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In a songbird, the black redstart, parents use acoustic cues to discriminate between their different fledglings

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Several studies on parental investment in territorial songbirds have reported the existence of brood division. This is a type of postfledging care in which each parent has long-term feeding preferences for different young within a brood, creating two family units. Recent theoretical work indicates that conflicts between individuals should select for brood division. However, little is known about the mechanisms involved in the onset and maintenance of this behavioural strategy. Given the high rate of fledglings' begging calls, we hypothesized that acoustic discrimination could explain the stability of feeding preferences at a proximate level. In a 3-year field study, we recorded the responses of parent black redstarts, *Phoenicurus ochruros*, a territorial songbird, to playback of the begging calls of fledglings fed by the male and by the female. Parents responded more to the calls of the fledglings that they preferentially fed. A principal component analysis of the calls suggested that parents may recognize individual offspring. To our knowledge, this study provides the first evidence that a bird can acoustically discriminate between two categories of its own offspring: those that it preferentially feeds and those fed by the other parent.

Individual acoustic recognition in vertebrates, and especially in birds, has been intensively studied during the last three decades (Falls 1982; Beecher 1990; Halpin 1991; Lambrechts & Dhondt 1995; Aubin & Jouventin 2002). Work carried out mostly in the field has revealed the existence of neighbour–stranger recognition in territorial songbirds (Stoddard 1996), mate recognition in monogamous birds (Lind et al. 1996; O'Loghlen & Beecher 1999), sibling recognition (Wanker et al. 1998) and parent–offspring recognition (Beecher 1990). However, evidence that parents discriminate between their offspring is lacking (Lambrechts & Dhondt 1995).

Comparative studies have shown that parent–offspring recognition is better developed in colonial than in noncolonial species, suggesting that coloniality is a strong selection pressure for the distinctiveness of calls (Beecher 1990). Nevertheless, other factors may lead to the recognition of offspring within noncolonial species. One example is brood division, a strategy of parental investment characterized by parents' long-term feeding preferences for specific young within the brood during the postfledging stage. Preferentially fed young are defined as that parent's 'in-chicks' while unfed young are that parent's 'out-chicks' (Harper 1985); a parent and its in-chicks form a family unit (Nolan 1978). Brood division was first described by Nolan (1978) for prairie warblers, *Dendroica discolor*, and since then its existence has been reported for a dozen songbird species (reviewed in Leedman & Magrath 2003).

Most studies dealing with brood division have focused on the possible benefits of this behaviour and have proposed hypotheses attempting to explain its emergence. Theoretical work indicates that conflicts between individuals should select for brood division. For example, sexual conflict can lead to brood division if one of the sexes preemptively abandons part of the brood (Lessells 2002). Parent–offspring conflict may also lead to brood division, as parents can try to limit competition between different young in the brood, and restrict feeding to particular offspring (Slagsvold 1997; Lessells 2002). Recent empirical evidence provides some support for these models (Leedman & Magrath 2003).

Less is known about the mechanisms involved in the onset and maintenance of this behavioural strategy. In several species practising brood division, there is a spatial separation between the two family units (Anthonisen et al. 1997), so this feeding pattern could be explained

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by parents' use of different locations. Nevertheless, brood division sometimes occurs despite the absence of spatial separation (Weatherhead & McRae 1990; Leedman & Magrath 2003). Consequently, individual recognition could be helpful in maintaining long-term feeding preferences for particular young. Only one study has tried to distinguish between these two explanations (Kopachena & Falls 1991) and its findings suggested that only some parents can discriminate between their young. To conclude, clear-cut experimental evidence of individual recognition of offspring is still lacking and there is no evidence for the sensory basis of this possible recognition.

Given that family units are stable over periods of several days (Harper 1985; Byle 1990) and for up to 5 weeks (Leedman & Magrath 2003), we hypothesized that parents should be able to discriminate between the fledglings they feed and those they do not feed. Furthermore, because young are still dependent on their parents once they fledge and they beg intensely during the period of dependency, we predicted the existence of an acoustic basis for this recognition process. To test these hypotheses, we studied the black redstart, *Phoenicurus ochruros*, a small (16 g) territorial songbird. Brood division has been described for this species in a Swedish population (Andersson 1985) and documented by us in our French one (Draganoiu et al. 2005). A high density of breeding birds, which were easy to observe during the postfledging stage, was another reason to choose black redstarts as a model species for this study.

