

# Sex-specific provisioning of nutritious food items in relation to brood sex ratios in a non-dimorphic bird

Pamela Espíndola-Hernández<sup>1</sup> · Gabriel J. Castaño-Villa<sup>2</sup> · Rodrigo A. Vásquez<sup>1</sup> · Verónica Quirici<sup>3,4</sup>

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## Abstract

In birds, the frequency with which the parents feed the young can vary considerably. Because of sexual differences in the begging behaviour and/or differences in the food requirements of the nestlings, brood sex ratio (BSR) is an important factor that may influence parental provisioning behaviour. Disparities in the quantity and quality of prey received by the sexes have been reported in a range of sexually size-dimorphic birds. However, to our knowledge, no study has evaluated prey composition delivery to nestlings in relation to BSR in a non-dimorphic size bird species. Because BSR influences provisioning rate in dimorphic and non-size dimorphic species and because in dimorphic species, BSR influences prey composition delivered to the nest, we hypothesised that similar to dimorphic species, BSR may influence prey composition delivered to nestlings in non-size dimorphic species. We quantify parental provisioning rate and prey

composition of prey delivered to nestlings in relation to BSR in the Thorn-tailed Rayadito (*Aphrastura spinicauda*) a non-dimorphic and altricial passerine bird. At the population level, we found that Thorn-tailed Rayadito mothers delivered more insect larvae to the nest when compared to the father, who provided the brood with a diet more diverse in composition. However, when we considered BSR, mothers delivered a greater quantity of arachnida and lepidoptera items (high-quality foods) in male-biased BSR. In addition, nestling weight gain increased in line with the proportion of high-quality food in the diet. Our results suggest that when considering non-dimorphic species, there may be more subtle, but nevertheless important, differences, in explaining parental care behaviour in species with bi-parental care.

## Significance statement

In birds, the frequency with which the parents feed the young can vary considerably. Because of sexual differences in the begging behaviour and/or differences in the food requirements of the nestlings, brood sex ratio is an important factor that may influence parental provisioning behaviour in sexual size species. For the first time, we evaluated prey composition delivery to nestlings in relation to BSR in a non-size dimorphic bird species. We found that the mother of the Thorn-tailed Rayadito delivered a greater quantity of lepidoptera and arachnida (high-quality food) items in a male-biased brood. In addition, nestling weight gain increased with the proportion of high-quality food in the diet. Our results suggest that in non-dimorphic species, there may be more subtle, but nevertheless important, differences in explaining parental care behaviour in species with bi-parental care.

**Keywords** Thorn-tailed Rayadito · *Aphrastura spinicauda* · Avian nutrition · Bi-parental care

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✉ Verónica Quirici  
rosina.quirici@unab.cl; vquirici@gmail.com

<sup>1</sup> Instituto de Ecología y Biodiversidad and Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Santiago, Chile

<sup>2</sup> Grupo de Investigación en Ecosistemas Tropicales, Facultad de Ciencias Agropecuarias, Universidad de Caldas, Calle 65 No 2610, Manizales, Colombia

<sup>3</sup> Departamento de Ecología y Biodiversidad, Facultad de Ecología y Recursos Naturales, Universidad Andres Bello, República 440, Santiago, Chile

<sup>4</sup> Centro de Investigación para la Sustentabilidad, Universidad Andres Bello, República 440, Santiago, Chile

## Introduction

In birds, the frequency with which the parents feed the young can vary considerably (Grieco 2002). In general, a larger brood size demands a greater amount of food; so, parents respond to the increased demand by increasing the provisioning rate or by providing larger-sized prey (e.g. Henderson and Hart 1993; Chamberlain et al. 1999; Leckie et al. 2008; Ryser et al. 2016). Another factor that may influence parental provisioning behaviour is brood sex ratio (BSR). Differences in provisioning behaviour in relation to BSR may arise because of the following: (i) differences in the begging behaviour of the nestlings. Such differences may arise because the feeding rate of parents may increase with the level of begging by the brood (Grieco 2002). For example, male and female barn swallow nestlings differ in their begging behaviours (Saino et al. 2003) and parents react to this difference by adjusting their provisioning rules (Saino et al. 2000; Sacchi et al. 2002; Boncoraglio et al. 2008). (ii) Differences in the food requirements of the nestlings. In size-dimorphic species, the larger sex will present higher metabolic rate and higher growth development (Teather and Weatherhead 1988; Anderson et al. 1993; Krijgsveld et al. 1998); so, it is expected that parents react to such requirements. Disparities in the quantity of prey received by the sexes have been reported in a range of sexually size-dimorphic birds (reviewed by Anderson et al. 1993). For example in Wandering Albatrosses (*Diomedea exulans*), sons received more food than daughters (Weimerskirch et al. 2000), and in the Brown Songlark (*Cinclorhamphus cruralis*), sons not only received more prey than their smaller sisters, but also prey of apparently higher quality, like arachnida and lepidoptera (Magrath et al. 2004).

