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Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*

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The sexes' share in parental care and the social mating system in a marked population of the single-brooded Lesser Spotted Woodpecker *Dendrocopos minor* were studied in 17 woodpecker territories in southern Sweden during 10 years. The birds showed a very strong mate fidelity between years; the divorce rate was 3.4%. In monogamous pairs, the male provided more parental care than the female. The male did most of the nest building and all incubation and brooding at night. Daytime incubation and brooding were shared equally by the sexes, and biparental care at these early breeding stages is probably necessary for successful breeding. In 42% of the nests, however, though still alive the female deserted the brood the last week of the nestling period, whereas the male invariably fed until fledging and fully compensated for the absent female. Post-fledging care could not be quantified, but was likely shared by both parents. Females who ceased feeding at the late nestling stage resumed care after fledging. We argue that the high premium on breeding with the same mate for consecutive years and the overall lower survival of females have shaped this male-biased organisation of parental care. In the six years with best data, most social matings were monogamous, but 8.5% of the females (N = 59) exhibited simultaneous multi-nest (classical) polyandry and 2.9% of the males (N = 68) exhibited multi-nest polygyny. Polyandrous females raised 39% more young than monogamous pairs. These females invested equal amounts of parental care at all their nests, but their investment at each nest was lower than that of monogamous females. The polyandrously mated males fully compensated for this lower female investment. Polygynous males invested mainly in their primary nest and appeared to be less successful than polyandrous females. Polyandry and polygyny occurred only when the population sex ratio was biased, and due to strong intra-sexual competition this is likely a prerequisite for polygamous mating in Lesser Spotted Woodpeckers.

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Monogamy is the dominant social mating system in birds (Lack 1968, Silver et al. 1985) but a number of facultative polygamous mating systems have been described (Davies 1991). Further, the norm in birds is that both parents provide parental care, e.g. nest building, incubation, brooding and feeding (Silver et al. 1985, Clutton-Brock 1991). There is, however, large interspecific variation in the degree to which the male and the female provide parental care, and the specific organisation of parental care is closely related to variation in mating system (Silver et al. 1985, Clutton-Brock 1991). In passerines, for example, the female usually takes the larger share of parental care and facultative multi-nest polygyny, where one male is paired with two or more females with separate nests in a season, is relatively frequent in this group (Lack 1968, Emlen and Oring 1977). Substantial male parental care and multi-nest (classical) polyandry, where one female is paired with two or more males with separate nests in a season, is far less common (Lack 1968, Silver et al. 1985). It occurs more or less facultatively in some 15 species of shorebirds Charadriiformes, which lay a small clutch of fixed size and have precocial young which facilitates uniparental care (Oring 1986). Multi-nest polyandry in birds with altricial young is very rare and has been reported only in a handful of species (Vernon 1971, Ralph 1975, Fulk et al. 1987, Middleton 1988, Seutin et al. 1991, Willimont et al. 1991, Hasselquist and Langefors 1998, Kotaka 1998).

In a number of woodpecker species, family Picidae, the male's contribution to parental care is equal to or greater than that of the female (Lawrence 1967, Ivanchev 1996, Hogstad and Stenberg 1997, Michalek 1998). This includes male nocturnal incubation and brooding which is very rare in birds overall (Ligon 1993). Hence, woodpeckers show features which in theory would promote multi-nest polyandry (Ligon 1993, Winkler et al. 1995). Still, to our knowledge multi-nest polyandry has been reported only twice (Willimont et al. 1991, Kotaka 1998) and woodpeckers are, except for cooperative breeders, viewed as being strictly monogamous since biparental care is supposed to be necessary for raising a brood (Short 1982, Ligon 1993, Winkler et al. 1995). Except for some cooperatively breeding species, there is a paucity of detailed long-term studies of parental care and social mating system of marked woodpecker populations, and much of the available information on the organisation of parental care is anecdotal and often contradictory (e.g. Glutz and Bauer 1980, Cramp 1985) which makes it difficult to quantify the share of the sexes. In this paper we report on the organisation of parental care and social mating system in a marked population of the Lesser Spotted Woodpecker *Dendrocopos minor* as observed during a 10-year study.

Material and methods

The Lesser Spotted Woodpecker

The Lesser Spotted Woodpecker is a small (body mass 24 g) non-migratory inhabitant of deciduous woodlands of the Palearctic region. In the non-breeding season, the birds in our study area live solitarily within a several 100 ha large home-range, usually with the 50–100 ha breeding territory in the centre (Wiktander 1998). As a rule, individuals show life-long fidelity to the territory where they first settled (Wiktander 1998). Established birds are highly territorial and intra-sexual competition is strong (Wiktander 1998). The eggs are incubated for 10–12 days. In clutches up to 5 eggs hatching is synchronous, but in larger clutches (6–8) one egg commonly hatches one day later than the rest (Wiktander 1998). The nestling period lasts 19–22 days (Cramp 1985, Wiktander 1998). Only one brood is reared in a season (Cramp 1985, Wiktander 1998) but renesting may follow failure at an early breeding stage (Wiktander et al. 1994).

