

A case of cooperative breeding in the Black Redstart *Phoenicurus ochruros* – labor division and a pattern of food distribution among nestlings

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Recent increase of studies on birds' mating systems and breeding ecology have resulted in new records of cooperative breeding across the species. The aim of the present study is to report on an event of cooperative breeding in the Black Redstart *Phoenicurus ochruros*. We also analyze the investment of all individuals involved in rising the brood and the pattern of food distribution among nestlings. Three adult birds participated in brood rearing: breeding pair in typical adult plumages and a female-like helper, whose sex was not confirmed. No aggressive encounters were observed among nest attendants. The breeding female and the helper participated equally in provisioning the nestlings while the breeding male fed young occasionally. Nestlings closer to nest entrance were fed significantly more often than nestlings in the second row. This resulted in nestling rotation within the nest. There was strong and significant correlation between the proportion of feedings in the first row and nestling rotation. Interestingly, the rotation was not initiated by the sibs from the back row and no competition for the first row was observed. It seems that the rotation was performed by the first row nestlings as they turned back to defecate after feeding. This move made them relocate to the back row. Such simple mechanism ensured nestlings rotation between front and back row and even distribution of food among nestlings without the need of signaling or competition.

Key words: cooperative breeding, food distribution, Black Redstart *Phoenicurus ochruros*

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1. Introduction

Cooperative breeding involves individuals other than genetic parents assisting in raising offspring (Stacey & Koenig 1990, Emlen 1991). A group that provides care for nestlings consists of breeders and one or few helpers that perform parent-like behaviour toward young that are not genetically their own offspring (Brown 1987). Studies on species with such social system demonstrated that helpers may participate in nest construction, incubation, feeding nestlings and territory defence (Brown 1987,

Stacey & Koenig 1990). Cooperative breeding may originate in delayed dispersal of independent offspring from their natal territories (Cockburn 1998) or strong philopatry resulting in formation of kin flocks (Russel & Hatchwell 2001; Hatchwell et al. 2001a, b). The examples of former strategy come from the Florida Scrub Jay *Aphelocoma coerulescens coerulescens* (Woolfenden & Fitzpatrick 1984) or the Seychelles Warbler *Acrocephalus sechellensis* (Komdeur 1996). Delayed dispersal and reproduction of helpers are explained by environmental constraints. Alternatively, helping may be uncoupled from delayed reproduction in species where helpers join neighbouring breeding relatives after own breeding failure. Such strategy is observed in the Long-tailed Tit *Aegialos caudatus* (Russel 2001) and the European Bee-eater *Merops apiaster* (Lessells et al. 1994). In both scenarios helpers are close relatives of breeders and they gain indirect benefits due to inclusive fitness (Dickinson & Hatchwell 2004). They may also gain some direct benefits in form of experience ('experience' hypothesis; Selander 1964) or access to communal resources ('pay-to-stay' hypothesis; Mulder & Langmore 1993). However, testing direct benefits proved difficult and studies brought mixed results (review by Koenig & Walters 2011). Another model of cooperative breeding involves groups of unrelated individuals that reproduce together. The example of such strategy is the Dunnock *Prunella modularis*, a species in which cooperative polyandry frequently occurs (Davies 1992).

Cooperative breeding was reported for less than 3% of all avian species (Arnold & Owen 1998, Ligon & Burt 2004) and seems relatively rare. Among passerines with biparental care cooperative breeding was described as prevalent in 18.5% of species and sporadic in another 3.7% species (Cockburn 2003). However, it may be underestimated due to limited data on patterns of nestling care with the use of marked individuals (Cockburn 2003). Recent increase of studies on birds' mating systems and breeding ecology (e.g. Gill 2004, Round 2006) have resulted in new records of cooperative breeding across the species. The aim of the present study is to report on the event of cooperative breeding in the Black Redstart *Phoenicurus ochruros*. We also analyze the investment of all individuals involved in rising the brood and the pattern of food distribution among nestlings.

2. Material and methods

The Black Redstart is a small migratory passerine bird nesting in holes and niches of alpine cliffs and rocky slopes (primary breeding habitat) as well as in human settlements (Glutz von Blotzheim & Bauer 1988). Within human settlements, nests are located in walls or roofs. The species is multibrooded and may produce up to three broods per season (Wegglar 2006). Adult birds are sexually dimorphic, however males may exhibit delayed plumage maturation during their first breeding season. As a result, yearling males in spring may be female-like dull grey, whereas older males are black with a white wing-patch (Cramp 1988).

