldest nestling in a box was 40 d old (± 1 d, near fledging) when we stopped feeding all nestlings to avoid causing the oldest to leave the nest too early.

MYIASIS (SUBCUTANEOUS FLY PARASITISM)

Our interest here was to measure development and growth of nestlings, therefore we decided that if infested with flies, we would remove larvae from nestlings during regular nest box checks. Larvae were easily removed using tweezers with no apparent effects on the nestlings. Larvae were stored for later identification and some they were reared so that we had adult samples for identification.

Larvae could present challenges to nestling growth, so we used Richards' equation to measure those effects as compared to nestlings without larvae.

ANALYSIS

We estimated nestling growth curves using nonlinear mixed models (Tjørve and Tjørve 2010, Svagelj and Quintana, 2017), applying Richards models using weight, bill length, tarsus length, wing length and tail length (each a separate univariate test) as follows:

$$y_t = A*(1+(d-1)\exp(-K*(t-T_i)/d^{d/(1-d)}))^{1/(1-d)}$$

Here, y_t is the measurement of the variable at age t, A is the upper asymptote estimate, K is the maximum relative growth rate, T_i is age at the maximum growth rate and d is a shape parameter (curve estimate using package nlme in R). We used three treatments for estimating growth curves: control (nestlings neither fed nor with flies), food (those we fed, restricted to nestlings in 2017 when the feeding was carried out), and flies (those with flies that we removed on more than one occasion, in 2016 and 2017).

We first tested (using control nests of both years) whether nest box (parents), clutch size or year, influenced nestling growth to determine whether those covariates should be controled in subsequent analyses of food supplementation. We did this because Richards' formula as calculated in R requires convergence which may not occur with small sample sizes. To test for these variables, we plotted age against each morphological variable by nest box, clutch size, and year and with Richards' formula when possible or the "lm" smoothing function in ggplot. In these plots, it was visually clear that growth was independent of all of these variables (box, clutch size, year, see Supplement). Thus, we compared growth curves using individual nestlings as independent samples to compare the three treatments (control, fed, fly).

We compared curves (coefficients A, K, T_i) between treatments using analysis of variance (d, as a shape parameter, was not compared by treatment, but was allowed to vary by model, Giudigi et al. 2017). Curve estimation was carried out in R (version 3.5.1, R Core Team 2018), using the package nlme (Pinheiro et al. 2019) with the function glm, and packages ggplot2 (Wickham 2016) and cowplot (Wilke 2019) were used for analyses and figures.

RESULTS

A total of 98 eggs were laid in 18 nests (nine boxes each year) of which 72 hatched and so the number of nestlings reared in each box varied from 2 – 7 (3 nests with 2, 5 with 3, 6 with 4, 2 with

5, and 2 each with 6 and 7 nestlings). Four of the 72 nestlings died, one for unknown reasons five days after hatching (November 2016). Two died, apparently due to myiasis, about 14 days after hatching (~15 January 2017). One died for unknown reasons (26 October 2017), four days after hatching, he was the last at hatched of five nestlings. Sixty-eight nestlings survived to fledge and comprised our sample for measuring growth.

FOOD SUPPLEMENTATION TREATMENT

Two nest boxes in 2017 (with 3 and 4 nestlings) comprised the food supplement treatment. Nestlings consistently accepted food and consumed an average of 6% of their body weight at each feeding bout (SE = 0.24%, range 0 – 15%). Food consumption (measured as the percentage of body weight consumed) reached a peak at around 22 days of age, when their weight after feeding increased by an average of 9.8 g (SE = 0.61g, range: 6.5 – 11.8g), which was about 14% of their body weight at the time of feeding (range 11 – 15%, Fig. 1). We were unable to measure the caloric intake of our food, but if we assume that values in Table 1 of Petzinger et al. (2015) are similar (about 1 kcal mL^{-1}), then at peak consumption, we added nearly 20 kcal to their daily intake, which was more than half of their daily requirement. Considering that they were also fed on those days by their parents, we conclude that the quantity of food that we supplemented would have been sufficient to generate a measurable effect on growth if food was limiting. Nonetheless, food was apparently not limiting as growth in all variables (body weight, bill length, tarsus length, wing length and tail length) was similar among control and food supplemented treatments (Table 1, Fig. 2).