Field methods

From March 1989 to July 1998 we followed Lesser Spotted Woodpeckers in a 125 km^2 study area, located in the boreo-nemoral region of southern Sweden (56°40′N, 14°10′E). The study area contained a maximum of 17 potential territories, which were rather distinct patches of mature deciduous woods in a landscape dominated by lakes and spruce forest. The territories were distributed singly or 2–4 bordering each other in 8 different sub-areas, 1.5–4 km apart. Outside the study area, the nearest known potential territories were 6 km away. For a further description of the study area, see Olsson (1998) and Wiktander (1998).

Each territory was visited at least weekly from March through June each year in 1989–1997, except for 3, 2 and 1 potential territories which were not searched in the years 1989, 1990 and 1991, respectively. In 1998, only 10 territories were searched, with less frequent visits. In 1989, 50% of the adults present were individually colour-ringed, 75% in 1990, 90–100% in 1991–1997 and 80% in 1998. In 1993–1996, at least one individual in most territories was equipped with a radio-transmitter. This weighed 1.15 g and was tied to two central tail feathers. The woodpeckers were captured at the roosting or nesting hole by means of a bag net or mist net.

The determination of sex ratio was based on the observations we made during our regular visits to the territories in the years 1992–1997. In these years all potential territories were investigated thoroughly and most or all observed individuals were marked. Although 1–2 individuals were unmarked in some of these years, we believe we had control of all individuals that occurred in the study area. This includes both breeding birds and non-breeders (see also Wiktander 1998), and we think that the ratios given can be regarded as accurate estimates of the overall population sex ratio, not only including the breeding birds.

To calculate the date of the first egg we assumed that one egg was laid per day (Wiktander 1998). For nests found with a full clutch, we assumed an incubation time of 11 days and for nests found after hatching a nestling period of 21 days (Wiktander et al. 1994). We counted nestlings and weighed them with a Pesola spring balance to the nearest 0.5 g when they were 17 days old. Data on nestling weight refer to the mean weight of the chicks in the brood. After fledging, we opened the nests and sieved the nest contents to look for unhatched eggs and dead young.

In 1990–1996, we observed the nestling feeding at most nests for two hours from a distance using a spotting scope, first when the young were 5–6 days old and again when they were 19 days old. Additional observations of feeding were made for at least one hour at some nests on days 1–8 and days 14–20. The time of each feeding visit and the identity of the feeding bird were recorded. In the following we refer to nests with 1–8 days old young as early stage and nests with 14–20 days old young as late stage. Only nests where we know that both parents were alive and where they fed without paying attention to the observer are included in the analyses.

Results

Social mating system

Our results concerning the mating system are based on 68 breeding attempts (involving 34 individual females and 33 males) that occurred in the years of most intense study, 1992–1997. In these years the majority of the breeding attempts (53 attempts, 77.9%) were by socially monogamous pairs, but in 11 attempts (16.2%) males had social pair bonds with polyandrous females and in four attempts (5.9%) females had social pair bonds with polygynous males (Table 1).

Social polyandry: incidence, breeding success and survival

The mean annual frequency of social polyandry among females in 1992–1997 was 8.5% (Table 2), and was exhibited by three different individuals (Table 1). Within the years with documented social polyandry, 10.0–14.3% of the females exhibited polyandry, and 16.7–33.3% of all breeding attempts involved a polyandrous female (Table 2). We documented social polyandry only in years when there was a male-biased sex ratio in the population (Table 2).

In the polyandrous matings, one female laid eggs in the nests of two, and in one case three, different males in the same season (Table 1). The nests were 1.4–3.0 km apart, situated in different territories which were occupied by successfully breeding monogamous pairs in other years of the study. The female first laid a full clutch in the primary nest, starting to lay in the secondary nest only 2–5 days after the first clutch was completed (Table 1). Thus, she started to lay the second clutch long before hatching of the first clutch. Socially polyandrous females laid 10–14 eggs in a season (Table 1) and fledged on average 6.4 young (Fig. 1) (under the minimum assumption of two fledglings from the secondary nest in 1997, Table 1). Primary males fledged on average 3.0 young and secondary males 3.2 young (assuming 4 fledglings in 1997, Table 1) (Fig. 1). Socially monogamous pairs that laid eggs in the same years as we observed polyandry raised on average 4.6 young (Fig. 1). There were significant differences among groups (ANOVA, $F_{2,40} = 6.39$, $P = 0.004$), and to compare the success of polyandrous and monogamous birds we performed two planned contrasts. Polyandrous females fledged significantly more young than monogamous pairs ($F_{1,40} = 4.42$, $P = 0.042$) and polyandrously mated males fledged significantly fewer

