

Reproductive success and nestling diet in the Lesser Spotted Woodpecker (*Picoides minor*): the early bird gets the caterpillar

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Received: 20 June 2006 / Revised: 19 February 2007 / Accepted: 21 February 2007 / Published online: 17 April 2007
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Abstract Populations of Lesser Spotted Woodpecker (*Picoides minor*) are decreasing in size, necessitating management strategies. However, data on the reproductive biology of this species are scarce. The aim of this study was to investigate the influence of timing of breeding and nestling diet on the reproductive success of the Lesser Spotted Woodpecker and thereby contribute to an understanding of the determinants influencing its reproductive success. During 6 study years between 1996–2003, we investigated various variables of reproductive success in a Lesser Spotted Woodpecker population in the Taunus low mountain range, Germany. We observed nestling feeding at breeding holes to assess the composition of nestling diet and how it changes during the season. Clutch size, number of fledglings as well as body mass of the nestlings declined with the start of egg laying. Pairs composed of individuals that had breed together in previous years started egg laying earlier than newly established pairs. Nestling diet consisted mainly of aphids, caterpillars, craneflies and wood-living larvae. The composition changed considerably within the breeding season in both early and late broods. However, early broods were provided with caterpillars more frequently, whereas late broods received wood-dwelling larvae more often. Our results suggest that Lesser Spotted Woodpeckers time their breeding so as to coincide with the early nestling stage with the highest availability of cater-

pillars, since this is the time of highest energy demand. Moreover, food availability declines during the breeding season, and the decline in reproductive performance seems to be an effect of this development.

Keywords Clutch size · Nestling diet · *Picoides minor* · Reproductive success · Timing of breeding

Introduction

The Lesser Spotted Woodpecker (*Picoides minor*) is widely distributed over the whole Palaearctic continent (Cramp 1985; Glutz von Blotzheim and Bauer 1994). An alarming development in the form of a dramatic population decline has been reported in Sweden and Finland (Tiainen 1985; Nilsson et al. 1992), and a similar trend is assumed for many European countries (Mikusinski and Angelstam 1997). The underlying factors determining this negative population development remain unclear as, despite its wide distribution range, Lesser Spotted Woodpeckers are difficult to study due to their low density, small size and inconspicuous behaviour (Wiktander 1998). It is therefore not surprising that many aspects of its biology and ecology are still unknown. However, data on the demographic parameters of this endangered species are urgently needed in order to gain an understanding of the critical factors affecting its dynamics. One of the most important parameters for estimating population viability is reproductive success (Haig et al. 1993). Reproductive success can be influenced by several factors, such as resource availability or weather conditions. In birds, food supply during the brood care period is one of the main determinants of reproductive success (Van Balen 1973; Perrins 1991; Brinkhof 1997; Naef-Daenzer and Keller 1999). However,

Communicated by F. Bairlein.

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all of the available data to date on the composition of the nestling diet in the Lesser Spotted Woodpecker is anecdotal or has been gathered at single nests (Pynnönen 1943; Török 1990; Wiklander 1998). It is known that Lesser Spotted Woodpeckers change their foraging behaviour during the breeding period from preying only on wood-dwelling insects to additionally searching for surface-dwelling arthropods, such as caterpillars (Olsson 1998; Wiklander 1998). The developmental cycle of caterpillars is strongly synchronised with the development of tree foliage in early spring (Feeny 1970), and the peak of abundance of caterpillars in terms of duration and timing is influenced by ambient temperature (Perrins 1991). Consequently, within a short time window, an almost endless amount of energy-rich food is available to the Lesser Spotted Woodpecker. Therefore, it should be a great benefit to the Lesser Spotted Woodpecker to synchronise the timing of breeding to the abundance of the caterpillars, as has been found in Great Tits (*Parus major*) (Van Balen 1973; Perrins 1991; Naef-Daenzer et al. 2000) and Blue Tits (*Parus caeruleus*) (Dias and Blondel 1996).

The timing of breeding has been shown to influence reproductive success in several bird species; in general, the later the initiation of breeding, the lower the observed reproductive success (Verhulst et al. 1995; Siikamäki 1998; Naef-Daenzer et al. 2001; Arnold et al. 2004). There are two not mutually exclusive explanations for seasonal decrease in reproductive success. First, the timing of breeding per se could be the causal factor, due to seasonal variations in the environment, which mostly take the form of a deteriorating food supply (timing hypothesis; Klomp 1970; Murphy 1986; Ens et al. 1992; Brinkhof 1997; Siikamäki 1998). Alternatively, the decrease in success within season could be caused by variations in the quality of the birds, with high-quality parents breeding early on good territories and poor-quality parents breeding later on poor territories (quality hypothesis; Price et al. 1988; Verhulst et al. 1995).

