

Brood provisioning rate and food allocation rules according to nestling begging in a clutch-adjusting species, the Rufous-tailed Scrub-robin *Cercotrichas galactotes*

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Abstract. Brood reduction may be a strategy by which, when food is scarce, parents provision chicks differentially — this usually leads to the death of the smaller nestlings. In contrast, in species where brood reduction does not normally occur, parents may allocate food equally among nestlings. The Rufous-tailed Scrub-robin *Cercotrichas galactotes* is a species in which brood reduction does not occur (it is a clutch adjuster), so that all nestlings usually fledge. This study analysed the food allocation rules in this species. As predicted, begging behaviour in nestlings seems to indicate their need for food, because once fed, they reduced their begging levels. Parents provisioning the nest allocated food according to begging by nestlings. Those nestlings that got fed begged nearer the parents, with lower latency and higher intensity, and stretched up to a greater height while begging. Moreover, the feeding rate was higher when more nestlings begged in the nest. There were slight differences between males and females with respect to prey type brought to the nest. Bigger nestlings got a larger proportion of food because they begged more intensely, but there was no evidence of parental favouritism towards bigger chicks.

Key words: Rufous-tailed Scrub-robin, *Cercotrichas galactotes*, begging, breeding strategies, brood reduction, food allocation rules, parental investment.

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INTRODUCTION

The parent-offspring conflict hypothesis determines that, given the genetic differences which exist between siblings and between parents and their offspring, the offspring will demand a greater parental investment than is optimal for their parents to deliver (Trivers 1974, Lazarus & Inglis 1986, Clutton-Brock 1991). The within-brood parent-offspring conflict (Macnair & Parker 1979, Mock & Parker 1997) establishes that, whereas each nestling will solicit a larger share of the food than its siblings receive, parents will distribute food in a way that maximises their own fitness: for example, feeding all their young equitably or showing a preference for particular offspring (Davis et al. 1999, Jeon 2008, Rodríguez

et al. 2008). Such conflicts of interest between offspring and parents may be resolved if the former give honest signals of their requirements to their parents, which may occur thanks to the costs associated with begging behaviour (Macnair & Parker 1979, Godfray 1991, 1995). On the other hand, strong between-sibling competition may affect how food is distributed within a brood (Mock & Parker 1997). Larger offspring have a competitive advantage, which would explain why they receive a greater proportion of the food delivered to the nest (Schwabl et al. 1997, Smiseth et al. 1998, Cotton et al. 1999).

Birds frequently show a size hierarchy between nestlings, which tends to result from hatching asynchrony, brought about usually by parental incubation patterns (Magrath 1990,

Stenning 1996). It may be adaptive through facilitating brood reduction when food is scarce by bringing about the death of the smallest chicks and allowing the largest ones, which have the greatest fitness, to survive (Lack 1968, Magrath 1989, 1990, Forbes et al. 2001). For brood reduction to incur a minimum waste of resources by parents, in species where this strategy is frequent (i.e., brood reducers), the parents should feed the larger nestlings preferentially (Soler 2001). Conversely, in species where brood reduction occurs rarely (clutch-size adjusters), parents might distribute food to all nestlings equally (Soler 2001). Preferential feeding of larger nestlings has been demonstrated in various brood-reducing species (Rydén & Bengtsson 1980, Ostreiher 1997, Smiseth et al. 1998, 2003, Cotton et al. 1999, Moreno-Rueda et al. 2007). However, no attention has been put on the food allocation rules in clutch adjuster species.

In this work, we study how adults determine their provisioning rates and how food is distributed within a brood in relation to the nestlings' begging behaviour in a population of the Rufous-tailed Scrub-robins *Cercothrichas galactotes* where brood reduction is absent. The Rufous-tailed Scrub-robin is a small passerine, some 15 cm. long, with an almost non-existent size dimorphism between sexes, which builds open nests in shrubs (Cramp 1998). Brood reduction does not occur in the population studied here, since the complete brood fledges in almost 100% of successful nests, those from which at least one nestling fledged (Palomino 1997). Despite the species not being a brood-reducer, a slight size hierarchy exists within the brood when the chicks are small. Therefore, according to this information and the previous reasoning, we predicted that parents should distribute food quantity equitably in this population, despite the size hierarchy between the nestlings existing (Soler 2001).