Table 1. The sequence and outcome of socially polygamous breedings in the Lesser Spotted Woodpecker. Cases are labelled by the year in which they occurred. The relative laying date of the eggs in the clutch is the date relative to the annual population median (= 0). Number of eggs in the full clutch, number of young fledged from each nest, the identity of the birds and the distance between the nests are shown in the last five columns. (s) beside the individual identity code means that the bird survived to the following breeding season, (n) that it did not.

	Nest no.	Rel. date of 1st–last egg in clutch	Clutch size	No. young fledged	Female	Male	Distance (km)
Polyandry							
1993	1	−4–1	6	5	A (n)	A (n)	2.3
	2	4–8	5	3		B (s)	2.4
	3	11–13	3	0		C (s)	1.8
1995	1	−1–3	5	0	B (s)	D (s)	2.8
	2	5–9	5	4		E (s)	
1996:A	1	0–5	6	0	B (s)	E (n)	1.4
	2	10–14	5	5		F (s)	
1996:B	1	5–8(10)	4–6[1]	4	C (n)	G (s)	1.6
	2	11–16	6	3		H (n)	
1997	1	−1–4	6	6	B (s)	F (s)	3.0
	2	9–10(12)	2–4[1]	≥2[2]		I (?)	
Polyandry							
1994	1	≤1–3[3]	3	0	D (n)	J (n)	1.8
	2	≤7–12[3]	6	0	E (n)		
1996	1	6–10	5	5	F (s)	D (s)	2.8
	2	6–11	6	6	G (s)		

[1] Nest found after hatching. Shown is the minimum clutch size (i.e. = number of fledglings) and a possible clutch size considering the overall seasonal trend of clutch sizes in the population (Wiktander 1998).

[2] The exact number is not known, the minimum number is shown.

[3] The exact relative laying date is not known, the date shown is the latest possible.

Table 2. The annual sex ratio and incidence of multi-nest social polyandry in the Lesser Spotted Woodpecker population.

Year	No. of males	No. of females	Males/females	% females polyandrous	No. breeding attempts	% br. attempts with polyandry
1992	5	5	1.00	0.0	5	0.0
1993	10	7	1.43	14.3	9	33.3
1994	11	12	0.92	0.0	12	0.0
1995	12	10	1.20	10.0	12	16.7
1996	19	15	1.27	13.3	19	21.1
1997	11	10	1.10	10.0	11	18.2
Total	68	59	1.15	8.5	68	16.2

young than monogamous pairs ($F_{1,40} = 5.66$, $P = 0.022$). Nestling weight did not differ between primary (mean = 24.3 g, SD = 1.9, N = 3) and secondary polyandrous broods (mean = 24.7 g, SD = 3.3, N = 3) (ANOVA, $F_{1,5} = 0.020$, $P = 0.90$). Neither did nestling weight differ between monogamous (mean = 24.7 g, SD = 1.8, N = 27) and polyandrous broods (mean = 24.5 g, SD = 2.4, N = 6) (ANOVA, $F_{1,33} = 0.008$, $P = 0.93$). Of the socially polyandrous birds, 60% of the females, 60% of the primary males and 80% of the secondary males survived to the following season (Table 1).

Social polygyny: incidence, breeding success and survival

Two males were socially polygynous in 1992–1997, that is 2.9% of the males. In both these cases, one male formed social pair bonds with two females at different nests, 1.8 and 2.8 km apart (Table 1). The nests of the socially polygynous males were situated in different territories which were occupied by successful socially monogamous pairs in other years. In both cases, the male's two nests were rather synchronous, differing by 0–6 days in timing (for 1994 we do not know the exact laying dates) (Table 1). Both socially polygynous matings occurred in situations with an excess of females. In 1994 there was a female-biased sex ratio in the population (Table 2). In 1996, the female at the secondary nest first set out to breed with a male who was killed by a predator on the day their first egg was laid. The following day the polygynous male (D) was seen in the territory copulating with the female. Three days later the female started to lay a new clutch in the same nest.