To our knowledge, only two studies have evaluated parental provisioning behaviour in relation to BSR in non-sized dimorphic species. In Zebra Finches (*Taeniopygia guttata*), Mainwaring et al. (2011) observed that mothers provisioned sons over daughters, and in Great Reed Warblers (*Acrocephalus arundinaceus*), Nishiumi et al. (1996) observed that fathers feeding frequency increased with the proportion of sons in the brood. The results of these two studies in non-size dimorphic species suggest that similar to size-dimorphic species, BSR is an important component in explaining parental provisioning behaviour. However, to our knowledge, no study has evaluated prey composition delivery to nestlings in relation to BSR in a non-size dimorphic bird species. Because BSR influences provisioning rate in dimorphic and non-dimorphic size species and because in dimorphic species, BSR influences prey composition delivered to the nest (e.g. Magrath et al. 2004), we hypothesised that similar to dimorphic species, BSR may influence prey composition delivered to nestlings in non-size dimorphic species. So, our main goal was to quantify parental provisioning rate and prey composition delivered to the nest in the Thorn-tailed Rayadito

(*Aphrastura spinicauda*), a non-dimorphic and altricial passerine bird.

## Materials and methods

### Biology of the Thorn-tailed Rayadito and the study population

The Thorn-tailed Rayadito (Furnariidae: Passeriformes) is an insectivorous and endemic species of Argentina and Chile temperate forest (Remsen 2003). Thorn-tailed Rayadito have a socially monogamous mating system where both members of the pair contribute to nest-building, incubation and the feeding of nestlings (Moreno et al. 2007). Thorn-tailed Rayadito are small (11 g) and lay one clutch per breeding season during the austral spring, from October to December (Moreno et al. 2005; Quirici et al. 2016). The nest construction period lasts 6–15 days, the incubation period is 9–15 days, and fledging occurs at 20–21 days of age. Eggs are laid on alternate days, and the Thorn-tailed Rayadito postpones incubation until after the clutch is complete. We provided artificial nest boxes for the birds to breed inside. This study was carried out during two reproductive seasons, from the beginning of October to late December in 2011 and 2012 in Navarino Island, Chile (55°4' S, 67°40' W). At this site, the vegetation is almost pristine and is characterised by deciduous Magellanic forest, whose characteristic species are Lenga Beech (*Nothofagus pumilio*) and Ñirre Beech (*Nothofagus antarctica*) (Rozzi et al. 2004).

### Field methods

To check for nest box occupation, nest boxes were monitored on a weekly basis, and when occupied, nest boxes were checked daily in order to detect laying dates (date of first egg) and hatching dates. In 2011, nestlings were weighed every 3 days starting on day 2 until day 18. In 2012, nestlings were weighed every 2 days starting on day 3 until day 17. When nestlings were 12 days old, we collected a small blood sample (ca. 10 µL) by puncturing the brachial vein with a sterile needle and collecting blood into heparinised microhematocrit capillary tubes for further molecular sex analysis. We stored blood samples in FTA Classic Cards (Whatman®) for subsequent molecular sex determination. After blood sampling, nestlings were weighed and banded with individual metal bands (National Band and Tag Co., Newport, Kentucky, USA and Split Metal Bird Rings, Porzana Ltd., UK). Adults were captured in their nests with a manually triggered metal trap that sealed the entrance hole when adults entered to feed their 12-day-old nestlings. Similar to nestlings, we obtained a small blood sample, then weighed and banded the individuals with coloured metal bands in order to facilitate identification during video recording. When nestlings were

17 days old, we positioned a digital video camera (Sony DCR-68) 3–4 m from the nest box. Similar to other studies of feeding behaviour (e.g. Grieco 2002; Leckie et al. 2008), we recorded parental care behaviour in each nest box over a 4-h period between 07:00 and 14:00. Parental behaviour was recorded this particular day because peak food demand is likely to occur in the middle stages of the nestling's development, when growth rates are highest, and then subsequently decrease when nestlings are close to fledging (Leckie et al. 2008).

