

CHAPTER VI



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Cantarero A., López-Arrabé J., Palma A., Redondo A. J. & Moreno J. 2014. Males respond to female begging signals of need: a handicapping experiment in the Pied flycatcher *Ficedula hypoleuca*. *Animal Behaviour* 94: 167-173.

CHAPTER VI

Males respond to female begging signals of need: a handicapping experiment in the pied flycatcher, *Ficedula hypoleuca*

**Alejandro Cantarero¹, Jimena López-Arrabé¹, Antonio Palma¹,
Alberto J. Redondo² and Juan Moreno¹**

1 Department of Evolutionary Ecology, National Museum of Natural Sciences - CSIC, José Gutiérrez Abascal 2, 28006, Madrid, Spain

2 Department of Zoology, University of Córdoba, Spain

ABSTRACT. The ‘female nutrition’ hypothesis proposes that food provided by males during incubation is an important energy source for females in bird species in which females alone incubate. Females should be able to communicate their needs through begging signals to mates and males may compensate for the energetic limitations of females through their feeding visits, owing to their overlapping reproductive interests. To test whether female begging during incubation is an honest signal of energetic need and whether mates respond to it we experimentally handicapped female pied flycatchers at the beginning of incubation by clipping two primary flight feathers on each wing. Experimental manipulation led females to intensify begging displays arising from condition impairment and males accordingly increased their incubation feeding rates. Female begging intensity explained more than half of the variation in male incubation feeding rate, thereby showing that female nutrition is the main factor explaining male incubation feeding. Moreover, handicapped females consumed a higher proportion of male food deliveries during the first few days after hatching and weighed less at the end of the nestling period than control females. Handicapping had no influence on female incubation behaviour, hatching and breeding success, nestling and male condition or female nestling provisioning. The provisioning rates of males in the late nestling stage were higher in experimental nests. This is the first experimental study showing that males adjust incubation feeding rates to behavioural displays of need by their mates. The ability of females to modify their begging displays according to need may be an important adaptation that allows females to maintain a good energetic condition during incubation.

INTRODUCTION

Males of many avian species in which only the female incubates provision their mates during the incubation period (Lifjeld and Slagsvold 1986; Lyon and Montgomerie 1985; Ricklefs 1974). In some species, for example hornbills, females are totally dependent on males for food during the incubation stage (Poonswad et al. 2004). In a variety of other species it is more common for incubating females to receive only some of their food from their mates, although they also leave the nest to forage in order to maintain their energy requirements (Boulton et al. 2010). Mate feeding has evolved as a behavioural strategy to compensate for energetically costly activities for the female during reproduction (Galván and Sanz 2011), which may include the posthatching stage.

Food provided by males during incubation has been proposed to be an important energy source for females, a proposal termed the 'female nutrition hypothesis' (Niebuhr 1981). In fact, several studies have demonstrated that higher rates of male incubation feeding to their mates can improve female body condition (Lifjeld and Slagsvold 1986) and increase nest attentiveness by reducing the amount of time the female spends foraging off the nest (Halupka 1994; Leclaire et al. 2011; Lloyd et al. 2009; Matysioková et al. 2011; but see Lifjeld & Slagsvold 1989; Matysioková & Remeš 2010; Boulton et al. 2010; Stein et al. 2010; Moreno and Carlson 1989; Pearse et al. 2004; Smith et al. 1989; Stein et al. 2010) and thereby help to advance hatching (Lyon and Montgomerie 1985; Nilsson and Smith 1988), improve hatching success (Galván and Sanz 2011; Lyon and Montgomerie 1985; Nilsson and Smith 1988) or improve fledgling condition (Lifjeld and Slagsvold 1986; Røskaft 1983). This suggests that incubation feeding has evolved as a behavioural strategy to partly compensate for the energetic limitations of females while incubating (Galván and Sanz 2011). Although there are probable fitness advantages for the breeding pair derived from male incubation feeding, there may also be costs for males induced by intensified foraging activity at an early stage of the season (Leclaire et al. 2011; Lifjeld and Slagsvold 1986; Smith et al. 1989). Thus males may experience a trade-off between provisioning their mate and feeding themselves (Lifjeld and Slagsvold 1986; Lifjeld et al. 1987; Lyon and Montgomerie 1985; Moreno et al. 2011). They may also allocate more or less effort

to finding and copulating with extrapair mates (Hill et al. 2011; Wagner 1992). Male incubation feeding intensity could thus be more a product of differences in male age, condition and mating strategy than of female nutritional needs (Lifjeld and Slagsvold 1986; 1989; Lifjeld et al. 1987).