In 1994, none of the clutches hatched (Table 1). In 1996, young were raised to fledging in both nests (Table 1). Nestling weight in the primary brood in 1996 (25.3 g) was similar to the mean nestling weight of socially monogamous broods (mean = 24.7 g, SD = 1.8, N = 27). On the other hand, nestling weight in the secondary brood was one of the lowest recorded (21.7 g). None of the birds involved in social polygyny in 1994 survived to the following year, whereas all three birds in 1996 survived to the following year (Table 1).

Partnership

On 29 occasions both the male and the female of a monogamous pair survived to the following season. In all but one of these cases, the same birds bred together also the second year, i.e. a divorce rate of 3.4% (sensu Rowley 1983). Among those that re-united were four pairs whose breeding failed in the first year and three pairs that laid no eggs in the first year. In the only case of divorce, a successful pair split after two seasons; the male remained in the territory and bred with a new female the following year, whereas the female moved to a neighbouring territory where she bred with a widowed male.

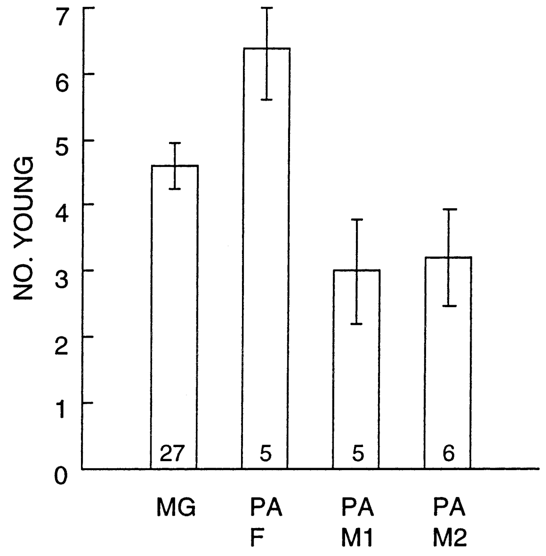

Fig. 1. Number of young fledged by socially monogamous and polyandrous Lesser Spotted Woodpeckers in 1993 and 1995–1997. Social pair bonds: MG = monogamous pairs, PA F = polyandrous females, PA M1 = primary males and PA M2 = secondary males. One standard error shown. Number of broods shown inside bars.

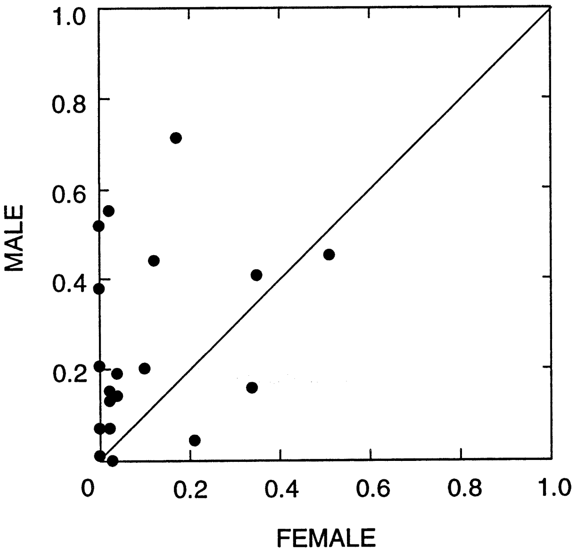

Fig. 2. The proportion of time male and female Lesser Spotted Woodpeckers spent nest excavating from 21 March to the time of oak bud burst (early–mid May). N = 21 monogamous pairs.

Relative contribution of male and female to parental care

Nest building

In all of the 125 breeding attempts that we monitored over the years, the birds excavated a new nesting hole in spring. To investigate the contribution of the sexes to nest building, we compared the proportion of time the male and female were excavating. In 17 out of 21 pairs monitored from 21 March to the date the oaks came into leaf (early–mid May), the male devoted more time to nest excavation than the female, and the mean proportion of time spent nest building was significantly larger in males (24%) than in females (10%) (Paired t-test on arcsin-transformed proportions, $t = 3.10$, $df = 20$, $P = 0.006$; Fig. 2).

Roosting behaviour

The male spent the night in the nesting hole at all but one of 66 inspections of 35 different nests over the years. The male started roosting in what became the nesting hole as soon as this was completed, $\geq 17-5$ days before the first egg was laid and continued to do so at least until the young were 15 days old. The only documented case where a female roosted in the nesting hole was the secondary female in 1996. (Her male spent the night in his primary nest, while the secondary nest was unattended at night until 1–2 days after the clutch was completed, and not until then did the secondary female start roosting there. Also in the 1994 polygyny did the male roost in his primary nest. In this case the secondary nest was probably never attended at night.)

In the 18 cases where we know where a socially monogamous female spent the night during breeding, she roosted in a hole 0.1–0.8 km from the nest. This was either the hole used during winter or a new hole made in spring. The roosting hole of three socially polyandrous females was situated in their primary territory, 1.7–3.0 km from their secondary nest.