MATERIALS AND METHODS

Study area

The study took place between 24 June and 11 August 1994 in a vinicultural region of south-west Spain (37°9'N, 5°56'E). The Scrub-robin nests were principally on vine stocks, a favoured habitat of this species (Seoane 2005). Nests were visited periodically from the start of the breeding season, so that nestling ages were known exactly. Adult birds were colour-ringed and sexed by brood patch and singing behaviour.

Videorecording nests

Ten nests (only first broods) were filmed, eight with broods of three and two with broods of four nestlings, which agree with the usual clutch size (3–4 eggs). The nestlings filmed were between seven and nine days old, with a mean mass which ranged from 17.5–23.0 g. Although begging behaviour varies with nestling age, this short difference in age presumably did not significantly affect begging (Rydén & Bengtsson 1980, Moreno-Rueda 2005, Leonard & Horn 2006). Recordings lasted approximately 120 minutes. Nine recordings were initiated between 7:10 and 7:45 (local hour), and one recording was initiated at 9:40. Visual plotting of this record showed no difference in feeding rate or prey size with respect to the whole sample. The videorecorder was placed close to each nest (0.5–1 m. away) in order to film the required details. Each nestling had its beak marked with non-toxic paint before filming began, to enable individual recognition. Nestlings were weighed on a field balance accurate to 0.1 g. The filming process did not seem to disturb the parents, who resumed feeding their broods as soon as the investigators withdrew.

Analysis of recordings

The recordings were later analysed using a viewer which permitted frame-by-frame examination, examining in detail where a feeding event occurred. Parents usually fed only one nestling in each feeding bout (89.1% of cases). Feeding bouts in which parents fed more than one nestling ($n = 32$) were not considered in the analyses. The type of prey brought by parents was identified at the level of Order, whenever possible. Prey size was estimated relative to the parents' beak size (ca. 11.5 mm), with items smaller than the beak scored 1, those similar to beak size scored 2, and those larger than the beak scored 3. The quantity of food supplied (measured in food units) was calculated by adding the products of prey size and number of items, for each size category. The number of chicks which begged during each feeding event was counted, to examine the influence of brood begging behaviour on feeding rate. It was assumed that the greater the number of begging chicks the higher the begging intensity of the brood as a whole (Kilner & Davies 1999).

In order to examine the aspects of nestling behaviour which affected parental food distribution decisions, when a feeding event occurred each nestling which begged was assigned a score for each of the following variables:

1) Latency, or relative begging order (henceforth 'order'): the order in which each nestling began begging, in response to the arrival of a parent or the uttering of a feeding call, which the adults sometimes made shortly before perching on the nest. Thus the nestling given order 1 was the first to beg, order 2 was the second, etc.

2) Position in nest relative to adult (henceforth 'position'): the distance between the beaks of begging nestlings and that of the feeding parent. The nestling assigned position 1 was the closest to a parent when begging, the next closest was in position 2, etc.

3) Relative begging intensity (henceforth 'intensity'): nestlings were ranked according to their begging intensity. Begging activity was assessed as in earlier studies (e.g. Redondo & Castro 1992), in ascending order of intensity, from begging with the beak open and legs flexed to begging with legs and necks completely extended while calling and wing-beating. A continuum of begging intensity was assumed to establish the ranking. Where two or more nestlings seemed to beg with equal fervour, the most active nestling was taken to be the most intense begger (Rydén & Bengtsson 1980). In this manner intensity 1 was assigned to the nestling which begged most actively.

4) Relative head height (henceforth 'height'): the relative order of head height among the nestlings. The chick assigned height 1 was the one whose head was raised higher than those of its nest-mates.