### Video recording and prey composition

In the lab, one of our research team (PE) replayed the video footage with SMPlayer© (version 0.8.0) and recorded the sex of the bird delivering the food, the provisioning rate and the prey type. Each prey item delivered to the nest was assigned to one of the following categories: lepidoptera, diptera, coleoptera, arachnida, neuroptera, larvae or other. In cases where the prey types delivered were not discernable, the visit was categorized as 'others', which represented less than 2% of the total records. Insects and arachnida have different nutritional value, which is related to the amount of chitin in the exoskeleton (because this carbohydrate is largely indigestible); so, prey with a lower amount of chitin represents a higher-quality food for birds, being in this case arachnida and lepidopteran (Karasov 1990). We combined food items into two categories: (i) high-quality food, which includes arachnida and lepidoptera, and (ii) low-quality food, which includes diptera, coleoptera and neuroptera. We recorded footage in 15 nest boxes in 2011 (60 h) and 14 nest boxes in 2012 (56 h), giving a total of 29 nest boxes. It was not possible to record data blind because our study involved focal animals in the field.

### Molecular sexing

Because the Thorn-tailed Rayadito exhibits an absence of visual sexual dimorphism, we used molecular methods to determine the sex of both nestlings and adults. Details of the protocol and validation of the method are described in Quirici et al. (2014). Briefly, DNA was extracted using a commercial kit (QIAGEN Inc., Valencia, CA). The sex of adults was determined using 2550F and 2718R primers (Fridolfsson and Ellegren 1999). PCR products were run in 1% agarose gels, pre-stained with ethidium-bromide and detected in a Fluorimager (Vilber Lourmat). Birds were sexed as females (heterogametic: WZ), when the CHD1W of 450 bp and CHD1Z of 600 bp fragments were amplified, and identified as males (homogametic: ZZ), when only the CHD1Z of 600 bp fragments was present.

### Statistical analysis

Because we observed no significant difference in the provisioning rate (per hour) between 2011 ( $11 \pm 5.0$  provisioning/h) and 2012 ( $10.9 \pm 5.2$  provisioning/h), data were pooled (permutation test,  $p = 0.15$ ). In order to identify differences between sexes, we compared the provisioning rate between fathers and mothers using a permutation test (resampling test). Secondly, we compared items provided to the nest by fathers and mothers using analysis of similarity (ANOSIM) and similarity percentage analysis (SIMPER). Analyses were conducted using Past 3.06 software.

In 2011, brood size ranged from 4 to 6 ( $5 \pm 0.75$  nestlings), and in 2012 from 1 to 6 ( $4 \pm 1.39$  nestlings). The data from the brood with only one nestling (one nest box in 2012) were excluded from the analysis of the relationship between parental provisioning rate and composition of prey delivered to the nest in relation to BSR because parental frequency for such brood was much lower than that for the other brood size. BSR for each nest was calculated as the ratio of the number of males to the total number of nestlings. Thus, the BSR varies from 1 (all nestling were males) to 0 (all nestlings were females).

We tested for differences in provisioning rate by both fathers and mothers. Data were analysed using a linear mixed effect model, with BSR and brood size as fixed effects and partner-provisioning rate as a random factor, using the lme package (Pinheiro et al. 2016) as implemented in R 2.4.1 software (R Development Core Team 2013). Parameter estimates for this model were obtained using the restricted maximum likelihood (REML) method. We included the following: (i) brood size in this and the following analyses because as mentioned in the "Introduction" section, it is known to influence parental provisioning behaviour (at larger brood size, higher provisioning rate), and (ii) the weight of the parent as a covariate because the item a parent might deliver to the nest could be related to the parent's size. For example, body size can affect the efficiency of flight, flight distance and hence the choice of feeding areas (e.g. Welcker et al. 2009; Randler et al. 2010; Diniz 2011). We chose weight instead of the residuals between tarsus length and body weight (Jakob et al. 1996), because it has been proposed as a better predictor of body condition (Green 2001).

In order to evaluate if the prey item delivered by the father or mother depends on BSR, brood size and parent weight, we performed Pearson's correlations for each item category.

In order to evaluate if the nutritional value of food affected nestling weight gain, we performed a linear mixed effect model, with nestling sex, the percentage of the prey item delivered (high quality and low quality) by parents (father and mother together), brood size and BSR as fixed effects and nest box and nestling ID as random factors. Nestling weight gain was calculated as the asymptotic weight minus the weight at the

intercept of a logistic regression. We chose a logistic regression curve because it has been used before in the study of this species (Moreno et al. 2005) and the model adjusts better than the von Bertalanffy or Gompertz curves ( $AIC_{\text{logistic}} = 22.37$ ,  $AIC_{\text{Gompertz}} = 28.55$ ,  $AIC_{\text{Bertalanffy}} = 106.47$ ). All statistical tests were two-tailed; data are reported as mean  $\pm$  SD.

