Parental care and brood division in a songbird, the black redstart

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Summary

Sexual conflict over parental care can be mediated through differences in male and female overall feeding rates, brood division or both. At present, it is not clear whether post-fledging brood division occurs due to sexual conflict over parental investment or is due to bi-parental cooperation, e.g. increase offspring fitness. We provide evidence suggesting that brood division in the black redstart, *Phoenicurus ochruros* is due to sexual conflict. Males and females had similar feeding contributions during the nestling stage, which is common for most passerine species. After fledging, each parent showed long-term feeding preferences for particular chicks within the brood. In most cases (74%; 17/23) both parents provided care but males tended to feed less fledglings than females did and in about a quarter of cases (26%; 6/23) females fed the whole brood by themselves. The relative amount of male to female post-fledging feedings showed a significant negative relationship with the proportion of fledglings cared for exclusively by the male. These results suggest (1) a close link between the amount of parental care and brood division; (2) sexual conflict can be mediated through brood division; (3) female redstarts appear to loose this conflict more often than male redstarts, with in the extreme cases males showing post-fledging brood desertion. A literature review shows brood division to occur in at least a dozen of songbird species but male black redstarts have the lowest relative post-fledging parental investment, expressed either as feeding rates or number of chicks in care.

Keywords: black redstart, brood division, parental care, sexual conflict.

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Introduction

In some species of birds parents feed some chicks more than others while in the nest. This may be the consequence of parental preferences, e.g. females preferentially feed smaller nestlings in budgerigars, *Melopsittacus undulatus* (Stamps et al., 1985), pied flycatchers, *Ficedula hypoleuca* (Gottlander, 1987) or tree swallows, *Tachycineta bicolor* (Leonard & Horn, 1996). Alternatively, this may come about due to sibling competition, e.g. larger and older chicks get more food than smaller ones in yellow-headed blackbirds, *Xantocephalus xantocephalus* (Price & Ydenberg, 1995), Arabian babblers, *Turdoides squamiceps* (Ostreiher, 1997) or starlings, *Sturnus vulgaris* (Cotton et al., 1999) or male chicks get more food than female ones (Teather, 1992).

Preferential feeding sometimes continues after fledging. Females preferentially feed smaller chicks in blue tits, *Parus caeruleus* (Slagsvold et al., 1994) and tend to do so in great tits, *Parus major* (Sasvári, 1990) whereas the opposite was found in robins, *Erithacus rubecula* (Harper, 1985) and Savannah sparrows, *Passerculus sandwichensis* (Wheelwright et al., 2003). An extreme case of preferential feeding is brood division, a form of post-fledging care with stable (several days to several weeks) parental feeding preferences for individual chicks within the brood (reviewed in Leedman & Magrath, 2003).

This pattern of care may be due to parental preferences, sibling competition or both. It is yet not clear if brood division represents a form of inter-individual conflict (sexual conflict, parent-offspring conflict or sibling competition) or no conflict at all. Hypotheses trying to account for the existence of brood division can be classified in four categories according to the hypothetical costs and benefits to the interactors (parents and offspring) and the potential conflicts arising. First, brood division may be beneficial to both parents and offspring (no conflict) due to increased offspring feeding rates or lower predation rate of the chicks, at a lower cost to both parents (Smith, 1978). At present, there is no support for this hypothesis (Byle, 1990; Leedman & Magrath, 2003). Leedman & Magrath (2003) proposed a mechanism which may lead to benefits of brood division to both parents and all their offspring, the 'social specialization' hypothesis. This hypothesis states that a close relationship between a parent and particular offspring could be selected for, because individuals knowing each other are better at 'working

together' and all behavioural interactions between a parent and its offspring could become more efficient through learning. Second, brood division may be beneficial to both parents, but not their chicks. For instance, if males take care of more chicks than females during early broods, this might minimize the inter-brood interval and increase future fecundity of both sexes. Supporting evidence for this hypothesis comes from studies with blackbirds, *Turdus merula* (Edwards, 1985), robins (Harper, 1985) and Savannah sparrows (Wheelwright et al., 2003). However, this might mean individual chicks are only fed by single parents, instead of two parents, leading to reduced survival of chicks in divided broods. Third, brood division could arise if one parent pre-emptively deserted part of the brood (sexual conflict). On one hand, parental benefits of reduced post-fledging care have been shown in Savannah sparrows, where both the number of chicks in care and the duration of the post-fledging care affect parental survival (Wheelwright et al., 2003). On the other hand, theoretical work indicates that sexual conflict should select for brood division, and this may be the case even if parents take care of equal numbers of chicks, when the cost of the reproductive effort is not the same for the two parents or if different chicks require different amounts of care (Lessells, 2002). Finally, the 'fledgling choice' or 'sibling rivalry' (Slagsvold, 1997) hypothesis states that sibling competition may lead to brood division if the largest offspring monopolized access to the best feeder, i.e. the male or female parent providing the best care. Evidence favouring this hypothesis has been found in the American robin, *Turdus migratorius*, where the heaviest chick was associated with the best feeder (Weatherhead & McRae, 1990; Slagsvold, 1997) and in the white-browed scrubwren, *Sericornis frontalis*, where there was a tendency in the same direction (Leedman & Magrath, 2003). A study with captive wood partridges, *Rollulus rouloul* (Davison, 1992) also supported this hypothesis: in this species, the most aggressive young were associated with the male, which provides longer care than females. In contrast, the less aggressive young were associated with the female and the least aggressive ones were not fed by either parent at all (Davison, 1992).