Daytime incubation

At our regular daytime inspections of nests during incubation, we noted which individual was in the nest upon our arrival. We expect that the sum of these observations gives a good estimate of the participation of the sexes in incubation. Out of 91 observations from 52 different monogamous nests over the years, the male was in the nest on 43 occasions, the female on 48. Using only data from our first visit to each nest each year, the male was in the nest on 27 occasions, the female on 25. Neither of these two observed frequencies deviate significantly from an equal participation of the sexes in daytime incubation ($\chi^2_1 = 0.20$, $P = 0.66$ and $\chi^2_1 = 0.083$, $P = 0.84$, respectively).

Our data on incubation by socially polyandrous females are very limited and do not allow a quantification of participation at different nests. In two cases, 1995 and 1996:A (Table 1), the female was observed incubating in both her nests. In 1993 the female was only observed incubating in her primary nest, but this does not exclude that she also took part in incubation in her other nests. In 1996:B, the female was observed incubating in the secondary nest; the primary nest was found after hatching. In all socially polyandrous nests, the male was observed incubating.

The socially polygynous male in 1996 incubated in both his nests.

Nestling feeding

At the early nestling stage, the socially monogamous pairs fed their young on average 8.8 times per hour ($SD = 3.8$, $N = 51$ nests). At the late nestling stage, the feeding rate increased to 13.6 times per hour ($SD = 5.0$, $N = 28$ nests), which was significantly higher (ANOVA $F_{1,77} = 22.82$, $P < 0.001$). The feeding rate was also significantly influenced by the number of young (being

Table 3. ANCOVA of factors influencing nestling feeding rate (per hour) of socially monogamous Lesser Spotted Woodpeckers. Nestling age refers to the early stage (nestlings 1–8 days old) and the late stage (nestlings 14–20 days old).

Factor	df	F-ratio	P
Nestling age	1	12.38	0.001
Number of young	1	13.43	<0.001
Mean daily temp.	1	0.04	0.839
Time of day	1	1.66	0.201
Error	58		

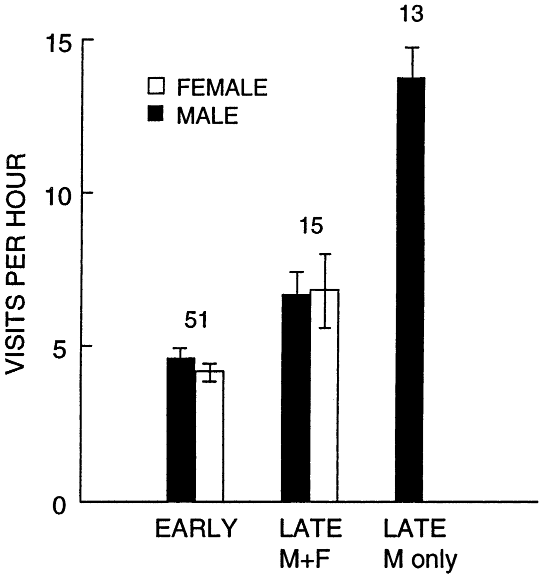

Fig. 3. Feeding rate per hour in socially monogamous male and female Lesser Spotted Woodpeckers during the early nestling stage (days 1–8) and the late nestling stage (days 14–20). 'Late M + F' represents the nests at the late stage where both parents fed, 'Late M' represents the nests at the late stage where only the male fed. Vertical lines represent one standard error. Number of nests shown above bars.

higher the larger the brood), but not by mean daily temperature or time of day (Table 3).

To examine the participation of the sexes in nestling feeding, we compared their feeding rates at nests where we know that both birds were alive. In monogamous pairs, at all nests both parents fed during the early nestling stage and there was no significant difference in feeding rate between the sexes (Paired t-test, $t = 1.43$, $df = 50$, $P = 0.16$) (Fig. 3). At the late stage, the male fed significantly more often than the female (Paired t-test, $t = 3.83$, $df = 27$, $P = 0.001$). This difference was, however, solely due to the fact that the female ceased feeding at the late stage in 42% of the pairs; looking only at pairs where both birds fed, there was no difference between the sexes (Paired t-test, $t = 0.28$, $df = 14$, $P = 0.78$) (Fig. 3). The number of young in nests where the female stopped feeding at the late stage did not differ from nests where she fed (ANOVA $F_{1,26} = 0.69$, $P = 0.41$). Still, the rate of feeding visits to nests where the male fed the young alone did not differ from nests where both parents fed (ANOVA $F_{1,26} = 0.77$, $P = 0.39$), showing that the male fully compensated for the absent female (Fig. 3). Our first observations of non-feeding females was from nestling age 14 days.