## Results

### Parental provisioning at the population level

At the population level, provisioning rate per hour was similar between fathers ( $10.7 \pm 5.64$ ) and mothers ( $11.0 \pm 5.05$ ) (re-sampling permutation test:  $p = 0.84$ ). Fathers and mothers combined provided the nestlings with a higher quantity of insect larvae (70.2%) compared to lepidopteran (10.7%), dipteran (8.9%), arachnida (7.2%) and ‘other’ adult insects (Table 1). When we compared items delivered by fathers and mothers, we observed that the prey composition delivered to the nest by fathers contained a higher proportion of adult insects (ANOSIM  $p < 0.01$ , Table 2).

### Parental provisioning rate in relation to brood characteristics

Parental provisioning rate (both male and female) increased as brood size increased (males:  $t_{22} = 2.93$ ,  $p < 0.01$ ; females:  $t_{22} = 2.23$ ,  $p < 0.01$ ) (Fig. 1). Neither BSR (males:  $t_{22} = 0.05$ ,  $p = 0.96$ ; females:  $t_{22} = 0.10$ ,  $p = 0.86$ ) nor parental weight (males:  $t_{22} = -1.21$ ,  $p = 0.24$ ; females:  $t_{22} = 1.11$ ;  $p = 0.28$ ) influenced parents’ provisioning rate.

### Prey items delivered by parents in relation to brood characteristics

Fathers decrease the quantity of larvae with increased father’s body weight ( $p = 0.05$ , Table 3) and a trend toward increased

**Table 1** Prey composition delivery by fathers and mothers in 29 broods in Navarino Island

	Fathers %	Mothers %	Total %
Larvae	60.0	78.8	70.2
Lepidoptera	14.7	7.3	10.7
Diptera	13.8	4.7	8.9
Arachnida	7.2	7.2	7.2
Coleoptera	2.4	1.4	1.9
Neuroptera	1.8	0.7	1.1

**Table 2** Results of ANOSIM and SIMPER analysis

ANOSIM	$R = 0.16$ ; $p < 0.005$ ; permutation $N = 9999$		
SIMPER	Item	Contribution % (mothers)	Cumulative % (fathers)
	Larva	59.11	59.11
	Lepidoptera	13.44	72.54
	Diptera	13.03	85.57
	Arachnida	9.33	94.90
	Coleoptera	3.16	98.06
	Neuroptera	1.94	100

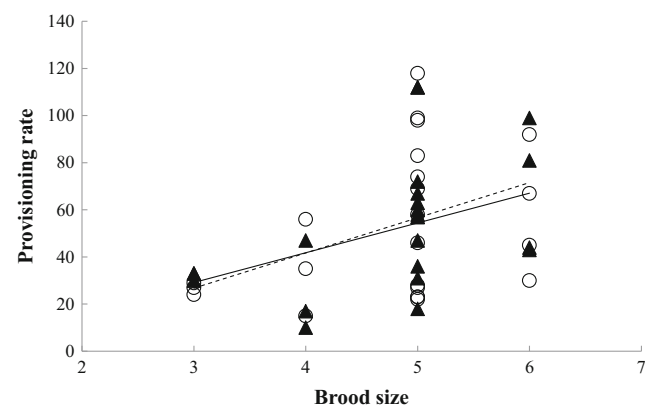
Based on Bray-Curtis distances, with Bonferroni correction

Contribution % = the contribution of that variable to the difference between groups (or similarity intra-group). Cumulative % = the cumulative sum of those percentages ordering highest to lowest

the quantity of larvae as brood sizes increased ( $p = 0.06$ , Table 3). Mothers increased the quantity of larvae as brood sizes increased ( $p < 0.01$ , Table 3). They also increased the quantity of lepidoptera with increases in brood size ( $p < 0.01$ , Table 3) and BSR ( $p < 0.01$ , Table 3) and increased the quantity of arachnida as BSR increased (BSR biased toward males) ( $p = 0.04$ , Table 3).

### Nestling weight gain in relation to brood characteristics, food items and parents’ weight

Nestling weight gain increased with the quantity of high-quality food (lepidoptera and arachnida) (Table 4, Fig. 2) and decreased as brood sizes increased (Table 4, Fig. 3). In addition, we observed a significant nestling sex effect (Table 4), with male nestlings presenting a higher weight gain ( $14.8 \pm 1.23$  g) than female nestlings ( $12.6 \pm 1.38$  g) (Fig. 2).