Recent studies have shown that climate changes also influence the onset of breeding, which in turn affects the reproductive success of the population (Visser et al. 1998; Bergmann 1999; Both et al. 2006). To understand how changes in environmental conditions due to climate change or habitat loss affect reproductive success, we need to gain insights into the relationships between timing of breeding and food supply of nestlings. Therefore, the aim of our study was to investigate reproductive success and composition of the nestling diet of a Lesser Spotted Woodpecker population in Germany. Since the timing of breeding is a crucial variable, we focused on gaining an understanding of the relationship between timing, food supply and reproductive success. Based on these findings, we discuss whether the timing or the quality hypothesis can be used to describe the current situation in this species.

Methods

Study area

The study was conducted in an area of 70 km² in a German low mountain range near Frankfurt/Main (Taunus). The study area is situated in a heterogeneous landscape with deciduous, mixed and coniferous forest, large areas of settlement and grassland as well as extensively used orchards. The area contains 12 Lesser Spotted Woodpecker territories, which were not all occupied in all of the study years.

Reproductive parameters

To investigate reproductive success, we collected data for six reproductive parameters: (1) laying date – defined as the date of the first egg in the clutch; (2) nesting success – defined as the proportion of pairs that fledged at least one young; (3) clutch size – the number of eggs in the full clutch; (4) fledgling success – the number of fledglings in successful nests; (5) body mass of nestlings; (6) duration of nestling period – defined as the time from the day the first nestling hatched to the day the young left the nest.

Laying date and size of the full clutch were determined by inspecting the breeding hole at least twice during the laying period, using a dentist's mirror and a small lamp. The exact laying date could then be calculated, based on the assumption that the females lay one egg per day (Wiklander 1998). To control for annual differences in timing, we set the annual median laying date of the population to zero and calculated the "relative laying date" for each pair using the deviation from 'time zero'. We refer to broods that were started before or on the median date as "early broods"; broods initiated later are referred to as "late broods".

The hatching date of nestlings was determined by inspecting the nest each day from the 9th day of incubation onwards. On the 16th nestling day, the nest chamber was opened, and the nestlings were counted and weighed with a Pesola spring balance (Pesola, Geneva, Switzerland) to the nearest 0.5 g. Nestlings were then marked with a metal ring and an individual combination of two colour rings for later identification. We decided in favour of the 16th day, since younger nestlings might be too small and lose the rings and older nestlings might try to escape their hole after having been put back (own observation). The number of young present in the cavity on day 16 was defined as fledging success, if no signs of predation were found the following days. From day 20, nests were visited each afternoon to determine fledging day.

Reproductive success was investigated each year between 1996 and 2003, with the exception of 1997 and

2001. We included only first broods in the analysis, i.e. secondary polyandrous nests were not considered.

Classification of birds

To identify the birds individually, we caught adults with a mist nest at their roosting or breeding holes and marked them with colour rings. During our observations in successive years, local recruits (i.e. territory holders that were marked the previous year as nestlings) were recorded and classified as yearlings. Adults that were known from previous years were defined as old birds. In 2002 and 2003 we had enough experience to classify caught birds by the moulting pattern of their greater wing coverts (following Wiktander 1998; Pasinelli 1999). We also defined a pair to be “old” if the partners had bred together the previous year; a pair was “new” if at least one partner was a yearling or the bird had mated with a different partner the previous year.

Observations of feeding

In 1998, 1999, 2002 and 2003, we investigated the feeding of the nestlings at 16 nests. To do this, we installed a telescope (Optolyth 30 × 80) in a place about 30–50 m from the nest that was hidden from the occupants and used this telescope to observe the nests for 2-h periods, adding up to a total of 454 observation hours. We visited each nest on 16 different days on average (minimum: 10 days). For each feeding visit, we recorded the identity of the parent, the time of arrival and departure to the nearest minute and the food item brought to the nest. Food items were identified to its major type (i.e. spider, aphids, crane fly, larvae), with finer levels of resolution (i.e. family of insect) whenever possible. The number of food items was recorded when they could clearly be identified. Furthermore, larvae were classified by their colour: for surface-dwelling larvae, brown, green or patterned; for wood-living larvae, white or bright red. Since the number and size of the prey items could not be identified if the parents fed very small items, (e.g. aphids or ants), we decided to calculate the relative frequency of occurrence for each type based on the number of feeding observations with identified prey type. Relative frequency of the prey type “a” ($F_a\%$) expresses the proportion of how many feedings (n_a) of all the feedings (n) was prey type “a” observed.

$$F_a\% = n_a/n \times 100$$

The sum of the relative frequencies of all prey types might exceed 100% because the different food items brought within one visit can belong to more than one group. To

investigate the change in food composition over the season, the period when nestlings were fed was divided into 5-day units, starting at the median time of egg laying each year.