The time that each nestling went without food (the interval since it was last fed) was recorded. This allowed a hunger ranking to be established within a brood, assuming that the longer a chick went unfed the hungrier it would be. Thus, value 1 was assigned to the nestling which went unfed longest, and so on. A ranking of body mass was also established.

Since brood sizes differed, all the variables concerning to nestlings were standardised in relation to brood size using the formula: $(\text{value} - 1)/(\text{brood size} - 1)$ (following Smith & Montgomerie 1991). This formula yields values between 0 and 1, such that values closest to 0 correspond to nestlings which had the lowest relative latency, were closest to the parent, raised their heads highest, were more time unfed, or were heavier, depending on the variable considered. It should be noted that the variables were expressed as a relative order and not as absolute values, so that the score given to a particular nestling in a given nest and during a given feeding event was not independent of the

scores of its siblings. Repeating the analyses only with the eight broods of 3 nestlings gave very similar results (data not shown).

Statistical analyses

The variables did not diverge significantly from a normal distribution, according to a Kolmogorov-Smirnov test, and thus parametric statistics were used (Sokal & Rohlf 1995, Quinn & Keough 2002). Values are given as means \pm standard deviations or as percentages. Each nest was considered as a statistical unit, using mean values for each nest, to avoid pseudoreplication (Hurlbert 1984). When multiple tests were applied simultaneously, Bonferroni's correction was employed, and the new critical α was indicated when necessary (Sokal & Rohlf 1995, Quinn & Keough 2002).

Student's t-test was used for pairwise comparisons between male and female parents at each nest, using mean values for each sex at each nest, and also to compare begging variables between fed and unfed young as well as the standardised orders of the periods which young went without food. Pearson's correlation was used where one of the continuous variables could be related to a nest parameter, such as provisioning rate or the total amount of food supplied to the nest. The non-standardised order of chick mass was used when comparing begging variables and the food received by nestlings, omitting the fourth nestling in broods of four. Exploratory analyses including the fourth chick in the two broods of four gave similar results. Between-variable comparisons were made using an ANOVA for repeated measurements, which permits pairwise comparisons at three levels. The χ^2 test was used for comparing frequencies (Siegel & Castellan 1988).

RESULTS

Quantities and types of food brought to nests by males and females

The provisioning rate by females was significantly higher than that by males (males: 5.6 ± 3.9 feeds/hour; females: 9.0 ± 5.0 feeds/hour; t-test for paired samples: $t_9 = 2.56$, $p = 0.03$). Females also brought more food than did the males (males: 18.6 ± 13.7 units of food/hour; females: 30.4 ± 17.7 units of food/hour; $t_9 = 3.23$, $p = 0.01$). Prey size did not differ significantly between the sexes (males: 1.52 ± 0.64 ; females:

1.77 ± 0.45 ; $t_0 = 1.03$, $p = 0.33$). Brood age did not affect feeding rate, prey size, or quantity of food brought to the nest (ANOVA, $F_{2,7} < 1.0$, $p > 0.40$). Average prey size did not vary with date ($r = 0.05$, $p = 0.89$), but feeding rate and quantity of food brought trended to decrease with date (respectively: $r = -0.60$, $p = 0.069$; $r = -0.57$, $p = 0.083$). Average nestling mass did not significantly vary with date ($F_{1,6} = 0.14$, $p = 0.72$; brood age as cofactor). With respect to prey type, the prey was identifiable to Order in 209 (64.3%) out of 325 cases. Over half of the identified items were lepidopteran caterpillars (59.8%; Table 1). There were significant differences in the proportions of different prey types brought by males and females ($\chi^2 = 15.94$, $p < 0.03$; Table 1).

