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Sex-related parental care strategies in the lesser spotted woodpecker *Picoides minor*: of flexible mothers and dependable fathers

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We investigated sex-specific parental care behaviour of lesser spotted woodpeckers *Picoides minor* in the low mountain range Taunus, Germany. Observed parental care included incubation, nest sanitation as well as brooding and feeding of nestlings. Contributions of the two sexes to parental care changed in progress of the breeding period. During incubation and the first half of the nestling period, parental care was divided equally between partners. However, in the late nestling stage, we found males to feed their nestlings irrespective of brood size while females considerably decreased feeding rate with the number of nestlings. This behaviour culminated in desertion of small broods by females shortly before fledging. The fact that even deserted nests were successful indicates that males were able to compensate for the females' absence. Interestingly, the mating of one female with two males with separate nests could be found in the population, which confirms earlier findings of polyandry in the lesser spotted woodpecker. We conclude that biparental care is not essential in the later stage and one partner can reduce effort and thus costs of parental care, at least in small broods where the mate is able to compensate for that behaviour. Reduced care and desertion appears only in females, which might be caused by a combination of two traits: First, females might suffer higher costs of investment in terms of mortality and secondly, male-biased sex ratio in the population generally leads to higher mating probabilities for females in the following breeding season. The occurrence of polyandry seems to be a result of these conditions.

Over 90% of the more than 9,000 bird species are socially monogamous and conduct biparental care (Lack 1968). Nevertheless, parental care is not always shared equally between the partners. Life-history theory suggests that effort in parental care is a trade-off between investment in current and future reproduction, since increased reproductive expenditure may reduce parental survival and therefore parental future reproductive output (Nur 1984, Horak 2003). In species with biparental care, the amount of expenditure is furthermore influenced by the effort of the mate (Johnstone and Hinde 2006). In most socially monogamous bird species, females take the larger part of brood care by doing most of incubation and brooding of the young (Clutton-Brock 1991). Since males are less involved in time consuming parental care, facultative multi-nest polygyny occurs frequently, i.e. one male is mated with more than one female with separate nests (Clutton-Brock 1991, Kempenaers 1995, Lubjuhn et al. 2000). In only two families of altricial birds (woodpeckers and cuckoos) the males contribute highly to brood care. Woodpeckers conduct biparental care, but males stay with the eggs and young during the nights and woodpeckers are generally monogamous (Winkler et al. 1995, Ligon 1993). It is assumed that this might favour females to become polyandrous (Andersson 2005) and resent studies indeed reported single occurrences of polyandry in woodpeckers (great spotted woodpecker *Picoides major* Kotaka 1998, lesser spotted woodpecker *Picoides minor* Wiktander et al. 2000, northern flicker *Colaptes auratus* Wiebe 2002, three-toed woodpecker *Picoides tridactylus* Pechacek et al. 2006).

However, simultaneous polyandry can only be successful, if also daytime parental care can largely be performed by males or males are at least able and willing to compensate the reduced investment of females. To understand the conditions under which polyandry might occur, investigations on parental care is needed. In our study, we focus on a woodpecker species for which polyandry has been reported in a Swedish population (Wiktander et al. 2000), and examine whether this behaviour can be confirmed for another population. Therefore, we investigated parental care behaviour and mating system of the lesser spotted woodpecker in a German low mountain range (Taunus). Our main objective was to examine the share of duties between the partners. Since optimal expenditures for the sexes might not be static but change within the season or differ with value of the current brood, we furthermore focused on the effect of age and number of nestlings on the effort in parental care by both sexes.

Methods

Study area

The study was conducted in an area of 70 km^2 in a German low mountain range (Taunus) 30 km NW of Frankfurt/Main in 1996, 1998, 1999, 2000, 2002 and 2003. The study area was situated in a heterogeneous landscape with deciduous, mixed and coniferous forest types, extensively used orchards as well as interspersed areas of settlement and grassland. The area contains 12 lesser spotted woodpecker territories, which were not occupied in all study years.