In early April 2010, a micro-camera was placed in a nest-box that was known to be occupied by a Black Redstart pair in previous years. The nest-box was located in a wall of a house in Kielnarowa near Rzeszow (49°56'N, 22°03'E), south-eastern

Poland. We planned to film a Black Redstart brood within a larger project on parent-offspring communication in passerines. The camera was placed about 30 cm above the bottom of the nest-box.

After nestlings hatched the brood was video-recorded for 7 out of 14 days (days 1–6 and day 12th). The nest was recorded from 5 to 14 hours a day. Altogether we recorded and analyzed 52 hours of video. Three adult birds provided care for nestlings: a breeding pair in typical adult plumages and a female-like helper. The latter bird was mist-netted and marked with two white spots on its head, thus identity of all adults was known during recording and observations. We chose marking the bird on its head instead of using a colour ring because we wanted all birds to be identifiable on camera images. We were not able to sex the helper from its plumage definitely. Thus it may have been a female or a 1-year-old male in female-like plumage. Using the films we analyzed the share of each individual in feeding nestlings as well as the patterns of food distribution among nest-mates.

Beside analyses of films, behavior of adult birds was regularly observed and noted.

3. Results

3.1 General description of cooperative breeding in the Black Redstart

At the beginning of breeding season only the breeding couple was present within the territory. A male was typically singing and accompanying a female. On 19 April the female started building a nest which was finished on 25 April. The first of five eggs was laid on 1 May and the remaining eggs were laid in consecutive days. The female started incubation on 5 May and continued until 21 May. The male did not participate in incubation. During the period of incubation a third bird in female-like plumage appeared within the territory. We did not observe any aggressive interactions between the newcomer and any member of the breeding pair. The newcomer neither sang nor presented precopulatory displays towards a breeding male, thus we had no behavioural clues on its sex. On 21 May five nestlings hatched. Similarly to breeding female, the helper started provisioning nestlings. Only the breeding female incubated hatchlings and cleaned the nest. Breeding male appeared at the nest occasionally, however he was present within the territory majority of the time. He also sang in vicinity of the nest. Surprisingly, despite of having a helper, the breeding pair did not re-nest after the first brood fledged.

3.2 Division of labour in cooperatively breeding Black Redstarts

The breeding female and the helper participated equally in provisioning the nestlings ($t = -0.32$, $df = 6$, $p = 0.98$; Fig. 1). Of 1061 of total feedings recorded on a camera 527 were performed by the breeding female and 532 by the helper. The remaining 12 feedings were performed by the breeding male. In nine cases he fed nestlings directly and in remaining three cases he passed food to the breeding female

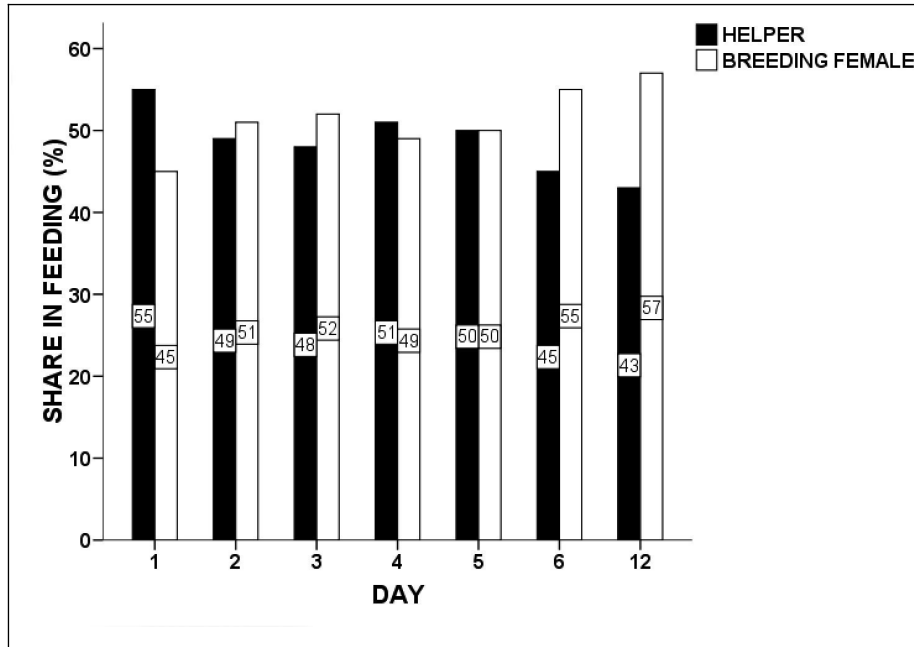


Figure 1. Labor division in feedings between the breeding female and the helper during 7 days of observation. Total amount of feedings delivered during 52 hours = 1059.