METHODS

Study Population

We studied a rural migratory population of black redstarts at La Valla sur Rochefort, France (45°45′N, 3°50′E) during three consecutive breeding seasons (2002–2004). The redstarts return from migration in March and most breeding pairs are established by the beginning of April; mate fidelity is the general rule for the two breeding attempts of the year. First broods fledge during late May and second ones fledge around mid-July. Adults were mist netted or trapped and chicks were banded while in the nest, when 7–9 days old, with authorization of the French Ringing Scheme (held by R.M.). All birds were colour banded, enabling individual identification.

Brood division is an optional trait in black redstarts (Andersson 1985; Draganoiu et al. 2005), a situation similar to that in other songbirds such as dunnocks, *Prunella modularis* (Byle 1990), and European robins, *Erithacus rubecula* (Harper 1985). Tests were carried out for 10 families that practised a clear and stable brood division (17 individuals; three birds were tested twice, during two breeding seasons). Mean brood size at fledging for the studied pairs ± SE was 4 ± 0.3 (range 3–5). Observations were made during days 1–12 postfledging and total association time between a parent and an in-chick was 3–12 days. Brood division is generally established 2–3 days after fledging and parents were tested after at least a 3-day period (including the test day) during which they were preferentially feeding a particular fledgling.

For a brood to be classified as divided, each of the two parents has to feed at least one young more than it would if it were feeding all siblings equally (Kopachena & Falls 1991) and more than the other parent (Harper 1985; Leedman & Magrath 2003). We present data for only two chicks in each family studied (preferentially fed by different parents), and we used the begging calls of these young for playback tests. Binomial two-tailed tests (Siegel & Castellan 1988) were used to assess both parent's preference for a particular fledgling versus its sibling and a fledgling's preferential association with one parent rather than the other.

Recording Design

Young fledge when 15–17 days old ($X \pm SE = 15.9 \pm 0.2$, $N = 27$ broods). Begging calls were recorded when they were 15–22 days old (1–8 days after fledging, with fledging day = 1) and tests were carried out when young were 17–23 days old (3–9 days postfledging). The begging calls used were recorded 0–2 days before the tests (we used a 3-day-old call only once). Fledglings' begging calls were recorded with a Telinga Pro4B (frequency range 40 Hz–18 kHz) microphone mounted on a parabola and connected to a Tascam DA-P1 digital audiotape recorder (frequency responses 20 Hz–20 kHz ± 0.5 dB). Recordings were digitized with 16-bit accuracy at a sampling rate of 22 050 Hz using Avisoft-SASLabPro version 4.1c (R. Specht, Berlin, Germany).

For the tests we used several calls from each fledgling: a mean ± SE of 11.7 ± 1.8 for males' in-chicks (range 5–24, $N = 10$) and 11.9 ± 2.3 calls for females' in-chicks (range 5–29, $N = 10$). We used a begging call rate of 24 calls/min. The mean duration of a begging call ± SE was 0.26 ± 0.005 s ($N = 156$ calls from 12 individuals, see also Figs 1, 2); calls were separated by a 2.25-s period of silence. This corresponds to a natural intense rate of begging in young black redstarts (mean silence period between successive calls ± SE = 2.06 ± 0.05 s, $N = 605$ calls from eight individuals, range 1.1–3.27). Calls were played back from Elipson C10 speakers (frequency range

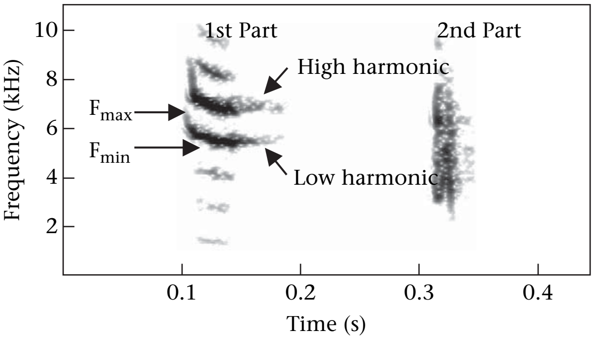

Figure 1. Begging call structure of an 18-day-old black redstart fledgling (fledged at 16 days). Window: flat top; fast Fourier transform length: 512; frame size: 100%; overlap: 96.87%. F_{max} = maximum frequency; F_{min} = minimum frequency.

