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Sex differences in the rate of food provisioning to nestlings red-breasted flycatchers (*Ficedula parva*)

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Parental care is one of the crucial factors affecting breeding success in birds. The level of parent investment can differ between males and females. We studied the sex-specific nestling-feeding effort by parents of the red-breasted flycatcher. Our study was carried out in the old-growth oak–lime–hornbeam stands in the Białowieża National Park (NE Poland). The frequency of nestling-feeding and relative nestling-feeding effort (number of visits by male or female expressed a percentage of all visits by both sexes at the nest) depended on sex of parents and age of nestlings but not on their number. Both sexes increased their feeding frequency as the nestlings became older. Sex differences in nestling-feeding have been found in a number of biparental-care bird species. There are many hypotheses to explain this phenomenon. In the red-breasted flycatcher, the most likely reason for differences in feeding efforts are differences in roles the parents play at different stages of brood develompent.

Introduction

In general, brood care is a necessity to many bird species because their young are initially incapable of independent life. The young of passerines are altricial (born naked, blind and helpless) and require care and feeding from the adults. The level of parental investment can be related to many factors such as age and number of young (Nur 1984, Blondel *et al*. 1991, Clutton-Brock 1991, Radford 2008), prey availability and territory quality (Barba & Gil-Delgado 1990, Bańbura *et al*. 1994, Naef-Daenzer 2000). One or both parents must bring food to the nestlings until they are ready to leave the nest. In most passerines, usually both parents take care of their young, but the males' and females' efforts may differ. Both similar and different rates of food provisioning by males and females have been observed in many studies (Breitwisch *et al*. 1986, Sasva'ri 1986, Wright & Cuthill 1989, Schadd & Ritchison 1998, Bańbura *et al*. 2001, Hamer *et al*. 2006). There are several factors influencing the intensity of male *versus* female parental effort. For example, sexual conflict, different life history or strategy, timing of breeding and the sex ratio of the offspring (Lessells 1999, Schwagmeyer *et al*. 1999, Champan *et al*. 2003, Houston *et al*. 2005, Wedell *et al*. 2006).

In most altricial bird species, both parents provide food to nestlings. In the red-breasted flycatcher *Ficedula parva*, females and males both take care of their young, but their individual effort is unknown. The red-breasted flycatcher is a small migratory bird species that breeds in forests in Europe and over-winters in the Indian sub-continent (Cramp & Perrins 1993, Mitrus *et al*. 2005). This species occurs mainly in dense deciduous and mixed forests (Mitrus *et al*. 2006). It is a socially monogamous species, but some males (10%) attempt to pair simultaneously with multiple females, although only two cases of polygyny have to date been recorded (Mitrus & Soćko 2005). This species breeds mainly in May and June, in natural tree cavities called "half cavities" (Mitrus & Soćko 2004, Mitrus 2006). In the oak–hornbeam forest stands of Białowieża National Park, the red-breasted flycatcher reaches breeding densities of up to 2 pairs per 10 ha (Wesołowski *et al*. 2002). So far, no detailed information on parental sex differences in the rate of food provisioning to nestlings has been published for this species.

The aim of this study was to investigate possible differences in parental care by males and females of the red-breasted flycatcher.

Study area and methods

The data were collected during three breeding seasons in 2005–2007, in the best preserved and strictly protected area of the Białowieża National Park (52°41´N, 23°52´E, NE Poland), dominated by old-growth oak–lime–hornbeam stands (*Tilio-Carpinetum*; Tomiałojć 1991, Wesołowski *et al*. 2002, 2006). Each year from May until the end of June, we searched for nests of the red-breasted flycatcher in three study plots (total area = 79.5 ha) and along the roads leading to these plots. Most of the nests were located by observing females during nest construction or incubation. Nestling feeding was observed using a telescope (32 × 82, Kowa TSN-821M) or recorded using a concealed digital camera (Sony DCR HC17E). The observations were carried out for 60 min in the morning (6:00–12:00), under good weather conditions, from a distance of about 3 m for the camera or 20 m for the telescope.

The age of the nestlings was estimated based on the date when the first egg had been laid or the hatching date. The date of laying of the first egg in the season was recorded directly or, if not observed, it was calculated based on the assumption that one egg is laid per day. The hatching and fledging dates were the dates when the first nestling hatched and fledged, respectively. For analyses, the nestlings were grupped into three age classes: 0–5-, 6–9-, and 10–14-day olds.

