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PADRÕES NO CUIDADO PARENTAL EM PASSERIFORMES TROPICAIS E TEMPERADOS

TALITA VIEIRA BRAGA

CURITIBA

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ecologia e Conservação.

Orientador: Dr. James Joseph Roper

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TERMO DE APROVAÇÃO

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 Tese de Doutorado de **TALITA VIEIRA BRAGA**, intitulada: "**Padrões no cuidado parental em passeriformes tropicais e temperados.**", após terem inquirido a aluna e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO.

Curitiba, 04 de Março de 2016.

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SUMÁRIO

RESUMO GERAL

O cuidado parental é um importante componente do investimento reprodutivo dos indivíduos, e a quantidade de cuidado investido é determinada pelo conflito entre as necessidades da prole e o cuidado que os pais podem investir. O investimento em cuidado parental pode variar com a latitude e com a taxa de predação do ninho, assim como com o número de adultos providenciando cuidado. Neste trabalho, primeiramente foram descritas a biologia reprodutiva de duas espécies de Parulideos, *Myiothlypis leucoblephara* e *Basileuterus culicivorus*, e contextualizadas com as características de história de vida de outras espécies tropicais e temperadas. Em seguida o cuidado parental e a taxa de predação dos ninhos durante a fase de ninhego foram comparados entre os parulídeos tropicais e temperados. Por último, a quantidade de cuidado parental investido durante os períodos de incubação e ninhego foram comparados entre diferentes modos de cuidado parental: uniparental, biparental parcial e biparental completo. Os resultados mostraram que as duas espécies de parulídeos estudadas diferiram em suas características de história de vida e não possuíram um padrão completamente tropical ou temperado. A taxa de visitas ao ninho e a taxa de predação durante o período de ninhego foram similares entre as espécies de parulídeos tropicais e temperados, enquanto a taxa de alimentação por ninhegos foi maior nas espécies tropicais apenas durante a segunda metade do período de ninhego. A quantidade total de cuidado parental investido durante o período de incubação e de ninhego foram maiores nos modos de cuidado biparental. O tempo investido na incubação dos ovos foi maior no modo biparental completo, e a alimentação dos ninhegos foi maior no modo biparental parcial. A alimentação dos ninhegos foi surpreendentemente similar entre os modos uniparental e biparental completo, sugerindo que a relação entre a quantidade total de cuidado parental e o número de adultos que providencia cuidado é mais forte durante o período de incubação. Esses resultados sugerem que as diferenças no cuidado parental entre espécies tropicais e temperadas devem ser críticas durante o final do período de ninhego, destacando a importância de estudos que diferenciem o investimento em cuidado parental entre as diferentes idades dos ninhegos. Adicionalmente, os resultados da comparação entre os modos de cuidado parental destacaram a importância em considerar a quantidade de adultos providenciando cuidado parental para alcançar um melhor entendimento da evolução desse comportamento.

Palavras-chave: período de incubação, período de ninhego, cuidado uniparental, cuidado biparental, taxa de predação de ninhos.

ABSTRACT

Parental care is an important component of reproductive effort of individuals. The amount of parental care is determined by a conflict between the offspring requirements and the amount that parents can provide. Parental care can vary with latitude and nest predation risk, as with the number of caregivers. Here, we first provide a description of the breeding biology of two warblers, the White-rimmed Warbler *Myiothlypis leucoblephara* and the Golden-crowned Warbler *Basileuterus culicivorus*. Then we compare their breeding traits with other tropical and temperate warblers. We follow with a comparison of nestling provisioning and nest predation rates during the nestling period between tropical and temperate warblers. Finally, we compared the total amount of parental care during incubation and nestling period between modes of parental care: the uniparental, partial biparental and complete biparental. The results indicated that breeding traits of the two studied warblers were different and did not fit completely in a tropical or temperate pattern. Total feeding and nest predation rates were similar between tropical and temperate warblers, while per nestling feeding rate was greater in tropical warblers only during late nestling period. The total amount of parental care was greater in biparental care than in uniparental care. Nest attentiveness was greater in complete biparental care, and nestling provisioning was greater in partial biparental care. Feeding rates were surprisingly similar in uniparental and complete biparental care, suggesting that the relationship between the number of caregivers and the total amount of parental care is stronger during incubation period. Our results suggest that differences in parental care between tropical and temperate species should be critical during late nestling period, highlighting the importance of studies that focus in parental care investment between different nestling ages. Additionally, comparisons between modes of parental care showed that accounting for differences in the number of caregirvers may provide valuable information to better understand parental care evolution.

Key-words: incubation period, nestling period, uniparental care, biparental care, nest predation

PREFÁCIO

O cuidado parental é um importante componente do investimento reprodutivo dos indivíduos (Clutton-Brock 1991, Martin et al. 2006). Nas aves o cuidado parental é representado principalmente pelos comportamentos de defesa de território pelos parceiros reprodutivos, construção do ninho, incubação dos ovos, incubação dos filhotes enquanto são incapazes de termorregular, alimentação dos filhotes, proteção dos filhotes contra predadores, e alimentação das fêmeas pelos machos antes da postura dos ovos e durante o período de incubação (Silver et al. 1985, Royle et al. 2012). Esse investimento em cuidado parental pode ser medido através da quantificação do tempo ou energia gasto por cada indivíduo em cada um desses comportamentos (Burger 1981).

Outro importante investimento reprodutivo nas aves é a produção dos ovos. A energia investida para a produção dos ovos, medida como porcentagem de gema no ovo, nas espécies com desenvolvimento altricial é menor que nas espécies com desenvolvimento precoce. Esse menor investimento de energia nas espécies altriciais é associado ao maior requerimento por cuidado parental após a eclosão dos ovos (Ar & Yom-Tov 1978). Assim, os filhotes dessas espécies necessitam ser nutridos através de alimento entregue pelos adultos, o que torna esse comportamento de cuidado parental primordial para a sobrevivência dos filhotes (Silver et al. 1985). Dessa forma, o estudo de espécies com desenvolvimento altricial é importante para o avanço do conhecimento sobre o investimento reprodutivo em cuidado parental.

O investimento em cuidado parental nas aves, assim como algumas características reprodutivas, pode variar com a latitude. Os padrões latitudinais de algumas características reprodutivas já foram bem estudados e são bem conhecidos, como o menor tamanho da prole, o longo período de desenvolvimento, a lenta taxa de crescimento dos ninhegos e a maior taxa de sobrevivência dos adultos nas espécies tropicais (Ricklefs 1976, Skutch 1985, Martin 1996, Cox & Martin 2009, Martin et al. 2011, 2015). Entretanto, a procura por diferenças latitudinais no investimento em cuidado parental é mais recente. Alguns padrões já encontrados durante o período de incubação foram o maior tempo investido na incubação dos ovos e a maior temperatura dos ovos nas espécies temperadas (Martin 2002, Martin et al. 2015). Durante o período de ninhego, os padrões encontrados indicam que a taxa de alimentação por ninhego é maior nas espécies tropicais apesar de não existir diferença latitudinal na taxa de alimentação total do ninho (Martin et al. 2011, Gill & Haggerty 2012, Llambías et al. 2015). Entretanto, esses padrões na taxa de alimentação ainda não foram analisados durante todo o período de ninhego, desde o nascimento até a saída do ninho.

As aves possuem distintos modos de cuidado parental que diferem de acordo com o número de adultos que participam do cuidado durante os períodos de incubação e de ninhego (Cockburn 2006, Martin et al. 2006). Os modos de cuidado parental mais raros são a cooperação (realizado por mais que dois indivíduos, 9%), apenas pela fêmea (8%) e apenas pelo macho (1%). O modo de cuidado biparental é o predominante (Lack 1968), ocorrendo em aproximadamente 81% das espécies de aves (Cockburn 2006). A evolução desses diferentes modos de cuidado parental é resultante do conflito entre os custos (diminuição da sobrevivência futura dos adultos) e os benefícios (aumento do sucesso reprodutivo) associados aos comportamentos de cuidado parental (Clutton-Brock 1991). Portanto, avaliar os padrões no investimento total em cuidado parental entre os diferentes modos é importante para entender a evolução desse comportamento (Matysioková & Remeš 2014).

O objetivo desse trabalho foi medir o investimento em cuidado parental para avaliar se existem padrões entre espécies tropicais e temperadas e entre distintos modos de cuidado parental nas aves. Para isso os comportamentos de cuidado parental de espécies de aves da ordem Passeriformes foram observados em uma região da Mata Atlântica no estado do Paraná, e foram feitas buscas na literatura por informações reprodutivas da família Parulidae. No Capítulo I as características reprodutivas de *Myiothlypis leucoblephara* e *Basileuterus culicivorus* foram descritas e contextualizadas no padrão das espécies tropicais e temperadas, e posteriormente o investimento em cuidado parental durante a fase de ninhego foi comparado entre espécies tropicais e temperadas da família Parulidae. No Capítulo II foi comparado o investimento em cuidado parental, durante o período de incubação e de ninhego, entre diferentes modos de cuidado.