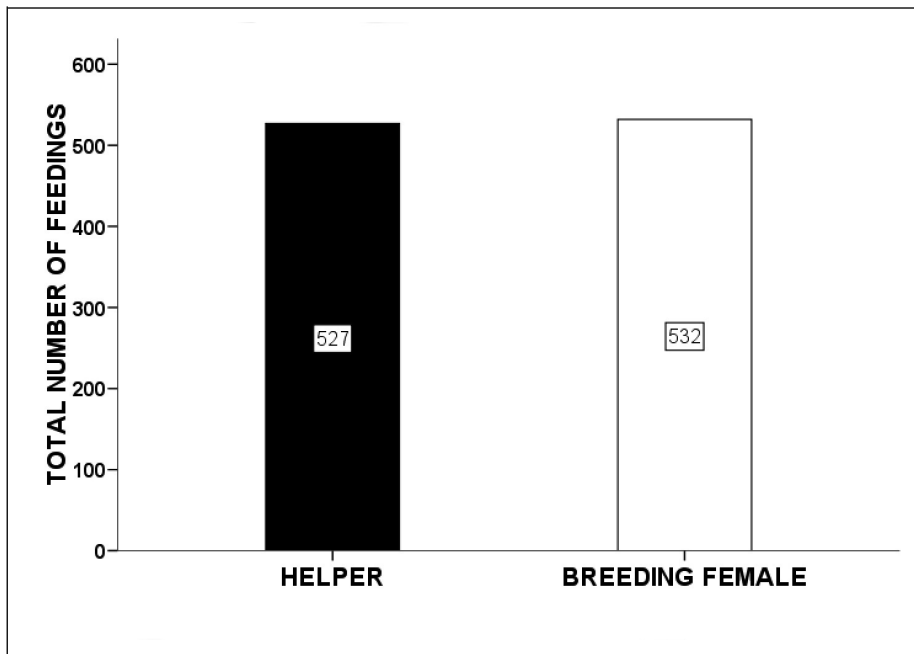


Figure 2. Total share of the breeding female and the helper in feeding nestlings (n = 1059 feedings).

which subsequently fed nestlings. The male appeared at the nest only when his mate was present.

3.3 Pattern of food distribution among nest-mates

Nestlings in the first row (closer to nest entrance) were fed more often (73% of all feedings) than nestlings in the second row (27% of all feedings). The difference in feedings of the first and the second row was highly significant ($t = 3.99$, $p = 0.007$). It shows that nestlings in the first row were fed preferentially. This preference increased in subsequent days of nesting period and the difference between feedings of the first and the second row became more pronounced (Fig. 3). The preference to feed nestlings from the first row was demonstrated both by the breeding female (69% of feedings) and the helper (67% of feedings). There was no significant difference between both individuals in feeding pattern (Mann-Whitney U-test: $U = 21$, $p = 0.71$; Fig. 4).

As the result of presented feeding pattern nestlings rotated from the second row to the first row and the tendency to rotate increased simultaneously with the parental preference of feeding the first row (Fig. 5). There was strong and significant correlation between the proportion of feedings in the first row and nestling rotation