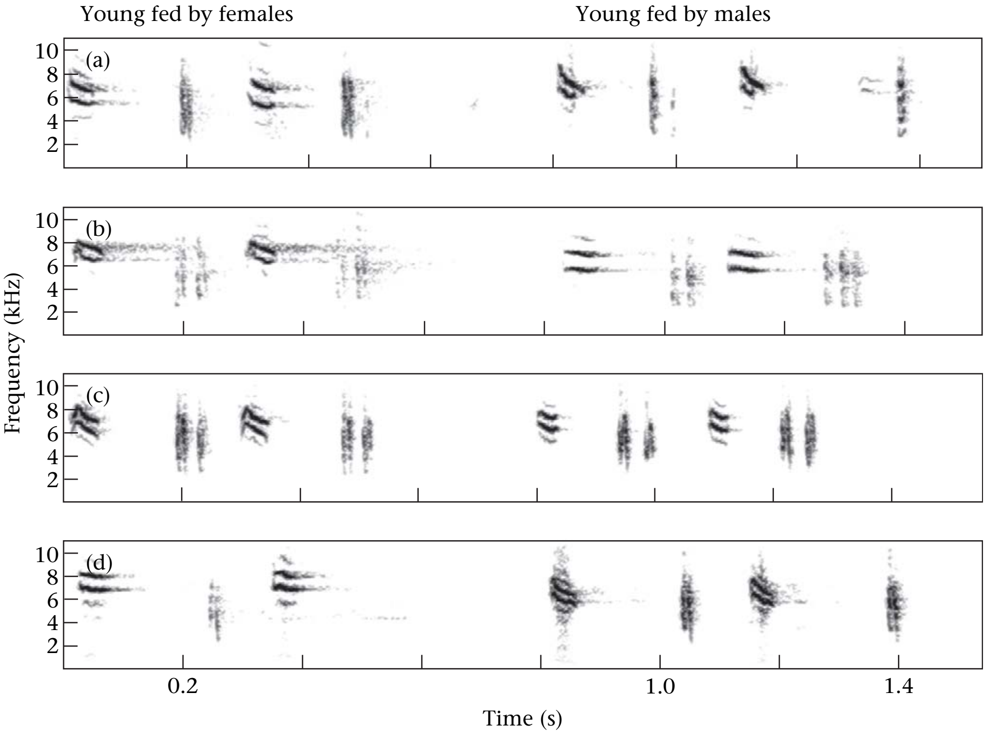

Figure 2. Sonagrams of four pairs of fledglings: preferentially fed by females (two calls each) and preferentially fed by males (two calls each). Sonagrams a–d correspond to four different broods. Window: flat top; fast Fourier transform length: 512; frame size: 100%; overlap: 96.87%.

180 Hz–18 kHz ± 4 dB; 25-W amplifier) powered by 12-V batteries. The intensity level matched the natural intensity and was fixed to 70 ± 0.4 dB at 1 m, measured with a Roline Sound Pressure Level Meter RO-1350.

Playback Procedures

For the playback choice tests we used stereo files broadcasting simultaneously the begging calls of a fledgling fed by the male and of a fledgling fed by the female. We tried to match the begging calls within a test by age but we had three 1-day mismatches (in two cases the fed fledgling's call was more recent) and two 2-day mismatches (in one case the fed fledgling's call was more recent). Parents will strongly respond to a call even 2 days after its recording (T. Draganoiu, personal observation).

Loudspeakers were placed 10 m from one another, in crevices of walls or on fence poles at 0–1.5 m above the ground; within a test, the two loudspeakers were at the same height. A test session consisted of two 15-min periods of continuous playback, separated by a minimum 30-min silent period. Files were interchanged between tests in a test session to avoid a location preference. We used the same pair of calls for both periods within a test session. During tests we recorded the time taken to appear (first detection of the bird being tested), the time taken to enter a 1-m circle around the loudspeaker, the number of entrances within this circle and the total time spent within it. A 15-s period of continuous presence within 1 m of the loudspeaker was necessary for us to record that a bird responded to our test. When no responses were recorded a test session was repeated up to three times; if tests were repeated, we used the same pair of calls as before.