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CAPÍTULO I

TROPICAL AND TEMPERATE NESTLING PROVISIONING RATES DIFFER FOR LATE NESTLINGS IN THE NEW WORLD WARBLERS

Abstract

The influence of nest predation in tropical and temperate birds and its influence on nestling provisioning have been debated. The nest predation hypothesis states that birds should reduce activity at nests to avoid attracting predators, and such effects may be more important in the tropics. However, recent statistical simulation proposes that avoiding nest predation is more important for species with shorter breeding seasons and fewer nesting attempts – common traits of temperate birds. Here, we first provide a description of the breeding biology of the White-rimmed Warbler (*Myiothlypis leucoblephara*) and the Golden-crowned Warbler (*Basileuterus culicivorus*) in the Atlantic Forest in southern Brazil and compare their life history traits to other tropical and temperate warblers. We follow with a comparison of nestling provisioning (measured as total feeding and per nestling feeding rates) and daily nest predation rates during the nestling period between tropical and temperate warblers using data from the literature. Breeding traits of the sympatric species, White-rimmed Warbler and Golden-crowned Warbler, show that they differ in their nesting strategies and do not fit completely in a tropical or temperate pattern. Total feeding rates and daily nest predation rates were not correlated and were similar between tropical and temperate warblers, suggesting that nest predation risk is not affected by activity at the nest. Per nestling feeding rate was greater in tropical warblers only in late nestling period, suggesting that differences between tropical and temperate species in nestling provisioning must be critical only during this period. These patterns allow a better understanding of the role played by nestling provisioning and highlights the importance of age-dependent differences in parental investment on life history evolution.

Key-words: parulids, *Myiothlypis leucoblephara*, *Basileuterus culicivorus*, feeding rate, nest predation rate.

Introduction

Understanding latitudinal variation in nesting biology and parental care of birds remains incomplete despite the great historical interest (Moreau 1944, Lack 1947, Skutch 1949, Ricklefs 1968a, 1976, Skutch 1985, Martin 1996, 2004, Roper et al. 2010). Some latitudinal patterns are well known, such as smaller clutches, longer developmental periods, slower growth rates and greater adult survival in tropical birds (Ricklefs 1976, Skutch 1985, Martin 1996, Cox and Martin 2009, Martin et al. 2011, 2015). Data and theory with respect to these issues are biased due to emphasis on north temperate species while most species of birds are from southern temperate and tropical regions (Martin 1996, 2004). However, recent studies of southern temperate and tropical species have improved the knowledge about latitudinal breeding variation and their influence on life history theory (Auer et al. 2007, Cox and Martin 2009, Lima and Roper 2009, Roper et al. 2010, Martin et al. 2011, 2015, Marini et al. 2012, Llambías et al. 2015, Marques-Santos et al. 2015).

Although understanding causes of variation in parental care is crucial for life history theory, latitudinal patterns in nestling provisioning are especially understudied. Nest predation is commonly suggested to be influential in life history evolution and in provisioning rates (Skutch 1949, Auer et al. 2007, Martin et al. 2011, Gill and Haggerty 2012). This idea suggests that greater nest predation probability in the tropics can favor reduced clutch size to reduce activity at nests and thereby decrease probability of activity attracting predators. Therefore, total feeding rates (as number of visits to the nest) should be lower in tropical birds. Contrary to this idea, a statistical simulation showed that birds with a short breeding season and fewer nesting attempts should avoid nest predation even when nest predation rates are low, while high nest predation rates for birds with long seasons and time for multiple attempts simply favor repeated nesting (Roper et al. 2010). Thus, avoiding nest predation may often be more important for temperate than tropical species due to their shorter breeding season and, if so, total feeding rates should be lower in temperate birds if parental activity is correlated with nest predation risk. These hypotheses have not been supported by recent analysis of feeding rates during the second half of the nestling period (advanced age of nestlings; Martin et al. 2011, Gill and Haggerty 2012, Llambías et al. 2015). Therefore, understanding differences in feeding rates with age of nestlings in widely latitudinally distributed taxa should provide better understanding of how nest predation influences patterns in tropical and temperate birds.

New World Warblers (family Parulidae) comprise approximately 110 species distributed throughout the Americas (Curson et al. 1994, Lovette et al. 2010, Gill and Donsker 2016) and provide the opportunity to test these predictions while controlling for phylogeny. Warblers have latitudinal life history patterns, with tropical species tending to have smaller clutches, lower nest attentiveness and longer developmental periods (Martin et al. 2000a, Martin 2002, Auer et al. 2007, Cox and Martin 2009, Marques-Santos et al. 2015). Yet, they are much better studied in temperate North America than elsewhere. As a consequence, basic breeding traits (such as incubation and nestling periods, nest attentiveness, nestling feeding and growth rates) remain unknown for most southern and tropical species, making latitudinal comparisons difficult (Curson et al. 1994, Cox and Martin 2009).

The White-rimmed Warbler *Myiothlypis leucoblephara* (Vieillot, 1817) is endemic to the Atlantic Forest of South America, from southern Brazil to Uruguay, northeastern Argentina and eastern Paraguay. The Golden-crowned Warbler *Basileuterus culicivorus* (Deppe, 1830) is more widespread, found from northeastern Mexico to northern Argentina (Olson 1975, Curson et al. 1994). These monomorphic species are common in forest patches throughout their ranges, and are sympatric in the Atlantic Forest of southern Brazil. Both parents feed the nestlings but only the female incubate the eggs (pers. obs.) and lay eggs on consecutive days (Marques-Santos et al. 2015). However, information about their reproductive traits is restricted to nest and egg description, clutch size and incubation period for White-rimmed Warbler, and egg description, clutch size, nest attentiveness, incubation and nestling period for Golden-crowned Warbler (Skutch 1967, Cox and Martin 2009, Firme et al. 2009, Lopes et al. 2013, Marques-Santos et al. 2015).

Here, we first provide detailed description of the breeding biology of White-rimmed Warbler and Golden-crowned Warbler and compare these traits to other tropical and temperate warblers. We then use nestling provisioning data for New World Warblers (from White-rimmed Warbler, Golden-crowned Warbler and the literature) to test for variation between tropical and temperate species in feeding rates during the entire nestling period.

Material and Methods

Literature search

We used New World Warbler breeding traits reviewed by Cox and Martin (2009) supplemented with information from the literature. We searched for warbler life history traits using the following key words in combination with the name of species (cf. Gill and Donsker 2016): reproductive, reproduction, breeding, nest, parental care, incubation, egg, attentiveness, nestling and feed. We used The Birds of North America, ISI, Scopus, Scielo and studies cited in those publications (Supplementary material Table A1). When more than one value of a life history trait was available for a given species we used the mean or the midpoint value if only a range of values was provided. For latitudinal comparisons we gathered tropical and subtropical species (following the classification of Cox and Martin 2009) because breeding information are still scarce for a separate comparison. Despite the fact that birds from these latitudes can differ in some breeding traits, in general they are similar and differ from temperate species (Martin 1996, Auer et al. 2007, Marques-Santos et al. 2015).

Study area

Field work was carried out at Marumbi State Park (*Parque Estadual Pico Marumbi* - 25º 29' S, 48º 59' W, 938 to 1,016 m elevation) in the state of Paraná, southern Brazil. This study area is subtropical and in the largest remaining Atlantic Forest fragment (Ribeiro et al. 2009), and is a transitional region between Araucaria Forest and Montane Atlantic Rainforest (Reginato and Goldenberg 2007).

Nests

We searched for nests of White-rimmed Warbler and Golden-crowned Warbler during three consecutive breeding seasons (2012 – 2015 from August to January). To find nests, we used adult behavioral cues and followed birds when carrying nesting material or food for young. We also searched for nests in potential places in the area, such as ravines, or after adult birds were observed flushing and performing a distraction display. Nests were checked every 2 – 3 days, and more often when nesting stages (laying, hatching and fledging) were expected to change (Martin and Geupel 1993, Cox and Martin 2009). At least one adult of each pair was banded and their sex was determined as only females develop a brood patch and only males sing. We used a unique combination of color plastic bands and a numbered metal band provided by the Brazilian banding agency (CEMAVE – *Centro Nacional de Pesquisa e Conservação de Aves Silvestres*).

Incubation period and nest attentiveness

We estimated the duration of the incubation period as the interval in days between the last egg laid and hatching (Cox and Martin 2009). To estimate female attentiveness during the first breeding season, we visited the nest hourly (6 – 8 times a day) and noted the presence of the female from a distance to avoid disturbance. In subsequent breeding seasons, we used the time-lapse function of a Trail Camera (M-990i, Moultrie Products, LLC., Birmingham, AL) and took pictures at five minute intervals for 5.7 ± 0.5 (mean ± SE) consecutive hours. Nest attentiveness in the first breeding season was estimated as the proportion of nest visits with the female on the nest. In the following breeding seasons, nest attentiveness was the proportion of photographs in which the female was on the nest. Thus, nest attentiveness was always the probability that female was incubating. We tested whether the two methods differed using linear mixed models. We built models with method as a factor, $\log_{10}$ transformed embryo age as a predictor and nest identity as a random effect on the intercept and slope. We compared models with and without the factor (method) by the likelihood ratio test. To estimate nest attentiveness for each species we obtained the least squares means of a linear mixed model with $\log_{10}$ transformed embryo age as a predictor and nest identity as a random effect on the intercept and slope, thereby controlling for age effects in estimates.

Nestling period and growth rates

Nestling period was estimated as the interval in days between hatching and fledging (Cox and Martin 2009). Nestlings were weighed on a digital scale (0.01 g precision) every 2 – 3 days (Cox and Martin 2009), and growth rate constants (K) were estimated using the logistic growth model (Ricklefs 1968b, Sofaer et al. 2013).

Feeding rates

The nestling provisioning for White-rimmed Warbler and Golden-crowned Warbler were measured using video cameras for approximately one hour every 2 – 3 days until fledging or nest failure during all three breeding seasons. We noted how many times parents arrived at the nest to feed the nestlings to estimate the total feeding rate (visits h^{-1}) and per nestling feeding rate (visits nestling^{-1} h^{-1}). We used linear regression to test for a relationship between nestling age and total feeding rate ($\log_{10}$ transformed) for the White-rimmed and Golden-crowned Warblers.