We conducted a three-year field study on the black redstart and we aimed, through a correlational approach, to understand what between parental co-operation and sexual conflict is more likely to explain brood division. Black redstarts are known to practice brood division and males have been reported to take care of less fledglings than females (Andersson, 1985). We measured

parental feeding rates of chicks during the nestling and post-fledging phase, and related post-fledging feeding rates to the extent and potential sex-biases in post-fledging brood division (henceforth abbreviated with 'brood division'). If brood division is a form of bi-parental cooperation, we predicted male-biased brood division during the first broods compared to the second broods.

Methods

Study population

We studied a rural migratory population of black redstarts at La Valla sur Rochefort (France-Loire (department 42), 45°45′N, 3°50′E) during three consecutive breeding seasons (2002-2004). Birds arrived from the wintering grounds in March and most breeding pairs were formed by the beginning of April. As a general rule, males and females form stable, monogamous pair-bonds and produced two broods each breeding season. First broods fledged during late May (mean number of chicks per nest when 7 days old was 4.41 ± 0.14 SE, $N = 32$), while second broods fledged around half July (3.87 ± 0.2 SE chicks, $N = 30$). Adults were mistnetted or trapped, colour-banded and released. Chicks were colour-banded in the nest when 7 to 9 days old (banding conducted under authorization of the French Ringing Scheme, held by RM). Therefore, all birds were individually recognizable from their unique colour-bands.

Parental feeding during the nestling stage

We measured male and female feeding rates at nests of 8 pairs (seven broods of 5 nestlings and one brood of 3 nestlings). Nests were monitored during a three-year period (five in 2002, one in 2003 and two in 2004), both during the first (five nests) and the second brood (three nests). Two of the eight males were in their first breeding year, the six others were at least in their second breeding year (black redstarts have a delayed maturation plumage and first year breeders have a female like plumage). Two of the females were of unknown age and the other six had bred at least once before. Male and female feeding visits to each nest were counted separately when chicks were 10-13 days old. These observations were conducted using an Optolyth telescope

TBS 20-60 × 80 and the observers were about 20 m away from nests. Nests were observed during 1 to 4 days (mean ± SE: 3.13 ± 0.4 days, $N = 8$) for 1 to 10 hours in total per nest (mean total duration ± SE: 4.69 ± 1.11 hours, $N = 8$).

Parental feeding during the fledging stage

Feeding events were observed using the same optical material as before; observers were 10-30 meters away from birds. Chicks fledged when 15-18 days old (mean ± SE: 16 ± 0.2 days, $N = 23$). One to two hour observation periods per day were performed for 23 nests (mean brood size was 4.09 ± 0.17 SE, range 3-5) over a span of 3-12 days (average span ± SE: 7.6 ± 0.5 days). Each pair was observed on average during 6.5 ± 0.5 different days (mean ± SE, range 3-10), for an average duration of 780 ± 101 minutes (± SE, range 185-1785) and a mean of 190 ± 23 feedings per family were recorded (± SE, range 41-510, $N = 23$). All observations were performed during the first 12 days after fledging but were finished by day four or five for 5 out of the 23 nests due to predation.

Unfortunately, not all observations could be used to calculate male and female feeding rates, either because not all chicks could be observed, or because feedings could not be attributed to a particular chick ('incomplete observations'). Consequently, we used a sub-sample of the observations with complete information ('complete observations') to calculate feeding rates. These data came from 14 nests observed during days 2 to 6 after fledging, with fledging day set as day 1 (mean observation periods of 222 ± 30 min for males and 166 ± 21 min for females and a total number of observed feedings which is 42 ± 9 for males and 48 ± 9 for females, ± SE throughout). Subsequently, we compared the male and female feeding rates determined during the incomplete observations to the same values obtained during the complete observations per nest. It appeared that the incomplete observations underestimated male and female feeding rates by an average factor of 2.13 and 1.98 respectively, the differences between the males and females being non-significant and showing no biases. Therefore, all observations of all nests were used to assess the relative parental feeding rate, i.e. the difference between female and male feeding rates.

