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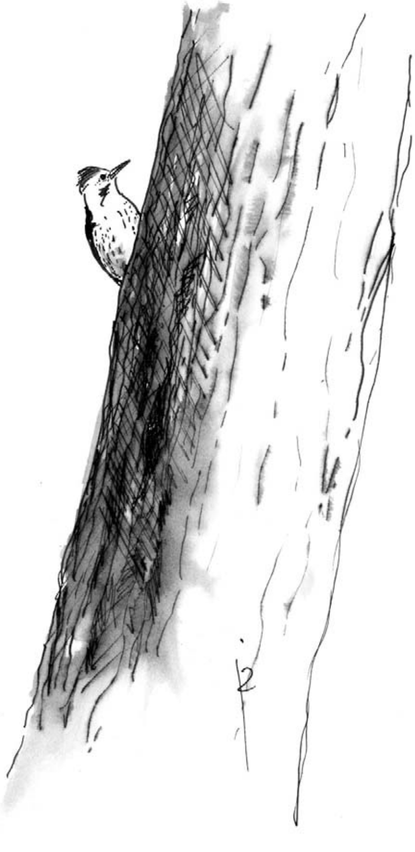
Reproduction of the Middle Spotted Woodpecker *Dendrocopos medius* in the Nerussa-Desna woodland, SW Russia, with particular reference to habitat fragmentation, weather conditions and food supply

Serguei M. Kossenko[1,*] & **Evgeniya Yu. Kaygorodova**[1]



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The Nerussa-Desna woodland (south-western Russia) is one of the core areas for the Middle Spotted Woodpecker *Dendrocopos medius*, a habitat specialist restricted mainly to mature oak forests. Recent studies have shown a lower breeding density of the species in fragmented compared with continuous habitat. To evaluate reproduction as a possible mechanism underlying the fragmentation effects, we studied reproductive performance of the species in both continuous habitat and fragmented habitat in the forested landscapes of the Nerussa-Desna woodland. During 1997–2001, annual variation of reproductive indices in both continuous and fragmented habitat was insignificant. None of the indices was significantly lower in fragmented habitat though nestling losses were significantly higher in fragments. Timing of breeding in 2000 was later in fragmented than continuous habitat, probably due to differential landscape phenology. In fragments, fledging success in a year was inversely related to the mean amount of rain. On the basis of individual pairs, fledgling production also correlated significantly and negatively with the amount of rain during the nestling period in food-poor fragments only. In 1999–2001, abundance of Lepidoptera larvae, main food for the Middle Spotted Woodpecker during nestling phase, varied significantly in continuous habitat, whereas in fragmented habitat the patterns of variation differed between fragments. No significant correlation was found between larval density and reproductive performance of individual pairs in either habitat. Large oak density, a habitat feature related to potential food abundance, was higher in fragments than in continuous habitat but was not related to the reproductive performance. The lower larval density within some territories in fragments as opposed to continuous habitat is likely to explain higher nestling mortality in fragmented compared to continuous habitat. Generally, we found little evidence for lowered reproductive performance in relation to fragmentation. Therefore, this seems unlikely to be responsible for the fragmentation-sensitive patterns of density.

Key words: *Dendrocopos medius*, Nerussa-Desna woodland, habitat fragmentation, reproductive performance, nesting mortality, weather, food supply

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INTRODUCTION

The Middle Spotted Woodpecker *Dendrocopos medius* is regarded as a habitat specialist restricted mainly to mature deciduous forests rich in oaks *Quercus* sp. (Glutz & Bauer 1980, Winkler *et al.* 1995, Pasinelli 2003). Continued loss and fragmentation of these forests have decreased the numbers and increased the isolation of extant local populations (Mikusiński & Angelstam 1997). In Russia, the woodpecker has been included in the Red Data Book as a species in decline (Ilyashenko & Ilyashenko 2000). One of the core areas for the Russian population of the species is the Nerussa-Desna woodland where its numbers have been estimated at 500 breeding pairs (Kossenko & Kaygorodova 1999, Kossenko 2004).

In Switzerland, presence and breeding density of the Middle Spotted Woodpecker in oak woods depended on size of the woods and degree of isolation from other oak woods (Müller 1982). Pettersson (1984) suggested that the low density of the Swedish population before its extinction was caused by fragmentation and that low reproduction, mainly emanating from poor breeding success, was an important factor in the extinction process. In Russia, Kossenko & Kaygorodova (1999) found lower breeding density in fragmented compared with continuous habitat. All these findings suggest that habitat fragmentation is a serious threat to the persistence of the Middle Spotted Woodpecker.

Habitat fragmentation is considered as one of the major issues in conservation biology (Simberloff 1995, Haila 2002). Its effects on wildlife populations have been well described for many taxa including birds (Saunders *et al.* 1991, Opdam 1991). At the same time, there is little knowledge about the mechanisms underlying effects of fragmentation (Wiens 1995). Our main approach to the problem is to describe reproduction and other population processes in variously fragmented habitats to identify possible mechanisms emanating from fragmentation (Kossenko 2002). Opdam *et al.* (1995) proposed comparing the reproduction rates in habitat fragments with those in continuous habitat in order to understand spatial factors regulating processes in fragmented populations. In fact, there are indications that reproductive success is essential in determining the effects of habitat fragmentation (e.g. Redpath 1995, Robinson *et al.* 1995). However, there is a remarkable lack of consistency in results across studies on this topic. Some studies have shown negative effects of fragmentation on reproduction (e.g. Hinsley *et al.* 1999, Roberts & Norment 1999, Luck 2003), whereas others have found no such effects (e.g. Matthysen & Adriaensen 1998, Walters *et al.* 1999, Buehler *et al.* 2002). As a result, it is difficult to make generalizations about the effects of habitat fragmentation on breeding productivity (Tewksbury *et al.* 1998, Stephens *et al.* 2003).