We did not measure the food availability directly. However, presuming that individuals always decide for the most profitable prey item, we expect that observed differences in the composition of nestling diet between pairs or between time periods reflect differences in the availability of the preferred food. This is supported by studies of Kristin (1992), who showed for several passerine species a strong correlation between availability of a prey type and its relative frequency in the nestlings’ food composition. Moreover, Naef-Daenzer et al. (2000) reported that changes in the diet of Great Tits were entirely related to the seasonal development of prey biomass, i.e. size and number of available food items.

In addition, we determined feeding rates per nestling by dividing the number of feeding visits per hour by the number of young in the nest. We divided the nestling period in two parts and calculated feeding rate per nestling for both stages: first to 12th nestling day, and 13th day to fledging day.

Statistical analysis

Statistical analyses were performed with SPSS ver. 11.0 (SPSS, Chicago, Ill.). We used a significance level of 0.05. Unless otherwise stated, reported *P*-values were based on two-tailed tests. When data were not normally distributed (clutch size and laying date), we used nonparametric tests and referred to median values. We used analysis of variance (ANOVA) and Kruskal–Wallis tests to examine between-year variation in reproductive success.

Results

We investigated the reproductive success of 31 first broods with the time interval spanning 1996–2003. Of these, 14 pairs were identified as new pairs and five as old pairs. Reproductive success did not show large variations in the study period: there were no significant differences in fledging success between years, neither on the basis of all pairs (one-way ANOVA, $F = 0.656$, $P = 0.660$) or when considering only successful pairs ($F = 1.023$, $P = 0.439$). The same was true in terms of clutch size ($F = 0.597$, $P = 0.708$), mean body mass of nestlings ($F = 0.699$, $P = 0.608$) and duration of nestling period ($F = 0.165$, $P = 0.952$). Even though some annual variation in these parameters can not be excluded, we pooled data from all years for analysis due to the small sample sizes.

Table 1 Causes of the failure to produce fledglings (n = number of breeding attempts)

n	Cause of failure
1	Female died before egg laying
1	Male died during first nestling stage
1	Eggs did not hatch
2	Complete predation by Eurasian Jay <i>Garrulus glandarius</i>
3	Complete predation by Great Spotted Woodpecker <i>Picoides major</i>

Timing of breeding

Within all years, the beginning of egg laying ranged from 14 April to 10 May. Both the latest and the earliest laying dates were observed in 1 year (1999), resulting in 26 days being the maximum range of days within which all pairs had started egg laying. Between years, the median dates of egg laying were not significantly different (Kruskal–Wallis test: $n = 6$, $P = 0.416$) and varied between 24 April and 1 May.

The laying date relative to the median was not different in pairs with yearling females compared to those with older females (unpaired t -test: $T = 1.774$, $n = 17$, $P = 0.096$), and the same was found for age classes of males ($T = 1.329$, $P = 0.207$, $n = 15$). The relative laying date for old pairs, however, was significantly earlier than that for new pairs ($T = 3.208$, $n = 19$, $P < 0.01$). Thus, a longer pairing bond had a positive effect on the relative laying date.

Reproductive success

Nesting success Of 31 breeding attempts, 23 pairs (74.2%) fledged at least one young. The causes of failure are listed in Table 1, with the most common cause of brood

loss being nest predation. From eight broods without fledglings, one belonged to an old pair and six belonged to a new pair, while in one case, the duration of the pair bond was not known. Hence, the proportion of failure did not significantly differ in old and new pairs (Fisher's exact one-tailed test: $P = 0.366$). Nevertheless, failure seemed to be related to the timing of egg laying, since late broods were more likely to fail than early ones (Fisher's exact one-tailed test: $P < 0.05$).

Clutch size The number of eggs in the full clutch was determined in 23 broods and varied from three to six eggs; the median size of each full clutch was six, and the mean clutch size was 5.4. Clutch size was strongly influenced by relative laying date ($r^2 = 0.346$, $P < 0.01$, $n = 23$; Fig. 1a). The number of eggs decreased by one egg in 11 days (clutch size = $5.36 - 0.09 \times \text{day}$)

Fledging success Successful nests produced on average 3.6 ± 0.25 (SE) fledglings ($n = 21$). Following the same seasonal trend as clutch size, fledging success decreased with relative laying date ($r^2 = 0.200$, $P < 0.05$, $n = 21$). The slope of the decreasing number of fledglings was similar to that of clutch size (number of fledglings = $3.54 - 0.10 \times \text{day}$).

