
Sexual differences of labour during breeding activities and territory use in the Lesser Spotted Woodpecker *Dendrocopos minor*

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The breeding activities and spatial use of territory in the nearly monomorphic Lesser Spotted Woodpecker *Dendrocopos minor* were studied in a subalpine forest in central Norway. The male tended to take a greater share than the female in nest construction (65 %) and nestling feeding (64 %), whereas their contribution was nearly equal in the incubation period (male 52 % vs female 48 %). During the last ten days the young were in the nest, the male fed the nestlings 6.9 times/h, significantly more often than the female (5.6 times/h). The two sexes showed little spatial overlap in their territory during the nestling period, suggesting that male and female Lesser Spotted Woodpeckers practise horizontal separation of their territory.

Key words: Lesser Spotted Woodpecker; sexual differences; breeding activities; territory use

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INTRODUCTION

Most birds are monogamous and both parents usually provide parental care, although there is often a bias towards the female investing more than the male (Black 1996). However, the sex roles are reversed in woodpeckers and males invest most heavily in breeding activities, i.e. nest construction, incubation and brooding of the young, and feeding of nestlings (Short 1982, Winkler *et al.* 1995, Wiebe & Elchuk 2003). Woodpeckers are also exceptional in that females practise classical polyandry, i.e. they nest with two or more males. Polyandry has recently been documented in many woodpecker species that have been considered as monogamous, and

reports of classical polyandry are accumulated as populations are studied in detail (e.g. Mumme *et al.* 1990, Willimont *et al.* 1991, Kotaka 1998, Wiktander *et al.* 2000, Wiebe 2002, Pechacek *et al.* 2006). If polyandrous females divide their effort in feeding nestlings in several nests, males have to compensate for the reduced contribution of females.

The Lesser Spotted Woodpecker *Dendrocopos minor* is generally monogamous and pair-bond may extend over several years. However, in a comprehensive study in a lowland forest in southern Sweden, Olsson (1998) and Wiktander (1998) recorded an excess of males in most years, and on average 16% of females were then poly-

androus. Males in these pairs devoted more time to breeding activities than females, especially in feeding the nestlings (Wiktander *et al.* 2000). In the present study, I report sexual differences in the breeding activities of Lesser Spotted Woodpeckers living in a subalpine forest in Norway. The species does not breed annually in the area, and I have never found more than one nest in a year. As the possibility for polyandry therefore probably can be ignored, the breeding activities actually recorded should be representative for monogamous pairs of the Lesser Spotted Woodpecker.

Incubation and parental care may be an energetic bottleneck in many birds (Nilsson 1994) and the Swedish study revealed that the survival of adult Lesser Spotted Woodpeckers that raised young was lower than for birds that did not (Wiktander 1998). Lesser Spotted Woodpeckers living in subalpine forests with unpredictable weather conditions may have difficulty obtaining sufficient food for their own requirements and for their growing nestlings within a reachable radius of the nest. Contrary to sexual dimorphic woodpeckers that may reduce competition by differences in foraging behaviour (e.g. Peters & Grubb 1983, Hogstad 1991), it may be suggested that the foraging behaviour of the nearly monomorphic Lesser Spotted Woodpecker (Cramp 1985) should result in intersexual competition, leading to a low spatial overlap between the sexes. This paper gives some information on the way birds use their territory during the nestling period.

MATERIAL AND METHODS

The study was carried out in a mixed, subalpine (altitude 550-650 m) forest of Scots pine *Pinus silvestris* and birch *Betula odorata* in Budal, 90 km south of Trondheim, in central Norway from 1986 to 2005. Scattered Norway spruce *Picea abies*, aspen *Populus tremula* and rowan *Sorbus aucuparia* trees also occur, and grey alder *Alnus incana* and willow *Salix caprea* are relatively common along rivers and streams. The study area was approximately 10 km².

Most of the study area is still covered by snow in early May, but the area is normally snow-free by the last days of the month. During the study period, the mean temperature in May varied between 3.1 and 9.4 °C, in June between 6.7 and 12.6 °C with a daily temperature between -3 and +25 °C. In some years, up to 6 days in June had a temperature below zero and 7 days experienced snowfall. Most winters have several periods with temperatures between -15 and -25 °C.