**Fig. 1** Provisioning rate (number of feeds per 4-h recording period) of fathers (filled triangles) and mothers (open circles) in relation to brood size

**Table 3** Pearson's correlations between the amounts of each item delivered to the nest, BSR, brood size and the parent's body weight

	Mother	Father
<b>Larvae</b>		
BSR	0.09 ( $p = 0.66$ )	-0.25 ( $p = 0.22$ )
Brood size	0.51 ( $p < 0.001$ )**	0.37 ( $p = 0.06$ )
Body weight	-0.32 ( $p = 0.11$ )	-0.40 ( $p = 0.05$ )*
<b>Diptera</b>		
BSR	0.07 ( $p = 0.73$ )	-0.20 ( $p = 0.32$ )
Brood size	0.19 ( $p = 0.34$ )	0.09 ( $p = 0.67$ )
Body weight	-0.14 ( $p = 0.48$ )	-0.18 ( $p = 0.39$ )
<b>Coleoptera</b>		
BSR	0.24 ( $p = 0.23$ )	0.03 ( $p = 0.89$ )
Brood size	0.23 ( $p = 0.26$ )	0.24 ( $p = 0.23$ )
Body weight	-0.16 ( $p = 0.44$ )	-0.09 ( $p = 0.68$ )
<b>Neuroptera</b>		
BSR	-0.06 ( $p = 0.77$ )	-0.05 ( $p = 0.80$ )
Brood size	0.00 ( $p = 1.00$ )	-0.03 ( $p = 0.88$ )
Body weight	0.31 ( $p = 0.12$ )	-0.05 ( $p = 0.80$ )
<b>Lepidoptera</b>		
BSR	0.52 ( $p < 0.01$ )**	0.27 ( $p = 0.18$ )
Brood size	0.50 ( $p < 0.01$ )**	0.27 ( $p = 0.19$ )
Body weight	-0.03 ( $p = 0.89$ )	0.34 ( $p = 0.09$ )
<b>Arachnida</b>		
BSR	0.40 ( $p = 0.04$ )*	0.37 ( $p = 0.06$ )
Brood size	0.00 ( $p = 0.99$ )	0.10 ( $p = 0.62$ )
Body weight	0.22 ( $p = 0.28$ )	0.22 ( $p = 0.28$ )

Significance codes: \* $p < 0.05$ , \*\* $p < 0.01$ 

## Discussion

### Provisioning behaviour in relation to BSR and brood size

The main objective of our study was to evaluate parental provisioning rates and prey composition delivery to nestlings in relation to BSR and brood size in the Thorn-tailed Rayadito, a non-dimorphic species. As expected, and similar to other species, we observed that the provisioning rate of parents increased with brood size (Henderson and Hart 1993; Chamberlain et al. 1999; Leckie et al. 2008; Ryser et al. 2016). Contrary to our predictions, and to studies by Mainwaring et al. (2011) in Zebra Finches and Nishiumi et al. (1996) in Great Reed Warblers, but similar to the findings in the Western Bluebird (*Sialia mexicana*, Leonard et al. 1994), we were unable to provide any evidence of differences in parental provisioning rate (by mothers and fathers) in relation to BSR. However, when we analysed the diet delivery to nestlings, we observed a positive correlation between the quantity of lepidoptera and arachnida delivered by mothers to the nest and the proportion of male nestlings in the brood (Table 3). Magrath et al. (2004) observed a similar result in the

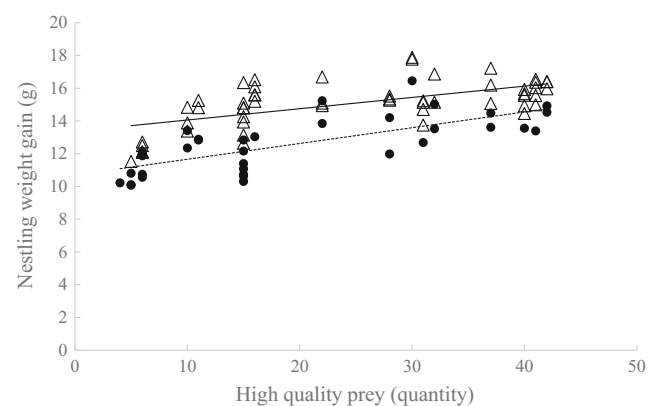
**Table 4** Results from linear mixed effect model testing the relationship between nestling sex, food item (low and high quality), brood size and BSR on nestling weight gain