In this paper, we test the hypothesis that reproductive performance of the Middle Spotted Woodpecker is lower in fragmented compared with continuous habitat, thus providing a possible explanation for previously documented differences in density between fragmented and continuous habitats in the Nerussa-Desna woodland (Kossenko & Kaygorodova 1999). Preliminary results of this study covering the period 1997–98 have been published by Kossenko & Kaygorodova (2001). Here we present the results for the entire 5-year period (1997–2001) of the study, and evaluate the effects of factors as weather conditions and food supply. Weather is known to influence breeding performance in the Middle Spotted Woodpecker (Pasinelli 2001), and food availability has been recognized as an important factor affecting reproductive performance of birds (Lack 1968). Furthermore, Zanette *et al.* (2000) suggested that the role of food supply should receive greater consideration in fragmentation studies. Specifically, we compared the effects of weather and food supply on reproductive performance of the Middle Spotted Woodpecker between continuous and fragmented habitats.

METHODS

The study was carried out in the Nerussa-Desna woodland (centred at 52°32'N, 34°05'E), which is known as Important Bird Area (international code RU077, Heath & Evans 2000) and as the Biosphere Reserve "Nerusso-Desnyanskoe-Polesie". It lies in the European southwest of Russia within the Bryansk administrative region along the left bank of the Desna River (Fig. 1), with altitudes ranging from 130 m to 270 m a.s.l. Climate is moderately continental with a mean annual temperature of +5.4°C and a mean annual precipitation of 655 mm.

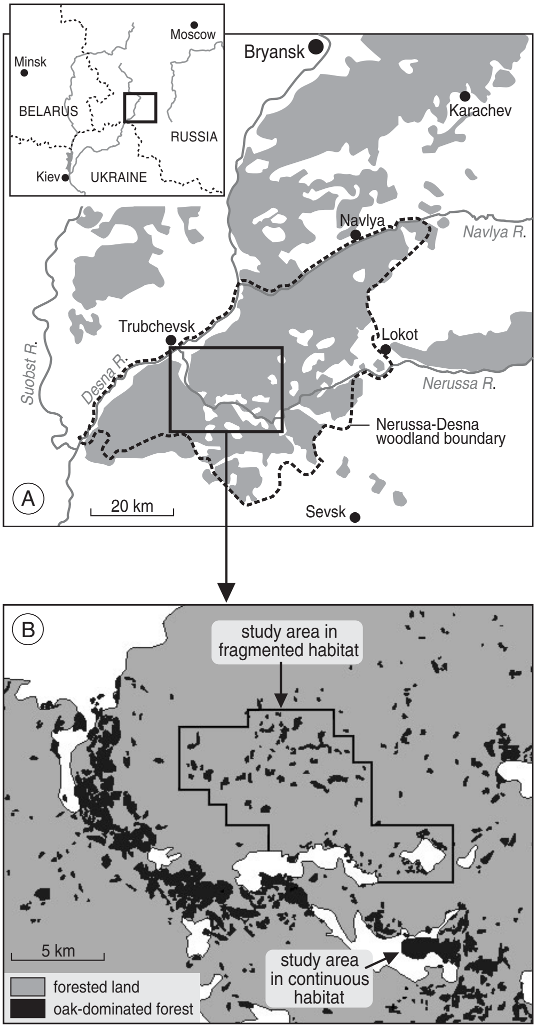

Figure 1. (A) Location of the Nerussa-Desna woodland. (B) Location of the study areas in continuous and fragmented habitats (compiled from forestry maps).

Forests cover more than 60% of the area. Although old-growth oak forests have declined during the last decades due to extensive timber harvesting, continuous and fragmented oak-dominated forests both still occur. This offered an opportunity to study the reproduction of the Middle Spotted Woodpecker both in fragmented habitat and in continuous habitat at the landscape scale. For comparison, we established two adjacent study areas differing in their degree of fragmentation of the main habitat (Fig. 1). A study plot of about 90 ha with continuous oak-dominated forest was established within a larger floodplain forest located along the middle river. This study area consisted of a 130-year old unmanaged oak-ash forest with over-aged oak trees. Oak *Quercus robur* and Ash *Fraxinus excelsior* dominate the upper storey. Other commonly occurring tree species are Norway Maple *Acer platanoides*, Common Maple *A. campestre* and Aspen *Populus tremula* with some admixture of Wych Elm *Ulmus glabra*, European White Elm *U. laevis*, Common Birch *Betula verrucosa* and Black Alder *Alnus glutinosa*. The other study area was a set of remnants of mainly unmanaged oak-dominated forest located along the small rivers and streams outside the floodplain area at 0.8–8.2 km from continuous oak-dominated forest. The fragments are surrounded by a matrix of closed-canopy non-oak forests of various age and composition, young regeneration stands and swamps. They are similar in terms of vegetation and physiographic features. The forest canopy is composed mostly of Oak, while Aspen, Common Birch, Scots Pine *Pinus sylvestris* and Norway Maple are found in small numbers with some scattered clumps of Black Alder and Norway Spruce *Picea abies* (see Kossenko & Kaygorodova 2001 for a more detailed description of the study area). Within the study area, the fragments ranging from 0.3 to 19 ha in size (total area c. 309 ha) are scattered over an area of about 75 km^2 with a degree of fragmentation of about 4%. The threshold, below which the importance of patch size and isolation for birds increases rapidly, has been estimated at 10–30% (Andren 1994). Moreover, we have found that only fragments with an area of at least 7 ha were occupied by the Middle Spotted Woodpecker for breeding. There are 17 fragments of sufficient area (total area c. 178 ha) within the study area, but only eight of them were used for breeding at least once during our study.