Nestling-feeding frequency (visits per hour) and relative nestling-feeding effort (number of visits by male or female expressed a percentage of all visits by both sexes at the nest) were calculated separately for males and females, and for each nestling age-class.

A Generalized Linear Mixed Model (GLMM) was used to predict changes in the nestling-feeding frequency and relative feeding effort depending on the sex of the parents (dependent variable) and the age and number of nestlings (predictors). Because several samples per nest (from 3 to 4) were recorded, nest was included as a random factor in the models. Statistical analyses were performed using Statistica for Windows ver. 6.0.

Results

We obtained 77 (60 minute) samples (847 feeding visits) at 14 nests of pairs of the red-breasted flycatcher.

The number of feeding trips to broods per hour by adult birds varied from 4 to 32 (mean ± SD = 22.4 ± 11.4). The frequency of feeding depended on age of nestlings ($F_{2,131} = 17.86$, $p < 0.001$) and sex of the parents ($F_{1,131} = 13.15$, $p = 0.001$) but not on number of nestlings ($F_{2,131} = 1.13$, $p = 0.33$). The nest as a random factor had no effect on the frequency of feeding ($F_{13,131} = 1.29$, $p = 0.23$). No interactions between variables were observed. During the first five days of life of the nestlings, the males fed them almost twice as often as did the females (mean ± SD = 10.1 ± 4.10 *vs*. 5.4 ± 3.29 visits/hour, respectively). Both sexes increased their feeding frequency as the nestlings became older (Fig. 1).

The relative male nestling-feeding effort (mean ± SD = 59.0% ± 12.9%) was significantly higher than that of the female (mean ±

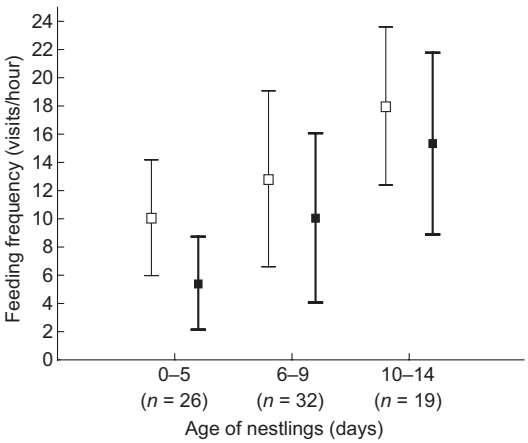

Fig. 1. Mean (± SD) nestling-feeding frequency by males (open squares) and females (filled square) of the red-breasted flycatcher depending on nestlings' age.

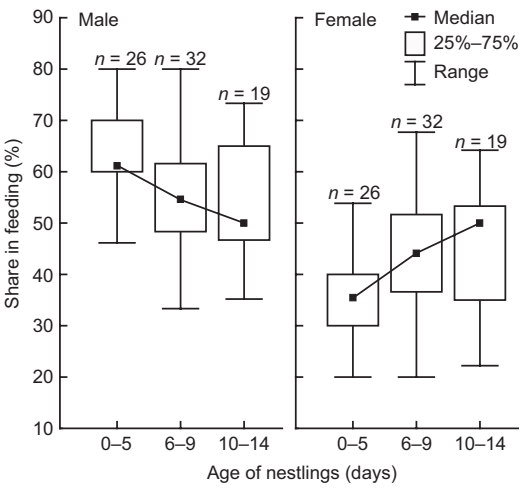

Fig. 2. Nestling-feeding effort by males and females of the red-breasted flycatcher depending on nestlings' age.

SD = 41.0% ± 13.1%) and decreased with their age, whereas the relative female nestling-feeding effort increased with nestling's age (Fig. 2). As in the case of feeding frequency, the relative male and female nestling-feeding efforts depended significantly on nestling's age ($F_{2,60} = 7.80$, $p < 0.001$; and $F_{2,60} = 3.33$, $p = 0.04$, respectively) but not on their number ($F_{2,60} = 0.79$, $p = 0.46$; and $F_{2,60} = 0.08$, $p = 0.93$, respectively). In both males and females, the nest had no effect on the share of feeding ($F_{13,60} = 0.94$, $p = 0.51$; and $F_{13,60} = 1.66$, $p = 0.11$, respectively). No interactions between variables were observed.