We searched for nestling provisioning data for other warblers species in literature. Some warbler feeding rates found were estimated by nest, as total feeding rate, without regard for the number of nestlings present. Thus, we estimated the expected per nestling feeding rates as total feeding rate divided by the average clutch size in each species. When only the per nestling feeding rate was reported, we estimated the total feeding rate similarly.

To compare tropical and temperate warbler feeding rates, we first separated feeding rates estimated for White-rimmed Warbler, Golden-crowned Warbler and from the literature into early (first half of the nestling period, by species) and late periods (after the middle of the nestling period, by species), when the age of the nestlings was reported. When feeding rates were estimated for a period longer than one day (but not more than five days) we used the midpoint of that period as the nestling age in the analysis. Feeding rates may vary with nestling age, so we used linear mixed models to test whether feeding rates ($\log_{10}$ transformed rates) during early and late nestling periods differed between tropical and temperate warblers. We built models separately for early and late nestling periods with nestling age as a covariate, location (tropical or temperate) as a fixed factor and species identity as a random effect on the intercept and slope. We compared models with and without the factor (location, tropical or temperate) by the likelihood ratio test.

Nest predation and feeding rate

To test the relationship between daily nest predation rate during the nestling period and activity at nests we restricted our literature search for nest predation rates to those studies that included feeding rate estimates. We tested for a correlation between daily nest predation rates and total feeding rates ($\log_{10}$ transformed). Additionally, we compared daily nest predation rates by tropical and temperate warblers using the *t*-test.

Statistical tests were carried out in R version 3.1.3. Linear mixed model were carried out with the lme4 package (Bates et al. 2015) and least square means with the lsmeans package (Russell 2015). Descriptive statistics and tests include sample sizes, means and standard errors (± SE), or as specified.

Results

Nests

We found a total of 33 nests (21 White-rimmed Warbler and 12 Golden-crowned

Warbler). Both species built a somewhat domed nest with a lateral entrance on the ground. Nests were on level ground or hillsides in ravines and valleys. Nine of the 21 White-rimmed Warbler (43%) and two of the 12 Golden-crowned Warbler (17%) nests were successful. Nests failed due to predation (6 White-rimmed Warbler and 8 Golden-crowned Warbler), abandonment (5 White-rimmed Warbler and 2 Golden-crowned Warbler) and heavy rain (1 White-rimmed Warbler). Both species laid eggs on consecutive days and clutch size was invariably 3 in the White-rimmed Warbler (n = 14) and 2.9 ± 0.1 eggs in the Golden-crowned Warbler (n = 9, only one nest had 2 eggs, the rest had 3) similar to other tropical warblers (Fig. 1A).

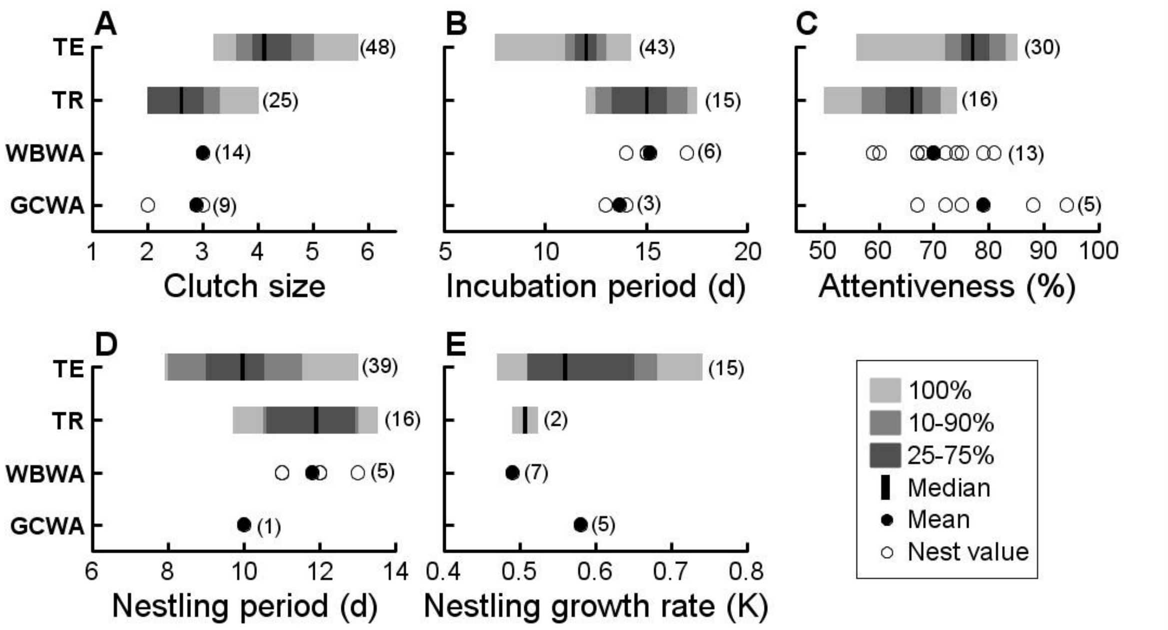

Figure 1. Breeding biology traits of temperate warblers (TE), tropical warblers (TR), White-rimmed Warbler *Myiothlypis leucoblephara* (WBWA) and Golden-crowned Warbler *Basileuterus culicivorus* (GCWA). Values in parenthesis indicate the number of temperate and tropical species, and the number of White-rimmed Warbler and Golden-crowned Warbler nests. Temperate and tropical warblers values are presented as median and quantiles of the species means. White-rimmed Warbler and Golden-crowned Warbler are presented as mean of nests values.

Incubation period and nest attentiveness

Incubation lasted 15.2 ± 0.4 days (n = 6) in the White-rimmed Warbler and 13.7 ± 0.3 days (n = 3) in the Golden-crowned Warbler. In neither species did males incubate, and we observed White-rimmed Warbler males feeding the female during incubation at two nests. The two methods used to estimate nest attentiveness similar for both species (White-rimmed

Warbler: $\chi^2 = 3.3$, df = 1, p = 0.069; Golden-crowned Warbler: $\chi^2 = 0.8$, df = 1, p = 0.365), so we combined data from the three breeding seasons to estimate nest attentiveness. White-rimmed Warbler nest attentiveness was 71 ± 2% in 10.0 days embryos old (13 nests, 41 observation days) and Golden-crowned Warbler was 77 ± 7% in 10.4 days embryos old (five nests, 21 observation days). Incubation periods of both species were similar to other tropical warblers (Fig. 1B), while nest attentiveness of White-rimmed Warbler was similar to tropical and Golden-crowned Warbler was similar to temperate warblers (Fig. 1C).

Nestling period and growth rates

The nestling period was 11.8 ± 0.4 days (n = 5) in the White-rimmed Warbler and 10 days in the one nest in which it could be measured in the Golden-crowned Warbler. Nestling growth rate constant (*K*) in White-rimmed Warbler was 0.49 ± 0.03 (seven nests, 19 nestlings) and in Golden-crowned Warbler was 0.58 ± 0.02 (five nests, 15 nestlings, Fig. 2). The nestling period and growth rate constant in the White-rimmed Warbler were similar to tropical warblers, while the Golden-crowned Warbler was more similar to temperate warblers (Figs. 1D and 1E).

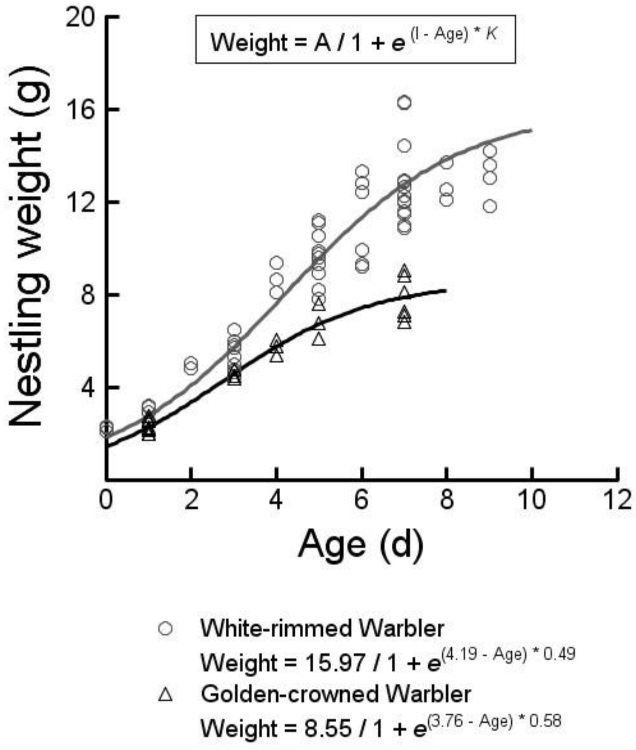

Figure 2. Nestlings growth curves of White-rimmed Warbler (*Myiothlypis leucoblephara*, open circles and gray line) and Golden-crowned Warbler (*Basileuterus culicivorus*, open triangles and black line).

Feeding rates

Nestlings were fed by both sexes in both species (White-rimmed Warbler: eight nests, 28 observation days and 28 hours of video monitoring; Golden-crowned Warbler: five nests, 14 observation days and 15 hours of video monitoring). As nestling age increased, so did total feeding rate (White-rimmed Warbler: $r^2 = 0.51$, $p < 0.001$; Golden-crowned Warbler: $r^2 = 0.33$, $p = 0.019$; Fig. 3).