Despite some differences in tree species composition between fragmented and continuous habitats both are similar in such important feature as Oak dominance and general forest structure: tree stands with broad-leaved and small-leaved tree species alternate with small swampy alder stands. Low density of Ash in fragments compared with continuous habitat may be at least partly compensated by the higher density of Oak (see below) since Ash can be an Oak substitute for the Middle Spotted Woodpecker (see e.g. Pasinelli 2003) and vice versa. Conifers (Pine and Spruce) occurring in fragmented habitat in small numbers are generally not avoided by the Middle Spotted Woodpecker if they do not affect Oak dominance (Müller 1982). Therefore, the differences are not likely to confound our inferences concerning the effect of habitat fragmentation.

Data on reproductive performance were collected over the breeding seasons of 1997–2001. In order to monitor reproduction, we located nests within known breeding territories during building or egg laying. We then recorded parental behaviour and inspected all accessible breeding cavities using a mirror and a lamp during scheduled nest checks. The nests were reached with a ladder or spikes. Over all years, of the 54 nests found in continuous habitat within c. 67 breeding territories overlapping with the study plot, 48 could be reached without a serious risk to observer or nest tree (some nests were in rotten stems). In fragmented habitat, all of the 23 nests with eggs found within 26 breeding territories were climbed. Before the young fledged, we cut a hole of standardized size (just to pass a hand through) in the nest chamber with chisel and hammer to count and measure the nestlings. After this, the hole was closed with a standardized wooden plug fitting the hole and fixed with plasticine and nails. In all cases following this procedure the adults continued to bring food and no nest was abandoned after the nest chamber had been opened in this way. After the young had fledged, the nests were opened again and inspected closely to look for possible losses among the young or traces of predators.

The following reproductive indices were calculated: clutch size (number of eggs in the completed clutch), brood size (number of hatched young per nest where eggs were laid), fledgling production (number of young at fledging per nest where eggs were laid), nesting success (% nests with eggs where one or more young fledged), hatching success (% eggs hatched), fledging success (% eggs fledged). Only the closely inspected nests found before or during egg laying were included in calculations of the reproductive indices except the number of young in successful nests. Timing of breeding is known to be an important component of reproduction in birds (Lack 1968). We estimated the date the first egg hatched directly or by back-dating from nestling age. The latter was calculated from the length of the second primary (counted ascendently) or wing length. To determine the sources of variation in reproductive performance, we also identified failures during nest-building, and egg - and nestling stages.

In the Nerussa-Desna woodland, the Middle Spotted Woodpecker nestling diet consists primarily of caterpillars gathered from foliage (Kossenko & Kaygorodova 2003). This resource is characterized by periodic irruptions that provide abundant food. In 1999–2001, when data on food supply were sampled, the larvae of the Plumed Prominent *Ptilophora plumigera* (family Notodontidae) were most abundant among defoliating Lepidoptera. It was also the dominant species in the nestling diet (Kossenko & Kaygorodova 2003). This species specializes on the Norway and Common Maple. The larvae of the Plumed Prominent are usually found in the first half of May when leaves of maples open. We estimated the abundance of larval Lepidoptera directly on foliage by visually searching 100-leaf samples. Each sample was taken from five neighbouring maple trees (20 leaves each) in a plot. Sample plots were regularly positioned approximately every 100 m throughout the woodpecker territories. We counted larvae in the second half of May when most of them are half-grown to full-grown. This period coincides with the nestling phase of the Middle Spotted Woodpecker. We counted larvae on the Norway Maple foliage only because this tree species is well presented in the lower storey of the forest, easily accessible from the ground, and hosts larvae of the Plumed Prominent and other defoliating Lepidoptera larvae. The larval density for a habitat or breeding territory was calculated as the median number of larvae per 100 leaves from a range of sample plots.

A study of Pasinelli and Hegelbach (1997) has revealed the outstanding importance of oaks with a diameter at breast height (dbh) of ≥ 36 cm as foraging trees for the Middle Spotted Woodpecker. In our study, the role of large oaks could be crucial before the emergence of Lepidoptera larvae, as a female needs an abundance of surface-living insects to initiate laying. We determined large oak density within breeding territories by measuring the distance between two nearest oak trees with dbh ≥ 36 cm at the intersections of a 100x100 m grid (one distance per intersection).

Weather data were taken from the meteorological station Navlya located c. 50 km northeast of the study areas within the same physiographic district as the study areas. We examined the influence of local weather conditions on reproductive performance using the daily temperature means and the amount of rain during the nestling period.