Assessment of post-fledging brood division

Two criteria must be met in order to classify a brood as divided. First, each of the two parents has to feed at least one fledgling more than expected (Kopachena & Falls, 1991). Separate chi-square tests per parent per brood on the parental feeding frequency per fledgling were used to assess if a parent had one or more favourite fledglings within a brood (so called 'in-chicks'). Second, each parent has to feed at least one young more than the other parent (Harper, 1985; Leedman & Magrath, 2003). Separate binomial two-tailed tests per brood and per fledgling, comparing male to female feedings to this chick, were used to determine whether individual fledglings were preferentially fed by one parent (Siegel & Castellan, 1988). If both criteria were met the brood was defined as divided, and the number of male and female in-chicks were used for further analyses.

We determined the sex for a sample of 19 chicks. For a total of 15 birds coming from 4 broods of the 2004 season, sex was determined through chromosomal sexing using feathers from 7 to 9 day old chicks (Labofarm, France). The remaining four chicks were philopatric birds and were sexed when one year old using behavioural criteria (singing or brooding).

Results

Feeding rates: nestling versus fledging periods

No significant difference was found between the total male and total female nestling feeding rates (means per hour $\pm$ SE: males, 9.55 ± 1.08 feedings; females, 10.11 ± 0.99 feedings; t-test, $t_{14} = 0.38$, $p = 0.71$, Figure 1). Males provided on average 48.6% of the feedings to their nestlings ($N = 8$ nests, range 25.6-61.2%). In contrast to the nestling period, during the post-fledging period males fed their chicks significantly less than their mates (means $\pm$ SE of the total feeding rates per hour: males, 11.03 ± 0.96 feedings; females, 16.24 ± 1.44 feedings; t-test, $t_{26} = 2.14$, $p = 0.04$, Figure 1).

Patterns of post-fledging care

Eighty of the 95 fledglings were preferentially fed by one parent whereas 15 of them were equally fed by both parents (Figure 2, Table 1). Among the 80 chicks that had a primary carer, 56 were preferentially fed by the
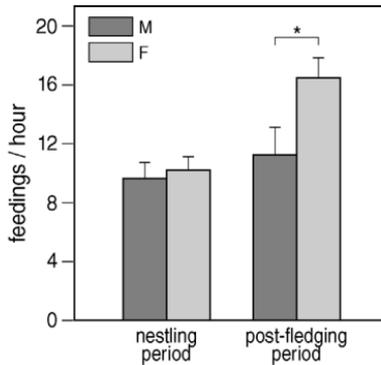
Figure 1. Total feeding rates for males (M) and females (F) during the nestling period (days 10-13, $N = 8$ nests) and during the post-fledging period (days 2 to 6 after fledging, $N = 14$ broods). Depicted are means $\pm$ SE (* indicates $p < 0.05$; *t*-test, see text for statistics).
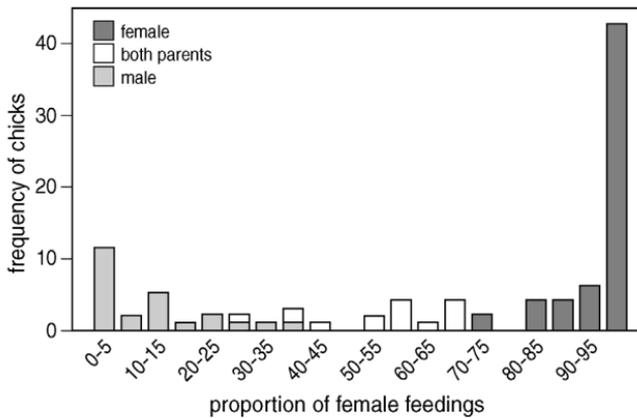
Figure 2. Proportion of female feedings (female feedings/total feedings) per chick ($N = 95$ chicks from 23 broods). Most chicks were preferentially fed by one parent: dark grey bars show chicks preferentially fed by the female (female in-chicks, binomial tests, all $p < 0.05$) and light grey bars show chicks preferentially fed by the males (male in-chicks, binomial tests, all $p < 0.05$). White bars show chicks equally fed by both parents (binomial tests, non-significant).

females, receiving 70.3-100% of the feedings from their female parent and only 24 were preferentially fed by the males, receiving 64.7-100% of the feedings from the male parent (Figure 2). On average, females fed significantly more individual chicks than their mates (Wilcoxon's test, $z = 2.9$, $p = 0.004$, $N = 95$). Most parents (39 out of 46) provided unequal numbers of feedings to their different fledglings and consequently they had one or

Table 1. Number of fledglings cared for by the male, female, or both, depending on brood size and whether post-fledging brood division occurred (yes) or not (no).