MYIASIS

Nestlings had myiasis to varying extent in seven nests, two in 2016 and five in 2017. Thus, one nest box with two parasitized nestlings in 2016 and one box with three nestlings together comprised the myasis treatment. Myiasis occurred in these two boxes at different nestling ages: in 2016, age was 2 – 10 days and in 2017 was 16 – 24 days. We began removing larvae upon discovering the infestation in both years, so nestlings suffered myiasis for longer time intervals before larvae were removed in 2016 (seven days) than in 2017 (two days, Fig. 2). In one 2016 box, two of six nestlings (12 and 21 days old) had very few larvae on 2 January and after the first remove, none larvae were found during subsequent nest checks. In a nest with four nestlings, we removed larvae at each check (46 larvae total, in 3 weekly nest checks) between 15 January and 5 February 2017. Two of those nestlings died at ages 7 and 10 days and the other two survived to fledge. During 2017, 11 nestlings (ages ranging from 18 – 38 days) in five boxes had myiasis between 25 November and 21 February.

In four boxes no additional larvae were found after the first check when we found larvae. In the remaining box, we removed 132 larvae (1 – 13 larvae removed each session, mode = 5 larvae) from the three nestlings between 3 – 23 January 2018. All of these nestlings survived to fledge.

Comparisons of the growth curves of the five nestlings with myiasis and the controls demonstrate that myiasis can cause slower growth in flight feathers. Only tarsus length was unaffected by myiasis (Table 2). Weight growth was somewhat slower with myiasis (*K*, a reduction of of 0.57 g day^{-1}, following g_{max} = A K, Tjørve and Tjørve, 2010) and so maximum growth rate occurred at a slightly later age (T_i, somewhat less than a day). Bill length also grew somewhat slower and T_i was delayed by almost two days in the myiasis treatment. Wing length grew more slowly by about 0.34 mm day^{-1} (*K*) in the myiasis treatment, and the maximum growth rate in both wings and tails was delayed by 2 – 3 days in the myiasis treatment, while maximum tail-length (*A*) was 15 mm shorter in the myiasis treatment (Table 2, Fig. 2).

DISCUSSION

All nestlings without myiasis grew at similar rates, regardless of clutch size, hatching order, parents, year of study, and food supplementation. Thus, these parakeets seem to feed young at optimal rates at all times, at least during the two years of this study. As a consequence, our data do not inform the peak-load hypothesis because food was never limiting and nestling crops were almost always full at any time during nest checks. Brood reduction due to starvation was absent and crops were full in the unexplained deaths of a few nestlings. Moreover, these nestlings died well before the peak load and their deaths appeared to be accidental, as if they were simply, inadvertently, suffocated by their larger siblings (Taylor and Perrin, 2009). Nestling growth was independent of hatch order and nestlings of any age always seemed equally well-fed. Thus, the lack of a relationship between hatch order and growth rate implies that all parents were able to feed young such that growth was at their maximum or physiologically optimal rates (Krebs 1999, Budden and Beissinger, 2009).

Nestlings that we fed usually had food visible in their crops before we began to feed them, yet they often accepted food, and we assumed that the food we added would provide a benefit if food was limiting at any time. Thus, the similar growth rates of supplemented and control treatments (and the lack of an effect of box, date, clutch size and so on) indicates that food was never limiting to growth. Consequently, the lack of a relationship with food and growth neither refutes nor supports hypotheses of hatching asynchrony. Similarly, in the parrotlet *Forpus passerinus*, experimentally synchronous clutches had similar nestling growth rates with naturally asynchronous clutches (Stoleson and Beissinger 1997) and hatching asynchrony was not associated with nestling growth in the flycatcher *Ficedula albicollis* (Szöllosi et al. 2007).