Observations

Before egg laying started, the area was searched for breeding holes and adult birds were caught and marked with two colour rings for individual identification. Over all years, we studied 31 breeding attempts. To examine influence of offspring value on parental care behaviour, we determined the size of the full clutch and the number of nestlings (brood size) in the breeding holes, using a dentist mirror and a small lamp. Number of young was counted twice: shortly after hatching and on d 16, when the nestling were marked with colour rings. If signs of predation were found (e.g. large pecking signs in the bark), nestlings were counted additionally. In our analyses, sample sizes for the calculation of clutch size and brood sizes differ for two reasons: (1) 8 nests failed during egg laying or nestling time, and (2) 5 nests could only been reached with large rope and ladder systems, which cause a disturbance for more than 30 min at the nests. Since this would be too long during incubation or brooding period, we only assessed brood size at the 16th nestling d on those nests.

We investigated parental care in its narrowest sense, meaning the care of eggs or young when they are detached from the parent's body (Clutton-Brock 1991). This included incubation, brooding, feeding and nest sanitation (i.e. removal of faecal sacs). Observations were conducted in the breeding seasons of 1998 to 2003, except for 2001. Pairs were observed at their breeding holes from a hidden place at a distance of 30 to 50 m with a telescope (Optolyth 30 × 80). We recorded identity of the visiting bird, time of arrival and leaving to the nearest minute for each visit and removal of faecal sacs. If an individual stayed for more than two minutes in the breeding hole with hatched young, we defined this behaviour as brooding.

Over all years, we observed incubation on 11 nests (7 monogamous and 4 polyandrous broods) in 49 time periods of 3 h (1998) or 2 h (2002 and 2003), and on minimum of 4 different ds per nest. During our observations in 1998, we recorded an average duration of one incubation bout of 38 min (maximum 74 min). Therefore, we decided 2 h of observation periods as long enough. After hatching, we observed parental care on broods with known brood size (19 broods over all years, 15 monogamous and 4 polyandrous pairs). The observations took place in 304 periods of 2 h and we visited every nest on 16 different ds on average (minimum 10 ds). Observation ds were distributed evenly over the whole nestling period. Observations were cancelled in heavy rain, since we found parents to decrease feeding frequency noticeably under these conditions.

Data analysis

To investigate parental effort in incubating and brooding, we calculated the relative percentage of time spent on this behaviour based on the observation time at the nest. In terms of providing for the young, we calculated the feeding frequency, i.e. number of feeding visits per h. Since individuals that feed more frequently are also more likely to remove faecal sacs, we calculated number of visits with faecal sac removal based on all feeding visits per observation to exclude influence of feeding frequency.

We analysed parental care on the pair level and on the individual level: first, on the pair level, we analysed parental care in the course of the nestling period to test for the effect of nestling age on brooding and feeding by the parents. Therefore, we applied mixed linear effects models for brooding and feeding frequency resp. and included pair as random factor, age of the nestlings and mean daily temperature (just for brooding) as fixed factors. Age of nestlings was included as repeated measurement, to model the possible correlation of the residual errors within each pair.

Second, we investigated the effects of sex and brood size on brooding and feeding frequency of the individual. Therefore, we calculated the mean proportion of brooding and feeding frequency resp. for each breeding individual over all observation ds for the early and late nestling stage. In three pairs, number of nestlings declined within the season, since nestlings starved to death or were killed by predators. In these cases, we calculated the mean nestling number over the observation ds.

For both dependent variables (proportion of brooding and feeding frequency resp.) we fitted a mixed linear effects model in which the pair was a random factor, sex of the parent, nestling stage (only for feeding frequency) and number of nestlings were included as fixed factors.

Statistical analyses were performed with SPSS 15.0. We used a significance level of 0.05 and, unless otherwise stated, reported p-values are based on two-tailed tests. In cases when data were not normally distributed we used nonparametric tests and referred to median values instead of mean values.

Results

Beside the section about polyandrous pairs, all results consider only broods of monogamous pairs.