To distinguish between the 'female nutrition' and alternative scenarios it is necessary to experimentally manipulate female condition and study male responses, as males may adjust their feeding activity to the optimal level of attendance at each nest in a nonexperimental situation (Moreno et al. 2011). Only according to the 'female nutrition' hypothesis would we expect a direct male response by either increasing (experimentally reduced female condition) or reducing (experimentally increased female condition) his provisioning rate. Both experimental approaches have provided support for the female nutrition hypothesis (reduced condition: Moreno et al. 2011; improved condition: Smith et al., 1989; Paillisson et al., 2007; Wright and Cuthill 1989; 1990a; 1990b).

To improve their condition during incubation, females should be able to communicate their needs to mates. As both sexes have at least partially overlapping reproductive interests (Moore and Rohwer 2012), communication between incubating females and their mates should be reliable (Searcy and Nowicki 2005). Begging by nestlings has received a fair amount of attention as an honest system of communication (Cotton et al. 1996; Mock et al. 2011; Wright and Leonard 2002), whereas begging between mates has received scant attention. Females beg to their mates in courtship contexts (Clancy 2005; East 1981; Ellis et al. 2009; Otter et al. 2007; Tobias and Seddon 2002), while incubating (Ellis 2008; Moore and Rohwer 2012; Tobias and Seddon 2002) and also during the nestling feeding phase before apportioning food to the nestlings (Clancy 2005). Female begging displays include loud vocalizations, body postures and wing fluttering, which closely resemble the begging displays of older nestlings (Ellis et al. 2009; Godfray 1991; Harper 1986). The striking similarity of female and nestling begging displays suggests the retention into adulthood in females of typically juvenile behaviours (Moore and Rohwer 2012). Otter et al. (2007) manipulated the hunger levels during egg laying of black-capped chickadee, *Poecile atricapillus*, females and showed no effect on male provisioning, even finding a decrease in female food

solicitation. Furthermore, Moore and Rohwer (2012) found a correlation between begging displays of incubating yellow warbler, *Setophaga petechia*, females and mate provisioning rate in relation to environmental conditions. However, to our knowledge, it has never been confirmed experimentally that males adjust incubation feeding effort to female begging intensity. To test this link, begging intensity could be manipulated directly although this is difficult. Several behavioural components (posture, vocalizations, wing fluttering) presumably contribute to begging behaviour but the information content expressed in each component is still unknown. Alternatively, begging behaviour may be manipulated through hunger. Hunger depends on energy balance which may be experimentally altered through either food supplementation or handicapping (see above).

In many passerines such as the pied flycatcher, females incubate alone and receive some of their food from their mates (Cantarero et al. 2013b; Moreno et al. 2011). Some experimental studies have shown that pied flycatcher males seem able to adjust incubation feeding to female requirements (Moreno et al. 2011), although the behavioural mechanism behind male responses remains unknown. To test whether female begging during incubation is an honest signal of energetic need and whether mates respond to it in the pied flycatcher we followed previous experiments with this species (Lifjeld and Slagsvold 1986) by experimentally handicapping some females by clipping two primary flight feathers (Moreno et al. 2011). Handicapping is a useful and widely employed method to study the effects of energetically challenging situations on bird behaviour (Harrison et al. 2009). We assumed that clipping should increase the female's flight costs and therefore her energy requirements during incubation (Matysioková and Remeš 2011; Pennycuik 1982). We then compared control and experimental females by videoing their behaviour within the nestbox during incubation (before and after female manipulation) and at two stages of the nestling period (3 and 9 days of age).

We predicted following the 'female nutrition hypothesis' that impaired flight ability caused by handicapping would (1) lead to increase female begging displays during incubation because of the manipulation of female condition and hunger and (2) induce more male incubation feeding in response to female needs. Depending on the effects of the experiment on male incubation feeding rate, we

might or might not expect changes in female incubation behaviour and in body mass loss between incubation and the nestling phase.

METHODS

Study area and species

The study was conducted during the spring of 2013 in a montane forest of Pyrenean oak, *Quercus pyrenaica*, at 1200 m above sea level in Valsaín, central Spain (40°54'N, 4°01'W) where pied flycatchers breeding in nestboxes have been studied since 1991 (see Sanz et al. 2003 for a general description). Of 570 nestboxes, 102 were occupied by pied flycatchers (see Lambrechts et al. 2010 for dimensions, structure and placement of nest-boxes).