The influence of the number of chicks begging on provisioning rates

There was a positive correlation between the mean number of begging chicks (standardised by brood size) in each nest and the overall provisioning rate ($r = 0.75$, $p = 0.01$, $n = 10$), which was not altered by date of records (partial $r = 0.68$, $p = 0.04$). The total amount of food brought to a nest did not correlate significantly with the standardised number of begging chicks ($r = 0.53$, $p = 0.11$, $n = 10$). The standardised number of begging nestlings had a strong effect on the provisioning rate by females ($r = 0.79$, $p < 0.01$, $n = 10$), and on the quantity of food brought by females ($r = 0.64$, $p < 0.05$, $n = 10$), but had no corresponding significant effect on the males' provisioning behaviour (provisioning rate: $r = 0.48$, $p = 0.16$, food quantity: $r = 0.32$, $p = 0.37$, $n = 10$). This suggests that females are more responsive to the needs of their broods.

Table 1. Number of prey items delivered to nests by males and females. Percentages in parentheses. Parental sex was unknown in some cases.

Prey type	Brought by		Total
	males	females	
Caterpillars	55 (69.6)	66 (53.2)	125 (59.8)
Orthoptera	9 (11.4)	19 (15.3)	28 (13.4)
Hymenoptera	2 (2.5)	11 (8.9)	13 (6.2)
Heteroptera	4 (5.1)	5 (4.0)	10 (4.8)
Lepidoptera	0 (0.0)	6 (4.8)	6 (2.9)
Coleoptera	4 (5.1)	1 (0.8)	5 (2.4)
Others	4 (5.1)	9 (7.3)	13 (6.2)
Grapes	1 (1.3)	7 (5.6)	9 (4.3)
Total	79 (100)	124 (100)	209 (100)

The influence of begging behaviour on food distribution

In general, begging variables were positively correlated among themselves, especially between 'intensity' and 'height', while 'position' was the variable less correlated with the rest (Table 2). On average, those nestlings which received food were those which were closest to the parents, begged sooner and more intensely than their unfed siblings and reached upwards higher (paired-sample t-test for the four variables $t_0 > 5.0$, in all cases $p < 0.001$; Fig. 1a). In order to control for a possible effect of relative nestling size on the probability of being fed, the begging behaviour of a randomly selected nestling was compared when it was fed and when it went unfed. The chosen nestling was closer to the provisioning parent, begged sooner and more intensively and reached higher when it succeeded in being fed than when it went unfed (paired-sample t-test, $t_0 > 5.0$, $p < 0.001$; Fig. 1b). Begging values of the feed nestlings did not vary with date (always $p > 0.15$).

The influence of nestling mass on food distribution

The coefficient of variation of within-brood nestling mass was $8.7 \pm 4.9\%$, with a range of 3.4–19.3% ($n = 10$ nests). The rate at which chicks were fed differed significantly according to their relative mass, heavier nestlings receiving more food (ANOVA for repeated samples, within-nests component: $F_{2,18} = 8.26$, $p < 0.003$; Fig. 2a). The total quantity of food received by nestlings also differed significantly in the same direction according to relative mass ($F_{2,18} = 5.24$, $p < 0.02$; Fig. 2b). Thus heavier nestlings received a greater quantity of food than lighter ones. The scores for the four begging variables of fed nestlings did not differ according to relative mass (for the four variables, $F_{2,18} < 2.00$, $p > 0.15$). This suggests that parents

Table 2. Matrix of average correlations (Pearson product-moment) among begging variables (mean \pm SD). A randomly selected chick in each nest was used to estimate the correlations. Range in parentheses.

Variables	Position	Order	Intensity
Order	0.25 ± 0.14 (0.07–0.50)		
Intensity	0.23 ± 0.27 (-0.16–0.76)	0.41 ± 0.25 (0.03–0.84)	
Height	0.24 ± 0.25 (-0.04–0.78)	0.43 ± 0.23 (0.08–0.77)	0.71 ± 0.18 (0.33–0.95)