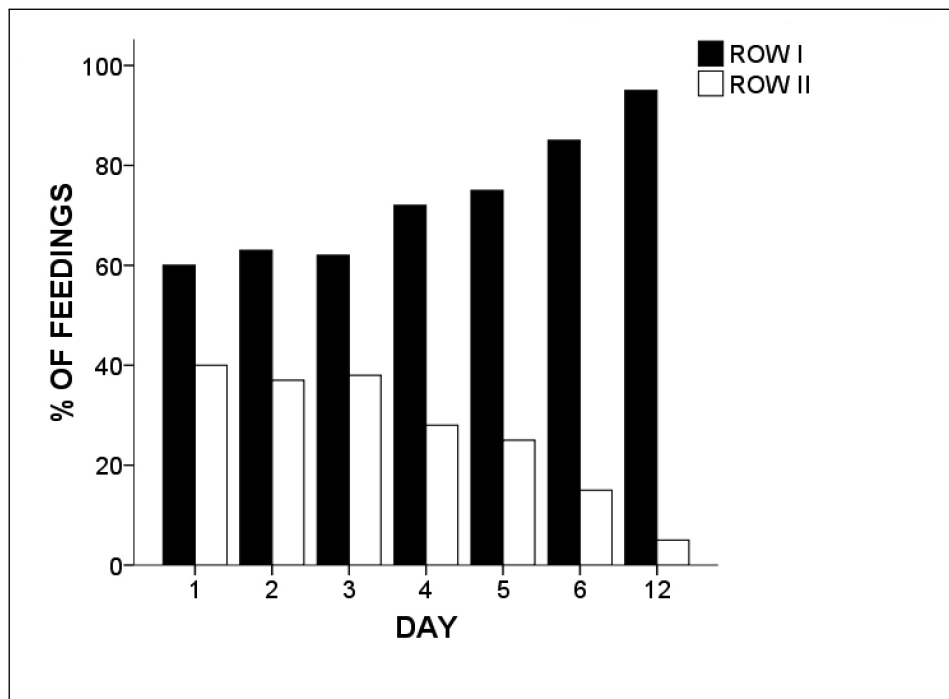


Figure 3. Percentage of feedings delivered to nestlings in a first and a second row in the nest during 7 days of observation (52 hours, 1059 feedings).

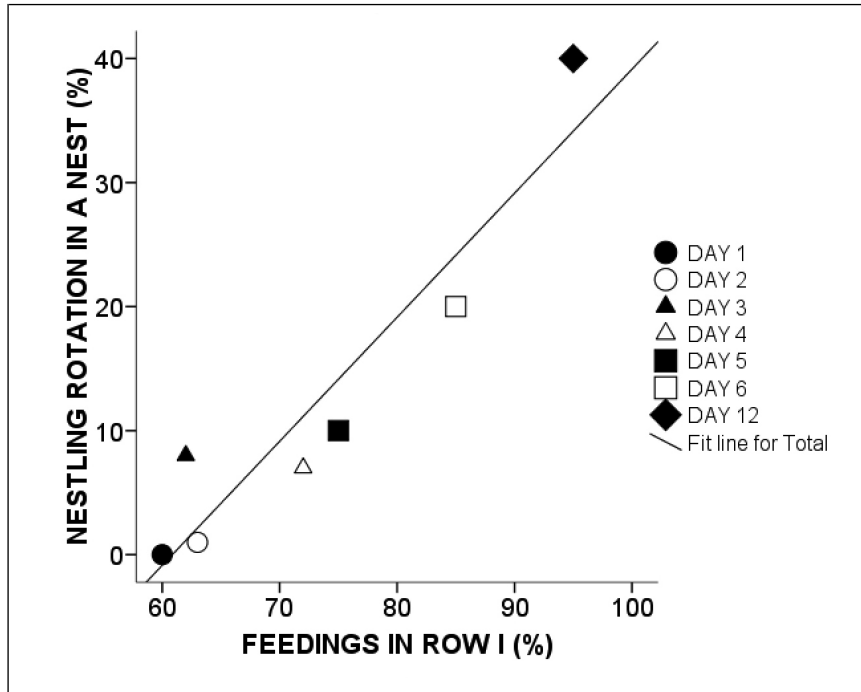


Figure 4. Relation between the proportion of feedings nestlings from the first row and rotation of nestlings between rows ($n = 1059$ feedings).