Brood division	Caring parent	Brood size (N = number of nests)			Total number of chicks (N = 95)
		3 (N = 6)	4 (N = 8)	5 (N = 9)	
Yes	Male	7	8	9	24
	Female	7	11	18	36
	Both	1	1	8	10
No	Male	0	0	0	0
	Female	3	10	7	20
	Both	0	2	3	5

A Hierarchical Loglinear model with backward elimination of non-significant terms from the fully saturated model brood division (yes or no) * brood number (1st or 2nd brood) * caring parent (male or female) * brood size (3, 4 or 5) * in-chick (female, male or both) * male age (1st or more than 1st year breeder) showed significant interaction effects between brood division * brood number * brood size (Likelihood Ratio LR $\chi^2 = 21.2$, $p < 0.0001$); brood division * in-chick (LR $\chi^2 = 17.4$, $p = 0.0002$); and brood size * male age (LR $\chi^2 = 61.8$, $p < 0.0001$).

more 'favourite' chicks within a brood (Figure 3). Typically, the males had one or two in-chicks, whereas females had up to four in-chicks (Figure 3).

We recorded two different patterns of post-fledging care (Table 1). First, most broods (74%; 17/23) were divided, with each parent taking care preferentially of at least one chick within one particular brood and a few chicks that were fed by both parents (henceforth called 'brood division' nests). Within divided broods, females tended to care for a higher proportion of chicks than did males (Wilcoxon's test, $z = 1.72$, $p = 0.09$, $N = 70$). Second, in the remaining 6 of the 23 broods (26%) all chicks were fed by the females whereas males provided no help at all or only occasionally fed one chick (henceforth called 'no brood division' nests). A Hierarchical loglinear model (see Table 1) showed that (1) brood division was less likely to occur in first broods, with females progressively taking a larger number of in-chicks in larger broods; (2) without brood division females have more in-chicks than males; (3) older males cared for larger broods.

Neither males nor females showed a preference for chicks of a particular sex: 7 fledglings were fed by parents of the same sex and 12 others were fed by parents of the opposite sex.
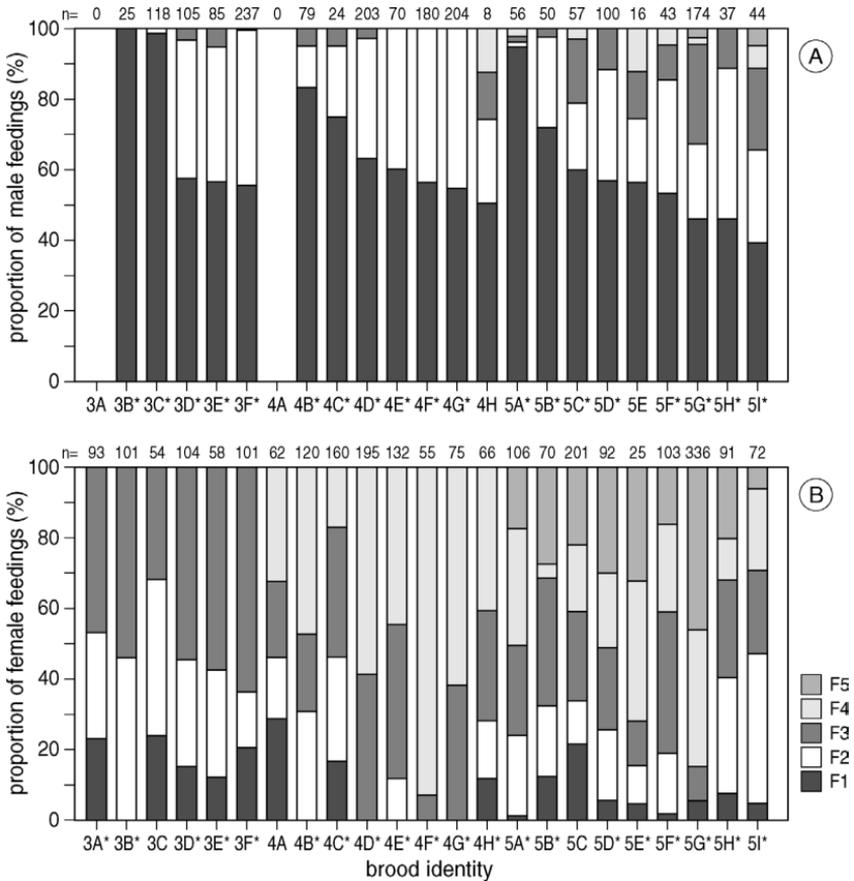
Figure 3. Proportion of male (A) and female (B) feedings to each fledgling (F1-F5) of the 23 studied broods (6 broods of 3 chicks: 3A-3F; 8 broods of 4 chicks: 4A-4H; and 9 broods of 5 chicks: 5A-5I) during the first ten days after fledging. Most parents provided unequal numbers of feedings to their fledglings (χ^2 tests (*), all $p < 0.05$; N = total number of feedings recorded for one parent). Different colours represent different fledglings in an arbitrary order.