As male and female fed their young at separate places (mean distance between the two family units at test time ± SE was 64 ± 8 m, range 28–96 m, $N = 10$) in all but one case, we carried out two test sessions, within areas occupied by the male's and female's family units, respectively. Loudspeakers were positioned near places where we had observed feeding events on previous days. A parent and its in-chicks may move more than 50 m during a day (T. Draganoiu, personal observation). As the speakers were only 10 m from each other, the two positions were equally likely to be associated with the presence of a parent's in-chick and two birds responded to test sessions carried out near both their own family unit and the other parent's family unit (total number of tests attended by birds = 0–4).

The main difficulty with our playback procedure was that, unlike other similar experimental designs (Beecher et al. 1986), we could not capture fledglings during playbacks, because they were already highly mobile. To compensate for this, we either carried out the tests when they were not actively begging or chased them away before testing; when we chased them, we did not notice any particular vocalizations that could alter the parents' behaviour. During all but one test the young were not visible and parents actively searched for them. If the young were present we temporarily stopped the tests. Parents' responses were thus unlikely to be influenced by the fledglings' behaviour. Our experimental design matches a natural situation where a family unit meets after an accidental separation. For example, when fledglings change places after being disturbed, parents will look for them at the last known feeding location but afterwards they will give contact calls and often find each other after a vocal exchange (T. Draganoiu, personal observation). To compare the responses of the parents, we used a two-tailed sign test (Siegel & Castellan 1988).

Begging Calls Analysis

To see whether male and female responses could be based on different decision rules, we analysed the begging calls of eight pairs of fledglings from different broods; half of the fledglings were preferentially fed by females and half by males. We analysed 278 calls: a mean ± SE of 14 ± 3 calls/fledgling for females' in-chicks (range 5–30) and 17.4 ± 3 calls/fledgling for males' in-chicks (range 5–50). The age of the fledglings was the same within the two groups: mean age ± SE was 17.6 ± 0.5 days for the female group and 17.5 ± 0.5 days for the male group (range 16–20 days in both cases, with a maximum 1-day mismatch within a pair).

Begging calls (Fig. 1) have two distinct parts: a first element with a descendant slope (fundamental frequency and its harmonic series, with two reinforced harmonics which are always successive harmonics, called low and high) and a second part, composed of one or more very short elements which sweep a large frequency bandwidth. Five parameters in the frequency, amplitude and temporal domains were considered: minimum frequency (F_{min}); frequency bandwidth (maximum minus minimum frequency); the loudest frequency of the low harmonic; the difference between the loudest frequencies of the high and low harmonics (which is an approximation of the fundamental frequency); and the duration of the first part of the call. All parameters were measured with Avisoft-SASLabPro software. Minimum frequency, frequency bandwidth and duration were measured on sonagrams (flat top window; fast Fourier transform, FFT, length 1024; 98.43% overlap; frequency resolution 21 Hz for frequency parameters; same characteristics but FFT length 512 for time parameters and a resolution of 0.36 ms). Loudest frequencies were calculated from amplitude spectra: flat top window, frequency resolution of 11 Hz.

A principal component analysis (PCA) of a subsample of the analysed calls (five calls of each of the 16 fledglings studied; Fig. 2 gives examples) identified the minimum frequency of the low harmonic as the main parameter explaining variability of begging calls. We used *t* tests to compare mean values of this cue within each of the eight pairs of fledglings. Statistica 6.0 software (StatSoft, Maisons-Alfort, France) was used for the PCA analysis.

RESULTS

Feeding Preferences

Feeding events recorded during the 3 days before the playback tests showed that stable associations existed between parents and different fledglings within the brood. For the two fledglings studied within each of the 10 broods, each parent fed a particular fledgling more than its sibling (binomial two-tailed tests: $P < 0.001$ for 19 birds and $P < 0.02$ for the 20th one; Table 1) but also more than the other parent (binomial two-tailed tests for the 20 chicks: $P < 0.001$). In all cases, the two criteria needed to classify a brood as divided were satisfied: both fledglings had a different primary caretaker and both parents had different favourite fledglings within a brood. For each family, the begging calls of these two fledglings were used for playback choice tests.