The majority of the woodpecker observations were in moist parts of the forest, mostly along rivers or streams with large amounts of decaying wood, mainly birch and grey alder (Fig. 1). In some years, I searched for Lesser Spotted Woodpeckers using playbacks in February-April. Even though the woodpeckers responded to the playbacks with drumming or series of calls, I frequently did not observe the birds, probably due to their inconspicuous behaviour.

A total of 11 nests were found. At each visit to the nest tree, I recorded the sex of the bird that was observed excavating the nesting hole, that left the nest tree upon my arrival in the egg laying and incubation phase, and that fed the nestlings. To increase sample independence, I recorded each individual only once per day at six of the nests, in total 48 records. As only the first observation of the bird was recorded, the sum of these observations should give a fair estimate of the participation of the sexes in the reproduction (cf. Wiens *et al.* 1970). Five nests were inspected regularly with up to three records per day, always separated by more than one hour: 165 such records were made. At four of these nests, I recorded for one hour on each of two days the number of visits by the parents to feed their nestlings and the sex in each case. The feeding observations were made during the ten-day period before the young left the nest.

Two males were caught in mist nets close to their nest tree in May 1996 and 1998, respectively. Both were ringed with colour rings and were later recorded foraging in their territories during the time they had young in their nest.



Figure 1. The majority of the woodpecker observations were made along rivers or streams. Photo: Olav Hogstad.

All tests are two-tailed, and were performed using SPSS 15. Data were analysed using nonparametric tests. Mean are presented ± 1 SD.

RESULTS

Contribution in breeding activities

All nests found were excavated in dead tree stumps, height 2.5 – 3.5 m, situated in moist areas near a river or stream. These areas had a high density of dead or dying trees, suitable as nest trees. Nine nests were in grey alder and one nest each in birch and aspen.

Although the sample size from the six pairs observed irregularly is small, the distribution of the contribution by the sexes to nest excavation, incubation and nestling feeding corresponds with that found for the five pairs observed regularly (Table 1). Thus, the combined records show that the male Lesser Spotted Woodpecker tended to

take a greater share than the female in nest construction (65 %) and nestling feeding (64 %), whereas their contribution was nearly equal in the incubation period (males 52 % vs females 48 %; Fig. 2). The difference between the sexes, however, is statistically different only in the feeding phase (Sign Test, $p < 0.001$).

During their last ten days in the nest, the nestlings were fed significantly more often by the male (6.9 ± 0.8 times per hour, $n=8$) than by the female (5.6 ± 0.7 times per hour, $n=8$; Mann-Whitney Test, $z=-2.52$, $p=0.015$).

Territory use in the nestling period

The male colour ringed in 1996 (male 1) was mated and was always recorded close to the nesting place, within an area of approximately 400 m x 600 m. He was observed foraging within this area 12 times, and no female was seen in the same area. The female mated to male 1 was observed in another area close to the nest tree. Although

Table 1. Distribution of the effort of the sexes in nest construction, incubation and feeding nestlings based upon data from five regularly and six irregularly inspected nests.

	Male		Female	
	%	(n)	%	(n)
Excavating				
Nest inspected regularly	60	(15)	40	(10)
Nest inspected irregularly	83	(5)	17	(1)
Total	65	(20)	35	(11)
Incubating				
Nest inspected regularly	50	(12)	50	(12)
Nest inspected irregularly	56	(5)	44	(4)
Total	52	(17)	48	(16)
Feeding nestlings				
Nest inspected regularly	64	(74)	36	(42)
Nest inspected irregularly	58	(19)	42	(14)
Total	64	(93)	36	(56)

she was not ringed, it is reasonable to believe that the seven records of a female in this area concerned the same bird. Male 1 was observed in this area once, indicating that the pair utilised separate areas when foraging and finding food for their nestlings (Fisher's Exact Test, $p < 0.001$). The other ringed male (male 2) was caught close to his nesting tree about 200 m from the nest found in 1996. Male 2 was also mated and was observed within approximately the same area as male 1 during the breeding period in 1998 and once in March 1999. The total area where he was observed during the nestling period was about 300 m x 600 m. The record from March 1999, however, was about 1 km from the nesting area. Male 2 was seen foraging in the area eight times and no female was observed in this area. The female mated to male 2 was observed five times within a small area near the nest tree, and male 2 was recorded in this area once. Thus, this pair apparently also utilised separate foraging areas ($p = 0.003$). Both females foraged in an area that had more dead grey alder trees than the areas used by the males.