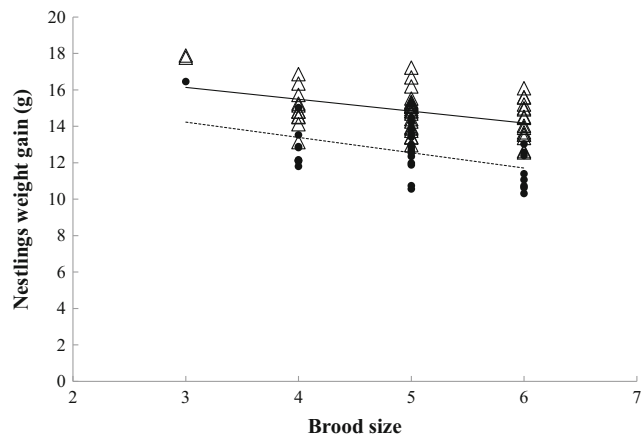
	value	SE	df	t value	p value
(Intercept)	15.58	1.06	61	14.71	<0.001***
Nestling sex	2.60	0.63	61	4.13	<0.001**
Larvae	0.00	0.00	61	0.09	0.93
Low nutrition	-0.05	0.03	61	-1.82	0.07
High nutrition	0.06	0.03	61	2.07	0.04*
Brood size	-0.88	0.35	61	-2.48	0.02*
BSR	1.21	1.42	61	0.85	0.40
Nestling sex $\times$ larvae	-0.00	0.00	61	-0.99	0.37
Nestling sex $\times$ low nutrition	0.01	0.02	61	0.72	0.47
Nestling sex $\times$ high nutrition	-0.03	0.02	61	-1.74	0.09

Significance codes: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ 

nests of Brown Songlarks, with BSR biased toward males receiving a higher quantity of arachnida and lepidoptera.

As mentioned above, insects and arachnida have different nutritional value. A strategy of some species is to remove those parts of the insect or arthropods with a high amount of chitin (Karasov 1990; Kaspari 1991; Klasing 1998), or alternatively, birds can select prey with low amount of chitin (Magrath et al. 2004). Although we did not quantify the content of indigestible chitin of prey items delivered by Thorn-tailed Rayadito adults, previous studies have determined the amount of chitin in insects and arthropods. For example, orthoptera and coleoptera contain almost twice the level of chitin as arachnida or lepidoptera (Kaspari 1991; Magrath et al. 2004); so, arachnida and lepidoptera represent a high-quality food. Other studies focussing on the diet of altricial nestlings have also concluded that arachnida and lepidoptera are among the most preferred prey items because of their relatively low chitin content (Cowie and Hinsley 1988; Grundel and Dahlsten 1991), but also because of their high content of

**Fig. 2** Weight gain (g) of male (open triangles) and female (filled circles) nestlings in relation to the quantity of high-quality food (lepidoptera and arachnida). Continuous line: male tendency curve; dotted line: female tendency curve



**Fig. 3** Weight gain (g) of male (open triangles) and female (filled circles) nestlings in relation to brood size. Continuous line: male tendency curve; dotted line: female tendency curve

certain amino acids (Ramsay and Houston 2003). Consequently, the higher quantity of arachnida and lepidoptera provided to BSR biased toward males is likely to be both energetically and nutritionally superior. This conclusion is also supported by our data of nestling's weight gain, which revealed that the gain in weight, for both sexes, increased with the proportion of lepidoptera and arachnida in the diet.

### Mother nutritional bias

The observation that at the population level, mothers provide greater quantities of larvae (Table 1) than fathers, and that when we consider BSR, mothers deliver more arachnida and lepidoptera items than fathers, it suggests nutritional favouritism toward sons. Nutritional favouritism (either in parental provisioning or food quality) by mothers (Leckie et al. 2008; Mainwaring et al. 2011) or fathers (Clotfelter 1996; Nishiumi et al. 1996; Ryser et al. 2016) in relation to BSR has been observed in size-dimorphic (Weimerskirch et al. 2000; Leckie et al. 2008) and non-dimorphic (Clotfelter 1996; Nishiumi et al. 1996; Mainwaring et al. 2011) species. One plausible explanation for nutritional bias can be attributed to differences in growth rates between nestlings of different sexes; we observed that weight gain was higher in male nestlings than in female nestlings (Table 4). So, the possibility exists that females are reacting to the higher energy demands of males. The possibility that females react to energy requirements is supported by our observation of a positive correlation between high-quality food delivered to the nest and brood size (Table 3). In addition, we observed that, as in Blackbirds (*Turdus merula*—Chamberlain et al. 1999), the provisioning rate of parents increased as brood sizes increased; also, the quantity of larvae delivered to the nest by parents increased as brood sizes increased, so both fathers and mothers reacted to the nutritional requirements of the brood. However, contrary to Chamberlain and collaborators (Chamberlain et al. 1999), nestling weight gain decreased as brood size increased; so, the

increased provisioning rate of parents did not fully compensate for the greater energy requirements of a larger brood size.

Another plausible explanation for nutritional bias is that it is due to the high level of extra pair paternity (EPP) in our study population. In a previous study, Castaño-Villa (2015), using eight species-specific micro-satellite loci (Yáñez et al. 2015), observed that 43% of broods contain extra-pair offspring. EPP leads to some offspring being genetically unrelated to the social father providing care (e.g. Griffith et al. 2002); so, males are likely to invest less in offspring that may have resulted from extra-pair copulations. In addition, offspring within broods are less related to each other and so have more incentive to compete against each other over evolutionary timescales (Royle et al. 1999). For example, in Reed Buntings (*Emberiza schoeniclus*), fathers provide more paternal care to nests that contain a lower proportion of extra-pair young (Dixon et al. 1994). Future studies should address if males of the Thorn-tailed Rayadito can assess their likelihood of paternity and adjust their nestling provisioning rates accordingly.

