

# The effect of forest patch size on the breeding biology of the great spotted woodpecker *Dendrocopos major*

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Received 7 Oct. 2005, revised version received 21 Mar. 2006, accepted 21 Mar. 2006

Mazgajski, T. D. & Rejt, Ł. 2006: The effect of forest patch size on the breeding biology of the great spotted woodpecker *Dendrocopos major*. — *Ann. Zool. Fennici* 43: 211–220.

Forest fragmentation leads to a decrease in total forest area and patch size, which enhances predation pressure on birds' breeding success. Existing data suggest that because hole nesters occupy relatively safe nest sites, their breeding success is not negatively affected by this process. However, fragmentation effects on other reproductive parameters are possible and could have important influences on population growth rates. We examined the hypothesis that a decrease in forest patch size does not influence some aspects of breeding biology of a primary cavity nester — the great spotted woodpecker. We compared clutch size, the number of fledglings, breeding phenology, and nesting success between birds nesting in large forests (> 120 ha) and in small woodlots (2–55 ha). We found that almost all the parameters studied differed in relation to patch size, and were worse in small forests. Only breeding success was similar in both groups of birds.

## Introduction

A decrease in areas suitable for wildlife due to habitat loss and landscape fragmentation may lead to many changes in avian ecology, such as patch occupation, the dynamics and densities of bird populations, as well as the structure of entire avian communities (e.g. van Dorp & Opdam 1987, Hinsley *et al.* 1995, Redpatch 1995, Mathysen 1999, Åberg *et al.* 2000, Zanette 2000, Tworek 2004). For many species, forest fragmentation was found to influence several aspects of reproductive biology, such as pairing success, nesting success, annual productivity, number and condition of nestlings, and even brood sex ratio (e.g. Hoover *et al.* 1995, Weinberg & Roth 1998, Roberts & Norment 1999, Zanette *et al.* 2000,

Bayne & Hobson 2001, Luck 2003, Suorsa *et al.* 2003). A few studies, however, did not find such negative effects on reproduction (e.g. Møller 1991, Friessen *et al.* 1999, Zanette 2001).

At the landscape scale, forest loss and fragmentation due to agriculture, urbanisation, roads, etc., may lead to an increase of edge areas and a resulting intensification of several unfavourable conditions, such as brood parasitism or nest predation (Gates & Gysel 1978, Robinson *et al.* 1995, Hobson & Bayne 2000). This latter factor is very frequently studied (review in Marzluff & Restani 1999, Stephens *et al.* 2003). Biotic and abiotic factors such as insolation, humidity, etc., may differ in edge gradients or even between fragments, and influence the organisms upon which birds forage (Murcia 1995).

Habitat loss and fragmentation are often studied in patch scale, because one obvious effect is an increase in patch number with a simultaneous decrease in surface area (Fahrig 2003). Most studies of the impacts of forest fragmentation on birds in patch scale have focused on breeding success. The breeding success of ground nesting birds decreases in small woodlots as a result of increased predation pressure. Such generalizations are made mostly from studies with artificial ground or shrub nests (review in Marzluff & Restani 1999). However, predator pressure is not only restricted to eggs or young. Adult birds are also more easily detected by predators when moving between forest patches as they search for food (Lima & Dill 1990). Also, more energy may be spent by parent birds in multi-patch territories (Hinsley 2000) thus affecting their survival rate.

Fragmentation may also influence food resources available to breeding birds. Invertebrates — the predominant food for many birds during the breeding season — may be influenced by the size of the forests studied (e.g. van Dongen *et al.* 1994, Abildsnes & Tømmerås 2000, van Dongen & Scott 2002, Summerville & Crist 2003). If food resources are affected, differences in nesting phenology could appear because food availability affects the dates of egg laying (Davies & Lundberg 1985). Many studies have not detected dramatic differences in the nutritional condition of birds in fragmented versus continuous forests, or near edges versus forest interiors (e.g. Nour *et al.* 1998, Huhta *et al.* 1999, Buehler *et al.* 2002, but Burke & Nol 1998). Indeed, some arthropods were even less numerous in a large forest (Jokimäki *et al.* 1998).