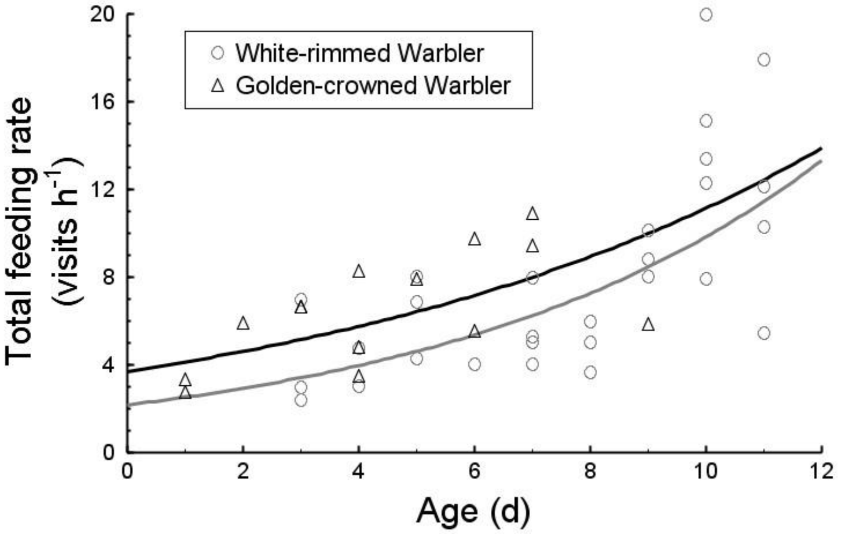

Figure 3. Total feeding rate increase with age of nestling for White-rimmed Warbler (*Myiothlypis leucoblephara*, open circles and gray line) and Golden-crowned Warbler (*Basileuterus culicivorus*, open triangles and black line).

For nestling provisioning comparisons between tropical and temperate warblers during the early nestling period we used information of 35 species (five tropical and 30 temperate). Tropical and temperate warblers had similar total feeding rate (additive effect: $\chi^2 = 0.19$, df = 1, p = 0.667; interaction effect: $\chi^2 = 0.15$, df = 1, p = 0.699) and per nestling feeding rate (additive effect: $\chi^2 = 1.18$, df = 1, p = 0.276; interaction effect: $\chi^2 = 0.23$, df = 1, p = 0.632; Fig. 4). During the late nestling period we used information of 38 species (nine tropical and 29 temperate). Tropical and temperate warblers had similar total feeding rate (additive effect: $\chi^2 = 0.29$, df = 1, p = 0.589; interaction effect: $\chi^2 = 0.22$, df = 1, p = 0.638), while per nestling feeding rate in tropical warblers (3.79 ± 1.23 visits nestling^{-1} h^{-1}) was greater than in temperate warblers (2.26 ± 1.12 visits nestling^{-1} h^{-1}; additive effect: $\chi^2 = 5.40$, df = 1, p = 0.020; interaction effect: $\chi^2 = 0.30$, df = 1, p = 0.587; Fig. 4).

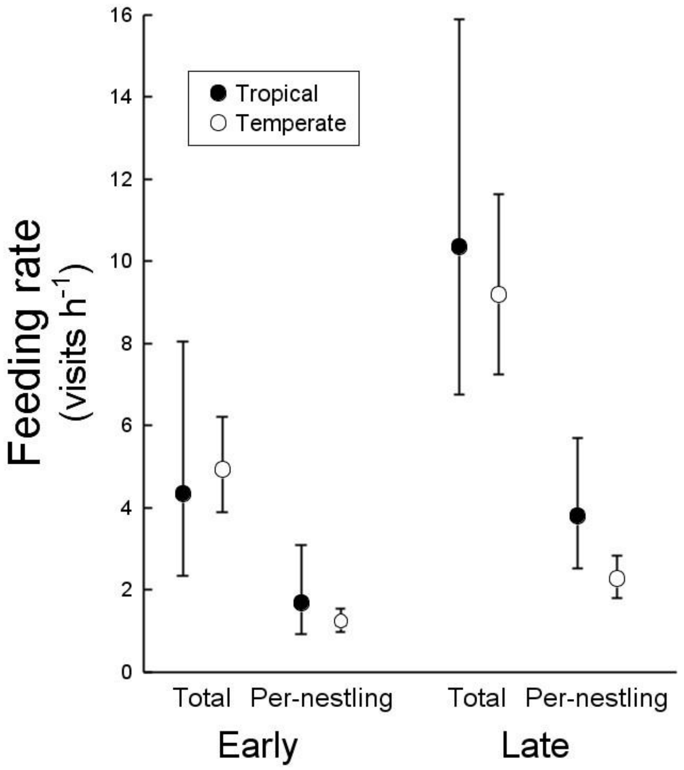

Figure 4. Total and per nestling feeding rates during early and late nestling period of tropical (filled circles) and temperate (open circles) warblers. During late nestling period per nestling feeding rate was greater in tropical warblers ($p < 0.05$). Values are presented as least square means, lower and upper confidence interval.

Nest predation and feeding rate

While nest predation was the main cause of nest failure, we were unable to estimate daily nest predation rates for the warblers due to sample size. Total feeding rates of species with daily nest predation rates available were estimated when nestlings were 6 to 8 days old. However, in some species feeding rates were estimated at different nestling ages, in which case we used the average total feeding rates during age 6 to 8 days in the analyses. Warbler daily nest predation rate was independent of total feeding rate ($t_{1,12} = 0.9$, $p = 0.390$), and both tropical (0.047 ± 0.007, n = 6) and temperate (0.034 ± 0.006, n = 8) nest predation rates were similar ($t = 1.5$, df = 12, $p = 0.155$; Fig. 5).

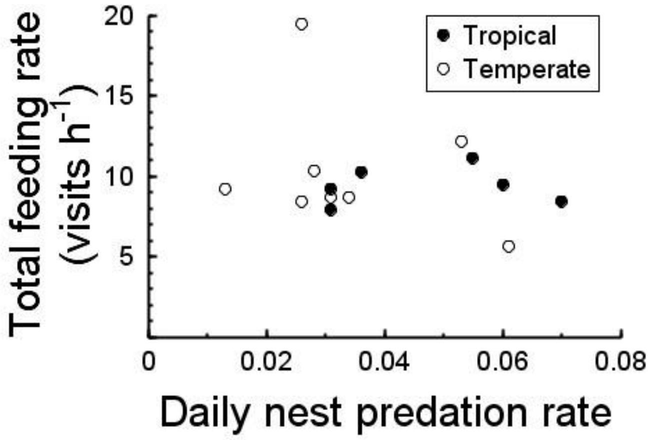

Figure 5. Total feeding rate is not correlated with daily nest predation in warblers, and daily nest predation is not different between tropical (filled circles) and temperate (open circles) warblers species.

Discussion

Contrary to predictions, nestling provisioning were similar in tropical and temperate warblers. However, when per nestling feeding rate was compared, we found that tropical and temperate warbler rates were only similar when nestlings were young (during the first half of the nestling period). At the same time, daily nest predation rates were independent of nest provisioning rate and were similar between tropical and temperate warblers, showing that activity at nests is unrelated to predation likelihood. We show that the two sympatric, ground nesting and simultaneously breeding warblers in southern Brazil have differences in their nesting strategies that do not fit into a tropical or temperate pattern (Marques-Santos et al. 2015).

Clutch sizes in the White-rimmed and Golden-crowned Warblers were smaller than temperate while similar to tropical warblers (Martin et al. 2000a, Auer et al. 2007, Cox and Martin 2009). Golden-crowned Warbler clutch size was within the interval reported in the literature (2 – 4 eggs; Skutch 1967, Cox and Martin 2009), and White-rimmed Warbler one egg smaller than the single nest reported in the literature (4 eggs; Firme et al. 2009). These findings suggest that clutch size in the species is variable, even if not in our study area. Incubation periods of both species were longer than those of temperate species while nest attentiveness in the White-rimmed Warbler only was clearly reduced and similar to that of other tropical warblers (Martin 2002, Auer et al. 2007, Cox and Martin 2009, Martin et al.

2015). This reduced nest attentiveness in tropical birds may be responsible for lower embryonic temperatures and consequent longer incubation period as compared to temperate species (Martin 2002, Martin et al. 2015). Nestling period and growth rate constant of the White-rimmed Warbler were also similar to those of tropical warblers, while these traits in the Golden-crowned Warbler were more similar to temperate species (Cox and Martin 2009). Different patterns in breeding traits of both species have been reported (Marques-Santos et al. 2015) and may be due to the wider distribution of the Golden-crowned Warbler (Olson 1975, Curson et al. 1994). Also, these results suggest that breeding patterns in this subtropical study site are not typical of either tropical or temperate patterns (Marques-Santos et al. 2015).

Contrary to predictions about nestling provisioning, total feeding rates were similar between tropical and temperate warblers. Both predictions were based on the idea of avoiding nest predation by reducing total feeding rates (activity at the nests; Skutch 1949, Roper et al. 2010). However, we also did not find differences in daily nest predation rates between tropical and temperate warblers, supporting the idea that nest predation is not consistently different between these regions (Snow and Snow 1963, Skutch 1985, Martin 1996, Martin et al. 2000b, 2006). Thus, feeding rates seem to be unrelated to daily nest predation in warblers, suggesting that nest predation risk is not affected by activity at the nests (Roper and Goldstein 1997, Martin et al. 2000b). Interestingly, this result may be unique to warblers because other recent studies found negative correlations between total feeding rate and daily nest predation rate across a more diverse array of other species (Martin et al. 2011, Martin 2015).

Looking at the similar total feeding rates we found between tropical and temperate warblers and the established pattern in clutch size, with smaller clutch sizes in tropical species (Martin et al. 2000a, Auer et al. 2007, Cox and Martin 2009), we expected to find greater per nestling feeding rates in tropical warblers. This predicted difference occurred only during the late nestling period. This result may be related to the difference in nestling growth trajectories between tropical and temperate species (Martin 2015). This greater per nestling feeding rate in tropical species may be necessary due to the greater nestling growth rate in tropical birds during late nestling period compared with temperate birds, which results in greater wing size (hence offspring quality) at the time of leaving the nest (Llambías et al. 2015, Martin 2015).