Egg laying in the pied flycatcher population under study typically begins in late May (Cantarero et al. 2013b), and the modal clutch size is six. The female incubates and broods alone and receives some of her food from her mate (Cantarero et al. 2013b; Moreno et al. 2011). No brooding is observed after nestlings attain 7 days of age (Sanz and Moreno 1995). Breeding activities are followed routinely every year and laying and hatching dates and brood sizes at hatching and fledging are determined (Cantarero et al. 2013a).

On day 3 (hatching day = day 1), we weighed jointly all nestlings with a digital scale to the nearest 0.1 g. On day 13, we ringed nestlings and measured their tarsus length with a digital calliper to the nearest 0.01 mm and their wing length with a stopped ruler to the nearest mm. Nestlings were also weighed with a digital balance to the nearest 0.01 g. The parents were captured in their nestboxes with traps and weighed and measured in the same way as nestlings. Parents were not inside the trap for more than 5 min. All the procedures between capture and release of the bird took less than 10 min.

Female handicapping

Of the 102 nestboxes occupied by pied flycatchers we selected those with laying dates between days 43 and 65 (1 April =day 1). We assigned 71 nests randomly to

two groups. We included 39 females in the control and 32 females in the experimental group.

Seven or eight days after clutch completion, incubating females were captured in the nestbox during the day without traps as they are not easily frightened away from the nest at this stage (see Moreno et al. 2011 for a similar protocol). They were banded if necessary, identified and weighed to the nearest 0.01 g with a digital balance. Primaries 7 and 9 on each wing (counting inwards from the distal margin of the wing) were clipped at the base of the rachis with scissors in experimental females while only the tips of these primaries were clipped in control females (Moreno et al. 1999; 2011). The whole procedure took around 5–10 min. The experimental manipulation was admittedly mild to simulate natural situations rather than to enforce drastic effects with possible repercussions on desertion probability (Moreno et al., 2011; but see Matysioková and Remeš 2011 for a more drastic manipulation). The wing manipulation had no observable effect on female behaviour outside the nestbox. No female deserted after manipulation.

Video recordings

Five and 10 days after clutch completion (days 6 and 11 of incubation) we recorded nest activity inside nestboxes for about 100 min ($101.68 \pm \text{SE } 17.42$ min, $N=135$) with a cold white light (LED 5 mm) powered by a 3 V battery and a camera (GoPro HD Hero1) mounted on the roof inside the nestbox (Cantarero et al. 2013a). We obtained two incubation records for each nest, before and after treatment.

Nestboxes were again filmed 2 days after the day of hatching of the young for periods of $99.63 \pm \text{SE } 9.47$ min ($N=69$) and 8 days after hatching of the young for periods of $97.08 \pm \text{SE } 14.93$ min ($N=67$). Because of technical problems, we failed to record the behaviour at seven nests during incubation and two nests with young nestlings. In four nests all chicks died after day 3 (one control and three experimental nests) but we have included earlier records for these nests. The death of nestlings was associated in all cases with rainy weather and occurred at least 10 days after female manipulation and 2–3 days after the nests were filmed in the early nestling phase. All the nestboxes in the study area are protected against predators. All films were recorded between 0800 and 1500 hours, and no

differences between experimental groups with respect to time of filming were found (first incubation record: $U=467.5$, $P=0.373$; second incubation record: $U=503.5$, $P=0.548$; nestling period day 3: $U=472.5$, $P=0.150$; nestling period day 9: $U=533.5$, $P=0.969$). As in previous studies (Cantarero et al. 2013a; 2013b), no evidence of stress or unnatural behaviour such as extremely long periods of absence from the nest or trying to peck at the camera system were observed after the first visit.

Behavioural data analysis

Recordings were displayed in the free VLC Media Player software. From records taken during incubation we estimated the proportion of time spent by the female inside the nestbox or 'egg attendance' which includes the time allocated to incubating and turning the eggs, and the mean duration of incubation sessions and recesses (Cantarero et al. 2013a). In addition, we counted incubation feedings by males. We also recorded female begging displays by quantifying the call duration, the posture during begging and the prey brought by the male (Fig. 1).

Female begging postures were assigned following a scale of increasing intensity: 0 = no arrival of male; 1 = female does not move upon arrival of male; 2 = takes the prey with low calls; 3 = takes the prey with loud calls; 4 = same as 3, but leaves the nest cup to approach the nest entrance without reaching it; and 5 = same as 3, but leaves the nest cup and puts her head out of the nest entrance in order to collect the prey. We identified prey as caterpillars (value 1) or other prey (value 0). On each visit of the male to the nest with food, we recorded the begging time of the female, the female posture during begging and the prey brought by the male. We then estimated the average value of these variables at each visit for the incubating female.