Thus, it seems that predators, not feeding conditions, could be a primary factor affecting birds' reproduction in relation to the process of forest fragmentation. Therefore, birds breeding in relatively safe nest sites, such as tree holes, are generally not considered particularly exposed to the negative aspects of habitat fragmentation (e.g. Lampila *et al.* 2005). No significant differences were found in studies of hole nest predation that tested edge effects rather than fragmentation itself (Sandström 1991, Pöysä *et al.* 1997, Deng & Gao 2005). It was found that

also other breeding parameters, such as laying dates, clutch size, fledgling condition, etc. that could be related to feeding conditions generally did not differ between birds breeding in small or large forests (Lens & Dhondt 1994, Matthysen & Adriaensen 1998, Nour *et al.* 1998, Matthysen 1999, but Hinsley *et al.* 1999, Loman 2003).

As primary cavity nesters that excavate their own breeding holes, woodpeckers *Picidae* achieved the highest breeding success among birds (e.g. Martin & Li 1992). Thus, if the process of forest fragmentation increases predator pressure, one could assume that this would not affect woodpeckers. Also, if food availability is not related to the size of forests, other aspects of woodpeckers' breeding biology should be similar. In fact, no differences were found for several breeding parameters of the black woodpecker *Dryocopus martius* (e.g., clutch size, number of fledglings, and fledgling condition) when examining breeding pairs in forested landscapes vs. farmland areas with highly fragmented forests (Tjernberg *et al.* 1993). Similarly, no differences were found in the reproductive success or adult annual mortality in the middle spotted woodpecker *Dendrocopos medius*, although differences in densities were found between a continuous forest dominated by oaks and fragmented woods (Kossenko & Kaygorodova 1998, Kossenko 2003).

Thus far, two factors — predators and feeding conditions — are considered to affect birds' reproduction with regard to forest fragmentation. However, other aspects of woodpeckers' breeding biology also should be studied in greater detail. First of all, the European starling *Sturnus vulgaris* is a powerful competitor for nesting sites and can usurp even freshly excavated woodpecker holes (e.g. Tracy 1938, Ingold 1989, Ingold 1994, Wiebe 2003, Smith 2005). The competitive pressure of this species is greater in small forests (Matthysen & Adriaensen 1998). Nest hole reuse by the great spotted woodpecker — as a measure of interference by other hole nesters — is less frequent in small forests (Mazgajski 2003). The impact of nest site competitors is greater along forest edges (Deng & Gao 2005), which suggests that birds breeding in smaller forests are more vulnerable to competition, as the edge areas constitute a relatively larger portion

of such patches. In addition, some variation in woodpeckers mating systems has been described in fragmented landscapes (Kotaka 1998, Wiebe 2002). Therefore, there are at least two other factors connected with forest fragmentation that could affect woodpecker breeding.

We chose the great spotted woodpecker *Dendrocopos major* to test the hypothesis that decreasing patch area — as an effect of forest fragmentation — does not affect woodpeckers. This is the most numerous woodpecker species in Europe (Flade 1997) and can breed in very small woodlots (the smallest recorded — 0.26 ha; Hinsley *et al.* 1995). It is a food generalist (e.g. Török 1990) and is known to achieve very high nesting success (e.g. Mazgajski 2002). Both factors related to forest fragmentation so far suggest that decreasing forest size should not influence the woodpeckers' breeding biology.

Our aim was to discover if increasing forest fragmentation, i.e. a decrease in forest patch size, affects aspects of the breeding biology of the great spotted woodpecker such as clutch size, number of fledglings, nesting phenology, breeding success, as well as starling pressure.