Nestling body mass Body mass was measured for 60 nestlings in 17 nests on their 16th day and was, on average, 21.0 g (range: 13.0–25.0, SE: ± 0.32). Again, a negative relation to relative laying date was found for mean nestling body mass per brood ($r^2 = 0.389$, $P < 0.01$, $n = 17$; Fig. 1b).

Duration of nestling period Nestlings fledged after 21–25 days (mean: 23.2 ± 0.29 , $n = 17$). In contrast to the other reproductive traits already mentioned, the duration of nestling period was not related to laying date ($r^2 = 0.129$,

Fig. 1 Influence of relative laying date on: **a** clutch size ($n = 23$, bubble size reflects number of data points), **b** mean body mass of nestlings per brood (\pm SE) ($n = 17$). ** $P < 0.01$

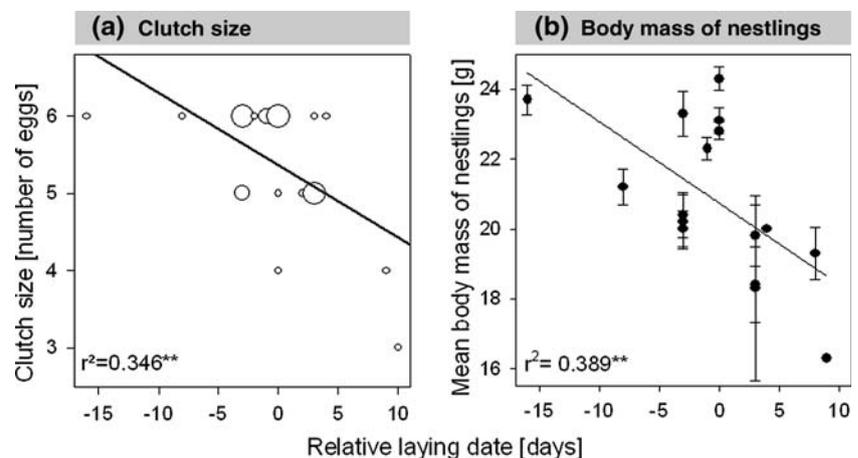


Table 2 Composition of nestling diet in Lesser Spotted Woodpeckers ($n = 3790$ feeding visits)

Prey type	Relative frequency (%) ^a
Sternorrhyncha (aphids)	51.6
Surface-dwelling larvae	24.6
Tipulidae (craneflies)	14.7
Wood-dwelling larvae	13.0
Arachnida (spiders and harvestman)	2.9
Formicidae (ants)	0.7
Cleoptera (beetles)	0.6
Lepidoptera (butterflies)	0.6
Diptera (excluding tipulidae)	0.7
Other items	1.4

^a Relative frequency refers to the proportion of feeding visits that include a certain prey type. Since one feeding visit might include several prey types, the sum of all relative frequencies exceeds 100%

$P = 0.156$, $n = 17$). However, it did increase with decreasing mean body mass of the nestlings on their 16th day ($r^2 = 0.314$, $P < 0.05$, $n = 16$).

Local recruits Overall, 46 nestlings had been marked in breeding seasons previous to the years we searched for local recruits. We recovered nine birds, which is a recovery rate of around 20%. Surprisingly, there was a non-significant trend for young from late broods to be relocated more often than young from early broods (Fisher’s exact two-tailed test: $P = 0.054$). However, body mass of nestlings did not predict the chance of being recovered, since mean body mass of recovered (21.1 ± 0.69 g) and non-recovered

(21.1 ± 0.45 g) individuals was the same (Fisher’s exact two-tailed: $P = 0.978$).

Feeding rate

In order to investigate the reason for a decreasing nestling body mass with laying date, we related the feeding rate per nestling (number of feeding visits per hour divided by number of young in the brood) of each pair to its laying date for the early (days 1–12) and late (day 13–fledging day) nestling stage. In the first stage, feeding rate per nestling showed a non-significant trend to increase with relative laying date ($r^2 = 0.278$, $P = 0.053$); thus, young from late broods were fed slightly more often than young from early broods. In the late stage, the number of feeding visits per nestling was not related to the timing of egg laying ($r^2 = 0.173$, $P = 0.157$).

Nestling diet

Overall, 4834 feeding visits were observed, and food was clearly identified in 3790 cases (78.4%). Based on these cases, we found the nestling diet of Lesser Spotted Woodpeckers to consist mainly of four prey types (Table 2): aphids (Sternorrhyncha), surface-dwelling larvae (mainly caterpillars), craneflies (Tipulidae) and wood-dwelling larvae. Other arthropod types were fed in less than 5% of the observed feedings and are therefore pooled in the group ‘‘other items’’.