Acoustic Choice Tests

Of the 20 parents, 14 responded to our playback tests (11 birds in total since three individuals were tested twice but during two different breeding seasons; see Tables 1, 2: M_1, M_7 and F_7). Six of them took care of only one fledgling whereas the other eight had two in care. The mean time for a parent to appear ± SE was 319 ± 65 s ($N = 14$, range 38–815) and the mean time to approach within 1 m of the speakers ± SE was 467 ± 71 s ($N = 14$, range 79–858). Three of the six birds that did not respond took care of two fledglings, two of them fed three and one fed four.

Of the 11 responding birds, nine (five males and four females) responded exclusively to begging calls of their preferentially fed fledglings, whereas two others responded equally to begging calls of both their preferentially fed young and the other young (two-tailed sign test: $P < 0.004$).

Table 1. Parents' feeding preferences for particular fledglings within a brood

	Feedings for in-chick of	
Bird	Male	Female
M_1	57	0
F_1	**3**	**14**
M_2	28	0
F_2	**0**	**18**
M_3	35	0
F_3	**1**	**22**
M_4	46	0
F_4	**2**	**28**
M_1	62	0
F_5	**0**	**22**
M_6	40	0
F_6	**0**	**42**
M_7	25	0
F_7	**0**	**32**
M_7	17	0
F_7	**0**	**42**
M_8	76	0
F_8	**1**	**76**
M_9	66	0
F_9	**0**	**19**

Number of observed feedings by the two parents (M = male, **F** = female) during last 3 days before playback tests were carried out (the 2 previous days and the day of the test) for the two fledglings whose begging calls were used for the acoustic choice tests: one preferentially fed by the male (male's in-chick) and one by the female (female's in-chick). Three individuals (M_1, M_7 and F_7) appear twice because they were tested during two different breeding seasons.

Table 2. Responses of 10 black redstart pairs to begging calls of in-chicks and out-chicks

Bird	No. of attended tests	Day after fledging	No. of approaches to speaker (<1m)		Total time spent within 1m (s)		No. of contacts with speaker	
			In-chick	Out-chick	In-chick	Out-chick	In-chick	Out-chick
M_1	1	D_4	1	0	18	0	0	0
F_1	3	D_4–D_5	1.3±0.3	0	60±28.9	0	0.33±0.3	0
M_2	1	D_8	1	0	15	0	0	0
F_2	0	D_8	–	–	–	–	–	–
M_3	1	D_6	1	0	116	0	1	0
F_3	0	D_7	–	–	–	–	–	–
M_4	0	D_6–D_7	–	–	–	–	–	–
F_4	1	D_9	1	0	15	0	0	0
M_1	4	D_3–D_5	2.8±0.9	0	172±70	0	2.8±0.9	0
F_5	1	D_5	3	0	107	0	2	0
M_6	2	D_3	1	0	74.5±7.5	0	1.5±0.5	0
F_6	0	D_3	–	–	–	–	–	–
M_7	2	D_3	4.5±0.5	0	299.5±199	10.5±10.5	1±1	0
F_7	1	D_3	2	0	102	0	0	0
M_7	1	D_4	2	0	43	0	0	0
F_7	2	D_5	1.5±0.5	0	27±3	0	1±1	0
M_8	2	D_5	1±1	0.5±0.5	52.5±41.5	16.5±16.5	0	1
F_8	2	D_5	1±1	0.5±0.5	14.5±14.5	13±13	0	0
M_9	0	D_4	–	–	–	–	–	–
F_9	0	D_4	–	–	–	–	–	–

Fledging day = D_1. In-chicks are young preferentially fed by the tested parent and out-chicks are young fed by the other parent (M = male, F = female). For birds that responded for more than one test, responses (number of approaches to within 1 m lasting at least 15 s, total time spent within 1 m of the speaker and number of contacts with the speaker) are given as means ± SE. Bold characters indicate that both members of a pair responded during a test session. As in Table 1, three birds (M_1, M_7 and F_7) appear twice because they were tested during two different breeding seasons.

Parents actively searched for their young during playbacks and approached within 1 m of the speaker; some of them came into direct contact with the speaker and carried food in their beaks (Table 2).