Myiasis due to *Philornis* flies is clearly detrimental to and may be fatal for parakeet nestlings. Because we removed larvae as they were encountered, and more frequently in 2017, most nestlings survived and the two that died apparently did so because when first discovered, their myiasis was already well-advanced. Growth was slowed by myiasis, especially so in flight feathers (wing and tail). Also, myiasis seems to have a greater impact on younger nestlings (Rabuffetti and Reboreda 2007, Quiroga and Reboreda, 2012). Flies, therefore, can be very limiting to nestling growth and survival. As parasitism only began well after the earliest nests were initiated (and more than a month after those eggs hatched), the effect of flies should be a strong force selecting for early nesting.

When infested with flies, body (but not feather) growth, as measured by weight and bill and tarsus lengths, and asymptotic size were surprisingly similar to that of control nestlings. Apparently, when stressed with fly larvae, growing birds continue to allocate resources to growth of permanent parts of the body and reduce allocation to feather growth. While infested offspring reach the same asymptotic body size, the slowed flight feather growth may have consequences for young birds once they leave the nest. In fact, some studies find that infested nestlings take longer to fledge (Quiroga and Reboreda, 2012). As our infested nestlings neared fledging, flies ceased being a problem and we removed few or none at all after 35 days of age. Also, had we not removed the many larvae from the nestlings in both years we believe that they were likely to have died. Thus, the final effects of myiasis on parakeets will require future and probably long term studies and myiasis may need to be allowed to proceed uninterrupted.

A possible interaction with hatching asynchrony may come from the overlap between the beginning of myiasis and nesting age. Younger nestlings when flies begin to be a problem are more likely to be infected and the infection is more likely to be fatal. Myiasis in both years began when the earliest broods of the season were almost ready to fledge and fully feathered nestlings were never found with fly larvae. Thus, the biology of the fly suggests that climate may influence when it becomes more common (Antoniazzi et al., 2011), and here, this seems to be a strong selective pressure for early nesting. Hatching asynchrony may influence mortality due to flies if smaller, less-feathered siblings are more likely to be infested.

We find several implications of this study for conservation. First, if parakeets are nesting and young birds typically have food in their crops, then food is unlikely to be limiting and resolving food issues may not help in conservation. However, by monitoring the condition of nestlings is easy to discern and if crops are regularly empty when the nests are checked, food can easily be supplemented. More importantly, perhaps, providing more nest boxes will favor greater use, and appropriately built boxes can reduce predation risk. For example, in previous years, oppossums (genus *Didelphis*) were often found in nest boxes in this study area. Our boxes were built with a smaller hole and a short vestibule (tunnel) as an entrance, and they were suspended between two adjacent trees using pulleys and strong nylon line. Thus, the combined entrance and the line apparently reduced the likelihood of a predator finding the nest. Nests are also easily and quickly checked by this method, reducing the time birds are perturbed at the nest and making field work more efficient. The number of boxes available, and the number used, both increased over time and this suggests that using boxes may require placing them in the field well in advance of nesting, and perhaps they may need to remain in the field throughout the year. Parakeets are often observed visiting and sleeping in boxes well outside the breeding season (JJR, personal observation). Next, by using boxes, nests can be monitored so that should myiasis become a problem, fly larvae can be removed from the nestlings. Our study demonstrates that nestlings will recover and grow at normal rates if larvae are removed often enough.

The Maroon-bellied Parakeet (*P. frontalis*) has very good nesting success and there is no evidence in two breeding seasons to suggest that food abundance limits success. Thus, we have no support for any particular hypothesis about the causes and consequences of hatching asynchrony. Myiasis, on the other hand, can be fatal and can cause a reduction in growth that can have consequences for post-fledging survival. Also, myiasis appears to favor early nesting because the first signs of flies come about the same time as the first young are fledging. Finally, we suggest that nest boxes are very effective tools for conservation of other species of *Pyrrhura*, especially as part of a long-term monitoring plan in which boxes may be mounted and maintained for several years.