### Feeding rates versus number of fledglings in care

The parental feeding rates after fledging were analysed in relation to parental sex (male or female), type of brood (brood division or no brood division) and brood size (Figure 4, $N = 22$ broods). A repeated measures ANOVA on these feeding rates (male and female feedings as repeated measures) showed no overall effect of sex ($F_{1,19} = 0.49$, $p = 0.49$), type of brood ($F_{1,19} = 0.28$, $p = 0.6$) and brood size ($F_{1,19} = 2.15$, $p = 0.16$), but strong effects of two
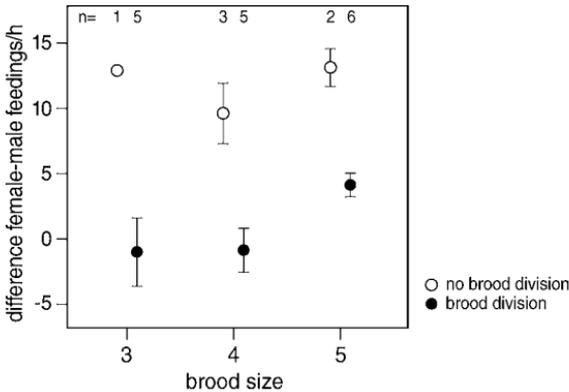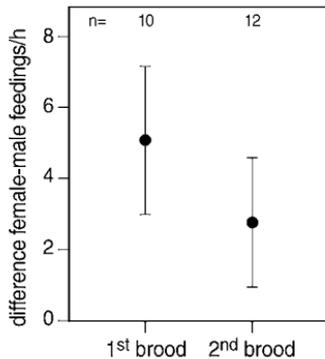
Figure 4. The difference in female to male post-fledging total feeding rates to the brood, in relation to brood size and whether brood division occurred or not. *N* denotes sample size.

interactions between these main effects. The first significant interaction was between the parental sex and whether brood division occurred or not ($F_{1,19} = 28.7$, $p < 0.001$). When the brood was divided parents had comparable feeding rates whereas if not divided, females had significantly higher feeding rates than males (Figure 4). The second significant interaction was between the parental sex and brood size ($F_{1,19} = 4.47$, $p = 0.05$). In small and medium broods (3 and 4 chicks) males and females had similar feeding rates, whereas in large broods (5 chicks) females showed a higher relative investment than males (Figure 4).

A higher relative feeding effort of females was accompanied by a greater proportion of chicks preferentially fed by the female parent (Figure 5a, Pearson $r = 0.63$, $p = 0.002$, $N = 22$) and a smaller proportion of chicks preferentially fed by the male parent (Figure 5b, Pearson $r = 0.75$, $p < 0.001$, $N = 22$). Finally, there was no significant difference in the relative parental effort comparing the first with the second broods (Figure 6, $N = 22$, ANOVA: $F_{1,20} = 0.71$, $p = 0.41$). Contrary to the hypothesis of bi-parental cooperation, (1) females rather tended to feed their fledglings more than their mates during the first broods (Figure 6), and (2) brood division was not significantly more likely, and, if anything, was less likely to occur in first broods (7 divided of 11 broods, 64%) than in second broods (10 divided of 12 broods, 83%, $\chi^2 = 1.2$, df $= 1$, $p = 0.28$), meaning that females were more often almost the sole care giver in first broods than in second broods.
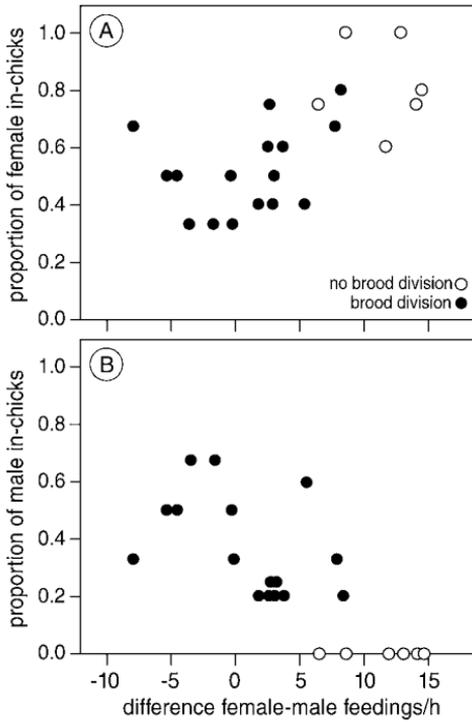
Figure 5. The proportion of chicks exclusively cared for by (a) the female and (b) the male (in-chicks) in relation to the difference in female to male total feeding rates to the brood. Black symbols denote broods where brood division occurred ($N = 16$) and white symbols denote broods where no brood division occurred ($N = 6$). For statistics see text.