Seven individuals responded to at least one complete test session (two tests with tapes interchanged between them) and five of them were consistent in their choice for the calls of their preferentially fed young, regardless of the speaker position (M_1, F_1, M_6, M_7 and F_7, Table 2). Two others (male and female from pair 8, M_8 and F_8) responded to their in-chick calls during the first test and it was only during the second one that they turned their attention towards the out-chick's calls. Four individuals (M_2, M_3, F_4 and F_5) responded during a single test of a test session and always for the calls of their preferentially fed chicks.

In three cases a male and a female responded simultaneously during the same test session (M_1 & F_1, M_1 & F_5, M_7 & F_7, Table 2). On each occasion, both parents chose the begging calls corresponding to their preferentially fed young.

The three birds tested during two different breeding seasons (M_1, M_7 and F_7) all responded positively only towards their in-chicks' calls on both occasions. If we consider these responses as statistically independent points, the results are even clearer (two-tailed sign test: $N = 14$ reponses, $P < 0.001$).

Begging Calls Analysis

The PCA based on five acoustic cues did not clearly separate begging calls of young fed by males and females as two distinct groups, but did separate the male's in-chick from the female's in-chick within each brood (Fig. 3). The first factor extracted explained 41.86% of the variability and the second one 24.11%. The minimum frequency and the loudest frequency of the low harmonic had the most important loading factors for the first factor (−0.96 and −0.95, respectively) and the approximation of the fundamental frequency had the most important loading factor for the second factor (0.74). The loading factors of the five

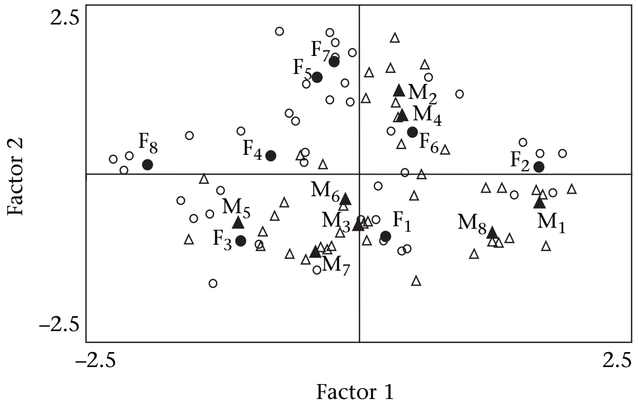

Figure 3. Begging calls of 16 black redstart fledglings, eight fed by females (F) and eight by males (M). Five calls were analysed for each fledgling (○: calls of females' in-chicks; △: calls of males' in-chicks). ●: Females' in-chicks average factorial scores; ▲: males' in-chicks average factorial scores. Pairs F_1–M_1 to F_8–M_8 indicate different broods except F_3–M_3 and F_4–M_4, which represent four fledglings from one brood.

variables on the first and second PC axes were: minimum frequency (−0.96; −0.14), loudest frequency of the low harmonic (−0.95; −0.07); frequency bandwidth of the low harmonic (0.26; 0.58); fundamental frequency (−0.17; 0.74); duration of the first part of the call (−0.41; 0.54).

Minimum frequency of the low harmonic was significantly different within each of the eight pairs of fledglings (Fig. 4). Nevertheless, in four cases (pairs 1, 3, 4 and 8) the calls of the fledgling fed by the female had significantly higher values than those of its sibling (which was in the male's care) and in the other four cases, the opposite was true.

DISCUSSION

The key finding of this study is that several days after their young fledge, parent black redstarts are able to discriminate between the begging calls of the offspring that they preferentially fed and did not feed. Vocalizations of preferentially fed young (in-chicks) attracted parents more than calls of those fed by the other parent (out-chicks). Several of our findings suggest that the birds' responses were due to the different identities of broadcast calls.

First, five of the seven individuals that responded to a complete test session were consistent in their preference for the calls of their preferentially fed young, regardless of the speaker's position. This suggests that our results are not biased by a preference for a particular location. Both of the two birds that responded at only one location (and thus to two different young) responded first to their in-chick and only then to their out-chick. This could reflect a priority order. For those individuals that responded only once, the initial speaker position was critical but, as stated in the Methods, there should be no bias in parents' responses in this case either. Second, simultaneous responses of males and females during a test session indicate that parents responded to the identity of the caller and not to some other parameter, such as the motivational value of the stimuli. Lastly, three birds were tested during two different breeding seasons and on each occasion they responded positively only towards their in-chicks' begging calls.