Figure 1. Example of female begging behaviour when males visit the nestbox with prey during incubation.

From recordings during the early nestling phase we obtained hourly provisioning rates by males and females and the amount of time spent by females on ‘nestling attendance’. ‘Nestling attendance’ includes the proportion of time spent by the female inside the nestbox (Cantarero et al. 2013a). We also counted male feeds aimed at the female and those aimed at the nestlings. We quantified the posture of females and the prey brought by the male while the female was brooding. These variables were estimated in the same way as during the incubation stage. From recordings during the late nestling phase we obtained hourly provisioning rates by males and females.

Data analyses

Breeding variables were normally distributed and were therefore analysed with GLM models (STATISTICA, Statsoft, Tulsa, OK, U.S.A.) assuming a normal error with treatment as explanatory factor. Clutch size and brood size were analysed with GLM models assuming a Poisson distribution with treatment as explanatory factor. The effects of treatment on brood-averaged nestling morphometric measurements and mass near fledging were analysed with GLM models with treatment as explanatory factor and hatching date and brood size as continuous predictors. Hatching success (proportion of eggs that hatched) and fledging success

(proportion of hatched chicks that fledged) were analysed as frequencies (Yes-1/No-0 cases of all chicks hatched and Yes-1/No-0 cases of all chicks hatched becoming fledglings) with chi-square contingency tables.

All parametric behavioural variables for the incubation stage were analysed with repeated measures ANOVA with treatment as explanatory factor and time as repeated measures effect (before or after female capture). All parametric behavioural variables for the young nestling phase were analysed with treatment as explanatory factor and hatching date, brood size and mate provisioning rate as continuous predictors. All parametric behavioural variables for the late nestling phase were analysed with treatment as explanatory factor and hatching date and brood size as continuous predictors.

Ethical note

We were authorized to handle pied flycatchers by Consejería de Medio Ambiente de Castilla y León and J. Donés, director of 'Centro Montes de Valsain' to work in the study area (protocol number EP/SG/193/2013). The experiments comply with current Spanish laws, and grant holder and field researchers were officially licensed for animal manipulation following current EU regulations on animal manipulation (authorization types C and B by regional authorities).

RESULTS

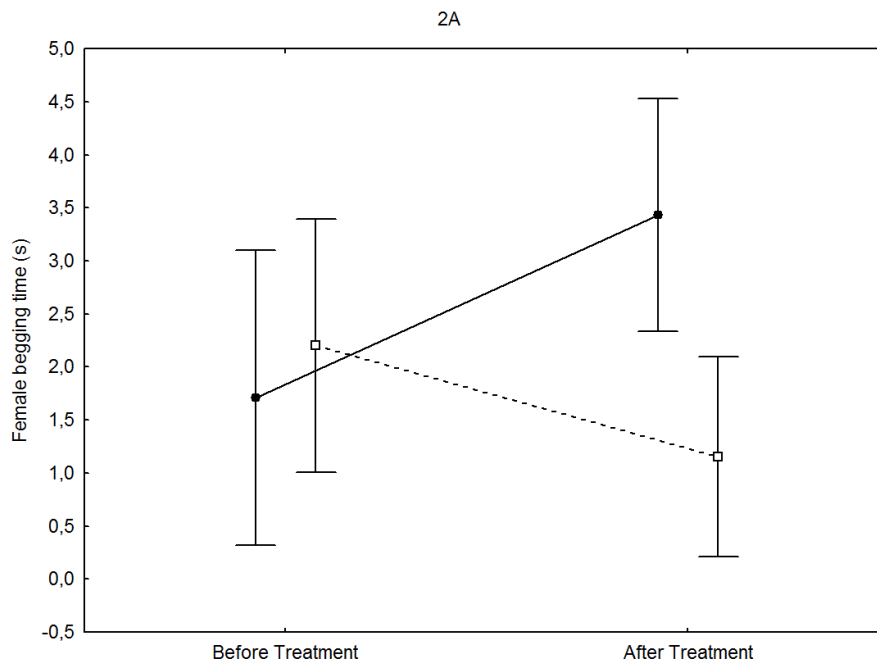
Females in the two treatments did not differ with respect to breeding variables or mass at incubation during capture (Table 1). Female mass during the nestling phase was positively correlated with female incubation mass ($r_s=0.56$, $F_{1,60}=17.201$, $P<0.001$), and was affected by treatment (control: 12.57 ± 0.70 g, $N=38$; experimental: 12.17 ± 0.68 g, $N=30$; $F_{1,65}=5.28$, $P=0.025$). Male mass during the nestling phase was similar in the two treatments (control: 12.17 ± 0.51 g, $N=34$; experimental: 12.20 ± 0.59 g, $N=29$; $F_{1,61}=1.35$, $P=0.820$).