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TABLE 1

Table 1. Final growth models for nestling Maroon-bellied parakeets using Richards' equation. These models include both controls and fed nestlings because growth curves were similar in both treatments (in 2017, measured every other day and so had greater precision). Coefficients are the upper asymptote (*A*, adult size), maximum relative growth rate (*K*), age at the maximum growth rate (T_i), and a shape parameter (*d*). *N* = 28 individuals for all variables, number of measurements = 606.

Variable (N)	Coefficients	Values (*SE*)
Weight	*A*	87.3 (1.05)
	K	0.0567 (0.0011)
	T_i	12.3 (0.28)
	d	2.03 (0.14)
Bill	*A*	13.9 (0.15)
	K	0.0239 (0.0004)
	T_i	14.1 (0.75)
	d	4.69 (0.51)
Tarsus	*A*	16.1 (0.04)
	K	0.0493 (0.0011)
	T_i	7.4 (0.44)
	d	4.23 (0.47)
Wing	*A*	149.3 (5.92)

	K	0.0224 (0.0011)
	T_i	25.1 (0.41)
	d	1.37 (0.12)
	A	128.3 (9.24)
Tail	K	0.0273 (0.0022)
	T_i	32.2 (0.64)
	d	1.39 (0.15)

TABLE 2

Table 2. Growth curves for nestling Maroon-bellied parakeets. Coefficients: upper asymptote (*A*, adult size, predicted controls ≥ myiasis), maximum relative growth rate (*K*, control > myiasis), age at maximum growth rate (T_i, control < myiasis), shape parameter (d).

Variable	Regression Coefficient	Values (*SE*)	$F_{1, 861}$	*p*
Weight	*A*	86.54 (0.455)		
	K Control[1]	0.0557 (0.0011)	5.39	0,021
	K Myiasis	0.0491 (0.0029)		
	T_i Control	12.2 (0.31)	5.66	0,018
	T_i Myiasis	13.0 (0.34)		
	d	1.88 (0.265)		
Bill Length	*A*	14.024 (0.088)		
	K	0.0231 (0.0004)		
	T_i Control	14.2 (0.77)	24.35	0,000
	T_i Myiasis	16.0 (0.37)		
	d	4.48 (0.481)		
Tarsus Length	*A*	16.04 (0.036)		
	K	0.0491 (0.0011)		
	T_i	6.6 (0.44)		
	d	3.60 (0.381)		

Wing Length	*A*	145.77 (0.455)		
	K Control[2]	0.0231 (0.0012)	15.96	< 0.001
	K Myiasis	0.0208 (0.0006)		
	T_i Control	25.2 (0.31)	142.27	< 0.001
	T_i Myiasis	28.3 (0.34)		
	d	1.47 (0.265)		
Tail Length	*A* Control	120.95 (8.532)	12.90	< 0.001
	A Myiasis	105.04 (4.429)		
	K	0.0291 (0.0023)		
	T_i Control	31.6 (0.49)	7.41	0,007
	T_i Myiasis	33.6 (0.76)		
	d	1.52 (0.167)		