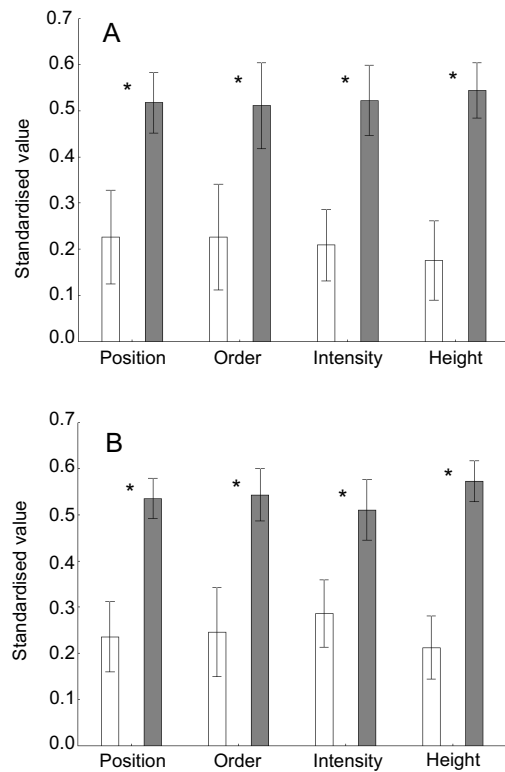


Fig. 1. Mean relative standardised orders for the four begging variables for: A) fed nestlings (white) and unfed nestlings (grey), B) a randomly selected nestling per brood, when fed (white) and unfed (grey). Lower values indicate closer position, earlier, more intense begging, as well as higher relative head height, respectively. Bars indicate standard deviations. Analysis performed with the Student t-test, * — $p < 0.001$, critical $\alpha = 0.0125$. Begging variables description in 'Analysis of recording' section.

followed the same norms when distributing food to heavier and lighter nestlings. However, heavier nestlings were the closest to the provisioning parent more often ($F_{2,18} = 6.55$, $p < 0.01$, critical $\alpha = 0.0125$; Fig. 3a), and they tended to beg sooner and more intensely, and to reach higher, but these latter differences were not significant (for these three variables, $F_{2,18} < 2.30$, $p > 0.10$; Figs. 3b–d).

The influence of hunger on begging intensity and food distribution

The period that nestlings went unfed did not significantly affect their probability of being fed (mean hunger ranking — of time since last feed: of fed nestlings: 0.30 ± 0.11 ; of unfed nestlings: 0.37 ± 0.08 ; paired-sample t-test, $t_9 = 1.53$; $p = 0.16$). To test whether nestlings reduced their begging levels after being fed, the means of these were compared for fed nestlings with those which they exhibited in the subsequent

feeding event. The four variables (relative position, begging order, relative begging intensity and relative height reached) gave higher standardised scores during the feeding event following that in which a nestling was fed (paired-sample t-test, $t_9 > 5.0$; $p < 0.001$, Fig. 4), showing that satiated nestlings reduced their begging levels. The effect of the size of the prey received did not significantly affect begging behaviour in the next feeding event (paired t-test; $t_9 < 1.6$; not significant for any variable after Bonferroni corrections).

Parental provisioning behaviour

Nestlings fed by females tended to show higher mean begging level scores than those fed by males, but no variable showed significant effect (after Bonferroni corrections; data not shown). There was no evidence that females fed smaller chicks preferentially ($t_9 = 0.32$; $p = 0.76$). Females spent significantly longer than males at nests when feeding young (males: 14.04 ± 6.31 sec.; females: 36.80 ± 30.70 sec.; Wilcoxon test, $z = 2.29$; $p = 0.02$; this variable did not approach a normal distribution).