Males respond to female begging signals

	Control	Experimental	Statistic	<i>P</i>
Laying date	57.308 ±	58.406 ±	$F_1 = 0.851$	0.359
Hatching date	76.231 ±	77.281 ±	$F_1 = 1.340$	0.252
Clutch size	5.256 ± 0.938 (39)	5.344 ± 0.971(32)	Wald=0.025	0.874
Brood size 13 days	4.462 ± 1.274 (39)	4.218 ± 1.660(32)	Wald=0.238	0.626
Female incubation mass	14.184 ±	14.159 ±	$F_1 = 0.010$	0.917

Table 1. Average \pm SE (*N* in parentheses) values for breeding variables of nests included in the two treatments prior to manipulation and results of GLM analyses.

Treatment did not interact significantly with the repeated measures effect for any female incubation variable (all $P > 0.20$), nor for type of prey delivered ($F_{1,63} = 0.007$, $P = 0.935$). There was a significant interaction between treatment and the repeated measures effect during incubation for female begging displays and male feeding. While females in the control group showed a similar duration of calling during the two sequential observation periods, females in the experimental group showed a marked increase in begging time after being handicapped (Fig. 2a; interaction of treatment with repeated measures: $F_{1,57} = 7.133$, $P = 0.009$). The same pattern was observed in female begging posture (Fig. 2b; interaction of treatment with repeated measures: $F_{1,57} = 7.031$, $P = 0.010$).



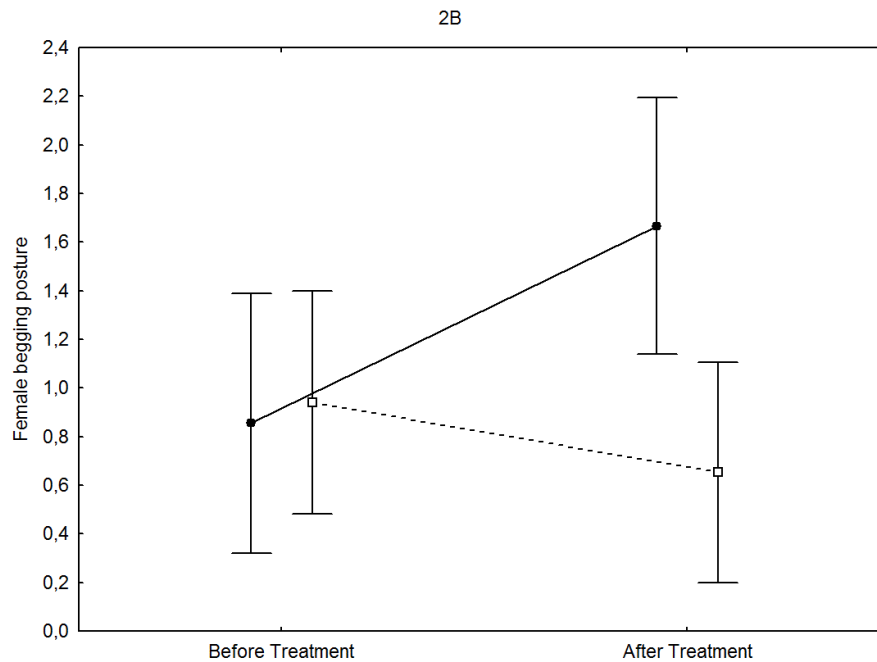


Figure 2. Variation in begging displays of pied flycatcher females during incubation, comparing control (□) and experimental females (●). Means \pm SE of (a) female begging time and (b) female begging posture before and after manipulation are presented.

Males increased their incubation feeding rates to females between observations in the experimental group but not in the control group (Fig. 3; interaction of treatment with repeated measures: $F_{1,62}=7.382$, $P=0.008$). Controlling for treatment, postmanipulation male incubation feeding rate was strongly positively associated with female begging time ($F_{1,60}=71.231$, $P=0.008$). Female begging time explained 57% of the variation in male incubation feeding. Female mass loss between the two captures was not related to postmanipulation male incubation feeding rate when controlling for treatment ($F_{1,56}=0.018$, $P=0.894$). However, this mass loss covers the whole posthatching period of adaptive mass loss (Sanz and Moreno 1995) and not just the period for which male behaviour was studied.