The sympatric White-rimmed Warbler and Golden-crowned Warbler have different breeding strategies which suggest that different breeding or behavioral strategies may be solutions to similar environmental pressures at the same latitude in the same environment

(Martin et al. 2011, 2015). This implies that breeding patterns and life history strategies are not merely latitudinally related, but that they may also be variable within locations as alternative ways that species can solve local exigencies of nesting and survival. Also, the breeding traits of these species show that the subtropical region cannot be fit neatly within a tropical or temperate pattern (Marques-Santos et al. 2015). Our results about per nestling feeding rates suggest that differences in behavioral strategies between tropical and temperate birds may be critical during the late nestling period and allowed a better understanding of the role played by nestling provisioning in life history evolution.

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Supplementary material

Table A1. Breeding biology traits of temperate and subtropical/tropical warblers. Species names follow the IOC World Bird List (Gill and Donsker 2016). CS = clutch size; IP = incubation period (days); A = attentiveness (%); NP = nestling period (days); K = nestling growth rate; EFR = species with early feeding rate data used in analysis; LFR = species with late feeding rate used in analysis; DNP = daily nest predation rate during nestling period; Bold = additional data from literature, not present in the review made by Cox and Martin (2009); PS = present study.

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
<u>Temperate</u>									
Ovenbird (*Seiurus aurocapilla*)	4.3	12.2	85	7.9	0.47	**X**	**X**		1, 2, 3
Worm-eating Warbler (*Helmitheros vermivorum*)	4.8	13.0		9.0					1
Louisiana Waterthrush (*Parkesia motacilla*)	5.0	12.7	79	10.8	0.59	**X**	**X**		1, 4, 5
Northern Waterthrush (*Parkesia noveboracensis*)	4.1	12.0	75	9.0					1
Bachman's Warbler (*Vermivora bachmanii*)	**4.2**								6
Golden-winged Warbler (*Vermivora chrysoptera*)	5.0	11.0		9.5		**X**	**X**		1, 7, 8

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
Blue-winged Warbler (*Vermivora cyanoptera*)	4.4	10.5		9.3	0.56	**X**	**X**		1, 8, 9
Black-and-white Warbler (*Mniotilta varia*)	5.0	11.0		10.0		**X**			1, 4
Prothonotary Warbler (*Protonotaria citrea*)	4.6	12.5	56	10.0	0.65	**X**	**X**		1, 10, 11, 12
Swainson’s Warbler (*Limnothlypis swainsonii*)	3.2	13.9	78	9.9		**X**	**X**		1, 13, 14, 15
Tennessee Warbler (*Leiothlypis peregrina*)	5.6	7.5		**11.5**	0.65				1, 8
Orange-crowned Warbler (*Leiothlypis celata*)	4.5	12.6	80	11.3		**X**	**X**	**0.028**	1, 8, 16, 17
Lucy's Warbler (*Leiothlypis luciae*)	**4.5**	**12.0**		**11.0**					8, 18
Virginia’s Warbler (*Leiothlypis virginiae*)	3.6	12.3	73	11.4		**X**	**X**	**0.031**	1, 8, 16, 17
Nashville Warbler (*Leiothlypis ruficapilla*)	4.7	11.5	73	10.0		**X**	**X**		1, 19
Connecticut Warbler (*Oporornis agilis*)	**4.5**								20

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
MacGillivray’s Warbler (*Geothlypis tolmiei*)	4.1	12.5	77	10.4			**X**	**0.026**	1, 16
Mourning Warbler (*Geothlypis philadelphia*)	3.7	12.0	75	8.0		**X**			1, 21
Kentucky Warbler (*Geothlypis formosa*)	4.1	11.0		9.0	0.68				1
Common Yellowthroat (*Geothlypis trichas*)	4.0	12.0	80	9.8	0.54	**X**	**X**		1, 22, 23
Hooded Warbler (*Setophaga citrina*)	3.6	11.0		8.5		**X**	**X**		1, 24, 25, 26, 27, 28, 29
American Redstart (*Setophaga ruticilla*)	3.9	11.5	82	8.0	0.61	**X**	**X**		1, 4, 30, 31
Kirtland’s Warbler (*Setophaga kirtlandii*)	4.6	14.2	82	9.4	0.55				1
Cape May Warbler (*Setophaga tigrina*)	**5.8**								32
Cerulean Warbler (*Setophaga cerulea*)	3.6	11.4	83	10.4			**X**		1, 33
Northern Parula (*Setophaga americana*)	3.9	12.5	79	10.5		**X**			1, 34

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
Magnolia Warbler (*Setophaga magnolia*)	4.0	12.0	70	9.0		**X**	**X**		1, 4, 35, 36
Bay-breasted Warbler (*Setophaga castanea*)	5.4	12.5	80	10.5			**X**		1, 37
Blackburnian Warbler (*Setophaga fusca*)	4.0		72						1
Mangrove Warbler (*Setophaga petechia*)	4.1	11.3	78	8.4	0.58	**X**	**X**	**0.026,** **0.053**	1, 38, 39, 40, 41, 42, 43, 44
Chestnut-sided Warbler (*Setophaga pensylvanica*)	3.9	11.0	75	10.5		**X**	**X**		1, 4, 45
Blackpoll Warbler (*Setophaga striata*)	4.3	11.8	77	9.5	0.54	**X**	**X**		1, 8
Black-throated Blue Warbler (*Setophaga caerulescens*)	3.8	13.0	72	8.6	0.65	**X**	**X**		1, 4, 46, 47, 48, 49, 50
Palm Warbler (*Setophaga palmarum*)	4.6	12.0		12.0					1
Pine Warbler (*Setophaga pinus*)	**3.8**	**11.5**							4, 51
Myrtle Warbler (*Setophaga coronata*)	3.9	12.8	77	12.6		**X**	**X**	**0.013**	1, 8, 16

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
Yellow-throated Warbler (*Setophaga dominica*)	4.0	12.0							1
Prairie Warbler (*Setophaga discolor*)	3.9	12.0	77	9.6	0.51	**X**	**X**	**0.061**	1, 52, 53
Grace's Warbler (*Setophaga graciae*)	3.2	12.0							1
Black-throated Gray Warbler (*Setophaga nigrescens*)	**4.0**								20
Hermit Warbler (*Setophaga occidentalis*)	**4.3**								8
Townsend's Warbler (*Setophaga townsendi*)	5.7	12.5		9.9					1
Black-throated Green Warbler (*Setophaga virens*)	4.0	12.0	78	10.0	0.74	**X**	**X**		1, 54, 55, 56
Golden-cheeked Warbler (*Setophaga chrysoparia*)	3.9	12.1	74	10.5					1
Canada Warbler (*Cardellina canadensis*)	4.4	12.0	85	**8.0**		**X**			1, 8
Wilson's Warbler (*Cardellina pusilla*)	4.1	11.9	81	10.2		**X**	**X**		1, 57, 58

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
Red-faced Warbler (*Cardellina rubrifrons*)	4.2	12.8	75	11.1			**X**	**0.034**	1, 16, 17
Painted Whitestart (*Myioborus pictus*)	3.2	13.2	75	13.0	0.56	**X**	**X**		1, 59
<u>Subtropical/Tropical</u>									
Flame-throated Warbler (*Oreothlypis gutturalis*)	2.0	16.0	61	13.0					1
Crescent-chested Warbler (*Oreothlypis superciliosa*)	2.5	13.0	68						1
Colima Warbler (*Leiothlypis crissalis*)	3.5	12.0		11.0					1
Masked Yellowthroat (*Geothlypis aequinoctialis*)	3.1	13.3	61	9.7			**X**	**0.031**	1, 60
Grey-crowned Yellowthroat (*Geothlypis poliocephala*)	2.7	12.8		11.0					1
Tropical Parula (*Setophaga pitiayumi*)	3.1			13.0			**X**		1, 61
Adelaide’s Warbler (*Setophaga adelaidae*)	2.5		50						1

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
White-striped Warbler (*Myiothlypis leucophrys*)	**3.0**								62, 63
White-rimmed Warbler (*Myiothlypis leucoblephara*)	**3.0**	**16.4**	**69**	**11.8**	**0.48**	**X**	**X**		PS
Pale-legged Warbler (*Myiothlypis signata*)	2.6	16.6	65	12.5			**X**	**0.055**	1, 17, 60
Black-crested Warbler (*Myiothlypis nigrocristata*)	**2.0**								64
Buff-rumped Warbler (*Myiothlypis fulvicauda*)	2.0	17.5	71	13.5					1
Two-banded Warbler (*Myiothlypis bivittata*)	3.0	14.8	62	10.9			**X**	**0.031**	1, 17, 60
Gray-and-gold Warbler (*Myiothlypis fraseri*)	**4.0**								65
Russet-crowned Warbler (*Myiothlypis coronata*)	**2.0**								64
Rufous-capped Warbler (*Basileuterus rufifrons*)	3.0		66	12.0					1
Black-cheeked Warbler (*Basileuterus melanogenys*)	2.0		62						1

Species	CS	IP	A	NP	K	EFR	LFR	DNP	References
Golden-crowned Warbler (*Basileuterus culicivorus*)	**2.9**	**15.0**	**74**	**10.0**	**0.58**	**X**	**X**		PS
Three-banded Warbler (*Basileuterus trifasciatus*)	**2.0**								64
Three-striped Warbler (*Basileuterus tristriatus*)	2.0	15.8	57	10.5	**0.49**	**X**	**X**	**0.070**	1
Red Warbler (*Cardellina rubra*)	3.0	16.0	66	10.5					1
Pink-headed Warbler (*Cardellina versicolor*)	3.0	16.0	71	10.5					1
Slate-throated Whitestart (*Myioborus miniatus*)	2.7	14.4	67	11.8	0.52	**X**	**X**	**0.060**	1, 66, 67
Brown-capped Whitestart (*Myioborus brunniceps*)	2.6	16.6	67	12.6			**X**	**0.036**	1, 17, 60
Yellow-crowned Whitestart (*Myioborus flavivertex*)	**2.0**								68
Spectacled Whitestart (*Myioborus melanocephalus*)	**2.0**	**15.0**	**67**	**12.0**					69
Collared Whitestart (*Myioborus torquatus*)	2.5	15.0	74	13.0					1