## Study area

Our study area was purposely located in a landscape with very little forest cover because the negative effects of patch size and isolation may not occur until the landscape consists of only 10%–30% of suitable habitat (Andrén 1994). The study was carried out in the agricultural landscape of central Poland, where only about 6.2% of the total area of 145 km<sup>2</sup> was forested. Those forests that did exist were heavily fragmented. Arable fields and/or pastures surrounded all the forest stands. A total of 40 woodlots were studied: 3 large (122–190 ha), 6 medium (30–55 ha) and 31 small (2–12 ha). The woodpecker populations were quite stable in the large forests, with about 12–16 pairs breeding each year (own unpubl. data). Birch (*Betula* sp.), aspen (*Populus tremula*), alder (*Alnus glutinosa*), and oaks (*Quercus* sp.) dominated the smaller forests, while larger forests also contained mixed stands with pine (*Pinus silvestris*) and spruce (*Picea abies*).

## Methods

Our study began in 2001, but most of the data on breeding biology were obtained in 2002–2004. Nests identified in 2001 were used for the analysis of nest-site reoccupation.

Starting in mid-April each year, we searched for woodpeckers excavating holes and later in the season we looked for nests, guided by the begging calls of young. We also monitored old holes excavated in previous years (checked or observed from the ground), as it has been reported that great spotted woodpeckers may reuse old holes (e.g. Cramp 1985). In this way we also estimated the competitive pressure of the starling (Mazgajski 2003). All holes studied were monitored using a small light and mirror to determine the timing of egg laying, the number of eggs, and the number of nestlings. Nest holes were reached by ladder, so only nests of up to 6 meters high were checked.

We also colour-ringed woodpeckers. When the nestlings were quite large and did not require brooding, we waited for both parents to check their colour codes. Observations ceased when both parents were observed, or after 45 minutes had passed in cases when we did not see both parents bringing food. If we did not see the couple bringing food, we repeated another 45-minute observation period within a few days. Such observations were made from ca. day 8 up to day 17–19 of the nestlings' lives (based on feather development), because sometimes only a single bird, most likely the male, will feed its young after this period of their development (Cramp 1985). Adult birds generally make 7–9 feeding trips/45 minutes during this stage of the nestlings' lives (Woźniak & Mazgajski 2003). Feeding observations were conducted only during the 2002 breeding season.

After day 19, the nests were observed from the ground (to avoid causing the young to leave the holes prematurely) every few days to establish the approximate dates of fledging. We considered the date when all young left the nest as the fledging date. After the young fledged, we checked whether the holes held any dead birds.

We observed great spotted woodpecker re-nesting, with late broods producing fewer fledglings (Mazgajski 2002). As we were not able to reach all

the holes to check their contents, and we wanted to obtain a general pattern of fledging period in relation to forest patch size, we categorized the broods as early or late by dividing the nesting period into two almost equal parts (the cut-off dates were 8–9.6. in 2002 and 10–11.6. in 2003). Nests where young fledged before the cut-off date were defined as early broods, those which fledged after the cut-off date were defined as late broods.

## Data analysis

Two categories of forests were distinguished for the data analysis: (1) large forests (over 120 ha) and (2) small woodlots (2–55 ha), which also included medium-sized forests (30–55 ha). In total we obtained data on clutch size from 3 large and 7 small forests. Data on fledgling numbers were collected from 3 large and 15 small forests.

Only complete clutches found during the egg-laying phase were used in the comparison of clutch sizes. Nesting success was defined as the number of nesting attempts that produced at least one fledgling. Only successful nests, producing at least one fledgling, were considered when comparing the number of fledglings, using the number of young counted at the last nest check. A few nests were excluded from the analysis because the nestling count was made just before fledging and it was possible that at least one young had already left the nest.

Since mating with the same partner in subsequent seasons was extremely rare among individually marked birds, we assumed that the probability of mating with the same partner in the next breeding season among unmarked birds was also low. In 2002–2004, we observed 15 pairs in which both parents had been ringed in a large forest and only twice the same birds bred together in the following season during 2003–2005. There were no cases observed of the same individuals breeding together in following seasons in small forests (8 pairs observed). Data collected for other species revealed that multiple observations of the same individual can be treated as independent with respect to clutch size and breeding phenology (Meijer *et al.* 1988, Korpimäki 1990). Therefore, we assumed that the possibility of pseudoreplication was very low,

thus all collected data originating from forests of the same size-group were pooled together.