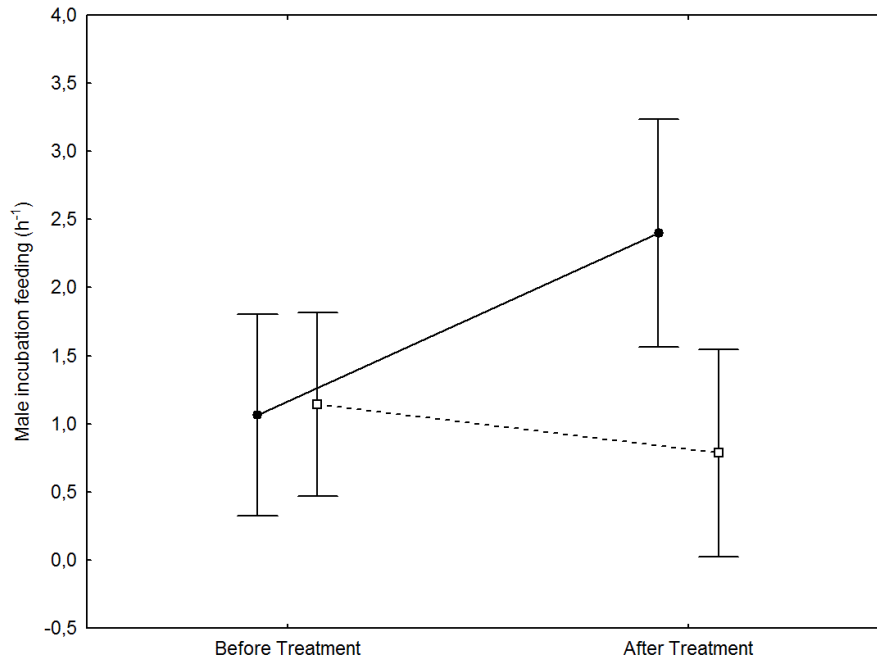


Figure 3. Variation in provisioning rates of pied flycatcher male during incubation, comparing control (□) and experimental nests (●). Means ± SE of male hourly provisioning rate before and after manipulation are presented.

On day 3, nestling attendance (proportion of time spent by the female inside the nestbox) did not differ between treatments and was positively related to male provisioning (Table 2).

Provisioning rates of males were similar in both treatments (Table 2). Female provisioning rates were lower in experimental nests, negatively related to mate provisioning and positively related to brood size (Table 2). There was no difference in direct male feeding rates to females (Table 2), but the proportion of prey consumed by the female with respect to total prey delivered by the male was higher in the experimental group (Fig. 4; $F_{1,41}=6.027$, $P=0.018$).

	Control	Experimental	Treatment statistic	Brood size statistic	Hatching statistic	Mate statistic
Nestling day 3						
Nestling attendance (%)	55.75 ± 22.65	59.27 ± 19.69	$F=1.403$	$F=0.598$	$F=0.868$	$F=4.431^*$
Male total provisioning (per h)	10.61 ± 4.30	11.18 ± 4.76	$F=0.011$	$F=0.352$	$F=0.065$	$F=2.746$
Male provisioning to female (per h)	5.62 ± 4.41	5.31 ± 5.31	$F=0.393$	$F=4.496^*$	$F=0.886$	$F=15.227^{**}$
Female provisioning (per h)	5.11 ± 3.86	4.80 ± 4.21	$F=4.841^*$	$F=11.309^{**}$	$F=1.273$	$F=6.863^*$
Female begging posture	1.37±0.39	2.00 ± 0.60	$F=14.818^{**}$	$F=0.005$	$F=0.192$	$F=1.311$
Nestling day 9						
Male provisioning (per h)	11.08 ± 4.24	13.77 ± 4.90	$F=4.457^*$	$F=4.053^*$	$F=0.235$	-
Female provisioning (per h)	12.57 ± 6.70	10.41 ± 5.95	$F=1.843$	$F=1.396$	$F=1.187$	-
Total provisioning by pair (per h)	19.52 ± 7.28	20.96 ± 9.40	$F=0.328$	$F=5.978^*$	$F=0.658$	-

$P<0.05$; $^{**}P<0.01$.

Table 2. Differences (means ± SE, N in parentheses) in behavioural variables between the two treatments and results of GLM analyses.