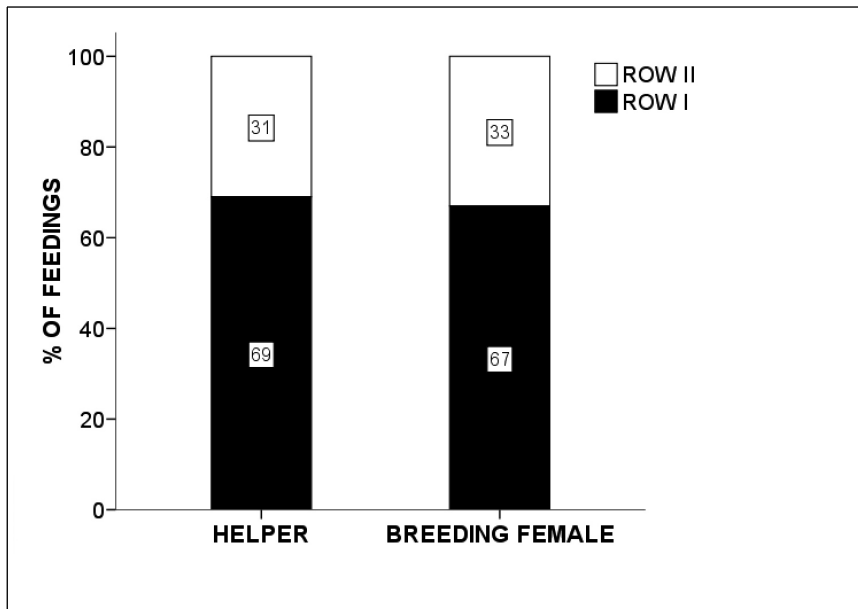


Figure 5. Proportion of feeding nestlings from the first and second row by the breeding female and the helper ($n = 1059$ feedings).

($r = 0.89$, $p = 0.007$). In 2-day-old nestlings rotation followed only 1% of feedings and it intensified in the following days (8% in day three, 7% in day four, 10% in day five, 20% in day six and 44% in day twelve).

4. Discussion

Our study describes a case of cooperative breeding in the Black Redstart and detailed analysis of investment of three nest attendants: breeding male and female and helping individual with female-like plumage. Black Redstarts are well studied in Europe (Cramp 1988; Weggler 2000, 2001, 2006; Draganoiu et al. 2005; Schwarzová et al. 2010) and the species is regarded as socially monogamous (Cramp 1988), however a recent study by Lu et al. (2011) demonstrated that in a Tibetan population of the Black Redstart a considerable number of nests (16.7%) were cooperatively cared for by both parents and one helper. Similarly to our study, all helpers observed in Tibet were in female-like plumage, however one of them proved to be a male. The proper sexing in such cases involves molecular techniques as one-year-old males may closely resemble females. Thus, the sex of the helper observed in our study remains unknown. Some behavioural clues suggest that it may have been a male, for example, during 52 recorded hours the helper never incubated nestlings or cleaned the nest which is a typical female biased behaviour in Black Redstarts (Mu et al. 2008, Lu et al. 2011). On the other hand, no aggressive encounters were recorded between the helper and the breeding male and this seems strange if the helper were a male. Studies on territoriality in Black Redstarts demonstrated that resident males were equally aggressive towards males in both adult and sub-adult (female-like) plumage (Landmann & Kollinsky 1995, Cuadrado 1995). However, in the majority of studied cases cooperative breeding in birds involves closely related individuals (Dickinson & Hatchwell 2004), mostly philopatric sons of a breeding pair (Hatchwell 2009). This may explain the lack of aggression between nest attendants, even though the helper was a male in the studied case. Unfortunately, there is a very few data on the structure of cooperatively breeding groups of the Black Redstart. The only study in which one helper was identified as a male, lacked data on its relatedness to the breeding pair (Lu et al. 2011).

To provide more data on organization of cooperative breeding in the Black Redstart we analyzed in detail labor division of all nest attendants. Contrary to findings of Lu et al. (2011), the breeding male seldom if ever participated in brood provisioning. This however did not result in decreased feeding of the brood, as the breeding male was fully replaced by the helper which fed nestlings at the same rate as the breeding female. It seems that it was the breeding male who took advantage of cooperative breeding at the expense of the helper. High level of commitment of the helper in feeding the brood remains poorly understood and more observations is needed to get the picture of the mechanisms of cooperative breeding in the Black Redstart.

Another finding of this study was that both breeding female and the helper preferred feeding nestlings close to the nest entrance (in the first row) and this tendency increased in consecutive days since nestlings hatched. However, it did not lead to

poorer development of offspring in back row as nestlings rotated in the nest and the level of rotation was proportional to the preference of feeding the nestlings in the front row. Interestingly, the rotation was not initiated by the sibs from the back row and no competition for the first row was observed. It seems that the rotation was performed by the first row nestlings as they turned back to defecate after feeding. This move made them relocate to the back row. Such simple mechanism ensured nestlings rotation between front and back row and even distribution of food among nestlings without the need of signaling or competition. Described pattern seems to be worth of further studies both in the Black Redstart and other species feeding their nestlings from nest entrance.

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