The composition of the nestling diet changed remarkably over the breeding season. While the relative frequency of aphids in the diet increased within the season, that of

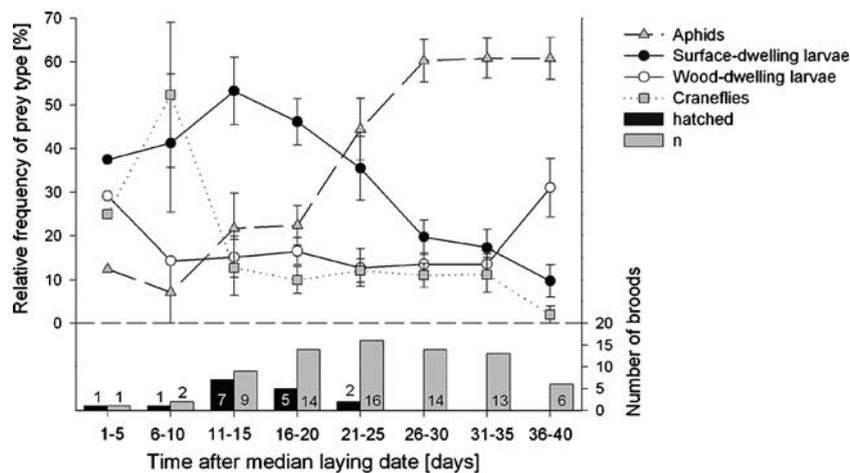


Fig. 2 Seasonal change in the nestling diet, combined over all the years. The relative frequency of occurrence in the observed feedings is shown for the four main prey types (mean \pm SE). Since one feeding visit might include several prey types, the sum of all relative frequencies in a certain time period can exceed 100%. Feeding period

is divided into 5-day units, beginning at the median laying date in each year. *Dark bars* The number of broods in which nestlings hatched at a certain time interval, *light bars* the number of broods containing nestlings

surface-dwelling larvae tended to decrease. Figure 2 shows that between days 11 and 20 most of the feeding visits contained surface-dwelling larvae; it is within this time interval that the nestlings in most broods hatched. The relative frequency of surface-dwelling larvae decreased thereafter, and from day 21 after the median laying date, the most frequent prey type in the feeding visits was aphids.

Seasonal variation in nestling diet was found in both early and late broods (Fig. 3). The declining trend for relative frequency in surface-dwelling larvae was observed in both groups at the same time unit.

The composition of the nestling diet of early and late broods (Fig. 4) differed significantly in terms of the relative frequency of surface-dwelling (unpaired *t*-test: $T = 2.464$, $P < 0.05$) and wood-dwelling larvae ($T = -3.754$, $P < 0.01$). Interestingly, a comparison of the relative frequency of any kind of larvae in the nestling diet did not reveal any significant difference between the groups ($T = 0.386$, $P = 0.706$). The relative frequency of aphids,

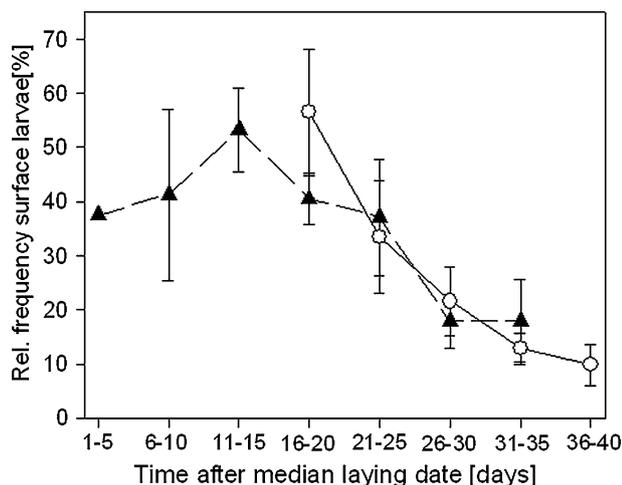
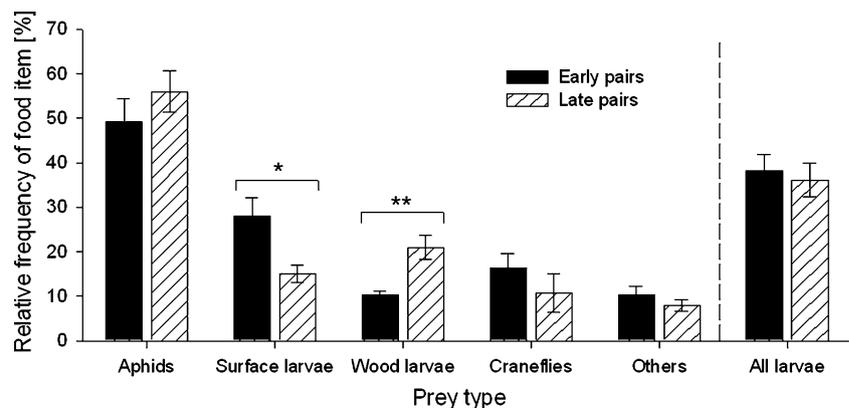