Behind the mechanism of nutritional biases, the existence of such a bias requires that parents discriminate between the sex of nestlings. It is accepted that in birds, parents are unable to discriminate between the sex of individual offspring prior to them attaining adult plumage. However, at least in the Barn Swallow (Boncoraglio et al. 2008), the two sexes differ in their begging behaviours and parents react to this difference by adjusting their provisioning rules. With respect to our study population, a possible explanation is that begging intensity differs between sons and daughters, and that, as occurs in the Barn Swallow, mothers use this cue to feed their sons higher-quality food. The mechanisms that allow female Thorn-tailed Rayadito mothers to discriminate between the sex of nestlings are currently unknown and future work could usefully examine how mothers are able to identify the gender of their offspring.

In conclusion, we found that mothers of the Thorn-tailed Rayadito, a non-dimorphic species, delivered more arachnida and lepidoptera to male-biased BSR and to larger brood sizes (only lepidoptera). This result, together with the increase in parental provisioning rate in relation to brood size, suggests that mothers react to the energy requirements of the brood. However, in this study, we are unable to discriminate between two possible scenarios: a higher energy demand on the part of males or a higher fitness return of males. Our results suggest that in non-dimorphic species, there may be more subtle, but nevertheless important, differences, in explaining parental care.

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## Compliance with ethical standards

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed. The study was performed with the permission of Servicio Agrícola y Ganadero (SAG) (permit number: 4668) and the Corporación Nacional Forestal (CONAF) (permit number: 54/2012) Chile. This article does not contain any study on human participants performed by any of the authors.

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**Conflict of interest** The authors declare that they have no conflict of interests.