We collected data from 22 broods where we could relate clutch size to first egg laying date (exact or approximated to 1–3 days; in such cases median date from the range was used for analysis). This allowed a detailed analysis of the relationship between laying dates and clutch size. Ten broods came from large forest, with the remaining 12 from small ones (7 from 2002, 12 from 2003 and 3 from 2004). In total, we collected clutch size data from 29 nests (16 from large and 13 from small forests).

The dates of first egg laying and number of fledglings for 18 broods (6 from 2002, 11 from 2003 and 1 from 2004), and data for the total number of fledglings were collected from 21 broods in large and 26 in small forests (23 from 2002, 21 from 2003 and 2 from 2004). We monitored 25 of the nests starting from the egg-laying phase to fledging of young, and 64 nests were classified as early or late broods.

For the analysis, we used the Univariate Analysis of Variance in SPSS 11 with clutch size and number of fledging as dependent variables (both were normally distributed). Rates of hole utilization as well as fledging phenology and nesting success were compared using the Fisher exact test (Statistica 4.3).

## Results

Woodpeckers in small woodlots excavated new breeding holes almost every year. Four holes (out of 28 checked — 14.3%) were reused. The frequency of hole reoccupation was greater in large forests (9 holes out of 31 checked — 29%), but those differences were not statistically significant (Fisher exact test:  $p = 0.218$ ).

Starling pressure was higher in small forests. The frequency of utilization of woodpecker holes from the previous season by starlings was significantly higher in small woodlots than in large forest (71.4%,  $N = 28$ ; and 38.7%,  $N = 31$ ; respectively, Fisher exact test:  $p = 0.018$ ). We also observed one freshly excavated hole usurped by a starling.

To search for factors affecting clutch size we used the hole histories of the 2002–2004 season (new vs. old), laying dates and size of the forest

patch (large vs. small). Those four variables were incorporated in the models. However, season and hole history were less related to the dependent variable ( $F_2 = 0.49$ ,  $p = 0.95$ ;  $F_2 = 0.133$ ,  $p = 0.876$ ; respectively) and were removed. After doing so, statistical significance for laying date was not achieved ( $F_1 = 2.32$ ,  $p = 0.14$ ). However, as a trend of decreasing clutch size in later broods was observed (Fig. 1), we restricted the final analysis only to broods that were started between 27 April and 6 May, the period when most great spotted woodpecker pairs started their laying. In this way, we excluded late broods, which could have been re-nesting due to hole competition or predation. The effect of laying date was not significant ( $F_1 = 0.67$ ,  $p = 0.424$ ). We found that only the size of the forest significantly affected clutch size ( $F_1 = 8.71$ ,  $p = 0.009$ ; Table 1).

Season and laying date did not influence the number of fledglings ( $F_2 = 1.19$ ,  $p = 0.34$ ;  $F_1 = 0.067$ ,  $p = 0.8$ ; respectively). Therefore, we included data from all holes in the final analysis and found that the size of the forest patch significantly affects the number of fledglings ( $F_1 = 4.31$ ,  $p = 0.044$ ), with pairs from large forests producing more young (Table 1).

In the above calculations, we controlled for laying date as a factor that could affect the results. However, we found that late broods were more numerous in small woodlots and early broods dominated in large forests (Fisher exact test:  $p = 0.036$ ; Table 1).