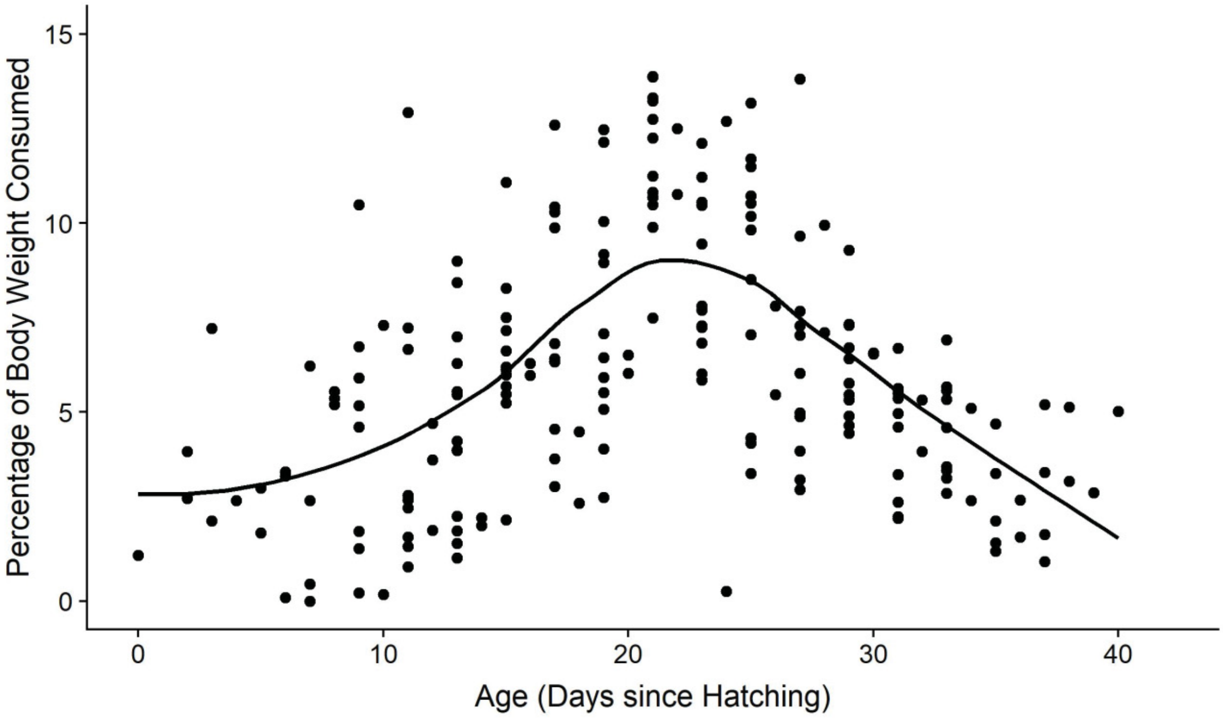
The differences in *K* result in a difference of [1]0.57 g day^{-1} and [2]0.34 mm day^{-1}.

FIGURE LEGENDS

Figure 1. The amount of food consumed during each feeding event as the percentage of the nestling weight at the time of feeding (calculated as the difference in nestling weight before and after feeding divided by after-feeding weight x 100).