All statistical analyses were carried out using STATISTICA v. 6.0. We calculated parametric and nonparametric statistics where appropriate. As both methods gave similar results, the latter were preferably used since sample sizes were mainly small. Correlation between variables was estimated with Spearman's coefficient of rank correlation. Only significant or strong effects are given in detail. Statistical significance was accepted at the 0.05 level. Data are presented as mean ± SD.

RESULTS

Reproductive performance and nesting mortality

For none of the reproductive indices we found significant differences between years (Table 1). Clutch size for all years combined was almost the same in fragmented and continuous habitat (6.7 vs. 6.5 eggs per pair, respectively) and overall fledgling production was only slightly lower in fragments compared with continuous habitat (4.5 vs. 5.0 young per pair, respectively). Pairwise comparisons of reproductive indices between continuous habitat and all fragments for particular years and all years combined revealed no significant difference (Table 1).

Beginning of egg hatching in the Middle Spotted Woodpecker usually coincides with the date of caterpillar emergence (Kossenko & Kaygorodova 2003). During the 5-year study period, the annual median dates of hatching were between 7 May and 18 May in continuous habitat and between 9 May and 20 May in fragments. The egg-hatching period varied between five (1997) and 15 (2001) days in continuous habitat, and between three (1997 and 2001) and six (1998) days in fragmented habitat. There was a significant effect of year on hatching dates both in continuous habitat (Kruskal-Wallis test, $H_4 = 32.29$, $n = 46$, $P < 0.001$) and fragments ($H_4 = 15.64$, $n = 24$, $P = 0.004$). In continuous habitat, eggs hatched on average slightly (0–2 days) earlier each year (Fig. 2), the differences being significant in 2000 (Mann-Whitney U-test, $Z = 2.53$, $P = 0.01$).

There was no significant variation from year to year in failures among nests, eggs or nestlings in continuous or fragmented habitats. For all years combined, three of the 42 nests with eggs found in continuous habitat failed to produce offspring (Fig. 3). Of them, two nests were destroyed during stormy weather. The third unsuccessful nest presumably contained unfertilized eggs. Of the 23 nests with eggs found in fragmented habitats, four were lost. Three nests containing nestlings were abandoned (one in 1997, 1998 and 1999). One

Table 1. Reproductive indices (mean or % ± SD) of the Middle Spotted Woodpecker in continuous and fragmented habitats during 1997–2001 (sample sizes in parentheses = no. of pairs or nests). See text for explanation of reproductive indices. Standard deviations of percentages are based on binomial sampling variation. Annual variations in clutch size, brood size and number of young are examined with Kruskal-Wallis test, and between-habitat differences in these indices with Mann-Whitney *U*-test. The percentage indices are examined with Fisher's exact test except hatching success and fledging success, for which none of the statistical tests is applicable as eggs and nestlings within nests are not independent. No statistically significant variation between years or habitats was found.

Index	Year					
	1997	1998	1999	2000	2001	All
Clutch size						
Continuous	6.3 ± 0.8 (7)	6.1 ± 1.4 (8)	6.9 ± 1.6 (7)	6.8 ± 1.6 (10)	6.0 ± 1.2 (9)	6.4 ± 1.3 (41)
Fragmented	6.0 ± 0 (3)	5.8 ± 1.0 (4)	7.0 ± 0.8 (4)	7.2 ± 0.8 (6)	7.2 ± 0.8 (6)	6.7 ± 0.9 (23)
Brood size						
Continuous	5.4 ± 1.3 (7)	5.1 ± 2.4 (8)	5.3 ± 2.7 (8)	5.2 ± 2.0 (10)	5.7 ± 1.3 (9)	5.3 ± 1.9 (42)
Fragmented	4.7 ± 0.6 (3)	5.5 ± 1.0 (4)	6.8 ± 1.0 (4)	6.3 ± 1.2 (6)	6.2 ± 1.7 (6)	6.0 ± 1.3 (23)
No. of young, all nests						
Continuous	5.4 ± 1.3 (7)	4.9 ± 2.2 (8)	4.1 ± 2.4 (8)	5.1 ± 1.9 (10)	5.4 ± 1.1 (9)	5.0 ± 1.8 (42)
Fragmented	3.0 ± 2.7 (3)	4.0 ± 2.9 (4)	4.0 ± 2.8 (4)	5.7 ± 1.4 (6)	4.7 ± 2.6 (6)	4.5 ± 2.4 (23)
No. of young, successful nests						
Continuous	5.4 ± 1.3 (7)	5.7 ± 0.9 (9)	4.8 ± 1.7 (8)	5.7 ± 0.7 (10)	5.5 ± 1.1 (10)	5.4 ± 1.1 (44)
Fragmented	4.5 ± 0.7 (2)	5.3 ± 1.5 (3)	4.5 ± 1.9 (4)	5.7 ± 1.4 (6)	5.6 ± 1.3 (5)	5.3 ± 1.4 (20)
Nesting success, %						
Continuous	100.0 ± 0 (7)	87.5 ± 11.7 (8)	87.5 ± 11.7 (8)	90.0 ± 9.5 (10)	100.0 ± 0 (9)	92.9 ± 4.0 (42)
Fragmented	66.7 ± 27.2 (3)	75.0 ± 21.7 (4)	75.0 ± 21.7 (4)	100.0 ± 0 (6)	83.3 ± 15.2 (6)	82.6 ± 7.9 (23)
Hatching success, %						
Continuous	86.4 ± 13.0 (7)	83.7 ± 13.0 (8)	85.7 ± 12.4 (8)	76.5 ± 13.4 (10)	94.4 ± 7.7 (9)	84.8 ± 5.5 (42)
Fragmented	77.8 ± 24.0 (3)	95.7 ± 10.1 (4)	96.4 ± 9.3 (4)	88.4 ± 13.1 (6)	86.0 ± 14.2 (6)	89.0 ± 6.5 (23)
Fledging success, %						
Continuous	86.4 ± 13.0 (7)	79.6 ± 14.2 (8)	67.3 ± 16.6 (8)	75.0 ± 13.7 (10)	90.7 ± 9.7 (9)	79.5 ± 6.2 (42)
Fragmented	50.0 ± 28.9 (3)	69.6 ± 23.0 (4)	57.1 ± 24.8 (4)	79.1 ± 16.6 (6)	65.1 ± 19.5 (6)	66.5 ± 9.8 (23)