## References

- Anderson DJ, Reeve J, Martínez Gomez JE, Weathers WW, Hutson S, Cunningham HV, Bird DM (1993) Sexual size dimorphism and food requirements of nestling birds. *Can J Zool* 71:2541–2545
- Boncoraglio G, Martinelli R, Saino N (2008) Sex-related asymmetry in competitive ability of sexually monomorphic barn swallow nestlings. *Behav Ecol Sociobiol* 62:729–738
- Castaño-Villa GJ (2015) Selección sexual en un ave socialmente monógama, *Aphrastura spinicauda*, (Furnariidae). PhD thesis, Universidad de Chile
- Chamberlain DE, Hatchwell BJ, Perrins CM (1999) Importance of feeding ecology to the reproductive success of blackbirds *Turdus merula* nesting in rural habitats. *Ibis* 141:415–427
- Clotfelter ED (1996) Mechanisms of facultative sex-ratio variation in zebra finches (*Taeniopygia guttata*). *Auk* 113:441–449
- Cowie RJ, Hinsley SA (1988) Feeding ecology of great tits (*Parus major*) and blue tits (*Parus caeruleus*) breeding in suburban gardens. *J Anim Ecol* 57:611–626
- Dimiz P (2011) Sex-dependent foraging effort and vigilance in coal-crested finches, *Charitospiza eucosma* (Aves: Emberizidae) during the breeding season: evidence of female-biased predation? *Zoologia* 28:165–176
- Dixon A, Ross D, O'Malley SLC, Burke T (1994) Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* 371:698–700
- Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* 30:116–121
- Green AJ (2001) Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82:1473–1483
- Grieco F (2002) Time constraint on food choice in provisioning blue tits, *Parus caeruleus*: the relationship between feeding rate and prey size. *Anim Behav* 64:517–526
- Griffith S, Owens I, Thuman A (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol Ecol* 11: 2195–2212
- Grundel R, Dahlsten DL (1991) The feeding ecology of mountain chickadees (*Parus gambeli*); patterns of arthropod prey delivery to nestling birds. *Can J Zool* 69:1793–1804
- Henderson IG, Hart PJB (1993) Provisioning, parental investment and reproductive success in jackdaws *Corvus monedula*. *Ornis Scand* 24:42–148
- Jakob EM, Marshall SD, Uetz G (1996) Estimating fitness: a comparison of body condition indices. *Oikos* 77:61–67
- Karasov WH (1990) Digestion in birds: chemical and physiological determinants and ecological implications. *Stud Avian Biol* 13:319–415
- Kaspari M (1991) Prey preparation and the determinants of handling time. *Anim Behav* 40:118–126
- Klasing KC (1998) Comparative avian nutrition. CAB International, Wallingford
- Krijgsveld KL, Dijkstra C, Visser GH, Daan S (1998) Energy requirements for growth in relation to sexual size dimorphism in marsh harrier *Circus aeruginosus* nestlings. *Physiol Zool* 71:693–702
- Leckie FM, Arroyo BE, Thirgood SJ, Redpath SM (2008) Parental differences in brood provisioning by hen harriers *Circus cyaneus*. *Bird Study* 5:209–215
- Leonard ML, Teather KL, Horn AG, Koenig WD, Dickinson JL (1994) Provisioning in western bluebirds is not related to offspring sex. *Behav Ecol* 5:455–459
- Magrath MJL, van Lieshout E, Visser GH, Komdeur J (2004) Nutritional bias as a new mode of adjusting sex allocation. *Proc R Soc Lond B* 271:347–349
- Mainwaring MC, Lucy D, Hartley IR (2011) Parentally biased favouritism in relation to offspring sex in zebra finches. *Behav Ecol Sociobiol* 65:2261–2268
- Moreno J, Merino S, Vásquez R, Armesto J (2005) Breeding biology of the thorn-tailed rayadito (Furnariidae) in south-temperate rainforests of Chile. *Condor* 107:69–77
- Moreno J, Merino S, Lobato E, Rodríguez-Gironés MA, Vásquez R (2007) Sexual dimorphism and parental roles in the thorn-tailed rayadito (Furnariidae). *Condor* 109:312–320
- Nishiumi I, Yamagishi S, Maekawa H, Shimoda C (1996) Paternal expenditure is related to brood sex ratio in polygynous great reed warblers. *Behav Ecol Sociobiol* 39:211–217
- Pinheiro J, Bates D, Debroy S, Sarkar D, R Core Team (2016) nlme: Linear and nonlinear mixed effects models, R package version 3.1–124. <https://CRAN.R-project.org/package=nlme>
- Quirici V, Venegas CI, González-Gómez PL, Castaño-Villa GJ, Wingfield JC, Vásquez RA (2014) Baseline corticosterone and stress response in the thorn-tailed rayadito (*Aphrastura spinicauda*) along a latitudinal gradient. *Gen Comp Endocrinol* 198:39–46
- Quirici V, Guerrero CJ, Krause JS, Wingfield JC, Vásquez RA (2016) The relationship of telomere length to baseline corticosterone levels in nestlings of an altricial passerine bird in natural populations. *Front Zool* 13:1
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>
- Ramsay SL, Houston DC (2003) Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. *Ibis* 145:227–232
- Randler C, Pentzold S, Teichmann C (2010) Weather conditions and sexual differences affect the foraging behavior of the insectivorous Cyprus wheatear, *Oenanthe cyprica* (Aves: Passeriformes: Muscicapidae). *Vertebr Zool* 60:175–181
- Remsen JV (2003) Family Furnariidae (ovenbirds). In: del Hoyo JH, Elliott A, Christie DA (eds) Handbook of the birds of the world. broadbills to tapaculos, vol 8. Lynx Edicions, Barcelona, p 162–357
- Royle NJ, Hartley IR, Owens IPF, Parker GA (1999) Sibling competition and the evolution of growth rates in birds. *Proc R Soc Lond B* 266: 923–932
- Rozzi R, Massardo F, Mansilla A et al (2004) La Reserva de Biosfera Cabo de Hornos: un desafío para la conservación de la biodiversidad e implementación del desarrollo sustentable en el extremo austral de América. *An Inst Patagonia* 35:55–70
- Ryser S, Guillod N, Bottini C, Arlettaz R, Jacot A (2016) Sex-specific food provisioning patterns by parents in the asynchronously hatching European hoopoe. *Anim Behav* 117:15–20
- Sacchi R, Saino N, Galeotti P (2002) Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behav Ecol* 13:268–273

- Saino N, Ninni P, Incagli M, Calza S, Møller AP (2000) Begging and parental care in relation to offspring need and condition in the barn swallow (*Hirundo rustica*). *Am Nat* 156:637–649
- Saino N, Suffritti C, Martinelli R, Rubolini D, Møller AP (2003) Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). *Behav Ecol* 14: 318–325
- Teather KL, Weatherhead PJ (1988) Sex-specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. *J Anim Ecol* 57:659–668
- Weimerskirch H, Barbraud C, Lys P (2000) Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. *Ecology* 81:309–318
- Welcker J, Steen H, Harding AM, Gabrielsen GW (2009) Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis* 151:502–513
- Yáñez DI, Quirici V, Castaño-Villa GJ, Poulin E, Vásquez RA (2015) Isolation and characterisation of eight microsatellite markers of the Thorn-tailed Rayadito *Aphrastura spinicauda*. *Ardeola* 62:179–183