All socially polyandrous females were observed feeding at all their nests. Their feeding rate did not differ between primary and secondary nests (ANCOVA with nestling stage as a factor and number of young as a covariate, the effect of nest status: $F_{1,9} = 1.98$, $P = 0.19$). Hence, socially polyandrous females devoted the same feeding effort to all their nests. The female, however, fed less frequently than the male at most polyandrous nests (Fig. 4). In the four cases where the female was not feeding during our observation (Fig. 4), we know she attended her other nest. At both the early and the late stage, the difference in feeding rate between the sexes was close to significant (Paired t-test, $t = 2.18$, $df = 9$, $P = 0.058$ and $t = 2.98$, $df = 3$, $P = 0.059$, respectively) (Fig. 4). For both stages combined males had significantly higher feeding rates than females (Paired t-test, $t = 3.27$, $df = 13$, $P = 0.006$). This difference was not entirely due to the cases where the female was attending her other nest during our observation period. Analysing only the cases where the female participated in feeding, the male still fed more frequently (Paired t-test, $t = 2.30$, $df = 9$, $P = 0.047$). In spite of the female's lower participation, the total feeding rate at polyandrous nests did not differ from that at monogamous nests (ANCOVA with nestling stage as a factor and number of young as a covariate, the effect of mating system: $F_{1,88} = 0.31$, $P = 0.58$), showing that the male compensated for the female's lower attendance.

The socially polygynous male in 1996 fed the young in his primary nest throughout the nestling stage. On the other hand we never saw him feeding at the secondary nest, and he apparently deserted this brood after the eggs hatched.

Brooding

Until the young were at least 8 days old, parents usually stayed in the nest brooding the young after feeding until the partner arrived. We have no observations from nests with 9–13 days old young, but at least

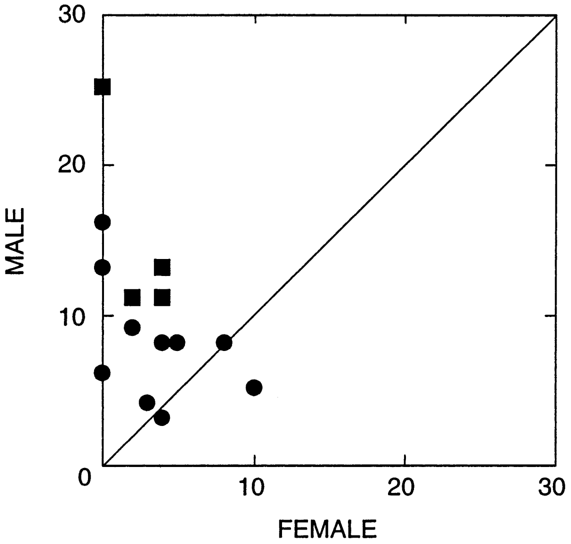

Fig. 4. Feeding rate per hour in socially polyandrous male and female Lesser Spotted Woodpeckers. Filled circles represent the early nestling stage (days 1–8), squares the late stage (days 14–20).

Table 4. Multiple regression analysis of variables influencing the proportion of time parent Lesser Spotted Woodpeckers spent brooding 1–8 days old young. Monogamous nests only. Overall model statistics: $r_{44} = 0.72$, $P < 0.001$.

Variable	t	P
Age of young	−5.22	<0.001
Number of young	−2.66	0.011
Mean daily temp.	−3.35	0.002
Time of day	−1.89	0.065
Constant	9.23	<0.001

from day 14, parents entered the nest after feeding only to collect faecal sacs. At monogamous nests, an adult bird was in the nest brooding on average 66% of the time during days 1–8. Brooding time, however, decreased significantly with age of the young, from nearly 100% on the first two days to about 50% on days 7–8 ($r_{46} = -0.48$, $P = 0.001$). The proportion of time brooding also decreased with number of young in the nest and with mean daily temperature and tended to decrease in the course of the day (Table 4).

The mean time spent brooding per feeding visit at monogamous nests did not differ significantly between males (mean = 355 s, SD = 246) and females (mean = 384 s, SD = 281) (Paired t-test, $t = 0.92$, $df = 46$, $P = 0.36$), showing that the brooding of young nestlings was shared equally by the parents.

The proportion brooding time in polyandrous nests (mean = 0.60, SD = 0.23) was not significantly different from monogamous nests (mean = 0.66, SD = 0.21) (ANCOVA, with the four variables in Table 4 as covariates, the effect of mating system: $F_{1,48} = 0.12$, $P = 0.74$).