Fig. 3 Seasonal changes in the relative frequency of caterpillars in the diet of early (triangle, $n = 8$) and late (circle, $n = 6$) broods

Fig. 4 Food composition of early ($n = 8$, black bars) and late ($n = 6$, white bars) pairs. The relative frequency based on all observed feedings is shown (mean \pm SE). * $P < 0.05$, ** $P < 0.01$



craneflies and other items also did not differ significantly (aphids: $T = -0.927$, $P = 0.372$; craneflies: $T = 1.087$, $P = 0.298$; other items: $T = 0.914$, $P = 0.379$).

Feeding visits with larvae

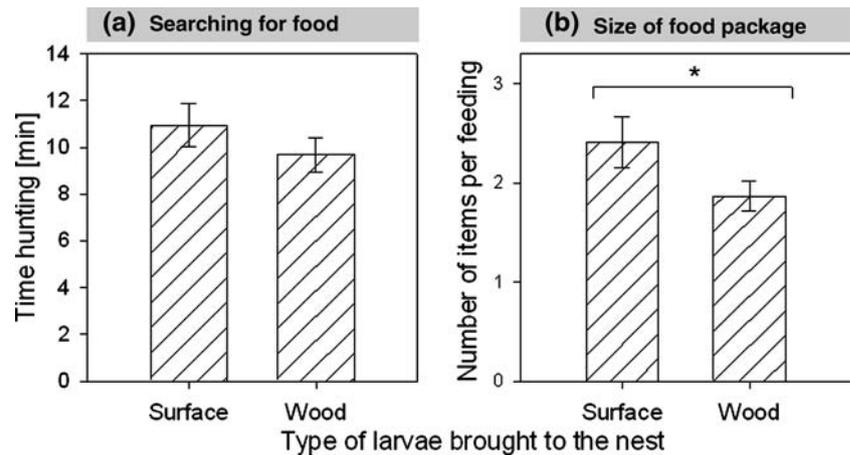
Since the composition of the nestling diet differed in terms of the type of larvae between early and late broods, we compared feeding observations in which surface-dwelling larvae had been recorded with those where wood-dwelling larvae had been recorded. We focused on the time an individual spent away from the nest before feeding the nestlings with larvae and the number of prey items in those feeding visits where larvae were fed to the young.

The time one adult spent away from the nest did not differ when feeding visits with surface-dwelling larvae were compared to those with wood-dwelling larvae (paired *t*-test: $T = -0.283$, $P = 0.782$, $n = 14$; Fig. 5a). Figure 5b shows that if surface-dwelling larvae were fed to the nestlings, the adults brought more food items back to the nest in that feeding than they did when wood-dwelling larvae were fed to the nestlings (paired *t*-test: $T = 2.689$, $P < 0.01$, $n = 6$).

Discussion

In this paper, we present the first detailed study on reproductive success and nestling diet of the Lesser Spotted Woodpecker in Central Europe. One major result of this study is that we were able to determine that timing of breeding influences reproductive success. Some bird species that feed their nestlings on a diet of caterpillars have adapted their timing of breeding to the seasonal pattern in caterpillar abundance. One example of this has been found in the well-studied Great Tits (*Parus major*): the optimal time of breeding has been adjusted so that the nestlings are approximately 10–18 days old (i.e. the second half of the nestling period) at the peak times of

Fig. 5 Comparison of the time between feeding visits with surface-dwelling and those with wood-dwelling larvae. **a** Time spent hunting by the parents (mean \pm SE, $n = 16$ pairs). **b** Number of items fed in one feeding visit (mean \pm SE, $n = 6$ pairs) in 1998 and 1999 only. * $P < 0.05$