Male and female Lesser Spotted Woodpeckers were observed at the same time only in the

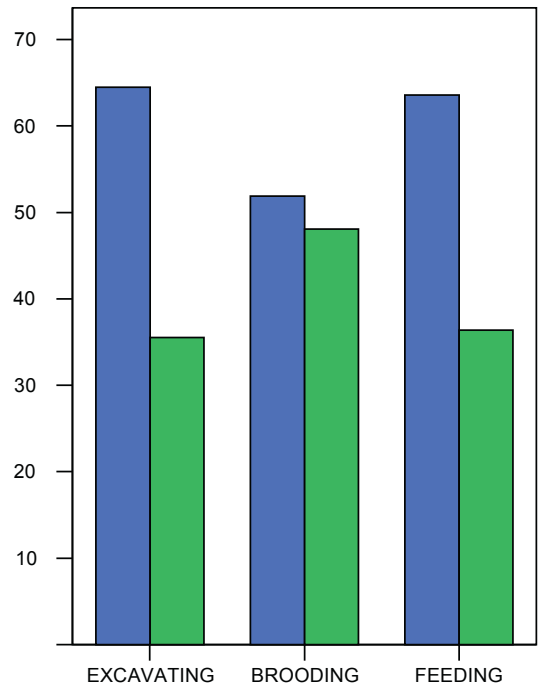


Figure 2. Distribution (%) of male (blue) and female contributions to nest construction ($n = 31$), incubation and brooding ($n = 33$) and feeding of nestlings ($n = 149$).

breeding phase, and then always in the vicinity of their nest tree. Even then, the birds seemed to maintain some distance from each other. When the parents arrived at the nest tree with food for their nestlings, they came from different directions, each bird from the same part of the forest. After they had fed their young, they left the nest area in the direction they entered. This may suggest that the parents found food in different parts of their territory. This suggestion is strengthened by observations of the colour ringed males that were always seen foraging in the same area, whereas a female was never observed in that area. It may therefore be suggested that the sexes of all these Lesser Spotted Woodpecker pairs practised horizontal separation of their territory, at least during the nestling phase.

DISCUSSION

The male Lesser Spotted Woodpecker took a larger share in breeding activities than the female, as also found by Wiktander *et al.* (2000) in southern Sweden. Both in the subalpine forest in Budal and the Swedish lowland forest, the Lesser Spotted Woodpecker male apparently devoted more time than the female to nest excavation and feeding nestlings, whereas incubation and brooding was shared nearly equally by the sexes. However, in the Swedish study, females took an equal share in incubation and brooding in daytime and in feeding nestlings in the early stage. In more than 40 % of the nests, the females stopped feeding at the late nestling stage, and the male responded by increasing his feeding rate (Wiktander *et al.* 2000). However, in areas where the Lesser Spotted Woodpecker is far more abundant than in the subalpine forest in Budal, the smaller contribution by the females in breeding activities may to some degree be explained by the polyandrous system, and that the females may benefit from spending more time looking for mates (Olsson 1998, Wiktander 1998).

Moreover, egg production takes its toll. Females seem to have greater energetic demands than

males during the pre-breeding and breeding periods, mostly because they produce eggs and this is energetically rather costly (Monaghan & Nager 1997). Females are therefore probably forced to rate energy higher than males do (Olsson 1998). The skewed distribution of the effort which the sexes put into nest construction and nestling feeding found in the present study may therefore partly be explained by a higher energy demand for the females. Fitness costs incurred at the time of egg production and egg laying depend strongly on environmental conditions, such as ambient temperature (Hogstad & Stenberg 1997, Visser & Lessels 2001). The harsh climate in the Budal area may therefore influence the contribution of Lesser Spotted Woodpecker females to breeding activities. The reproductive success may be related to the food availability long before breeding, and because foraging is the most dangerous activity for woodpeckers, this may explain the observation that females suffer higher mortality prior to egg laying (Olsson 1998). The females thus pay a high cost for the increased energy gains.