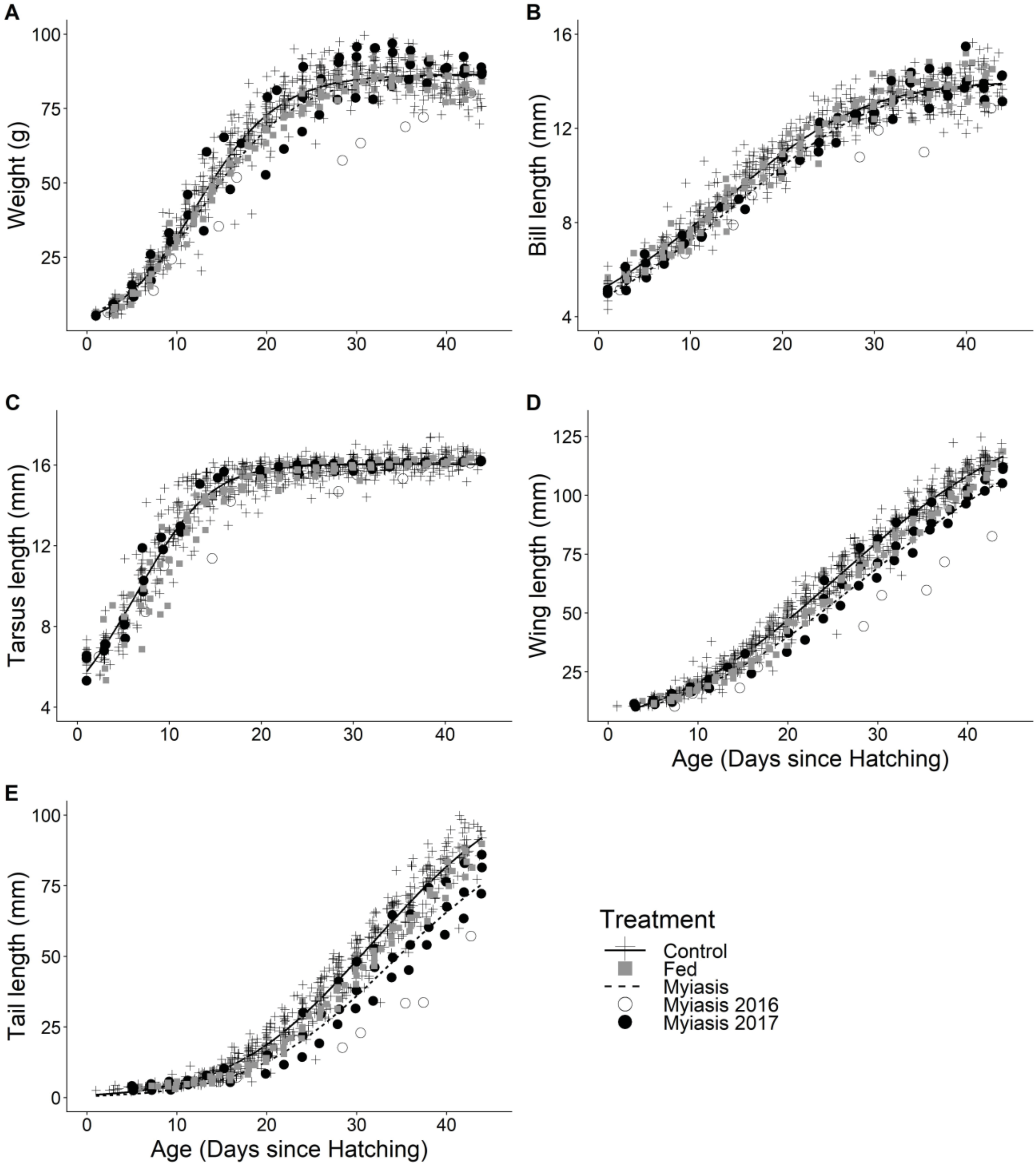
Figure 2. Comparison of growth curves of *P. frontalis* nestlings combining controls (unfed, without flies, 2016 and 2017, crosses), nestlings fed in 2017 (grey squares), with myiasis (2016 open circles, 2017, black circles). A) Body weight (g), B) bill length (mm), C) tarsus length (mm), D) wing length (mm), E) tail length (mm). Only tarsus length was independent of all treatments and some coefficients (especially K and T_i) in different variables varied only between controls and nestlings with myiasis (Table 2).