caterpillar abundance and size (Perrins 1991; Wesolowski 1998; Naef-Daenzer and Keller 1999). The late nestling stage is assumed to be the most energy demanding in Great Tits, since energetic needs increase with nestlings' growth (Naef-Daenzer and Keller 1999). In the Lesser Spotted Woodpecker, however, we observed that the highest frequency of caterpillars in the feedings occurred when the nestlings in most broods had just hatched (Fig. 2). Thus, the timing of breeding seems to be later in Lesser Spotted Woodpecker than in the Great Tit. A relatively late timing of breeding in the Lesser Spotted Woodpecker compared to other non-migratory bird species, including the Great Tit, was also found in Sweden (Wiktander et al. 2001b). One advantage of starting later in the season may be the enhancement of mean day temperatures as well as the declining probability of frost. Moderate temperature might be particularly important to woodpeckers, since they do not use insulating nesting materials other than a thin layer of woodchips on the ground of the breeding hole (personal observation of authors; Wiktander 1998) and the broods are relatively small (two to six nestlings). Consequently, heat loss can be expected to be higher in woodpecker broods than in Passerine hole-nesting species that usually have larger broods and nests with a thick layer of insulation material. Furthermore, woodpeckers incubate their eggs for only 10–11 days. The young hatch therefore relatively immature compared to other altricial species and need a longer time to grow feathers and develop thermoregulatory abilities (Yom-Tov and Ar 1993). As a result, the first nestling days require intensive brooding, which reduces the parents' available time for foraging and nestling feeding (Rossmanith 2005). The early nestling stage of the Lesser Spotted Woodpecker would appear to be the most demanding and should, consequently, coincide with the time of highest food availability. This is further supported by Wiktander et al. (2001b) who found that most breeding

failures in Lesser Spotted Woodpecker appear in the early nestling stage. The time-consuming excavation of breeding holes may also explain the relatively late breeding in woodpeckers. Lesser Spotted Woodpeckers build a new breeding hole every year (Wiktander 1998) and often need several trial runs before successful completion of a breeding hole (personal observation of the authors). In addition, Lesser Spotted Woodpeckers suffer from competition for cavities by larger woodpeckers (e.g. Great Spotted Woodpecker, *Picoides major*) that take over, enlarge and use their breeding holes (personal observation of the authors). Thus, the later breeding start in the Lesser Spotted Woodpecker could also be the result of a competition for cavities; this has been discussed for other woodpecker species by Ingold (1994) and Pasinelli (1999).

Despite the general evolutionary trend in Lesser Spotted Woodpeckers to breed relatively late compared to other hole-breeding species, we found that within the population itself, the later the start of breeding, the lower the reproductive success. The seasonal decline in clutch size confirms earlier findings for this species in other climatic regions (Wiktander et al. 2001b) and is similar to the pattern found for many single-brooded birds (review in Klomp 1970; Wesolowski 2000). Furthermore, our results show that fledging success decreased with the same slope, indicating that clutch size is the major cause for the number of fledglings in successful nests.

However, not only did the number of eggs and fledglings decline with a later breeding start, but body mass of the nestlings at day 16 was also lower the later a pair started breeding. The lower nestlings' weight corresponded to a shift in the diet of the nestlings: in our study, Lesser Spotted Woodpecker nestlings in early broods were fed significantly more often with surface-dwelling larvae (namely caterpillars) than those in late broods. In turn, feeding visits in late broods contained wood-dwelling larva

more often (Fig. 4). Surface-dwelling larvae such as caterpillars can be collected easily, especially when highly abundant, since they are visible and relatively immobile (Kristin 1992). Conversely, wood-dwelling larvae are invisible and have to be pecked out of the bark. Consequently, we assume that preying on wood-dwelling larvae requires more time and energy.

Interestingly, the time spent by the parents searching for food did not differ when either wood-dwelling larvae or caterpillars were more frequent in the feedings, respectively (Fig. 5a); however, in the case of the former, fewer items were brought back per feeding (Fig. 5b). Our results suggest that parents did not exceed their allotted foraging time when food availability was lower, but instead delivered the food in smaller packages. A similar behaviour has been found for Great Tits, where parents became less selective in their choice of prey – in contrast to decreasing the feeding rate – when food was less available (Grieco 2002).

The difference in nestling diet between early and late broods can be explained by: (1) the timing hypothesis, where food availability decreases in time and (2) the quality hypothesis, where differences occur in the quality of the habitat between early and late breeders. If timing were to be the main cause of the observed deterioration in reproduction performance, we should see the same development in food supply within a season in both groups. If habitat quality were to be the ultimate cause, we would anticipate differences in food supply between early and late pairs, irrespective of seasonal changes. We found that the relative frequency of caterpillars in feedings was similar in early and late breeders at a given date in the season and decreased with time (Fig. 3). We therefore conclude that with a late start in egg laying, food availability decreases, thereby leading to an inferior supply of food to the nestlings of later broods. This would support the timing hypothesis as the main cause of the declining reproductive success within a season.

The duration of the nestling period increased with declining body mass of the nestlings, suggesting that nestlings stayed in the nests until they reached a sufficient body condition. Similar results have been found for Marsh Tits (*Parus palustris*), where the decision for a young to fledge was dependent on its body mass at day 13 (Nilsson and Svensson 1993), and for Great Tits, where the duration of the nestling period was negatively related to food availability (Seki and Takano 1998). In our study, we found no influence of body mass on the probability of local recruitment, and local recruitment was not higher for early than for late fledglings, which contradicts investigations on other species (Harris et al. 1994; Gaston 1997; Verboven and Visser 1998; Green and Cockburn 2001; Monrós et al.