Male and female Lesser Spotted Woodpeckers were never observed foraging together, except close to the nest tree. The different arrival and departure directions of the sexes may indicate separate foraging areas, at least during the nestling period.

Since the foraging patterns of the sexes seem relatively similar (Hogstad 1978, unpubl. data), an adoption of mutually exclusive territories, or at least maintaining a low spatial overlap, during the nestling period may be regarded as an adaptation to secure food supply without energy-wasting conflicts over foraging sites. Similar findings have been reported for the Three-toed Woodpecker *Picoides tridactylus* (Hogstad 1976), White-backed Woodpecker *Dendrocopos leucotos* (Aulén 1988) and Middle Spotted Woodpecker *Dendrocopos medius* (Pettersson 1984, Pasinelli 2000). As suggested for the Lesser Spotted Woodpecker in Budal, Pettersson (1984) found that the Middle Spotted

Woodpecker, a species showing a low degree of sexual dimorphism, tended to forage close to the territory border while the female foraged more in the parts richer in oaks (preferred tree species) in the centre of the territory. Among sexually dimorphic woodpeckers, however, intersexual segregation of the habitat has been reported to be vertical, the larger males with a longer bill than females foraging lower in trees with a larger stem diameter (e.g. Ligon 1968, Jackson 1970, Peters & Grubb 1983, Hogstad 1978, 1991).

Although the mates of Lesser Spotted Woodpeckers were rarely seen together and probably created few conflict situations over food resources, the sexes differed in foraging technique: males used bark pecking and probing more than females, which most often picked prey off the surface of trunks or branches (Hogstad unpubl. data). Even though males and females showed small differences in foraging niche dimensions in the subalpine forest in Budal, the intersexual overlap was smallest during the pre-breeding and breeding periods (Hogstad unpubl. data). These foraging differences may be interpreted as niche segregation, which is thought to reduce food competition between the sexes. Such sex-specific niche segregation may be a result of social dominance, as suggested for several *Picoides* species (e.g. Ligon 1968, Hogstad 1976, Peters & Grubb 1983). However, the slightly larger male was not observed behaving dominantly to his mate. The only two cases that gave a hint of male dominance, was when both sexes arrived at the breeding tree simultaneously and the female waited to enter the nest hole until the male had fed the nestlings and left the tree. In addition, I earlier observed a male chase a female that maintained a neighbouring winter territory (Hogstad 1978). Because the Lesser Spotted Woodpecker inhabits large territories (Wiktander 1998) and apparently most often forages singly, the apparently intersexual segregation of foraging niche recorded during the nestling phase is hardly influenced by social dominance.

To sum up, the significantly lower contribution of females than of males in feeding nestlings may be

due to higher energy demands of females than of males, leading to females being forced to prefer energy prior to nestling care. This may be related to monogamous as well as polyandrous females. The apparently intersexual horizontal separation of the territory of the nearly monomorphic Lesser Spotted Woodpecker in the nestling phase is difficult to explain, but a reduction of competition due to social dominance cannot be excluded.

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SAMMENDRAG

Forskjellig arbeidsinnsats av kjønnene hos dvergspett ved hekkingen og forskjellig bruk av territoriet.

En undersøkelse av hekkende dvergspettpar i en fjellskog i Budal, Sør-Trøndelag, viste at hannens gjennomsnittlige innsats ved reirhacking (65 %) og mating av reirunger (64 %) var større enn hunnens, mens paret delte jobben mer likt ved rugingen (hannen 52 %, hunnen 48 %). I løpet av ungenes siste 10 dager i reiret, matet hannen ungene 6.9 ganger/time, klart oftere enn hunnens 5.6 ganger/time. I denne tida ble hannen og hunnen alltid sett i forskjellige deler av territoriet, og det antas at paret delte territoriet mellom seg, muligens for å redusere konkurranse om føden.

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