Clutch and brood size

The median size of a full clutch was 6 eggs (mean 5.4) and varied from 3 to 6 ($n = 20$). Shortly after hatching, mean brood size in nests with hatched young was 4.2 (2–6 young, $n = 15$). Due to nest predation the mean number of nestlings on the 16th nestling d decreased to 3.6 (1–5 nestlings, $n = 17$).

Parental care within the breeding cycle

Over the 11 ds of incubation period, the eggs were incubated between 69% and 100% of the observation time, on average 92% ($n = 7$). When eggs had hatched, parents stayed in the breeding hole after feeding and nestlings were brooded. The proportion of time spent brooding decreased significantly with increasing aging of nestlings ($F_{11,\ 6.85} = 58.86$, $P < 0.001$, $n = 15$) from 77% on the first d to 10% on d 12 (Fig. 1). Furthermore, the proportion of brooding increased with decreasing mean daily temperature ($F_{1,\ 65.5} = 13.37$, $P < 0.01$, $n = 15$). After d 13, most parents entered the hole only to feed the nestlings or to remove faecal sacs but brooding was hardly observed (Fig. 1). Between d 22 and d 25, nestlings fledged. Following this pattern, the nestling period was divided into two stages for further analysis: (1) early stage: first d to d 12, (2) late stage: d 13 to fledging day.

When the nestlings were 3 ds old, parents started to remove faeces covered with woodchips to keep the breeding hole clean. In the early nestling stage, parents' feeding frequency increased with age of nestlings ($F_{11,\ 110.7} = 23.43$, $P < 0.001$, $n = 15$), whereas in the late nestling stage, feeding frequency did not increase with age ($F_{10,\ 9.8} = 2.19$, $P < 0.001$, $n = 14$; Fig. 1).

Share of the parental care between the partners

Males and females shared diurnal incubation equally (Wilcoxon 2-tailed: $P = 0.499$, $n = 7$, Fig. 2). In terms of nest sanitation, males removed significantly more often faeces when visiting the nest than females (paired t-test, $T = 2.934$, $P < 0.05$, $n = 15$). The proportion of time spend brooding by an individual was not influenced by its sex ($F_{1,12} = 1.78$, $P = 0.207$, $n = 15$) or the brood size ($F_{1,12} = 0.16$, $P = 0.70$, $n = 15$) or a combination of these two factors ($F_{1,12} = 1.87$, $P = 0.197$, $n = 15$). Individual feeding frequency was affected by the interaction between sex, brood size and nestling stage ($F_{1,46.7} = 6.53$, $P = 0.014$, $n = 15$). Nevertheless, in the early nestling stage, we found no effect of brood size on feeding frequency of males and females resp. (Fig. 3a). In contrast, in the late nestling stage, feeding frequency of females was positively related to brood size (Table 1), whereas feeding frequencies of males showed no relationship (Fig. 3b). As shown in Fig. 3b, females feed less frequently than males in nests smaller than 4 nestlings.

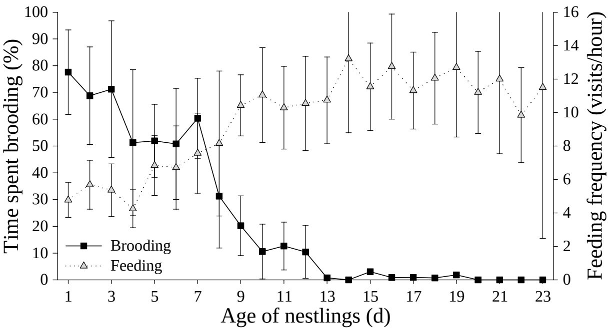

Figure 1. Change of parental duties in the course of the nestling period. Proportion of time parents spent brooding (squares) and feeding frequency (triangles; means ± CI).