2002). However, given our small sample size, we cannot conclusively exclude a positive effect of early breeding on local recruitment.

Since clutch size determines the number of fledglings, the question arises as to what is the ultimate cause of a reduced clutch size in late broods. We assume that food availability during nestling time becomes suboptimal the later the young hatch and that it may indeed be insufficient for a large brood. However, a strategic decision by late pairs should be considered as well. It is time-saving to produce smaller clutches, since for each egg the birds forego to lay, they can start incubating 1 day earlier, and the young hatch earlier (see Wesolowski 2000).

Interestingly, we found that pairs which bred together in consecutive years also started laying eggs earlier; This observation has been confirmed in another region (Wiklander et al. 2001a). A positive influence of pair bond duration on reproductive success is known for several long-living (Forslund and Larsson 1991; Pyle et al. 2001) and short-living birds (Perrins and McCleery 1985; McGraw and Hill 2004). Nevertheless, the factors underlying this phenomenon remains unclear (Ens et al. 1996). We assume that experience in the territory may lead to the observed pattern in the Lesser Spotted Woodpecker. Höntsch (2005) conducted a study investigating home ranges and found that many individuals do not have close neighbours, since the population density is low and the sizes of the home range are large during mating time. Therefore, individuals establishing a new pair have to shift their home range, whereas old pairs can stay in the same territories (Höntsch 2005). Since breeding experience in the same territory has been shown to increase reproductive success (Pyle et al. 2001), this may be one explanation of the inferior performance found in new pairs.

Conclusion

We have shown that the timing of breeding is an important determinant of reproductive success in the Lesser Spotted Woodpecker. In general, Lesser Spotted Woodpeckers time their breeding so that the early nesting stage coincides with the highest availability of caterpillars, since this is the time of highest energy demand. During the course of the breeding season, food availability deteriorates, and the observed decline in reproductive success seems to be a direct result of this development. Caterpillars play an important role in the diet of the nestlings. Consequently, it is likely that any variation in caterpillar availability caused by environmental changes may influence reproductive success in this species.

Zusammenfassung

Reproduktionserfolg und Nestlingsnahrung des Kleinspechts (*Picoides minor*)

Der Bestand des Kleinspechts (*Picoides minor*) ist in den letzten Jahren stark zurückgegangen. Bislang sind Informationen zur Autökologie der Art lückenhaft. Um Managementmaßnahmen zum Schutz der Art entwickeln zu können, sind Kenntnisse der Faktoren notwendig, die den Reproduktionserfolg beeinflussen. Ziel dieser Studie ist es daher, den Einfluss des Legebeginns und der Nestlingsnahrung auf den Reproduktionserfolg zu ermitteln. In sechs Untersuchungsjahren zwischen 1996 und 2003 nahmen wir verschiedene Variablen des Reproduktionserfolgs in einer Kleinspechtpopulation im hessischen Vordertaunus auf. An den Bruthöhlen wurde die Fütterung der Nestlinge beobachtet, um die Zusammensetzung der Nestlingsnahrung und ihre Änderung im Verlauf der Nestlingszeit zu untersuchen. Es zeigte sich, dass Gelegegröße, Körpermasse der Nestlinge und Zahl der ausgeflogenen Jungvögel mit späterem Legebeginn abnahmen. Paare, die schon im vorherigen Jahr zusammen gebrütet hatten, begannen früher mit der Eiablage als neu zusammengestellte Paare. Die Nestlingsnahrung bestand hauptsächlich aus Blattläusen, Raupen, Schnaken und holzlebenden Larven. Ihre Zusammensetzung änderte sich stark im Verlauf der Brutsaison, sowohl bei frühen als auch bei spät legenden Paaren. Frühe Bruten wurden häufiger mit Raupen und seltener mit holzlebenden Larven gefüttert als späte Bruten. Unsere Ergebnisse weisen darauf hin, dass es für Kleinspechte von Vorteil ist ihren Brutbeginn so zu wählen, dass die höchste Verfügbarkeit von Raupen zeitlich in die frühe Nestlingszeit fällt. Im Verlauf der Brutsaison sinkt die Nahrungsverfügbarkeit, so dass der reproduktive Erfolg mit spätem Legebeginn abnimmt.

Acknowledgements We wish to thank all of the field helpers for their dedication and Ulf Wiktander for comments on an earlier version of the manuscript. We thank the Deutsche Wildtierstiftung for financial support. The study was sponsored by the Scholarship Programme of the German Federal Environment Foundation (DBU). All work carried out within the framework of this project complies with the current laws of Germany.

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