Parents that took care of several young seemed to be less responsive to our tests: all six birds that took care of one fledgling responded, whereas only eight of the 11 parents that took care of two did and neither of the three birds that fed more than two responded. An explanation for this could be that in-chick recognition in our study was limited to discrimination between two fledglings. However, we think this is more likely to be related to the methodology. When parents took care of only one or two young we managed to carry out tests when the young were silent or we were able to chase them away before testing, but this was almost impossible when three or more young were cared for by one parent: fledglings begged during the playback test and parents preferred to direct their attention to them rather than to loudspeakers broadcasting begging calls.

There are several possible interpretations of the parents' ability to discriminate between begging calls of fledglings that they preferentially fed and those that they did not. First, a difference in parents' familiarity with the two categories of young could account for this result. The spatial separation of the two family units when playback tests were performed could support this explanation. Nevertheless, given the proximity of the family units, most of the time all young were within the adults' hearing range and often a parent ignored an out-chick's begging calls while flying over it in order to reach one of its in-chicks. Therefore, it is likely that begging calls of all young were familiar to parents when tests were carried out.

Second, males and females could react to different acoustic characteristics; consequently, each sex would feed any fledgling belonging to a category defined by some precise acoustic parameters. Our begging call analysis of males' and females' in-chicks does not support this interpretation. The PCA analysis based on five acoustic parameters did not separate begging calls of males' and females' in-chicks as two distinct groups. We chose parameters from time, frequency and spectral domains,

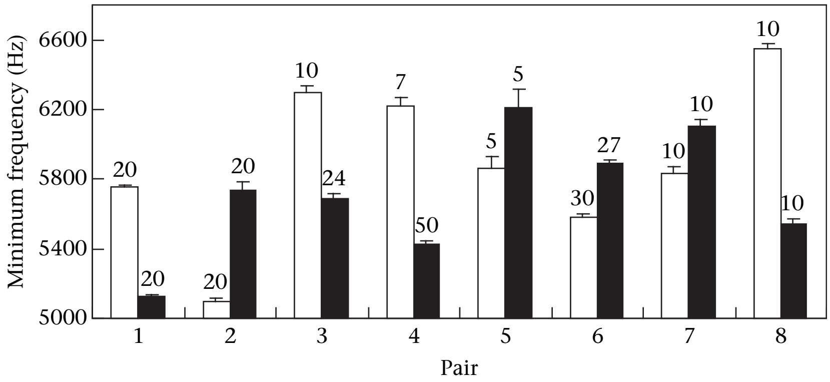

Figure 4. Average minimum frequency of the low harmonic + SE for eight fledglings fed by females (□) and eight by males (■). Number of calls analysed per fledgling is indicated above the bars. Pairs 1–8 correspond to distinct broods belonging to different birds except pairs 3 and 4, which represent four young of one brood; pairs 1 and 2 come from different broods of the same parents. Student's *t* tests comparing fledglings within a pair that were fed by male and female parents: pair 1: $t_{38} = 36.41$; pair 2: $t_{38} = 14.15$; pair 3: $t_{32} = 11.87$; pair 4: $t_{55} = 17.44$; pair 5: $t_8 = 2.88$; pair 6: $t_{55} = 9.34$; pair 7: $t_{18} = 5.72$; pair 8: $t_{18} = 24.28$; all $P < 0.001$, except pair 5, where $P < 0.05$).

known to be used by other species for kin recognition. For example, the use of pitch as a cue for acoustic recognition has been documented for several species, both birds and mammals: black-headed gulls, *Larus ridibundus* (Charrier et al. 2001), several penguin species, such as *Aptenodytes forsteri*, *A. patagonica*, *Pygoscelis adeliae* and *P. papua* (Aubin & Jouventin 2002), long-tailed tits, *Aegithalos caudatus* (Sharp et al. 2005) and sheep, *Ovis aries* (Searby & Jouventin 2003).