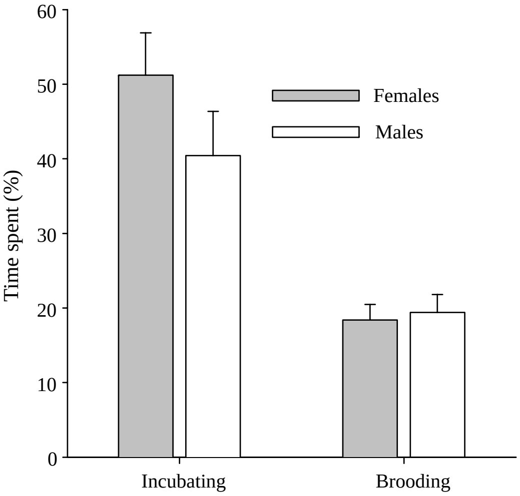

Figure 2. Share of parental duties between partners in the lesser spotted woodpecker. Percentage of time (mean ± CI) males and females spent incubating ($n = 7$ pairs), and brooding ($n = 15$ pairs).

We observed that almost half of the females (7 out of 15) stopped visiting their nest in the late nestling stage, most of them one or two ds before the young fledged. The earliest desertion appeared on the 13th nestling d at a nest with only one young. All females were seen alive after desertion and we observed three of them feeding young after fledging. All nests where females had stopped feeding were successful, i.e. at least one young fledged and none of the nestlings in deserted nests starved to death after the female deserted. The number of nestlings in deserted nests was significantly smaller (mean 2.5 young) than in non-deserted nests (mean 4.4 young) even before the female disappeared (unpaired t-test, $T = 3.980$, $P < 0.01$, $n = 15$).

Polyandrous pairs

From a total of 31 breeding attempts examined over all study years, 6 (19%) belonged to 3 different polyandrous female individuals in three different years. In all cases, the polyandrous female laid eggs in the nests of two males that were 0.8–1.2 km apart from each other (mean 1.0 km). After completing the clutch in the primary nests (5–6 eggs, mean 5.7) the female started one or two ds later a second clutch with an average of 4.7 eggs (4–5). Consequently, polyandrous females laid up to 11 eggs per season. The number of fledglings in primary nests was 4 on average. Only one out of three secondary nests was successful and produced two fledglings. The other two nests failed because the eggs did not hatch and the male died during early nestling stage, respectively. Polyandrous females produced 4.7 fledglings on average, i.e. 1.2 more nestlings than monogamous females. We observed parental care of a polyandrous female and its two males in two years (1998 and 2002), i.e. on 2 nests each year. In both years, the polyandrous female invested more time and energy in the primary than in the secondary nest (Table 2). We observed incubation on secondary nests on 3 ds (1998) and 8 ds