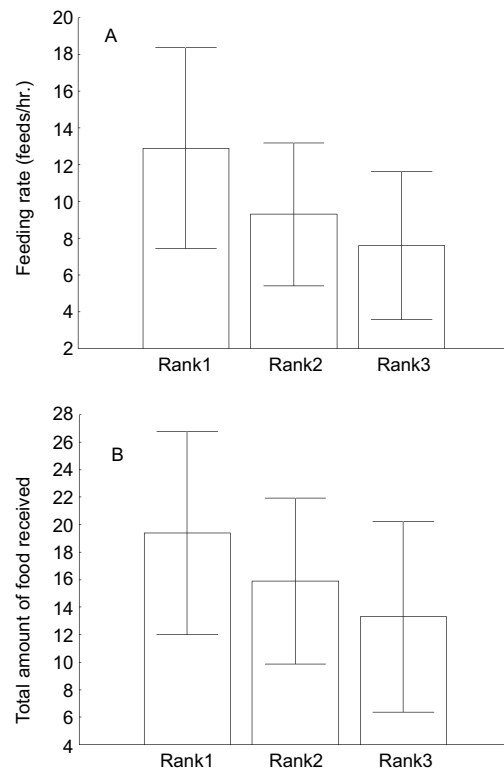


Fig. 2. Food received by the nestlings according to their relative body size. A) Mean feeding rates; B) Total food received. Bars include standard deviations. Rank 1 — largest nestlings; 2 — mid-size nestlings; 3 — smallest nestlings.

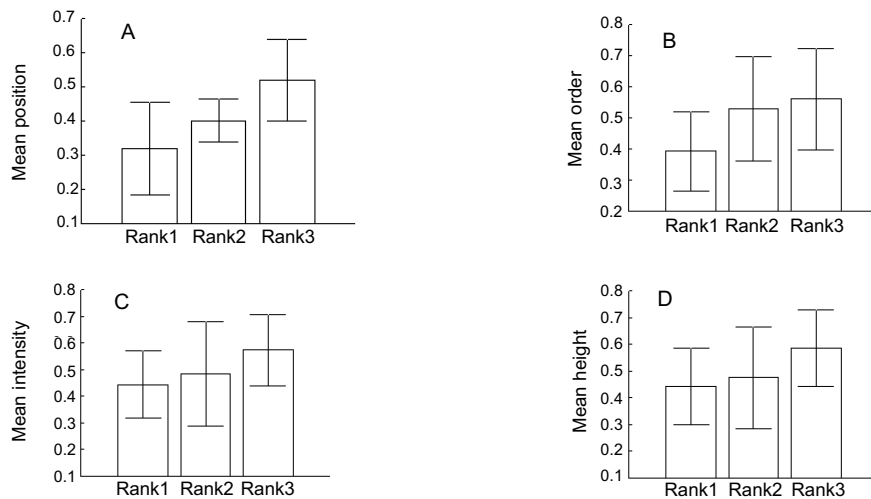


Fig. 3. Mean scores of nestlings according to their relative sizes for: A) position, B) begging order, C) begging intensity and D) relative height when begging, for nestlings according to their relative size. Lower values indicate closer position, earlier, more intense begging, as well as higher relative head height, respectively. Bars indicate standard deviations.

DISCUSSION

Is begging behaviour an honest signal of need in this species?

Many models of parent-offspring communication in birds predict that nestlings indicate their hunger to their parents via their begging behaviour (Harper 1986, Godfray 1991, 1995, Kilner & Johnstone 1997). The relationship between hunger and various parameters of begging behaviour has been confirmed in many studies (e.g. Iacovides & Evans 1998, Kilner et al. 1999, Budden & Wright 2008). In the present study, fed nestlings reduced their intensity of begging, the height to which they reached up and their relative proximity to the feeding parent, and took longer to start begging during the next feeding event. Larger nestlings begged closer to their parents (Fig. 3a), which accords with experimental studies showing that the largest nestlings succeed in getting nearest to parents (Cotton et al. 1999). Larger nestlings may have more advanced sensory and locomotory development, which may allow them to respond to the parents' arrival more quickly (Bengtsson & Rydén 1981, Leonard & Horn 2001, Moreno-Rueda 2005). Thus our results suggest that the nestlings of the Rufous-tailed Scrub-robin indicate their need via their begging level but that size may also have an influence on proximity to parents.

Do parents adjust their provisioning behaviour in response to begging behaviour?