However, the PCA did separate the calls of the male's and female's in-chicks within a brood. The minimum frequency of the low harmonic was identified as the main parameter explaining the variability of the begging calls. Further analysis revealed that significant differences existed between the male's and female's in-chicks in this parameter for all eight pairs of fledglings studied. Despite this, not all males and females used this parameter in the same way: in four cases the female's in-chick had a mean value greater than that of the male's in-chick and in the four other cases the opposite was true. Our analysis of begging calls is obviously not exhaustive and cannot rule out the 'two types of calls' hypothesis, but we suggest that parents' responses to playback tests are more likely to be explained by an individual recognition of particular fledglings within a brood. Pitch is one possible cue enabling parents to discriminate between their in-chicks and out-chicks. Frequency coding appears to be a simpler recognition system than time coding (Jouventin & Aubin 2002; Searby & Jouventin 2003) and may be applicable to our study, as the risk of misdirected parental care is low in territorial species. Variation also exists in frequency modulation (Fig. 2), another parameter known to be used in individual recognition (Charrier et al. 2001) which we did not investigate in our study. Only further playback experiments with modified signals (Aubin & Jouventin 2002) could establish which parameters black redstarts really use.

Two previous studies with noncolonial species found that, prior to the chicks fledging, parents reacted in the same way towards begging calls belonging to their offspring and to strangers (Medvin & Beecher 1986; Leonard et al. 1997). In contrast, the only study carried out once chicks had already left the nest (at least 2 weeks after fledging) showed that parents responded differentially to begging calls belonging to their own versus alien fledglings (Barg & Mumme 1994). In a study on discrimination of young within a brood in white-throated sparrows, *Zonotrichia albicollis*, only some parents responded differently to their in-chicks and out-chicks, 3 days after fledging (Kopachena & Falls 1991). The authors suggested that the differences between parents may be explained by the timing of recognition, as the fledging period is a time of transition between immobility and mobility of fledglings. Our results show that black redstarts are able to discriminate acoustically between their preferentially fed fledglings and fledglings fed by the other parent within a brood 3–9 days after fledging. One possible explanation for the different parental responses before and after the chicks fledge is that in territorial species parents develop offspring recognition only after they fledge, once they become more mobile and the risk of intermingling with strangers increases. This would not be the first example supporting the view that the development of offspring recognition coincides with the onset of brood mobility. A study of several colonial species belonging to the auk family showed that recognition appears earlier in precocial species (Jones et al. 1987) than in nidicolous ones (Ingold 1973; Lefevre et al. 1998). However, acoustic choice tests should be carried out both at the end of the nestling stage and during the postfledging stage to test this hypothesis. Further investigation is also needed to see whether parents can discriminate between an out-chick and a stranger.

Why brood division occurs is still puzzling. Our study showed that acoustic discrimination between offspring within a brood is one of the proximate mechanisms used to maintain this behavioural strategy. One hypothesis attempting to account for the existence of primary caretakers is that of social specialization (Leedman & Magrath 2003), which states that interactions between a parent and its young could become more efficient with learning. Indeed, individual knowledge of specific young could reinforce parent–young interactions and bring several benefits such as provisioning efficiency or predator avoidance. Our findings support the social specialization hypothesis: one main advantage of acoustic discrimination is that parents can identify their fledglings at a distance and thus reduce searching costs.

Our results are also consistent with the idea that evolutionary conflicts between individuals may lead to brood division (Lessells 2002). In the case of sexual conflict, if a parent pre-emptively deserts part of the brood, we should expect consistency in its feeding preferences (Leedman & Magrath 2003) and this could be achieved through individual recognition. Sexual conflict could explain brood division in black redstarts, as males generally take care of only one of the three to five fledglings in a brood (Andersson 1985; Draganoiu et al. 2005). Discrimination between offspring within a family should also enable parents to feed particular offspring exclusively and thus counteract possible sibling competition.

To our knowledge this is the first study showing that birds can acoustically discriminate between two categories of young within a brood (their preferentially fed young and those fed by the other parent), revealing a proximate mechanism enabling the maintenance of brood division. Furthermore, as brood division has been described for a dozen songbird species (Leedman & Magrath 2003), we suggest that parental acoustic discrimination of young within territorial species could be more widespread than currently thought. More studies of parent–offspring acoustic interactions of songbird species during the postfledging stage should be carried out to test this prediction.

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