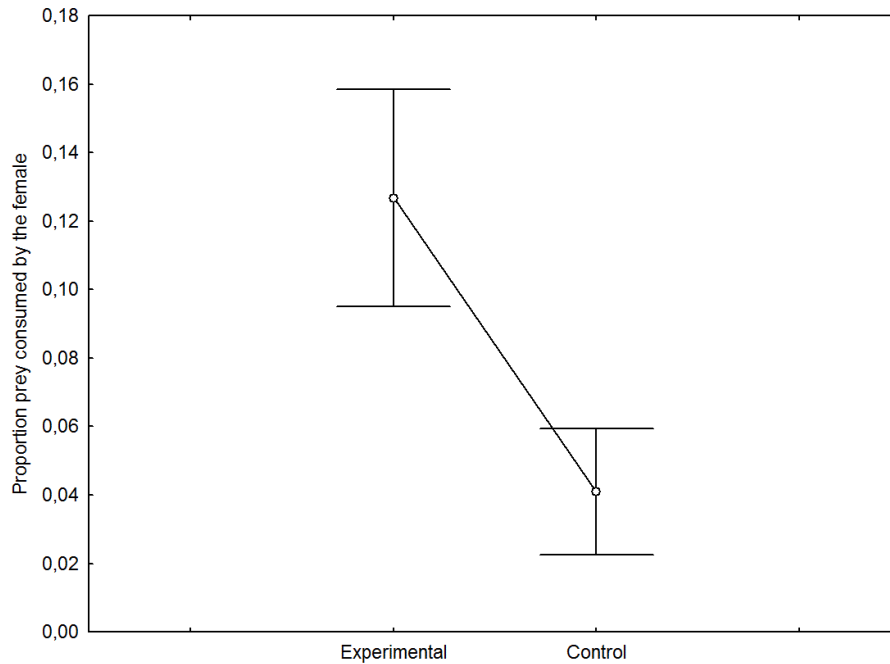


Figure 4. Differences in the proportion of food deliveries consumed by the female with respect to total prey deliveries by the male comparing control and experimental nests on day 3 of nestlings. Means \pm SE are shown for each treatment.

Females in the experimental treatment begged more intensely also at this stage (Table 2). On day 9, female provisioning rates were not related to treatment (Table 2) when controlling for brood size and hatching date. Males in the experimental treatment provisioned more at this stage while there was a positive effect of brood size on male provisioning (Table 2). The total provisioning rate by the pair was similar in both treatments and was positively affected by brood size (Table 2).

The control (3.02 ± 0.36 g, $N=39$) and experimental (2.99 ± 0.68 g, $N=32$) groups did not differ in mean nestling mass (g) on day 3 ($F_{1,69}=0.067$, $P=0.797$). There were no differences between treatments in nestling morphometric measurements on day 13 when controlling for hatching date and brood size (all $P>0.20$). Nestling body mass was negatively related to brood size ($F_{1,62}=6.428$, $P=0.014$). The nests from the two treatments did not differ in hatching success ($\chi^2_2=0.52$, $P=0.473$; control nests: 0.56 ± 0.50 , $N=39$; experimental nests: 0.69 ± 0.47 , $N=32$) or fledging success ($\chi^2_2=1.03$, $P=0.311$; control nests: 0.87 ± 0.34 , $N=39$; experimental nests: 0.78 ± 0.42 , $N=32$).

DISCUSSION

This study shows that experimentally handicapping female pied flycatchers during the incubation stage led to intensified begging displays arising from condition impairment and that males were able to respond by increasing their feeding rates to females. Experimental females produced longer vocalizations and modified their begging posture after being manipulated. Female begging largely explained male feeding behaviour. Handicapping had no influence on female incubation behaviour or hatching success. Moreover, handicapped females fed their chicks at the same intensity as control females, but they showed a greater decrease in body mass. They also took a higher proportion of male food deliveries to the nest for themselves than control females during the first few days after hatching. The provisioning rates of males in the late nestling stage were higher in experimental nests. Male and nestling condition were unaffected by the treatment.

Female begging displays are honest and adaptive if males can assess the nutritional state of their mates (Tobias and Seddon 2002) and males may gain an advantage by responding to female needs through food provisioning (Otter et al. 2007). Communication between females and their mates should be an honest system because of their common interests (Moore and Rohwer 2012; Searcy and Nowicki 2005). Females probably benefit from begging by increasing male incubation feeding rates (Moore and Rohwer 2012) and, by supplying food, males may directly enhance their own fitness. Our results are consistent with this scenario, as we found that incubating females communicate energetic needs to their mate and adjust their begging intensity when their nutritional state is manipulated through handicapping. Most studies involving flight feather removal assume that a reduced wing area affects wing loading and thereby increases flight costs (Slagsvold and Lifjeld 1988; Wright and Cuthill 1990a; Wright and Cuthill 1990b). The higher flight cost imposed by handicapping in experimental females could negatively affect foraging efficiency and thereby reduce energy input. Moreover, the short flights involved in foraging are energetically very costly which may increase energy output in small passerines (Carlson and Moreno 1992; Tatner and Bryant 1986). The combination of the two effects may therefore negatively affect energy balance.