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CAPÍTULO II

CONSEQUENCES OF THE NUMBER OF CAREGIVERS FOR THE AMOUNT OF PARENTAL CARE AT THE NEST

Abstract

Parental care is determined by a conflict between the needs of the offspring and the care that parents provide while maximizing their own survival. While efforts have been made to better understand how parents partition care, to better understand parental care sympatric species with different modes of parental care must be compared. Modes of parental care differ mainly in how many parents provide care, with uniparental care (a single parent) and biparental care (two parents) being the most often studied. Biparental care can be divided in partial biparental care, when one parent incubates eggs while both parents provision the nestlings, or complete biparental care, when both parents share egg incubation and nestling provisioning. Here, we compared the amount of parental care between uniparental (Blue Manakin *Chiroxiphia caudata*), partial biparental (Red-eyed Vireo *Vireo olivaceus*, Olivaceus Elaenia *Elaenia mesoleuca* and Highland Elaenia *Elaenia obscura*) and complete biparental care (Variable Antshrike *Thamnophilus caerulescens*) in the Atlantic Forest in southern Brazil. The total amount of parental care was greater in biparental care than in uniparental care. Nest attentiveness was greater in complete biparental care, and total and per nestling feeding rates were greater in partial biparental care. Feeding rates were surprisingly similar in uniparental and complete biparental care, which suggests that the relationship between the number of caregivers and the total amount of parental care is stronger during the incubation period. Our results support the idea that the total amount of parental care varies with the number of caregivers and that this difference influences important breeding traits in birds. Thus, considering the effects of the differences in the number of caregivers in life history traits is important to better understand parental care evolution.

Key-words: biparental care, uniparental care, attentiveness, feeding rate, parental effort

Introduction

Parental care is an important component of reproductive effort and influences reproductive success in birds (Royle et al. 2012). Increasing parental care should maximize offspring survival probability, while reducing care to the minimum requirements of the offspring should increase the parents survival and future reproduction (Martin 1987, Clutton-Brock 1991, Royle et al. 2012). Thus, the investment in parental care should be a balance between offspring demand and care that parents can provide (Godfray and Johnstone 2000, Royle et al. 2012). Offspring commonly beg to communicate hunger to their parents, and the energy required by offspring varies by hatching pattern, growth rate, brood size, thermoregulatory costs and age (Godfray and Johnstone 2000). In response, parents can invest in parental care according to offspring needs (Martin 1987, Carere and Alleva 1998, Wright et al. 1998). Therefore, this parent-offspring conflict is an important selective force for the evolution of parental care (Royle et al. 2012).

Attempts have been made to understand how parents partition their care to successfully rear their offspring (Harrison et al. 2009, Weeb et al. 2010), however, how parental care varies among species with different modes of parental care and in similar ecological circumstances remains to be studied. Modes of parental care in birds differ mainly in how many parents provide care (Cockburn 2006). Uniparental care is rare in birds, with only females providing care in 9% and only male in 8% of all bird species. Biparental care is the most common, comprising about 81% of species (Cockburn 2006). Biparental care can have either of two options: 1) one parent, usually the female, incubates eggs while both parents provide food for the nestlings (hereafter partial biparental care), and 2) both parents share egg incubation and nestling provisioning (hereafter complete biparental care).

Comparisons of the different modes of parental care can be made based on the number of caregivers, the trait used to classify species in modes of parental care (Cockburn 2006), and the total amount of care invested. The total amount of parental care can increase with the number of parents providing care, while the individual cost to the parents can be reduced by dividing care among more individuals (Skutch 1957, Emlen and Oring 1977). Therefore, the total amount of parental care should be greater in complete biparental care during the incubation period (Matysioková and Remeš 2014), and in partial and complete biparental care during the nestling period. However, how much greater the amount of care invested will be dependent on the resolution of sexual conflict between parents because both should attempt to minimize their own cost, increasing the cost of their partner, while insuring survival of the offspring (Trivers 1972, Winkler 1987, Olson et al. 2007).

In a hypothetical scenario we can assume that: 1) parents invest in parental care at the minimum offspring requirements, and 2) offspring requirements are independent of the mode of parental care. If so, then the total amount of care invested when both parents share parental care activities should be similar to the total amount invested when a parent provides care alone. However, we can also assume that: 3) parents invest in parental care to the maximum amount possible, without affecting their likelihood of survival, and 4) this maximum is similar between individuals and independent of the modes of parental care. If so, then the total amount of parental care invested when both parents share parental care activities should be twice the amount invested when a parent provides care alone. If the minimum amount of care for offspring growth and survival is lower than the maximum parental care each parent can provide, then the total amount of parental care in natural populations should be between the minimum offspring requirement and the maximum given by the parents. Thus, the total amount of parental care given will be a consequence of the number of caregivers and will increase offspring survival and future survival and reproduction of adults.

Here we compared parental care between three parental care modes (uniparental, partial biparental and complete biparental care) in five species of passerine birds to better understand how the total amount of parental care is affected by differences in the number of caregivers. We used nest attentiveness during incubation period and feeding rates (total and per nestling) during nestling period to compare the total amount of parental care. We expect an increase in the total amount of parental care with the number of caregivers. However, since sexual conflict may play a role, we expect that the total amount of parental care given by both parents will not be twice of the total amount when just one parent is caring. Additionally, we discuss implications of the number of caregivers and the total amount of parental care for the evolution of different modes of parental care and life history traits in birds.

Material and Methods

Study species

We compared three different modes of parental care using data collected at the same time and location from five passerine birds: the uniparental care Blue Manakin *Chiroxiphia caudata* (Shaw & Nodder, 1793), the partial biparental care Red-eyed Vireo *Vireo olivaceus* (Linnaeus, 1766), Olivaceus Elaenia *Elaenia mesoleuca* (Deppe, 1830) and Highland Elaenia *Elaenia obscura* (d'Orbigny & Lafresnaye, 1837), and the complete biparental care Variable Antshrike *Thamnophilus caerulescens* (Vieillot, 1816). The Blue Manakin (family Pipridae) is a dimorphic species with about 25 g (Snow 2016). This species is polygynous and males aggregate in leks to perform a display, while parental care is made by the female alone (Foster 1981, pers. obs.). This species feed predominantly on fruits but sporadically on insects (Lopes et al. 2005, Snow 2016). Breeding traits are virtually unknown, with the exception of the open cup nest and the clutch of two eggs (Snow 2016, per. obs.). The Red-eyed Vireo (family Vireonidae) is a monomorphic and monogamous biparental care species, with about 12 – 25 g (Brewer 2016). Little information is available for the species in South America. It is apparently mostly insectivorous, builds an open cup nest and clutch size is two or three eggs (Brewer 2016). The Olivaceus Elaenia (family Tyrannidae) is monomorphic, with about 16 – 20 g, insectivorous and frugivorous (Hosner 2016a), with biparental care (per. obs.). It uses an open cup nest, lays a clutch of two or three eggs with an incubation period of 15 – 16 days and nestling period of ca. 20 days (Hosner 2016a). The Highland Elaenia (family Tyrannidae) is also monomorphic, with about 24 – 27 g, insectivorous and frugivorous (Hosner 2016b), with biparental care (pers. obs.) using an open cup nest in which it lays a clutch of two eggs (Hosner 2016b). The Variable Antshrike (family Thamnophilidae) is dimorphic, with about 15 – 24 g, predominantly insectivorous (Lopes et al. 2005, Zimmer and Isler 2016), has biparental care with incubation by both sexes during the day, with an open cup nest and a clutch size of 2 – 4 eggs (Zimmer and Isler 2016, pers. obs.).

Study area and nests searching

We carried out this study in Marumbi State Park (*Parque Estadual Pico Marumbi* – 25º 29' S, 48º 59' W) in the state of Paraná, southern Brazil. The area is located in the largest remaining Atlantic Forest fragment (Ribeiro et al. 2009) and is a transitional region between

Araucaria Forest and Montane Atlantic Rainforest (Reginato and Goldenberg 2007).

We searched for nests during three consecutive breeding seasons (2012 – 2015 from August to February). Nests were found by searching appropriate locations in the vegetation and by following adult behavioral cues, such as birds carrying nesting material or food and performing a distraction display (Martin and Geupel 1993). Nests were checked every 2 – 3 days, aside from behavioral observation (see below). We checked the nest more often when nesting stages (laying, hatching and fledging) were expected to change. At least one adult of each pair was banded for monitoring. We captured adult birds, weight on a appropriate scale and used a unique combination of color plastic bands and a numbered metal band provided by Brazilian birding agency (CEMAVE – *Centro Nacional de Pesquisa e Conservação de Aves Silvestres*).

Incubation period and nest attentiveness

Incubation period was estimated as the interval (in days) between the date on which the last egg was laid and hatching. Nest attentiveness during the first breeding season (2012) was sampled by visiting the nest hourly (6 – 8 times per day) and noting whether an individual was incubating from a distance to avoid disturbance. During the remaining breeding seasons (2013 and 2014), nest attentiveness was sampled by using time-lapse cameras (M-990i, Moultrie Products, LLC., Birmingham, AL) that took pictures at five minute intervals during at least five hours each day used. Nest attentiveness in the first breeding season (2012) was estimated as the proportion of nest visits in which the adult was on the nest. In the following breeding seasons (2013 and 2014), nest attentiveness was the proportion of photographs in which the adult was on the nest. Both methods gave similar nest attentiveness estimations (similar to Chapter I).