FIGURE 1



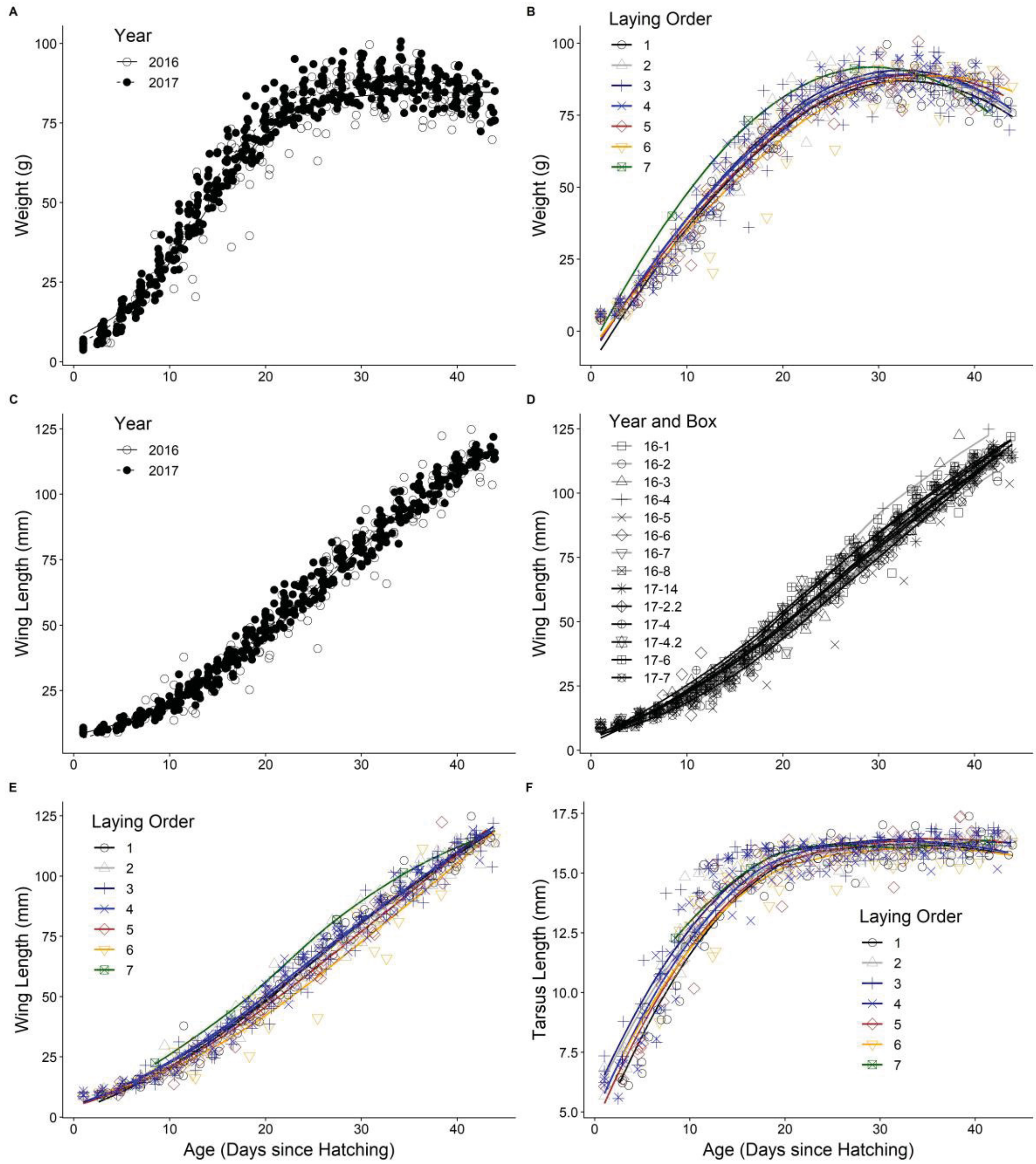
Percentage of Body Weight Consumed
15
10
5
0
0
10
20
30
40
Age (Days since Hatching)

FIGURE 2


A
Weight (g)
100
75
50
25
0
10
20
30
40
B
Bill length (mm)
16
12
8
4
C
Tarsus length (mm)
D
Wing length (mm)
125
Age (Days since Hatching)
E
Tail length (mm)
Treatment
Control
Fed
Myiasis
Myiasis 2016
Myiasis 2017

SUPPLEMENTARY INFORMATION

Figure 1. Comparisons of nestling growth (weight, wing length and tarsus length) by year, pair (box) and hatching sequence to demonstrate that none of these factors was important, thereby permitting comparisons of supplemented versus control nestlings and parasitized versus non-parasistized nestlings. Nestlings used in this figure were all from boxes in which young were not fed and young did not have flies (the two control groups). In panels A and C sample sizes permitted using Richard's formula to calculate curves. In the remaining, the "loess" function was used in ggplot in R. A), B) Body weight (g). C), D), E) wing length (mm). F) tarsus length (mm).



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