Post-fledging care

Our data on parental care after fledging unfortunately are very limited. All parents equipped with radio-transmitter after the young fledged (7 males and 9 females) were observed feeding fledglings, however, indicating that post-fledging care was shared by both parents. This includes five females who ceased feeding at the late nestling stage, suggesting that non-feeding females did not abandon the brood altogether but resumed care after fledging. We have observations of parents feeding young 14 days after fledging (3 broods). Still at this time the young appeared highly dependent upon food brought by the parents, and it seems likely that the time until independence may be far longer than this.

Discussion

Value of biparental care

In agreement with the general view (Short 1982, Ligon 1993, Winkler et al. 1995) the results of this study show that biparental care, at least during incubation and brooding, appears to be necessary for raising a brood in woodpeckers. This is further supported by the fact that all birds in our study population that were widowed during incubation and brooding (6 males, 6 females) gave up the breeding attempt (Wiktander 1998). This contrasts to the situation in, e.g. passerines, where experiments in which the male has been removed have shown that attendance by both parents may be beneficial but is generally not necessary for successful breeding (Wolf et al. 1988, Bart and Tornes 1989).

The necessity of biparental care in woodpeckers has been thought to preclude either form of social multi-nest polygamy (Short 1982, Ligon 1993, Winkler et al. 1995). However, we documented both multi-nest (classical) polyandry and multi-nest polygyny in the Lesser Spotted Woodpecker. Multi-nest social polyandry was achieved through an even division of parental care among the nests by the female and increased care by the males. Also socially polygynous males divided parental care between their nests, but less evenly. We expect that multi-nest social polygamy, and perhaps social polyandry in particular, may occur facultatively also in other single-brooded woodpecker species, as suggested by the observation of Kotaka (1998). Without the birds individually marked and a thorough knowledge of the distribution of potential territories, social polygamy is easily overlooked, however, and when individual birds are as mobile as in our study, may be impossible to detect without the aid of radio-transmitters.

The growing body of data from molecular studies on birds has revealed that there is often a discrepancy between the social and the genetic mating system, due to extra-pair paternity (EPP) (Gowaty 1985). The level of EPP, however, shows considerable variation between species (Birkhead and Møller 1992). In species where male assistance in parental care is essential for female reproduction, Birkhead and Møller (1996) predicted that levels of EPP would be low, because females can be expected to be less likely to engage in extra-pair copulations because of the risk of losing the male's help. In view of the apparent importance of biparental care, levels of EPP can be expected to be low in woodpeckers. Michalek (1998) found two extra-pair fertilised young (3.3% of all young) in one out of 37 broods of the Great Spotted Woodpecker *Dendrocopos major*, and none in any of 13 broods of the Middle Spotted Woodpecker *Dendrocopos medius*. A preliminary analysis of DNA fingerprinting of nine socially monogamous broods in our study population in 1996 revealed no extra-pair fertilised young (U. Wiktander, O. Olsson, M. Wink and H. Staudter unpubl.). This was true also for the four polyandrous broods and both polygynous broods in 1996. Hence, the social mating system may actually correspond with the genetic mating system in this population of Lesser Spotted Woodpeckers.

Social polyandry

We documented socially polyandrous females on five occasions, in four out of six years. Together with two cases discovered in Hessen, Germany in 1996 and 1998 (K. Hoentsch, pers. comm.), these are the first records of multi-nest social polyandry in the Lesser Spotted Woodpecker known to us. Admittedly, the number of observations is low, but the repeated occurrence both in our population and the population studied by K. Hoentsch in a totally different area, indicates that multi-nest social polyandry is recurrent in this species.

These observations of multi-nest social polyandry are also among the very few in altricial birds overall. We have found reports of its occurrence in Black Coucal *Centropus grillii* (Vernon 1971), Dwarf Cuckoo *Coccyzus pumilus* (Ralph 1975), Northern Mockingbird *Mimus polyglottos* (Fulk et al. 1987), American Goldfinch *Carduelis tristis* (Middleton 1988), Redpoll *Carduelis flammea* (Seutin et al. 1991), West Indian Woodpecker *Melanerpes superciliaris* (Willimont et al. 1991), Sedge Warbler *Acrocephalus schoenobaenus* (Hasselquist and Langefors 1998) and Great Spotted Woodpecker (Kotaka 1998). The socially polyandrous females in our study laid their clutches in rapid succession, starting to lay the second clutch only 2–5 days after the first clutch was completed. According to the classification of Oring (1986), they exhibited simultaneous polyandry and this applies also to the Black Coucal, Dwarf Cuckoo and Great Spotted Woodpecker. In the other species, socially monogamous pairs occasionally raise a second brood in a season. In the socially polyandrous cases, the female helped rearing the young in the first brood to near fledging or independence and then started the second brood with a new male. Middleton (1988) and Willimont et al. (1991) interpreted the female's desertion of the first brood near fledging as a strategy to be able to start the second brood earlier. According to Oring (1986), these species exhibit sequential social polyandry.