We frequently observed that only one adult bird, primarily the male, fed its young in small

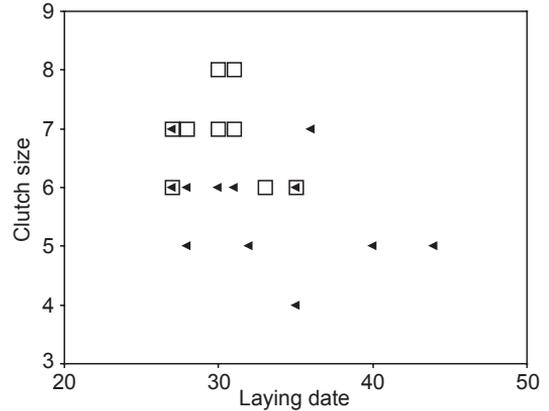


Fig. 1. Clutch size in large (□) and small forests (◄) in relation to laying dates. (1 = 1 April)

woodlots. During the same period, we observed both parents provisioning their nestlings in large forests (Fig. 2).

Nesting success was very high, with no difference between pairs breeding in small woodlots and large forests (Fisher exact test:  $p = 1.0$ ; Table 1). We investigated all nests that had experienced breeding failures — 2 nests were predated and 2 succumbed to natural losses. Both events were equally distributed in small and large forests.

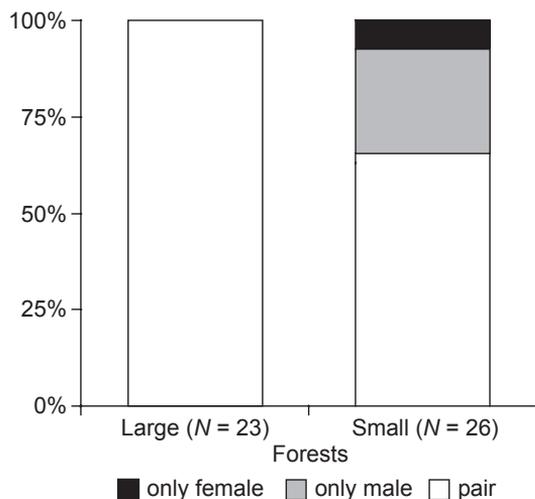
## Discussion

Our work supports the hypothesis that nesting success is high among cavity nesters and not related to the size of forest patches, as could be observed

Table 1. Breeding parameters (mean  $\pm$  SD) of great spotted woodpeckers from large (> 120 ha) and small forests (2–55 ha).  $N$  = sample size.

Parameters	Forests	
	Large	Small
Clutch size		
broods controlled for laying date*	6.9 $\pm$ 0.74 ( $N = 10$ )	5.8 $\pm$ 0.92 ( $N = 10$ )
all broods	6.5 $\pm$ 0.89 ( $N = 16$ )	5.69 $\pm$ 0.85 ( $N = 13$ )
Number of fledglings	4.48 $\pm$ 1.03 ( $N = 21$ )	3.92 $\pm$ 0.77 ( $N = 24$ )
Phenology		
early broods (%)	70	42
late broods (%)	30 ( $N = 40$ )	58 ( $N = 24$ )
Breeding success (%)	84.6 ( $N = 13$ )	83.3 ( $N = 12$ )

\*(egg laying started earlier than 7 May)



**Fig. 2.** Parental care pattern in relation to the size of forest patch.

in experiments with artificial open nests in the same area (Mazgajski & Rejt 2005). Therefore, forest fragmentation does not influence woodpeckers through increased predation pressure (see also Geng & Gao 2005). However, we found that decreasing forest patch size negatively affected almost all other breeding parameters of the great spotted woodpecker. Thus, other factors connected to fragmentation may affect woodpecker breeding.

Similar to other bird species, the number of eggs laid, as well as fledged young and their condition, could be influenced by breeding phenology (e.g. Ingold 1989, van Manen 1993, Hogstad & Stenberg 1997). In this study we did not find a relationship between the time of egg laying and clutch size. But some trends could be observed, and lack of statistical significance may be connected with insufficient data from late nests in large forests (Fig. 1). Delayed broods also occur in this habitat (as was noticed when comparing fledging periods), but we failed to find them during the egg laying phase. However, we found more late breeding attempts in small forests in this study. There are at least two factors affecting the time of egg laying that could be related to forest fragmentation. The first is connected with food and feeding conditions both for adults and nestlings. Second, the commencement of breeding could be related to nest hole competition.