Figure 6. The difference in female to male post-fledging feeding rates to the brood, for first and second brood separately.
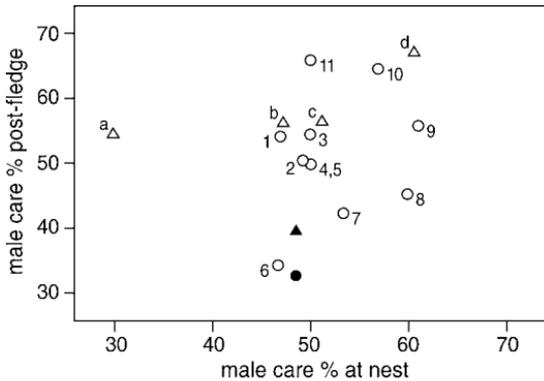
Figure 7. The relationship between male relative feeding effort during the nestling versus post-fledging period. Triangles indicate studies where post-fledging feeding rates were available whereas circles represent studies where the relative feeding effort is expressed in number of chicks preferentially fed by one parent. Filled symbols indicate black redstart values (our study) whereas open symbols correspond to other studied species: [a]*Passerculus sandwichensis* (Freeman-Gallant, 1998; Wheelwright et al., 2003), [b]*Mimus polyglottos* (Breitwisch et al., 1986; Zaias & Breitwisch, 1989), [c]*Parus major* (Sasvári, 1986, 1990), [d]*Erithacus rubecula* (East, 1981; Harper, 1985), [1]*Turdus migratorius* (Weatherhead & McRae, 1990), [2]*Melospiza melodia* (Smith, 1978; Smith & Merkt, 1980), [3]*Turdus merula* (Edwards, 1985; Snow, 1988), [4]*Prunella modularis* (Byle, 1990; Hatchwell & Davies, 1990), [5]*Oenanthe oenanthe* (Moreno, 1984, 1987), [6]*Luscinia svecica* (Anthonisen et al., 1997; Smiseth & Amundsen, 2000), [7]*Calcarius lapponicus* (McLaughlin & Montgomerie, 1985; Lyon et al., 1987), [8]*Zonotrichia albicollis* (Whillans & Falls, 1990; Kopachena & Falls, 1991), [9]*Wilsonia citrina* (Evans Ogden & Stutchbury, 1997), [10]*Sericornis frontalis* (Magrath & Yezerinac, 1997; Leedman & Magrath, 2003), [11]*Geospiza fortis* (Price & Gibbs, 1987; Grant, comm. pers.). Data come from brood division studies except for *Parus major* (c) and *Mimus polyglottos* (b) – where brood division occurred only occasionally.

Interspecific comparison

We have shown that male black redstarts provide about equal parental care to their broods as females do during the nestling phase, but less so during the post-fledging phase. For fifteen species, most of them practicing brood division as redstarts do, we collected data from the literature on the relative male to female feeding effort before and after fledging. When compared to other species, black redstart males have the lowest value of relative investment during the post fledging period: 33% when considering the number of chicks fed preferentially and 40% when considering the feeding rates (Figure 7). There was no correlation between the pre- and post-fledging relative feeding rates comparing across species (Pearson $r = 0.19$, $p = 0.49$, $N = 16$). This

result did not change when the outlying value for *Passerculus sandwichensis* was excluded from the analysis (Pearson $r = 0.36$, $p = 0.19$, $N = 15$).