According to current theoretical models, parents should adjust their provisioning rates according

to brood requirements (Hussell 1988, 1991, Godfray 1991, Kölliker et al. 2005), and should also distribute food within a brood according to the relative need of the nestlings (Godfray 1995, Kilner & Johnstone 1997). A relationship between the brood's begging level and feeding rate has indeed been found in other species (Bengtsson & Rydén 1983, Kilner 1997, Wright 1998). In the Scrub-robin, the parental feeding rate was positively correlated with the standardised mean number of begging nestlings in the nest, which is an indicator of need for the whole brood. Also, as other studies have found (Teather 1992, Leonard & Horn 1996, Lichtenstein 2001), food was distributed within the brood as a function of its begging behaviour, given

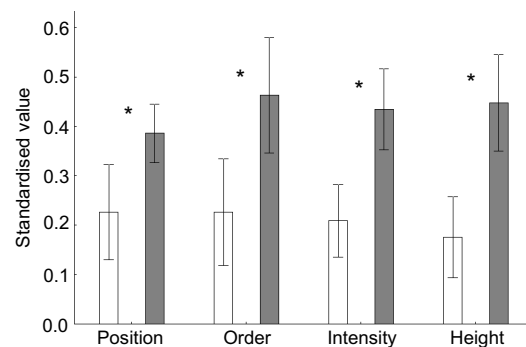


Fig. 4. Mean relative standardised orders for the four begging variables when nestlings received food (white) and in the subsequent feeding event (grey). Lower values indicate closer position, earlier, more intense begging, as well as higher relative head height, respectively. Bars indicate standard deviations. Student t-test, * — $p < 0.001$, critical $\alpha = 0.0125$.

that those nestlings which begged soonest, most intensely, closest to their parents and reached highest had a greater chance of being fed (Fig. 1).

Parents could feed larger nestlings preferentially, given that these have greater reproductive fitness (e.g. Smiseth et al. 2003). In the Scrub-robin, nestling mass did not affect the begging effort which nestlings had to make to get fed, suggesting that parents did not use nestling size per se (nor any size-related character such as gape dimensions: Kilner & Davies 1999) when deciding which nestlings to feed but only their begging behaviour. On the other hand, in the Magpie *Pica pica*, for example, larger nestlings did not need to make such a large effort to get fed as did smaller nestlings, suggesting that parents favoured larger offspring (Moreno-Rueda et al. 2007). Even so, larger nestlings succeeded in getting a larger percentage of feeds, which seems due to their competitive advantage, given that larger nestlings succeeded in getting closest to the parents more often. Other studies have shown that large nestlings get closer to parents more readily, permitting them to claim more feeds (Kacelnik et al. 1995, Cotton et al. 1999, Ostreiher 2001), that is to say, the results suggest that parents prefer to feed the nearest nestlings, which favours large brood members. This could be a parental strategy to feed fitter offspring (Bonabeau et al. 1998, Davis et al. 1999, Jeon 2008, Rodríguez et al. 2008), but other aspects of Scrub-robin biology make this explanation improbable, given that brood reduction rarely occurs in this population (Palomino 1997; see below).

Brood reduction and food distribution norms

Soler (2001) argued that the type of reproductive strategy — clutch-size adjustment or brood-size reduction — influences food distribution mechanisms. In brood-size reducers at least one nestling dies from starvation whereas in clutch-size adjusters the full brood tends to fledge. This population of Scrub-robin belongs in this latter category (Palomino 1997). These birds lay a clutch, which is equivalent to the number of nestlings, which they can raise and hence it is predictable that they will distribute food equitably among the brood (Soler 2001). Nevertheless, this did not occur: larger nestlings succeeded in getting more food thanks to their competitive advantage (getting close to their parents).

A possibility is that parents deliver sufficient food for all the brood to fledge, even though the larger ones will do so in better condition. This

could allow a considerable range of size in the brood at fledging, representing a higher phenotypic variation than if all the nestlings fledged in equal condition, which would increase the probability that, in a variable environment, some would survive to breed (Laaksonen 2004). Nevertheless, all the nestlings within a brood fledged at approximately the same mass (J. J. Palomino, unpublished data). Another possibility is that the smaller nestlings catch up with the larger ones at a later age, which has been showed in other species (Barba et al. 1993, Björklund 1997, Royle 2000).