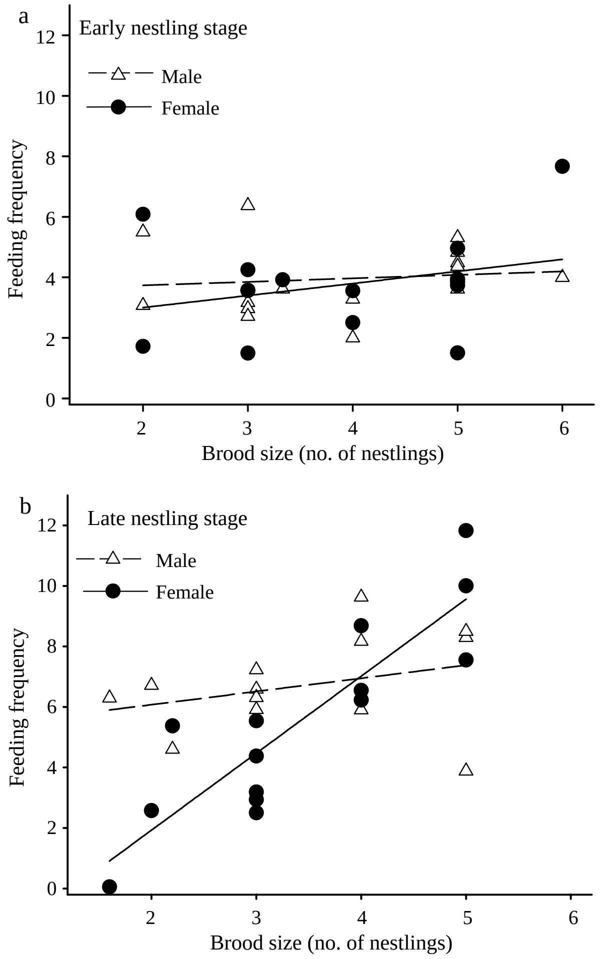

Figure 3. Feeding frequencies of males (triangles) and females (black circles) in relation to the number of nestlings: (a) early nestling stage, n = 15 and (b) late nestling stage, n = 14.

(2002) but never observed the female care for the eggs, though we cannot finally exclude incubation to a minor extent. In 1998, the secondary male died on the third nestling d. After its death, the polyandrous female kept feeding the nestlings and roosted in the nest. For the next 6 ds the female was feeding on both nests until it finally deserted the secondary nest and the young died. The results in Table 2 include only ds when both parents were alive. In 2002 the polyandrous female cared for the nestlings in the secondary nest only in the first nestling stage and was last seen at the nest on the 10th nestling d. All polyandrous females had been observed in previous years or were relocated in following years and in these years they were socially monogamous.

Discussion

Brooding intensity increased with decreasing temperatures, since parents have to spend more time to keep the nestlings at optimal temperature. This relationship confirms earlier results (Wiktander 1998), and was also reported in other woodpecker species, e.g. northern flickers (Wiebe and Elchuk 2003). Moreover, brooding declined with the age of the young. This is a typical trait in altricial species caused by improved thermoregulatory abilities of the young (Clark 1985, Sanz and Tinbergen 1999, Chastel and Kersten 2002). With decreasing time spent on brooding, feeding frequency increased, which is necessary because of the rising energy demand throughout the nestlings growing phase (Royama 1966, Ricklefs 1984).

During incubation and early nestling stage, parental care was provided by both parents equally. Brooding and feeding are both very time-consuming and we suppose that the early nestling stage is most challenging for parent lesser spotted woodpeckers and both parents are needed. In the late nestling stage, feeding frequency stopped to increase with the age of the nestlings and brooding became obsolete. In this stage, feeding frequency of females but not of males was related to the number of nestlings. The decrease in females' feeding frequencies in relation to brood size culminated in the complete stop of feeding in small broods. Desertion by females was found in the lesser spotted woodpecker before, although it was not related to brood size (Wiktander et al. 2000).

None of the deserting females had a second brood the same year, thus, the benefit of this behaviour is assumed to be long-term. However, desertion of the brood by one partner will only be favoured by natural selection if the present brood requires only little additional parental investment (Lazarus 1990). Indeed, all broods deserted by their mothers fledged nestlings and the number of nestlings did not decline during the time the male cared alone for the brood. This indicates that the care of both parents was not essential in the late nestling stage.

We assume two reasons for the influence of brood size on the parental effort in females: First, in small broods males might be able to feed nestlings alone due to a lower food requirement. Second, the value of small broods and therefore the benefit for the parents is lower.

Interestingly, in species where females take the larger part of parental care, studies found the opposite pattern, in that males adapt their parental investment to the brood size or that females compensated for a decreasing feeding rate in handicapped males *Tachycineta bicolour* (Whittingham et al. 1994) and *Parus major* (Sanz et al. 2000). One reason for these differences between males and females can be seen in the lack of confidence in paternity (Slagsvold and Lifjeld

Table 1. Parameter estimation from a mixed linear effect model analysing the combined effect of sex, nestling stage and brood size on the feeding frequency of individuals (with pair as a random factor).

Variable	Parameter estimation	df	T	P
Female × early stage × brood size	0.40	26	1.26	0.216
Male × early stage × brood size	0.11	26	0.36	0.720
Female × late stage × brood size	2.54	24	6.443	<0.001
Male × late stage × brood size	0.44	24	1.102	0.282

Table 2. Parental care in primary and secondary polyandrous nests in the years 1998 and 2002.