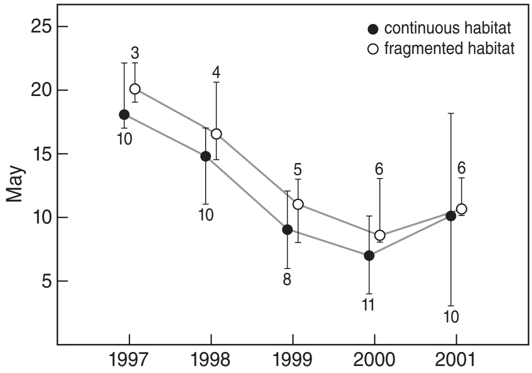

Figure 2. Medians and ranges of egg hatching dates in continuous habitat and fragmented habitat. Numerals indicate sample sizes.

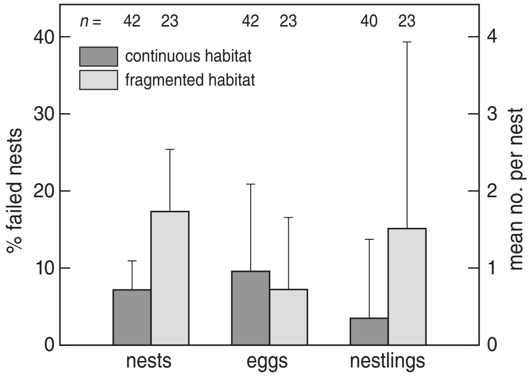

Figure 3. Failure rates among nests (%), eggs (number per nest where eggs were laid) and nestlings (number per nest where eggs hatched) of the Middle Spotted Woodpecker in continuous and fragmented habitats during 1997–2001; n = sample sizes. Vertical lines show one standard deviation. Difference in the loss of nestlings is significant (Mann-Whitney U-test, $Z = 2.80$, $P = 0.02$).

more nest was destroyed after the nest tree had fallen. Of the 264 eggs laid in continuous habitat, 34 failed to hatch and six were lost after the fall of the nest tree. In fragmented habitat, 17 of 155 eggs failed to hatch. Of the 224 nestlings hatched in continuous habitat, 14 perished probably due to starvation although adults still delivered food to the nest. In fragmented habitat, 35 of 138 nestlings died including 10, which probably perished from starvation. One brood of eight nestlings died after the fall of the nest tree. The other 17 nestlings were lost due to the three above-mentioned cases of nest abandonment.

We found no significant difference between continuous and fragmented habitats in the proportion of failed nests and number of eggs lost per pair in any year separately or all years combined (Fig. 3). Nestling losses for all years combined were significantly smaller in continuous habitat than in fragments (Fig. 3).

Weather

Over all years, weather conditions during the nestling period varied considerably, with 1999 being the wettest in both continuous habitat and fragments; year 1999 was also the coldest in continuous habitat, whereas 2001 was the coldest in fragments (Table 2). In continuous habitat, neither mean temperature nor mean amount of rain in the nestling period in a year were related to any of the reproductive indices. In fragments, the only significant correlation was found between the mean amount of rain and fledging success (Spearman rank correlation, $r_s = -0.90$, $n = 5$, $P = 0.037$). On the basis of individual pairs, the correlation between the reproductive indices and mean temperature or amount of rain during the nestling period of a pair was insignificant both in continuous habitat and in fragments.

Food supply

The food supply within breeding territories measured in 1999–2001 by the abundance of larval Lepidoptera varied significantly over the years in continuous habitat, declining from one year to the next (Kruskal-Wallis test, $H_2 = 75.65$, $n = 235$, $P < 0.001$; Table 3). In fragmented habitat, sampling distribution of the larval abundance was bimodal, indicating heterogeneity of the sample. The apparent reason of the heterogeneity was the differential larval density in fragments (Fig. 4). Cluster analysis by two-mean clustering method distinctly divides all fragments into subsets with high vs. low larval density. We did not find any

Table 2. Weather conditions during the nestling period in 1997–2001. Nestling period is timespan between first hatching and last fledging. Mean temperature is the mean of mean daily temperatures during each period. The differences between habitats in the weather conditions in a year are caused by differences in the timing of the nestling period between habitats.