Nestling period, feeding rate and nestling growth rate

The nestling period was the interval in days between hatching and fledging. The nestling provisioning rates were measured using video cameras for approximately one hour every 2 – 3 days until fledging or nest failure during all three breeding seasons. We noted how many times parents arrived at the nest to feed nestlings to estimate the total feeding rate (visits h^{-1}) and per nestling feeding rate (visits $nestling^{-1}$ h^{-1}). After each recording we checked the number of nestlings in the nest to estimate correctly the per nestling feeding rate and to weight each nestling on a digital scale (0.01 g precision) to determine nestling growth.

Statistical analysis

Nest attentiveness, total and per nestling feeding rates, and nestling growth vary with embryos and nestlings age in birds, so we used linear mixed models to compare the three modes of parental care. To place all species on the same scale, we standardized embryo and nestling age as the proportion of the duration of incubation and nestling period of each species, so that embryo or nestling age always varied from 0 to 100. Similarly, nestling weight was standardized as the proportion of the adult weight, with nestling weight varying from 0 to 100. To compare nest attentiveness we used models that included embryo age as a covariate, modes of parental care as a fixed factor, and species and nest identity as random effects on the intercept and slope. To compare total feeding rate and per nestling feeding rate (both $\log_{10}$ transformed to normalize residuals) we used models that included nestling age as a covariate, modes of parental care as a fixed factor, and species and nest identity as random effects on the intercept and slope. To compare nestling growth we used models that included nestling age as a covariate, modes of parental care as a fixed factor, and species and nest identity as random effects on the intercept and slope. We compared the mode of parental care with respect to nest attentiveness, total and per nestling feeding rate, and the nestling growth by comparing models with (additional and interaction effect) and without the fixed factor (mode of parental care) and covariate (age) by the likehood ratio test. Once the best model was found, we estimated nest attentiveness, total and per nestling feeding rates, and nestling weight for each mode of parental care using least squares means. When the factor was significant, we compared these estimates between the three modes of parental care using Tukey's method with a 0.05 level of significance.

Statistics were carried out in R version 3.1.3. For linear mixed models we used the lme4 package (Bates et al. 2015) and for least square means we used the lsmeans package (Russell 2015). Descriptive statistics and tests include sample sizes (n), means and standard errors (± SE), unless otherwise stated.

Results

Nests

We monitored 55 nests (22 Blue Manakin, 10 Red-eyed Vireo, 10 Olivaceus Elaenia, five Highland Elaenia and eight Variable Antshrike). All nests of the Olivaceus Elaenia (five nests) and Highland Elaenia (three nests) that we could examine had two eggs. Most Blue Manakin (17 of 21) and Red-eyed Vireo (5 of 8 nests) nests had two eggs, and most Variable Antshrike nests had three eggs (7 of 8, Table 1).

Table 1. Clutch size, incubation and nestling period of five passerine birds with three different modes of parental care in southern Atlantic Forest in Brazil. Clutch size is the number of eggs, and incubation and nestling period are the number of days.

Species	Mode of parental care	Clutch size			Incubation			Nestling		
		mode	range	nests	mean	SE	nests	mean	SE	nests
Blue Manakin (*Chiroxiphia caudata*)	Uniparental	2	1-2	21	16.50	0.27	10	18.88	0.40	8
Red-eyed Vireo (*Vireo chivi*)	Partial biparental	3	2-3	8	13.33	0.33	3	13.00*		1
Olivaceus Elaenia (*Elaenia mesoleuca*)	Partial biparental	2	2	5	15.00*		1	18.50	0.50	2
Highland Elaenia (*Elaenia obscura*)	Partial biparental	2	2	3	14.50	0.50	2	18.00*		1
Variable Antshrike (*Thamnophilus caerulescens*)	Complete biparental	3	2-3	8	13.40	0.24	5	10.50	0.50	2

*Incubation and nestling period estimated for only one nest.

Incubation period and nest attentiveness

Incubation period for the five species ranged from 13.3 to 16.5 days (Table 1). Nest attentiveness was estimated in eight Blue Manakin nests (4.5 ± 0.78 observation days per nest), five Red-eyed Vireo nests (2.4 ± 0.4 observation days per nest), three Olivaceus Elaenia nests (2.7 ± 0.3 observation days per nest), three Highland Elaenia nests (2 ± 0.6 observation days per nest) and eight Variable Antshrike nests (3.8 ± 0.8 observation days per nest). Nest attentiveness differed between modes of parental care (interaction effect: $\chi^2 = 7.51$, df = 2, $p = 0.023$; Table 2). Nest attentiveness was estimated in 59% of the duration of incubation period (embryos age) using least square means. Nest attentiveness was 82% for uniparental, 78% for partial biparental and

94% for complete biparental care. In the comparison of the least squares means using Tukey's test the complete biparental care had the greatest nest attentiveness, while partial biparental and uniparental care were similar and lower (Table 3, Fig. 1A and 1D).

Table 2. Comparisons of linear mixed models of nest attentiveness, total and per nestling feeding rates between three different modes of parental care in passerine birds in southern Atlantic Forest in Brazil. Models included random effects of species and nest identity on the intercept and slope.

Model	Log likelihood	χ^2	df	p
Nest attentiveness				
null	-362.47			
mode	-353.63	17.69	2	<0.001
mode + age	-353.17	0.92	1	0.338
mode * age	-349.42	7.51	2	0.023
Total feeding rate				
null	-9.75			
mode	3.76	27.02	2	<0.001
mode + age	11.99	16.46	1	<0.001
mode * age	12.81	1.66	2	0.437
Per nestling feeding rate				
null	28.74			
mode	39.33	21.17	2	<0.001
mode + age	46.69	14.72	1	<0.001
mode * age	47.22	1.07	2	0.585

Table 3. Comparisons of means of nest attentiveness, total and per nestling feeding rates between three different modes of parental care in passerine birds in southern Atlantic Forest in Brazil. Means are the least square means from a linear mixed model with embryos and nestlings age as covariate, and with random effects of species and nest identity on the intercept and slope.

Modes	*t*	df	p
Nest attentiveness			
Uniparental – Partial biparental	0.96	22.5	0.610
Uniparental – Complete biparental	3.42	14.0	0.011
Partial biparental – Complete biparental	4.33	22.5	<0.001
Total feeding rate			
Uniparental – Partial biparental	6.48	24.1	<0.001
Uniparental – Complete biparental	2.20	35.9	0.085
Partial biparental – Complete biparental	2.58	36.6	0.037
Per nestling feeding rate			
Uniparental – Partial biparental	4.85	27.3	<0.001
Uniparental – Complete biparental	0.71	29.2	0.762
Partial biparental – Complete biparental	3.39	28.8	0.006

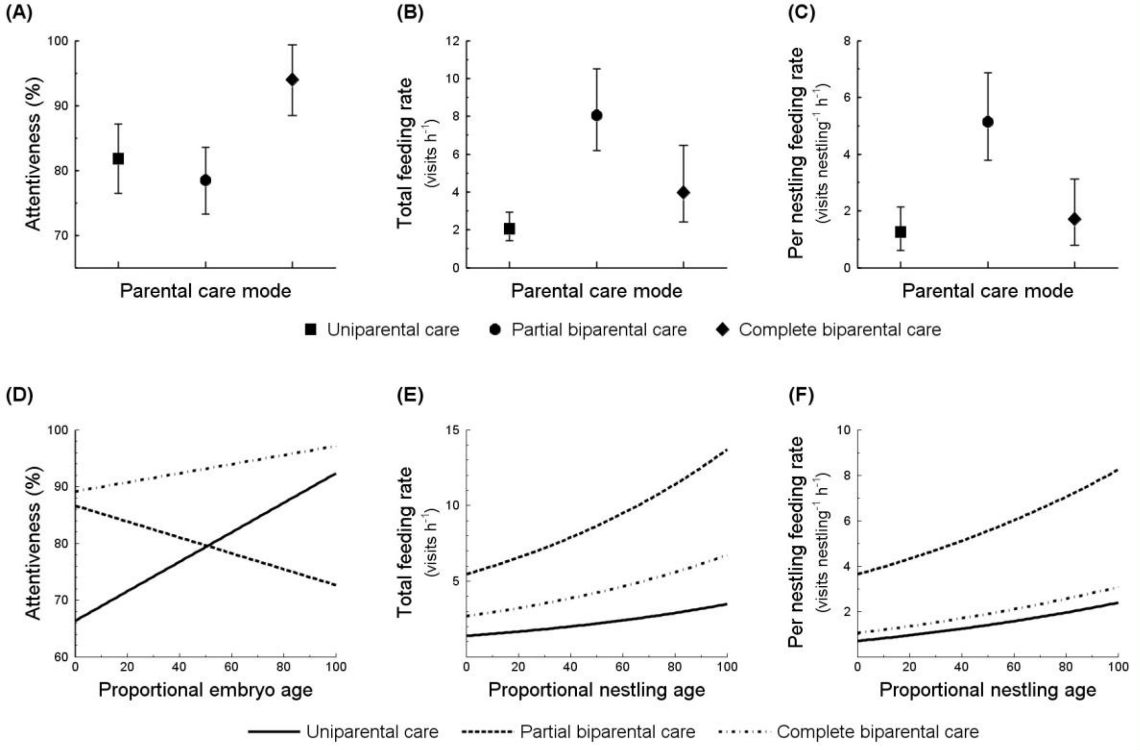

Figure 1: Comparison of nest attentiveness (A and D), total feeding rate (B and E) and per nestling feeding rate (C and F) between three different modes of parental care in passerine birds in southern Atlantic Forest in Brazil. Values in A, B and C are the least square means, lower and upper confidence intervals from a linear mixed model with embryos and nestlings age as covariate, and with random effects of species and nest identity on the intercept and slope. Lines in D, E and F are the linear regression of these models.