		1998		2002	
		Primary	Secondary	Primary	Secondary
Time spent incubating (%)	Male	56	68	50	67
	Female	38	0	41	0
Feeding visits with nest sanitation (%)	Male	21	0	15	27
	Female	19	0	18	13
Feeding frequency early nestling stage	Male	5.1	10.8	9.7	5.0
	Female	4.3	3.3	7.8	4.3
Feeding frequency late nestling stage	Male	11.5	failed	16.4	12.8
	Female	5.4	failed	11.1	0

1990), since extra-pair paternity occurs frequently in these species (Dunn et al. 1994, Lubjuhn et al. 1999, Griffith et al. 2002). In woodpeckers, however, a high confidence in paternity was found in socially monogamous pairs *Picoides borealis* (Haig et al. 1994) *Picoides major* and *P. medius* (Michalek and Winkler 2001), *Picoides tridactylus* (Pechacek et al. 2005), and can also be assumed for lesser spotted woodpeckers. Therefore, the value of the current brood should be the same for both females and males. Consequently, reasons for the difference in parental investment between the sexes should be found in the future reproductive value of the parents. Since lesser spotted woodpeckers are single brooded, the future reproductive value of the breeding individual depends on reproductive success in the following year. This includes survival to the following year and the chance to find a mate. Accordingly, the observed differences in investment between the sexes can be explained either by: (1) different chances for mating, or (2) different costs of parental effort in terms of survival rates. The chance to find a mate differs between the sexes, since lesser spotted woodpecker populations are often male biased (Wiktander et al. 2000, Rossmanith et al. 2007). An excess of males leads to a higher competition for females which makes future reproductive success for males uncertain. Therefore, it might be more beneficial for the male to increase his own effort in the current brood and compensate for the female's reduced care. Moreover, Wiktander (1998) found that survival rates were lower for lesser spotted woodpeckers that rose young compared to widowed birds that gave up the breeding attempt and these costs were higher for females than for males. Thus, the magnitude with which reduction of effort increases survival might be higher for females than for males. In addition, lesser spotted woodpeckers have lifelong pair bonds, and reproductive success was shown to be higher in pairs that breed together in consecutive years (Wiktander et al. 2001, Rossmanith et al. 2007). A higher survival rate of females is therefore increasing the likelihood for the male to mate the same partner and thus increase reproductive success. Consequently, males compensate for the lack of female effort, since survival costs might be higher for females and survival of the own mate is of benefit for the male. In the light of these assumptions we conclude that parental care of females is adjusted to the reproductive value of their offspring, to its importance on offspring fitness and to their cost for parental expenditure. It also indicates that the optimal level of parental expenditure varies with brood size for females but not for males. Males compensate for the decreasing or lacking feeding by females, because the mate's future physical condition is of direct importance for the male. The basis for this behaviour seems to be the male-biased sex ratio, which leads to a higher competition for females. An influence of the population's sex ratio on the share of parental care was also assumed in Breitwisch et al. (1986).

Mating system

We confirmed social polyandry in the lesser spotted woodpecker population in Taunus, Germany. Though being an exception from the general performed social monogamy in this species, polyandry occurs frequently with 19% of the breeding attempts in our study and 16% found by Wiktander et al. (2000), and can have a strong effect on the viability of the population (Rossmanith et al. 2006). Despite the fact that our observations on polyandrous broods are limited, the results tentatively suggest that polyandrous females did not share their effort in parental care evenly between their two broods. This is a further support by the trade-off theory. First, food availability deteriorates with time (see Rossmanith et al. 2007) and the secondary brood might be too late for optimal food supply. Second, the brood size and thus the value of the brood are lower in secondary broods. This is probably caused by late timing, however, lower male quality can not be excluded as well. We conclude that the pattern of expenditure in parental care in monogamous pairs is the prerequisite for the occurrence of polyandry. If the males were not able or 'willing' to compensate a reduced effort in parental care, it would be unlikely for females to have the opportunity to mate with additional males.

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