The laying period of birds generally coincides with caterpillar development (e.g. van Noord-

wijk *et al.* 1995), which could be connected with temperature, tree budburst dates, etc. (cf. van Dongen *et al.* 1997, Buse *et al.* 1999). Also, the date of egg laying could be connected with the age and condition of females prior to laying. It is known that older females (e.g. Wiklander *et al.* 2001), as well as those supplemented with food, start to lay their eggs earlier (e.g. Davies & Lundberg 1985). However, if factors affecting invertebrate populations, such as heat, solar radiation and other abiotic conditions, reach higher levels at edges as well as in more fragmented landscapes (e.g. Malcolm 1998), the abundance of invertebrates should be higher there (cf. Jokimäki *et al.* 1998). One would expect caterpillars, for instance, to appear earlier in these habitats than in larger forests, as was found by van Dongen *et al.* (1997). Therefore, egg laying in small forests should start earlier, but we did not observe this. Delayed breeding in small woodlots, as well as smaller clutch size and fewer fledglings observed in our study and by many other authors (Hinsley *et al.* 1999, Loman 2003), suggests that nutritional conditions worsen as the size of the forest decreases.

When analyzing the impact of forest patch size on egg laying and clutch size, the condition of females and age structure should also be taken into consideration, as “worse” (smaller/weaker/younger, etc.) birds may settle in small forests. In our study, we measured only a few birds, but there were no significant differences between females from small and large forests in wing length, the most frequently measured condition parameter (large forests  $14.0 \pm 0.33$ ,  $N = 19$ ; small forests  $13.89 \pm 0.32$ ,  $N = 14$ ,  $t_{31} = 0.94$ ,  $p = 0.36$ ).

Great spotted woodpecker nestlings are fed a wide spectrum of food, but Lepidoptera, mostly in caterpillar form, dominates (Török 1990). Similar food is delivered to nestlings of other hole nesters (tits, nuthatches) and it is known that caterpillar abundance and adult provisioning rates did not differ among tits in small woodlots or larger forests (Nour *et al.* 1998). However, Koszenko (2003) found that the pattern of caterpillar abundance in fragments and close forests may differ between seasons. Seki and Takano (1998) found a significant negative correlation between the length of the nestling period and food avail-

ability, which could explain the lower number of fledglings for the woodpeckers breeding in small forests in our study. Thus, possible differences in the nutritional factor related to forest patch size, such as food availability and provisioning rates, should be analyzed in more detail.

Interspecific competition for nest sites is another factor that could affect the time breeding commences. It is generally known that great spotted woodpeckers may reuse old holes excavated in previous years if they are available. If they do reuse an old nest hole, they lay their eggs earlier (e.g. Mazgajski 2003). However, nest hole reoccupation is rather rare due to pressure from secondary cavity nesters, especially starlings, and differs among forests of various sizes and starling populations (cf. Mazgajski 2003). Similarly, Matthysen and Adriaensen (1998) found that nuthatches *Sitta europaea* lost their holes in competition with starlings more frequently in small woodlots than in large ones.

In this study, starlings occupied the majority of holes from the previous season in small woodlots. The pressure of starlings forced woodpeckers to excavate new holes every year, which consumes time and energy. Additionally, the newly excavated hole could also be taken over by a starling (e.g. Tracy 1938, Smith 2005), as we observed in a small woodlot during the present study. Hole evictions probably occur very rarely and are difficult to observe. Smith (2005) observed only 7 such cases during almost 20 years of studying great spotted woodpeckers' breeding. Competitive pressure by the starling does not always lead to hole usurpation, but its harassment and the necessity to guard the hole may delay the woodpecker's egg laying (Ingold 1994). Several authors (Ingold 1989, 1994, Pasinelli 1999) suggest that later breeding helps woodpeckers avoid the usurpation of freshly excavated holes. This was confirmed quite recently by Smith (2006) who provides evidence that woodpeckers start laying eggs earlier with a decrease in starling abundance. Thus, the effect of forest patch size on great spotted woodpecker breeding could be related to competition for nest holes, better defined as cavity kleptoparasitism (cf. Mazgajski 2003), but the impact of hole competitors in relation to forest fragmentation both manifested as hole usurpa-

tion and interference interaction should be also studied in the future.