Nestling period, feeding rate and nestling growth rate

Nestling period for the five species ranged from 10.5 to 18.9 days and was shortest in the complete biparental care species (Variable Antshrike) and longest in the uniparental care species (Blue Manakin, Table 1). Feeding rates was estimated in nine Blue Manakin nests (3.1 ± 0.4 observation days per nest), seven Red-eyed Vireo nests (4 ± 0.4 observation days per nest), six Olivaceus Elaenia nests (4.7 ± 0.8 observation days per nest), four Highland Elaenia nests (3.8 ± 1.5 observation days per nest) and six Variable Antshrike nests (2.8 ± 0.5 observation days per nest). Total and per nestling feeding rates differed between modes of parental care (total feeding rate, additive effect: $\chi^2 = 16.46$, df = 1, $p < 0.001$; per nestling feeding rate, additive effect: $\chi^2 = 14.72$, df = 1, $p < 0.001$; Table 2). Total feeding rates was estimated in 45% of the duration of nestling period (nestling age) using least square means. Total feeding rate was 2.05 visits h^{-1} for uniparental, 8.06 visits h^{-1} for partial biparental and 3.97 visits h^{-1} for complete biparental care. Per nestling feeding rates was estimated in 46% of the duration of nestling period (nestling age) using least square means. Per nestling feeding rate was 1.25 visit $nestling^{-1}$ h^{-1} for uniparental, 5.13 visit $nestling^{-1}$ h^{-1} for partial biparental and 1.71 visit $nestling^{-1}$ h^{-1} for complete biparental care. In the comparisons using Tukey's test the partial biparental care had the greatest total and per nestling feeding rates, followed by lower and similar uniparental and complete biparental care (Table 3, Fig. 1B and 1E for total feeding rate, Fig. 1C and 1F for per nestling feeding rate).

Adult weight in the Blue Manakin was 25.3 ± 0.3 g (n = 20), in the Red-eyed Vireo was 16.8 ± 0.4 g (n = 7), in the Olivaceus Elaenia was 16.2 ± 0.7 g (n = 6), in the Highland Elaenia was 27.9 ± 0.6 g (n = 7) and in the Variable Antshrike was 20.9 ± 0.6 g (n = 4). For comparisons of nestling growth we used information about three of the five species: four nests and 11 nestlings of the complete biparental species (Variable Antshrike), five nests and 12 nestlings of the partial biparental species (Red-eyed Vireo), and nine nests and 16 nestlings of the uniparental species (Blue Manakin). Nestling growth varied by mode of parental care (interaction effect: $\chi^2 = 10.32$, df = 2, p = 0.006), yet growth rates were similar among parental care modes when compared by Tukey's test (Fig. 2). Nestling weight was estimated in 37% of the duration of nestling period (nestling age) using least square means. Nestling weighed 40.1% of adult mass for uniparental, 42.8% of adult mass for partial biparental and 39.5% of adult mass for complete biparental care.

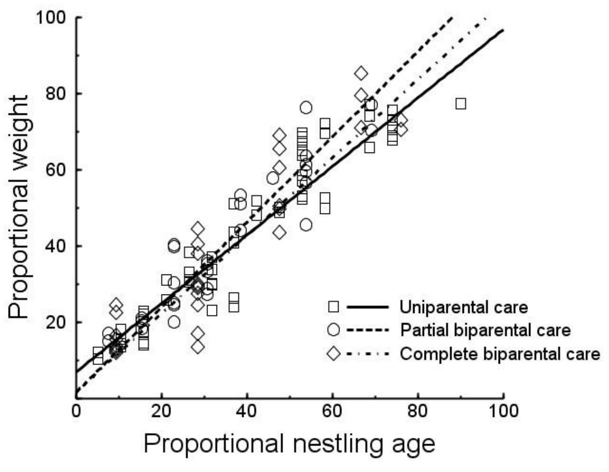

Figure 2: Nestling growth, measured as the proportion of adult bird weight (mean value), of three different modes of parental care in southern Atlantic Forest in Brazil. Uniparental care species is Blue Manakin, partial biparental care is Red-eyed Vireo, and complete biparental care is Variable Antshrike.

Discussion

While biparental care gave the greatest amount of parental care, nestling grew at a similar rate under care modes. Greater nest attentiveness occurred under complete biparental care (Matysioková and Remeš 2014), and greater total and per nestling feeding rates occurred under partial biparental care. These findings support the prediction that the total amount of parental care increases with the number of caregivers (Skutch 1957, Emlen and Oring 1977). However, while care was greatest when both parents participated in egg incubation, nest attentiveness was less than twice that of one parent incubating alone. Yet, in general, total and per nestling feeding rates in partial biparental care were twice (or more) that of uniparental care. Despite these differences, however, total and per nestling feeding rates in complete biparental care were similar to those under uniparental care.

Adults in the complete biparental species (Variable Antshrike) seem to always take turns incubating, one leaving the nest upon the arrival of its mate, so that nest attentiveness was almost 100%. In uniparental and partial biparental care, nest attentiveness was near 80%, indicating that the female spent very little time off the nest. Thus, the amount of time eggs are incubated is a consequence of care mode (Skutch 1957, Emlen and Oring 1977, Matysioková and Remeš 2014). Yet, time spent incubating by each individual adult in complete biparental care was less than that by the single female in uniparental and partial biparental care. This increase in nest attentiveness has important consequences for life history traits, as nest attentiveness and egg temperature are correlated (Martin et al. 2007, 2015). Also, incubation requires an optimal egg temperature for development, and so more constant incubation results in more uniform embryo development (White and Kinney 1974). Thus, greater nest attentiveness is also associated with shorter incubation periods. This relationship has been debated (Boersma 1982, Tieleman et al. 2004), but noted within species (Lyon and Montgomerie 1985, Martin et al. 2007), among species and over latitudes (Martin 2002, Martin et al. 2007, 2015). Nonetheless, our observed difference in nest attentiveness among parental care modes was not associated with incubation period.

Total feeding rate was greatest in partial biparental care. The uniparental and complete biparental care were similar in the statistical analyses, however total feeding rate in complete biparental care was more variable. Also, although statistically similar, total feeding rate in complete biparental care was twice that of uniparental care. Therefore, the total feeding rate in uniparental care suggests that one parent alone cannot provide food for offspring at the same rate as two parents can (Skutch 1957, Emlen and Oring 1977).

Uniparental care had the lowest total feeding rate, although the single caregiver (female) provided enough food to successfully rear young (only one from nine nests monitored during nestling period failed). The uniparental species (Blue Manakin) feeds nestlings by regurgitation (pers. obs.), so it is possible that uniparental care provides the same amount of food for the nestlings at a slower visit rate as compared to species that feed nestlings by providing individual items instead of regurgitation. For example, with complete biparental care, the Variable Antshrike parents fed nestlings with relatively large and visible individual items in comparison with partial biparental care species (pers. obs.), and so a slower total feeding rate (similar to the rate in uniparental care) may provide the same biomass of food as faster rates with smaller items. In this context, energetic costs of foraging by the parents to provision nestlings and the nestling diet are likely to be adaptations that account for differences in feeding rates in the modes of parental care. The uniparental care Blue Manakin is predominantly frugivorous, as are most birds with female only parental care (Snow 2004, Cockburn 2006, pers. obs.). The remaining species with partial and complete biparental care studied here are predominantly (Olivaceus Elaenia and Highland Elaenia eat fruit at times) or completely inseticvorous (Zimmer and Isler 2003, Hosner 2004a, 2004b, Brewer 2010). Therefore, biparental care, with sharing of feeding the nestlings may be crucial for parents of insectivorous birds, as the availability of this type of food is unpredictable and energetically expensive to catch (Williams 1988), while fruits are stationary and predictable and a single individual can successfully feed young.

Per nestling feeding rate had similar patterns among the three modes of parental care. However, per nestling feeding rate in complete biparental care was now less than twice that of uniparental care. This may be due to the difference in clutch size between studied species. The reduction in clutch size in the uniparental care species, even in just one nestling in relation to complete biparental care species, may have been sufficient to result in a lower total feeding rate (Wright et al. 1998, Martin 2015). Even though mean nestling growth was similar in the three modes of parental care, individual nestlings in uniparental care and complete biparental care received food at a slower rate than partial biparental care, which suggest a difference in quality of the food being provided. These species also differ in nestling period, with the uniparental care

Blue Manakin having the longest period. Thus, the longer nestling period with uniparental care may be required due to the difference in resource quality, as young ready to leave the nest must have reached the point of more likely survival upon leaving the nest (Lill 1986, Martin 2015).

The number of carergivers is the main difference between the three modes of parental care studied (Cockburn 2006), but consequences of this difference in total amount of parental care are understudied (Matysioková and Remeš 2014). Here we show that the number of caregivers determines the way parents participate in care activities and which suggests that the different total amount of care influences breeding traits and life histories. The difference in total amount of parental care due to the number of caregivers was more evident during incubation. Uniparental care species successfully rear offspring individually probably because the nestling diet is primarily predictable fruits, feeding behavior (regurgitation) and longer development period prior to leaving the nest. Future studies must attempt the difficult task of measuring food quality to better understand how differences in the number of caregivers have resulted in the evolution of different parental care strategies. Also, long term studies will be required to determine how these differences in investment in parental care between modes of parental care can result in different life time fitnesses and thereby shape these and other life history traits.

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