Year	Nestling period	Mean daily amount of rain (mm)	Mean temperature (°C)
Continuous habitat			
1997	17 May – 13 June	2.32	13.73
1998	11 May – 8 June	1.14	15.10
1999	6 May – 3 June	3.22	11.51
2000	4 May – 1 June	0.86	12.75
2001	3 May – 9 June	2.09	12.04
Fragmented habitat			
1997	19 May – 13 June	2.50	13.88
1998	14 May – 11 June	1.10	16.10
1999	8 May – 4 June	3.34	12.19
2000	8 May – 4 June	0.79	13.50
2001	10 May – 4 June	2.08	11.07

relation between larval density and fragment size, isolation or age of oaks that could explain this pattern. Even neighbouring fragments of similar tree species composition and area differed significantly in larval density. In larva-rich fragments, larval abundance did not vary over the years, while larva-poor fragments showed significant year-to-year variation ($H_2 = 8.91$, $n = 89$, $P = 0.01$) though remained larva-poor between years despite the large variation (Fig. 4).

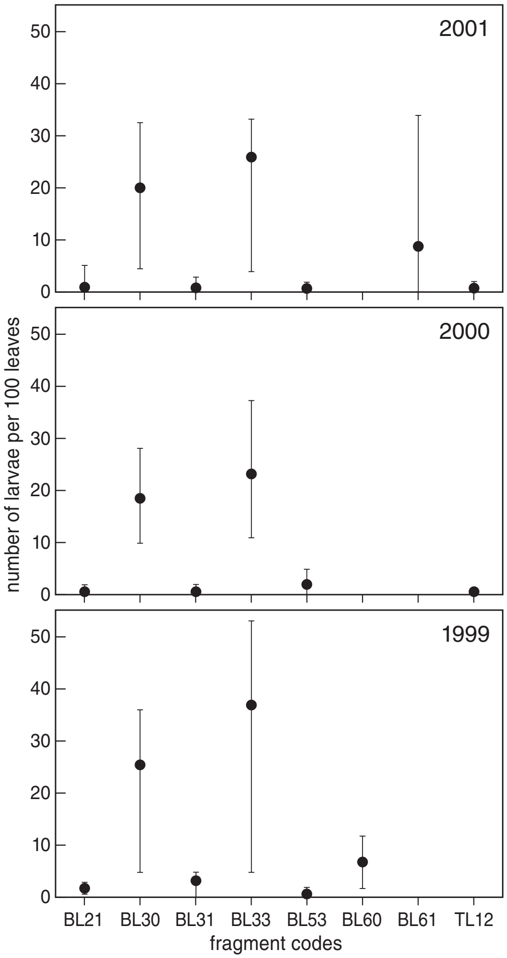

Figure 4. Patterns of larval density within breeding territories in habitat fragments in 1999–2001. Symbols are medians and vertical lines are ranges. Fragment BL60 was unoccupied in 2000 and 2001, BL61 in 1999 and 2000, and TL12 in 1999.

Table 3. Larval density (number of larvae per 100 leaves) in continuous habitat and fragments in 1999–2001 (n = number of plots).

Year	Continuous habitat			Larva-poor fragments			Larva-rich fragments		
	Median	Range	*n*	Median	Range	*n*	Median	Range	*n*
1999	13	2–27	27	2	0–5	16	17.5	2–53	16
2000	2	0–17	104	0	0–5	35	23	10–37	13
2001	1	0–5	104	0	0–5	38	19	0–34	32

Larval abundance in particular years was either not (1999) or significantly lower in continuous habitat than in the larva-rich fragments (Mann-Whitney *U*-test, 2000: $Z = 5.84$, $P < 0.0001$; 2001: $Z = 7.94$, $P < 0.0001$; see median values, ranges and sample sizes in Table 3). At the same time, it was significantly higher in continuous habitat compared to larva-poor fragments (1999: $Z = 4.95$, $P < 0.0001$; 2000: $Z = 4.56$, $P < 0.0001$; 2001: $Z = 2.68$, $P < 0.01$).

We did not find any significant correlation between larval density and reproductive performance of individual pairs in continuous or in fragmented habitat neither in any particular year nor in all years combined. The only nearly significant correlation was found in fragmented habitat between larval density and fledgling production in 1999, i.e. in the year with highest amount of rain (Spearman rank correlation, $r_s = 0.87$, $n = 5$, $P = 0.054$). We also found no significant difference in any of the reproductive indices between fragments with high vs. low larval density.

Mean distance between the two nearest large oak trees within the Middle Spotted Woodpecker territories in particular fragments ranged from 9.0 m to 26.4 m. Overall, pooled over the fragments, it was significantly lower in fragmented than in continuous habitat (13.0 ± 11.5 m ($n = 142$) and 16.7 ± 11.3 m ($n = 98$), respectively; Mann-Whitney *U*-test: $Z = 3.86$, $P = 0.0001$), i.e. large oak density was higher in fragmented than in continuous habitat. We found no correlation between large oak density and reproductive indices in both continuous and fragmented habitats. Large oak density showed also no correlation with larval density.