Discussion

The age of the nestlings was the most important factor affecting feeding frequency. Both females and males increased significantly their feeding visits with the age of the nestlings. It is probably related to the increasing reproductive value (Clutton-Brock 1991) and to the increasing of energy demands (for growth and thermoregulation) of the offspring. A similar pattern was observed in many other species (Nolan 1978, Johnson & Best 1982, Haggerty 1992, Goodbred & Holmes 1996). The number of nestlings was not the most important factor affecting the feeding rate in the red-breasted flycatcher, although many papers reported that the number of feeding trips increased significantly with number of nestlings (Lazarus & Inglis 1986, Winkler 1987, Montgomerie & Weatherhead 1988). A lack of such relation in our study was probably caused by small differences in the number of offspring among nests: in most cases there were five or six nestlings per nest (C. Mitrus unpubl. data).

Sex differences in nestling-feeding effort have been found in a number of socially monogamous birds with biparental care, but the reasons for that remain unclear. There are many hypotheses to explain this phenomenon. It is well known that investment in parental care reduces the future reproductive success and this fact can be a trigger of a sexual conflict (Clutton-Brock 1991). The conflict over offspring care can lead to a reduction of the parental effort or even desertion of one of the parents (Wedell *et al*. 2006). In many bird species, males can mate with the next female and reduce the parental care in the first brood (Alatalo *et al*. 1984, Birkhead & Moller 1992, Smith & Sandell 1998). Also 10% of male red-breasted flycatchers tried to pair up with a second female, but only one case of polygyny was observed in the studied population (Mitrus & Soćko 2005). The fact that in the same population many males remain unmated (Mitrus 2007) indicates a female-biased sex ratio and a difficulty to obtain a second partner. Although a potential polygyny in red-breasted flycatchers and in many other species was reported, males of these species brought food to nestlings more often than did the females

(Biermann & Sealy 1982, Johnson & Best 1982). These differences can be interpreted in several ways. In the case of the red-breasted flycatchers, advantages to investing into polygyny and extra-pair copulation can be less advantageous than into parental care for one brood. The red-breasted flycatcher is a long-distance migratory species that winters in the Indian subcontinent (Cramp & Perrins 1993). The birds arrive usually in May and breeding season is relatively short. Also breeding densities of this species are very low in the Białowieża Forest (up to 2 pairs per 10 ha; Wesołowski *et al*. 2002) and their territories are relatively large (authors' unpubl. data). Moreover, in the Białowieża Forest, only approximately 50% of males breed each year (authors' unpubl. data), which still further decreases a chance of mating with second females simultaneously. In some species, greater efforts of a male in feeding were usually ascribed to the influence of body size on foraging efficiency (Gonzáles-Solís *et al*. 2000, Weimerskirch & Lys 2000). In fact males of the red-breasted flycatcher have longer wings and are heavier but there is no evidence for differences in type and size of preys between sexes (Cramp & Perrins 1993). In the red-breasted flycatcher, the most likely reason for differences in feeding effort are differences in roles the parents play at stages of brood development. During the first stages of reproduction most of the costs are paid by one partner: only females build nests, incubate eggs, and protect small, naked chicks and keep them warm in the first four–five days of life. Hence a female's concern with food provisioning during this period could be a disadvantage for the nestlings, which results in a male feeding the nestlings. As chicks grow, proportional involment in feeding them becomes nearly equal for both sexes. Also in other species often males invest more in food gathering and females more in covering the young to keep them warm (or to shield them from sun or rain) and protecting them from predators (Clutton-Brock 1991). Olson *et al*. (2008) reported that parental conflict, as indicated by the disparity in care between the male and the female, depends on offspring development and mating opportunities, since in precocial as opposed to altricial species both males and females responded to increased mating opportunities. Theoretical analysis also predicts that each partner should respond to reduction in care by mate by increasing their own effort (Heuston & Davies 1985). It is the result of a negotiation process involving repeated interactions between the male and female (Houston *et al*. 2005).

The decreasing nestling-feeding effort of males' may not necessarily be a reaction to the increasing feeding intensity of females. Both sexes have to invest more in feeding as the chicks grow and before fledging they feed nestlings at almost equal rates.

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