Regardless of the reasons for delayed breeding, we controlled for laying date in our analysis and still found that clutch size and the number of fledgling is related to patch size, and that worse parameters are achieved in small forests. Thus, the negative effect of decreasing patch size on the great spotted woodpecker reproduction is evident. The mechanism of this phenomenon in the studied species is still not clear, and other studies are needed in the future.

Most of the nesting attempts were delayed in small woodlots when compared to those in large forests. Regardless of the reason (cavity kleptoparasitism, differences in food availability, etc.), this could negatively affect both the adult birds and fledglings. Adults molt after breeding (Cramp 1985). Those birds which breed later may postpone molting, possibly leading to a deterioration of their condition and subsequent winter survival (Hinsley *et al.* 2003). Fledglings in poor nutritional condition will likely experience greater mortality risks and may be forced to disperse over larger distances (Matthysen *et al.* 1995), which could negatively impact their survival. In such a way, differences in breeding biology related to the size of forest patches may lead to subsequent negative effects. And those effects may accumulate in the great spotted woodpecker population.

We observed solitary birds feeding their young only in small woodlots. It is known that reduced parental care can decrease the survival of nestlings and number of fledglings (Kuitunen & Suhonen 1991). There are some explanations for such differences in parental behaviour between pairs breeding in large forests and small woodlots. Higher predator pressure in forest fragments affects not only birds' breeding success, but also increases the mortality of adult birds. Feeding trips, especially in gaps between forest patches, can enhance predation (Lima & Dill 1990). Also, parents with late broods (such as woodpeckers in small woodlots) could be more vulnerable to predators (Götmark 2002). However, the probability that predators will kill an adult bird should be similar for both sexes, because males and females work equally in feeding their young (e.g. Cramp 1985, Woźniak & Mazgajski 2003). Except for a few females, we

frequently observed solitary males bringing food to the young in small woodlots. Therefore, other factors besides predation should be considered. The numerous cases of males being present at nests in small woodlots may also be explained by differences in the mating system. The extremely rare cases of polyandry in the great spotted woodpecker, as well as in other woodpecker species (northern flicker *Colaptes auratus*), were found in highly fragmented landscapes (Kotaka 1998, Wiebe 2002). It seems that both factors may be occurring together in the study area. Regardless of the reason (e.g. predation, differences in mating system, nest desertion), such solitary birds occurred only in small forests, and this was another factor which differentiated woodpeckers breeding in small and large forest patches.

The results of our study suggest that some breeding parameters and ecological aspects worsen for great spotted woodpeckers in forests smaller than 100 ha despite similar breeding success in fragmented and unfragmented forests. Thus, information on more than just breeding success is required to assess the true impact of fragmentation on cavity nesting species. As forest size decreases, the impact of changes on the population may increase. Additionally, given the keystone role spotted woodpeckers play by excavating cavities, influences on their population may result in changes to the entire avian assemblage present in forests.

## Acknowledgements

We are deeply grateful to Joanna Mazgajski, Robert Rudolf and Andriy Zatushchevskyi for field assistance, Przemysław Chylarecki for help with statistics, the Pichalski family for providing housing and Jerzy Mazgajski for all logistic support. We also thank the landowners who kindly allowed us access to their forests. Two anonymous referees provided valuable comments to an earlier draft. This study was financed by the Committee for Scientific Research (KBN) grant No. 6P04F 06920. Barbara Przybylska reviewed the English version of this paper.

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