Discussion

Our study shows that in black redstarts parental investment is equivalent for both sexes during the nestling period but that after fledging males have significantly lower feeding rates than females. We found two patterns of post-fledging care: either each parent will provide preferential care to particular chicks within the brood (brood division) or the female will take care of all the fledglings, with the male providing no help or occasionally feeding one chick. Similar results during feeding of nestlings have been reported for an Italian population of black redstarts (Cucco & Malacarne, 1997). Concerning the post-fledging investment, a lower male contribution was also found in a Swedish population, where in five cases of brood division the male took care of only one of the three or four fledglings (Andersson, 1985). Thus, males deserting part or the whole brood after fledging, despite an equal investment during the nestling stage, could be a general pattern of care in black redstarts.

Importance of male care during the nestling stage

One may ask why males do not desert broods during the nestling period? Male removal experiments in birds have shown that male's absence generally causes a decrease in hatchling survival or condition (Bart & Tornes, 1989) and sometimes leads to complete breeding failure (Dunn & Hannon, 1989). This could explain why similar contributions of males and females in feeding nestlings is a common pattern among monogamous songbirds (Schwagmeyer et al., 1999), including black redstarts. The importance of male care in redstarts is emphasized by a supplementary feeding experiment. It has been shown that supplemental food triggers a significant decrease in males' feeding rates but an opposite trend in females, leading to a similar combined feeding rate as in control couples (Cucco & Malacarne, 1997). In that study, males and females of control couples had equal feeding rates and this was also the case with our birds. These results suggest that equivalent investment during the nestling period could be valuable during normal conditions. It

has also been shown that feeding and brooding are competing parental behaviours (Whillans & Falls, 1990; Wolf et al., 1990). Female black redstarts intensively brood their chicks during the first week after hatching (Cramp, 1988) and this behaviour may be paramount to chick survival, given the low temperatures at our high altitude study site (850 m). In turn, this means females have less time to feed their chicks and consequently, a high relative male investment during the nestling stage may be invaluable to ensure chicks receive enough food to grow and survive until fledging.

Post-fledging care: evidence for sexual conflict?

Our correlative data do not enable us to test directly the four different hypotheses on why and to whose benefit brood division occurs. Nevertheless, our results are consistent with brood division occurring due to sexual conflict. First, brood division and the relative feeding rates of males and females were closely related, i.e. the parent with the highest feeding rate also cared exclusively for the highest proportion of fledglings in the broods. In a sense, sex-biases in feeding rates and sex-biases in brood division go hand-in-hand. This leads to partial brood desertion in the less extreme cases, or complete brood desertion in the most extreme cases. Second, brood division occurred equally often in first and second broods and the relative male feeding rates were higher during second broods. These results cannot be explained by the hypothesis that brood division occurs as a way to increase the fitness of both parents. Redstarts in our population remained paired for the whole breeding season and generally produced a second clutch. In that case, we predicted (1) more male-biased brood division occurring during first broods with (2) male-biased feeding rates during the first broods, e.g. to increase the likelihood of the females producing a second clutch, to decrease the within-brood interval or increase the clutch size of the second brood. Third, male relative investment was lowest in the largest broods. This result cannot be explained if males and females cooperate to increase the fitness of their brood. However, it can be accommodated by the sexual conflict hypothesis, since brood division and overall male and female feeding rates were closely linked.

The fact that a higher female relative investment is associated with both a greater number of chicks in female's care and fewer chicks in male's care suggests female redstarts usually lose this sexual conflict. Apparently, males are more likely to reduce their overall feeding rate and desert part or whole of

the brood in the post-fledging period. In turn, females appear to compensate for this reduction in male care by increasing their feeding rate and taking care of more fledglings than males do.

In addition, we found that parents do not show feeding preferences for chicks of a particular sex. This strenghtens previous findings from four other species for which robust samples of sexed chicks were presented: medium ground finches, *Geospiza fortis* (Price & Gibbs, 1987), hooded warblers, *Wilsonia citrina* (Evans Ogden & Stutchbury, 1997), Savannah sparrows (Wheelwright et al., 2003) and white-browed scrubwrens (Leedman & Magrath, 2003). In none of these species do parents divide their broods according to the sex of the chicks. The only indication that parents base their feeding preferences on the sex of the chicks comes from robins were all but one of seven chicks were fed by an opposite-sex parent (Harper, 1985), albeit the sample sizes were low.