DISCUSSION

Reproductive performance in fragmented vs. continuous habitat

In our study areas, reproductive performance of the Middle Spotted Woodpecker was noticeably high compared with that in other populations. Thus, the overall brood size was 5.6, and fledgling production was 4.8 young per pair (all nests) or 5.4 young per successful pair (fragmented and continuous habitats pooled), i.e. almost twice as much as the 2.3 young per pair (all nests) or 3.2 young per successful pair reported from north-eastern Switzerland (Pasinelli 2001). The estimate of breeding productivity of 2.7 fledged young per successful pair in the Swedish population (Pettersson 1985) came from a near-extinct population. Only in Austria an equally high number of 5.1 nestlings (when 5–16 days old) per successful nest was recorded (Michalek *et al.* 2001).

Year-to-year variation of reproductive indices was insignificant both in fragmented and in continuous habitats (possibly due to the relatively small sample sizes). The reproductive indices did not differ significantly between fragmented and continuous habitat. We cannot test the possibility that fragmentation might cause later fledging or lower body mass of fledglings since we did not determine exact fledging dates nor nestling weights.

Hatching dates of the Middle Spotted Woodpecker varied markedly over the years, being earlier in continuous habitat than in fragments in some years. The time of hatching in a year is closely linked to the emergence of Lepidoptera larvae (Kossenko & Kaygorodova 2003) which, in turn, coincides with the time when maples come into leaf (unpubl. data). As any particular stage of vegetation, the latter is attained when the sum of the mean daily temperatures reaches a certain value (Walter 1979). We feel confident that the differences in hatching dates between fragmented and continuous habitats were caused by the specific location of our study areas. Fragments were located outside the floodplain, whereas the study area representing continuous habitat was in a riverine forest. The spring development of vegetation, which determines the timing of caterpillar emergence, is usually earlier in floodplains than in neighbouring areas (unpubl. data). Individual quality or age are unlikely to be the factors accounting for the differences in hatching dates as no differences were found in the reproductive indices. Besides, participation of one-year old individuals in breeding did not differ between fragmented and continuous habitats (Kossenko 2002).

Neither nest, nor egg failures were significantly different between fragments and continuous habitat. A possible explanation of this pattern may be that cavities provide protection from predators, which have been shown to be a major factor in lowering reproduction of open-nesting birds in fragmented habitats (e.g. Hoover *et al.* 1995, Robinson *et al.* 1995). Besides, our fragments are located within a matrix of forest. This is very different from most studied fragmented habitats. We did not observe any evidence of nest predation. However, other cavity-nesting birds including woodpeckers have been shown to suffer from predators (see e.g. Wesołowski 1995, Walankiewicz 2002).

Although the fledgling production in successful nests was very similar in both habitats, loss of nestlings was significantly higher in fragments. This difference obviously arises from the abandonment of nests with nestlings in fragments. It is of particular note that in the Swedish population, just before extinction, the majority of failed nests were abandoned after incubation (Pettersson 1985).

In general, our data suggest that reproductive performance of the Middle Spotted Woodpecker is not affected significantly by habitat fragmentation in our study areas. Similar patterns have been found in other studies. Thus, Tjernberg *et al.* (1993) found no differences in reproductive indices or timing of breeding in Black Woodpeckers *Dryocopos martius* in a forested landscape area and in farmland with highly fragmented forests. Matthysen & Adriaensen (1998) also observed no differences in reproductive parameters of the Nuthatch *Sitta europaea* between fragments and two large forests. They also did not find effects of fragmentation on timing of breeding in this species. Nour *et al.* (1998) made similar inferences from studying other cavity-nesters, i.e. Great Tit *Parus major* and Blue Tit *P. caeruleus*, in small fragments vs. large forests.

Effects of weather and food supply

Our data suggest an adverse impact of rainfall on reproduction in fragments. Similarly, high amounts of rainfall as well as low temperatures during the nestling phase negatively affected breeding performance of the Middle Spotted Woodpecker in north-eastern Switzerland (Pasinelli 2001), but no clear correlation between breeding success and weather variables was found in Sweden (Pettersson 1985). In fragmented habitat, the negative relationship between the numbers of fledglings produced by individual breeding pairs and the amount of rain was significant after excluding the larva-rich fragments (Spearman rank correlation, $r_s = -0.66$, $n = 11$, $P = 0.03$). Therefore, it seems that food shortage may have increased the impact of rain. Increased vulnerability to harsh weather when food is in short supply has also been found in other birds. Thus, in the study of Hogstad (2000) the breeding success of Bramblings *Fringilla montifringilla* in cold, rainy summers was poor when food supply was low but normal when food was in good supply.

Significant annual variations of larval abundance in larva-poor fragments and continuous habitat did not appear to affect the yearly reproductive performance as neither significant correlations between larval abundance and reproductive indices nor significant year-to-year variations of most reproductive indices were found. Likewise, no clear correlation emerged between larval abundance and reproductive performance of individual pairs in any year or habitat, except a nearly significant positive correlation between larval density and fledgling production in 1999. We believe that harsh weather in that particular year contributed to the relationship.

Generally, our findings suggest that reproductive performance of the Middle Spotted Woodpecker does not respond to changes in the abundance of Lepidoptera larvae. We have no evidence that woodpeckers breeding in fragments have used resources in habitats surrounding the fragments. These consist of pure conifer forests, that are generally avoided by Middle Spotted Woodpeckers (see Pasinelli 2003), or small-leaved deciduous forests unsuitable for this woodpecker species. Probably, occupied fragments are large enough and adults normally are able to compensate for a reduction in the supply of larvae by enlarging foraging distances, as recorded in the Blue Tit *Parus caeruleus* (Tremblay *et al.* 2005), or by switching to other food items. The latter hypothesis is supported by numerous remains of Common Cockchafers *Melolontha melolontha* in many nests both in fragmented and in continuous habitats.