Differences between males and females in provisioning behaviour

Females brought food more often than did males (also see Martín-Gálvez et al. 2005). In species where extra-pair copulations are frequent, the males may be selected to invest less in consequence of having a reduced likelihood of relatedness with the brood (Westneat & Sherman 1993, Queller 1997). On the other hand, males may be involved in other activities at that stage of the breeding cycle, such as nest defence (Markman et al. 1995, Woodard & Murphy 1999, Álvarez 2000; but see Tryjanowski & Goławski 2004 for an exception). Although there was no difference in the size of prey items brought by males and females, prey types did differ (Table 1). Similar sexual difference in prey types has been found in other species, and probably is caused by sex foraging in different zones (Krupa 2004). Rates of feeding by females, but not by males, increased significantly with brood hunger, suggesting different responses by male and female parents. On the other hand, although females employed more time during feeding, there was no evidence of sexual differences in food allocation rules. Many studies have reported that males feed preferentially the largest nestlings (Rydén & Bengtsson 1980, Gottlander 1987, Leonard & Horn 1996). Recently, Wiebe & Slagsvold (2009) suggested that this may be a side effect of males bringing larger prey, which cannot be swallowed by smallest nestlings. Our results were consistent with this hypothesis, both males and females bringing similar-sized prey items, and therefore both sex employing the same food allocation rules.

Our results suggest that begging behaviour is a reliable signal of nestling need in the Rufous-tailed Scrub-robin, and parents respond to begging by increasing food provisioning. As predicted for a clutch-size adjuster species, there was

no parental preference for bigger nestlings, but heavier chicks achieved more food thanks to a superior competitive capacity. Food allocation rules did not differ between male and female parents.

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STRESZCZENIE

[Liczba karmień i rozdział przynieszonego pokarmu w zależności od żebrania piskląt u drożdówki rdzawej]

Wiele ptaków stosuje strategię redukcji lęgu, rozpoczynając wysiadywanie przed złożeniem ostatniego jaja, co prowadzi do powstania hierarchii wielkości młodych. Dostępny pokarm trafia przede wszystkim do większych piskląt, a w przypadku jego niedoborów najmłodsze piskląta giną. Z drugiej strony ptaki, mogą dopasować swe zniesienia do warunków pokarmowych i wyprowadzać następnie wszystkie wyklute piskląta. W takiej sytuacji powinny one karmić swe młode bez jakichkolwiek preferencji, a sygnałem o potrzebach piskląt może być sposób i intensywność ich żebrania. W pracy badano sposób rozdzielania pokarmu pomiędzy piskląta drożdówki rdzawej w zależności od intensywności żebrania młodych. Gatunek ten karmi zwykle jedno pisklątę za jednym przylotem do gniazda. Badaniami objęto 10 lęgów, z trzema i czterema pisklątami a zachowania ptaków analizowane były z nagrań wideo. Analizowano kolejność rozpoczynania żebrania i jego intensywność, położenie piskląt względem rodzica, biorąc pod uwagę osobnika, który został nakarmiony i te, które nie otrzymały pokarmu.

Stwierdzono, że samice karmiły młode częściej i przynosiły więcej pokarmu niż samce. Proporcja różnych grup zdobywcy przynieszonej do gniazda różniła się między samcami i samicami (Tab. 1). Im więcej młodych żebrało, tym liczba karmień była większa, szczególnie tych wykonywanych przez samice. Poszczególne elementy, które składały się na opis żebrania były ze sobą skorelowane (Tab. 2). Rodzice rozdzielali pokarm w zależności od sposobu żebrania, karmione były młode znajdujące się najbliżej rodzica i najintensywniej domagające się pokarmu (Fig. 1). Największe młode dostawały więcej pokarmu, gdyż zebrały bardziej intensywnie (Fig. 2, 3), ale nie stwierdzono jakiegokolwiek preferowania tych piskląt ze strony rodziców. Zebranie odzwierciedlało potrzeby piskląt, gdyż ptaki nakarmione, domagały się o pokarm mniej intensywnie (Fig. 4).