Mating systems should be regarded as outcomes of behaviours of individuals competing to maximise their fitness (Davies 1991). A prerequisite for socially polygamous mating is that one individual can economically monopolise access to several mates of the opposite sex (Emlen and Oring 1977). The opportunities for such monopolisation vary in relation to, e.g. the organisation of parental care, patterns of settlement and levels of intra-sexual competition (Davies 1991). In the Lesser Spotted Woodpecker, the occurrence of social polyandry varied in relation to the population's sex ratio, and was expressed only in years when there was an excess of males (see also Oring 1986). This may be a consequence of the apparently strong intra-sexual competition in this species; in the breeding season, established males and females are highly territorial and are seemingly prepared to spend a considerable amount of time and energy in disputes with same-sexed intruders. Intensive fights may last for hours and even extend over days (own observations). Hence, in situations with an equal sex ratio, the monopolisation of several males is probably too costly due to intra-sexual competition, which limits the opportunity for social polyandry. Therefore, a male-biased sex ratio is likely a prerequisite for a Lesser Spotted Woodpecker female to economically monopolise several males. However, it is likely the deficit of females, rather than the excess of males, that matters for economic monopolisation; in the polyandrous associations we observed, primary and secondary males occupied different exclusive territories, whereas polyandrous females expanded their territory to encompass the territories of several males.

From the females' perspective, social polyandry was successful. On the other hand, both primary and secondary males fledged fewer young and were less assisted by the female in parental care than the average socially monogamous male. A question then is why males decided to associate with an already mated female. A likely reason is that no other females were available, leaving males no other alternative but to mate with an already mated female if they were to breed at all in that season. The fact that socially polyandrous females divided care equally between their nests and the very long distance between the nests also make it tempting to speculate that males were unaware of their status and that they were deceived by the females (cf. Alatalo et al. 1981, 1982). Our presently available data do not, however, allow us to pursue this idea further.

Social polygyny

Social polygyny occurred less regularly than social polyandry and we documented it only twice. As far as we know, this is the first documentation of multi-nest social polygyny in woodpeckers. Both cases occurred in situations with an excess of females, suggesting that this was a prerequisite, for the same reasons as discussed concerning polyandry. Although our data are very limited, polygynous males, in contrast to polyandrous females, invested mainly in the primary nest and were less successful than polyandrous females. Our results support the view of male nocturnal incubation as a conservative (but apparently not completely inflexible) behaviour and a possible limit to successful social polygyny (cf. Ligon 1993, Winkler et al. 1995).

Organisation of parental care under social monogamy

Also in socially monogamous pairs did the male contribute more care overall than the female. A major difference was in chick feeding at the late nestling stage, when over 40% of the females deserted the brood. Males responded to this by increasing their feeding rate to fully compensate for the absent females. If there are costs in terms of lowered survival associated with parental care, the question is why males accepted such an increased workload. Males are expected to assume the bulk of parental care only when this increases their individual fitness (Emlen and Oring 1977). If the physical condition of the female is of direct importance to male fitness and reproductive costs are larger for females than males, males are expected to benefit from assuming a larger share of parental care (Emlen and Oring 1977, Houston and Davies 1985). Three findings support this explanation for the organisation of parental care in the Lesser Spotted Woodpecker. First, the woodpeckers in this study showed a very strong mate fidelity, and Wiktander (1998) found that pairs that bred together for consecutive years were significantly more successful (started egg-laying earlier and produced more fledglings) than newly established pairs. Because new pairs consisting of two old birds also had lower breeding success than stable pairs (Wiktander 1998), there clearly was a high premium on staying together. Hence, the fitness of the male is likely to be closely linked to the physical condition and survival of the female. Second, a survival cost of reproduction is suggested by the observation that individuals widowed during egg-laying or incubation that subsequently abandoned breeding, had higher survival than individuals that raised young to fledging (Wiktander 1998). Third, females had lower survival than males (Wiktander 1998) and this appeared to be related to their higher energy demands during the breeding season (Olsson 1998, Wiktander 1998), indicating a higher reproductive cost in females. Hence, the females' offspring-desertion behaviour may be regarded as an adaptive life-history decision (Székely et al. 1996). In conclusion, the high premium on breeding with the same mate for consecutive years, coupled with the difference in life history between males and females, may have shaped the male-biased organisation of parental care in the Lesser Spotted Woodpecker.

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