On the other hand, lower abundance of larvae in larva-poor fragments compared with continuous habitat may explain the higher nestling losses in fragmented habitat for all years combined. In some studies it has been shown that fragmentation may affect reproduction only when food is in short supply. For instance, Hakkarainen *et al.* (2003) found that landscape composition had the strongest effect on vole-eating Tengmalm's Owl *Aegolius funereus* breeding in the declining phase of a vole cycle. In another fragmentation study, the Eastern Yellow Robin *Eopsaltria australis* experienced relative food shortage in small fragments compared with large fragments, with negative consequences of low food supply on egg mass and nestling body size (Zanette *et al.* 2000). Lower food availability in small compared with large forest remnants has also been shown in other studies (e.g. Burke & Nol 1998, Luck 2003).

Since overall large oak density was somewhat higher in fragments than in continuous habitat, it cannot be ruled out that this could somehow compensate for the lower abundance of larvae in some fragments compared to continuous habitat. Anyway, the density of large oaks was not related to the reproductive performance. Interestingly, in the study of Pasinelli (2001) the density of large oaks also turned out to be a poor predictor of breeding success in the Middle Spotted Woodpecker.

CONCLUSIONS

We studied a rare species breeding in natural cavities, not in artificial nest-boxes. The results therefore may be subject to the problems associated with sample size. With these reservations, our data indicate that between-year variation in reproductive performance of the Middle Spotted Woodpecker in our study areas is small and reproduction in fragments seems to be more susceptible to variations in local weather conditions and food supply. The greater vulnerability to poor conditions might have as a consequence that subpopulations confined to fragmented habitat might decline in the long term if reproduction in good years or immigration could not balance a shortfall in poor years. This in turn would depend on the frequency and severity of poor conditions.

Vacant breeding territories are more common in fragmented than in continuous habitat (Kossenko 2002). An explanation for this pattern might be that reproductive performance in fragmented habitat is too low to compensate for adult annual mortality. However, as evidenced from our data, reproductive success in habitat fragments did not differ significantly from that in continuous habitat. We therefore conclude that reproductive performance is unlikely to be responsible for the lower breeding density in fragments compared to continuous habitat.

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SAMENVATTING

De Middelste Bonte Specht *Dendrocopos medius* wordt meestal als een echte habitatspecialist beschouwd, beperkt tot volgroeid loofbos met een fors aandeel eiken *Quercus* sp. Aaneengesloten oud eikenbos is overal in Europa schaars geworden door fragmentatie en omzetting in naaldbos. Hierdoor zijn populaties van Middelste Bonte Spechten versnipperd geraakt. In Rusland gaat de soort in aantal achteruit, en is hij op de Rode Lijst geplaatst. Een van de kerngebieden in Rusland betreft het Nerussa-Desna woud, gelegen langs de rivier de Desna in ZW-Rusland. In dit uitgestrekte bosgebied werden twee studieplots gekozen: (a) 90 ha aaneengesloten bos gedomineerd door 130 jaar oude Zomereik *Quercus robur* en Es *Fraxinus excelsior* gelegen in het rivierdal, en (b) een conglomeraat van snippers eik-gedomineerd bos buiten het rivierdal op 0.8–8.2 km afstand van het aaneengesloten bos. De snippers varieerden in omvang van 0.3–19 ha (in totaal 309 ha) en lagen verspreid over een gebied van 75 km^2. Legsel- en broedselgrootte, aantal uitvliegende jongen, en nest-, uitkomst- noch uitvliegsucces bleken tussen aaneengesloten en versnipperde habitats significant te verschillen. Evenzo werden geen weersinvloeden op de reproductiecijfers in het aaneengesloten broedgebied gevonden; in versnipperde bossen had alleen de hoeveelheid neerslag een negatief effect op het uitvliegsucces. De talrijkheid van rupsen in aaneengesloten bos schommelde sterk van jaar op jaar, maar in gefragmenteerd bos verschilde de rupsendichtheid vooral van snipper tot snipper. In geen van beide habitattypes werd een correlatie gevonden tussen voedselaanbod en reproductieve eigenschappen van Middelste Bonte Spechten, mogelijk met uitzondering van de gemiddeld lagere rupsendichtheid in gefragmenteerd bos en de grotere nestjongensterfte aldaar in vergelijking met aaneengesloten bos. Hoewel gebaseerd op kleine steekproeven, immers verzameld aan spechten broedend in natuurlijke holtes, zijn de verschillen in broedprestaties van Middelste Bonte Spechten nestelend in aaneengesloten en versnipperde habitats gering. De reproductie in gefragmenteerde bossen lijkt gevoeliger te zijn vooral lokale weersinvloeden en voedselaanbod. Wanneer het tegen zit, kunnen jongenaanwas in goede jaren en immigratie kennelijk niet compenseren voor slechte broedresultaten in daljaren. Dit zou ook het grotere aandeel vacante territoria in gefragmenteerd habitat kunnen verklaren (reproductie onvoldoende om sterfte van adulte vogels op te vangen), ware het niet dat de reproductiecijfers van Middelste Bonte Spechten in aaneengesloten en versnipperd bos niet significant van elkaar verschillen. (RGB)

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