During intense begging displays, females flutter their wings and are constantly calling to their mate during male visits. Different components of begging displays vary in the same direction to enrich the information content of the female signal (Gottlander 1987; Moore and Rohwer 2012) and our results show that this signal is honest over time. Begging behaviour may be a finer predictor of nutritional need as evidenced by several previous studies based on food deprivation experiments in nestlings (Budden and Wright 2008; Marques et al. 2009; Villasenor and Drummond 2007), food supply experiments in females (Otter et al. 2007) or by correlating environmental conditions with female condition (Moore and Rohwer 2012). In our study, female begging behaviour continued during at least the first 3 days after hatching. When males visited the nest during female brooding bouts, they were met by female begging which was more intense in handicapped females. As females can then allocate food to themselves or the nestlings, they can adjust self-feeding to their needs. This has only been observed previously in hornbills (Ng et al. 2011) and raptors (Durant et al. 2004; Sonerud et al. 2013). Contrary to our second prediction but in agreement with the results obtained by Matysioková & Remes (2010; Matysioková and Remes 2011) in great tits, *Parus major*, we found that male incubation feeding did not predict female nest attentiveness. Since handicapping increases wing loading and thus the costs of flight (Pennycuik 1982), male incubation feeding may compensate for changes in female energy demand, thereby removing effects on attendance or reproductive success (Moreno et al. 2011). Smith et al. (1989) found that males decreased their rate of incubation feeding when females increased incubation attentiveness as a result of a supplementary food experiment, a result that could be obtained by reduced female begging intensity in the experimental situation and not through direct observation by males of female nest attendance.

Handicapped females did not reduce parental care intensity as shown by nestling provisioning rates on day 9. In most manipulative studies, the main effect of handicaps is a decrease in the experimental birds' nestling provisioning rate (Sanz et al. 2000; Slagsvold and Lifjeld 1988; Slagsvold and Lifjeld 1990) or an increased mass loss (Ardia and Clotfelter 2007; present study; Sanz et al. 2000). To maintain the same provisioning effort and attendance as in control females, handicapped females may forage just enough to adequately feed their chicks but

not enough to sustain their own body condition (Leclaire et al. 2011), in this way bearing the costs of the handicap themselves (Matysioková and Remeš 2011, but see Moreno et al., 1999). The higher declines in mass observed in experimental females may be interpreted as a physiological consequence of reduced foraging efficiency (Winkler and Allen 1995) or as an increase in reproductive costs by reducing long-term physiological condition (Alonso-Álvarez and Tella 2001). Another possible explanation for body mass reduction may be an adaptation to compensate for the higher flight cost imposed by increased wing loading (Moreno 1989; Pennycuik 1982).

Although there were opposing trends in provisioning rates for males and females with respect to treatment, the difference was only significant for males. However, the total provisioning rate by the pair did not differ with respect to treatment which agrees with the lack of differences in nestling size and condition between treatments. The absence of effects of provisioning rates on male condition suggests that our measure of condition may be insufficiently precise to detect them.

To conclude, our study is the first to confirm experimentally a basic assumption of the 'female nutrition' hypothesis, namely that males adjust feeding rates to behavioural displays of need by their mates. Female begging behaviour should be considered a communication system enabling successful reproduction in birds with female uniparental incubation (Galván and Sanz 2011). The ability of females to modify their begging displays may be an important adaptation that allows females to maintain an adequate energetic condition during incubation. Further studies should explore the full information content of this intersexual communication channel.

ACKNOWLEDGMENTS

This study was financed by project CGL2010-19233-C03-02 to J.M. from Spanish MICINN. J.L.-A. and A.C. were supported by FPI and FPU grants from MICINN and MECD, respectively. We thank Dirección General de Desarrollo Rural y Política Forestal for donating the nestboxes and S. Merino, J. Rivero-de Aguilar, A. Díez-

Fernández and E. Pérez-Badás for collaboration in the field. This study is a contribution to the research developed at 'El Ventorrillo' field station.

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