Unusual reduced male care after fledging: possible benefits and costs

There have been numerous studies in birds on male and female parental investment during incubation and nestling feeding, but unfortunately less effort has been made in determining parental investment in the post-fledging period (Bart & Tornes, 1989). Most studies on parental investment after fledging have been made on species practicing brood division (for a review see Leedman & Magrath, 2003), with some exceptions such as northern mockingbirds, *Mimus polyglottos* (Zaias & Breitwisch, 1989) or great tits (Sasvári, 1990). For species where both nestling and post-fledging stages were studied, males and females were shown to provide an overall equivalent feeding effort to their chicks and sometimes males provide more care than females during the post-fledging stage. In this context, the black redstart is an exception: even if males participate equally during the nestling stage they provide less care than females once chicks fledge. The only other species presenting a similar pattern is the bluethroat (*Luscinia svecica*). However, in this case the relative effort was expressed in the number of fledglings in the care of each parent and a considerable number of fledglings could not be observed: when considering only the nests where all young were observed there was no significant difference between the numbers of chicks fed by males and females respectively (Anthonisen et al., 1997).

Why do male black redstarts show a lower relative investment compared to males of other related species? Redstarts are strictly territorial during the

breeding season and have a consistent singing activity before and during the breeding season but also in autumn (Weggler, 2000). Moreover, some birds are also territorial in winter (Cuadrado, 1995). One possibility is that highly territorial behaviour could be associated with a prolonged high testosterone level, which is known to interfere with paternal care (Wingfield et al., 1990; Beletsky et al., 1995).

By reducing their relative investment once the chicks leave nests, males will have more time for other activities. For example, males black redstarts that decreased their feeding rate in response to supplemental feeding spent more time singing and were out of view twice as much compared to control birds (Cucco & Malacarne, 1997). Prospecting adjacent territories could be of great importance for males, especially between the two breeding seasons. First, birds can obtain information about breeding success of other couples and indirectly about the quality of neighbouring territories (Doligez et al., 2002, 2004). Second, males can also check the mating status of neighbouring females. In our study we observed two cases when a male took advantage of the disappearance of a neighbour between the two breeding seasons, taking over his territory and female. For birds that occupy low quality territories prospecting should also be useful at the end of the second breeding season: males can take advantage of a missing neighbour and acquire a better territory. This may be of particular importance in black redstarts, because males defend territories in autumn which may be used for breeding in the next spring (Weggler, 2000). Moreover, it has been shown that in one songbird species the amount of post-fledging care affects parental survival (Wheelwright et al., 2003), thus reduced male care could represent a direct benefit, but this argument should apply to all species practicing brood division.

It seems obvious that males can take advantage from reduced parental care but is there also an associated cost? We have seen earlier that the absence of male care during the nestling stage often affects fledging success or chicks condition at fledging (Bart & Tornes, 1989). However, less is known about the importance of post-fledging male care in maximizing reproductive success. In great tits more fledglings remained unfed when one parent was removed (Sasvári, 1990) and in dark-eyed juncos, *Junco hyemalis*, male removal was associated with a lower survival of fledglings to independence (Wolf et al., 1988) but in this experiment males were removed since eggs hatched and it is not clear if lower post-fledging survival is due to the absence of male care during the nestling period, post-fledging period or both.

However, even if male black redstarts provide less care than females concerning feeding events they do not desert their territories and they might have an active role of defence against predators (alarm calling behaviour). For example, we observed that even if a male will exclusively feed its in-chicks in a divided brood, he will alarm in response to the approach of a potential predator both for fed and unfed young. We suggest that a late (post-fledging) decrease in relative male feeding investment, which is not associated with territory desertion, may be a strategy enabling males to prospect for additional mating opportunities and possibly to increase their survival chances to the next season without compromising the reproductive success of the current breeding attempt too much.

An interspecific comparison of 16 songbird species showed that the levels of relative parental care during the nestling and post-fledging period were not closely linked. The absence of a correlation may be explained by a greater importance of biparental care while chicks are in the nest. In fifteen out of sixteen considered species, males provided almost half or more (range 47-61%) of the feedings during the nestling period; this is consistent with data presented earlier, emphasizing the importance of male care at nest. After fledging there is a greater variability of the extent of male care (33-67%). A high male relative investment should enable females to more quickly initiate new breeding cycles (robins, multi-brooded white-browed scrubwrebs) and subsequently increase reproductive success of both sexes. Alternatively, a low post-fledging investment (redstart example, this study) could also benefit males by possibly increasing survival chances or allowing them to prospect for new mating opportunities.

Our approach is correlational and we acknowledge the need of experimental studies in order to understand the relationships between the relative parental investment during nestling, after fledging and the occurrence and timing of brood division. This study raises several questions that could be addressed by such experiments. First, are relative male to female feeding rates always correlated with the number of chicks in each parent's care, as found in our study species, and why is this the case? Second, are decisions and conflicts about parental investment mediated by brood division, as evidence in this study suggests? Third, what are the costs and benefits of post-fledging care to the parents and the offspring, and how are these affected by brood division?

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