

## FOREST SIZE AND ISOLATION HAVE NO EFFECT ON REPRODUCTIVE SUCCESS OF EURASIAN NUTHATCHES (*SITTA EUROPAEA*)

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**ABSTRACT.**—We collected data on breeding success, nestling mass, fledging date, and recruitment of Eurasian Nuthatch (*Sitta europaea*) nesting attempts in a number of small (<30 ha) forest fragments and parks, as well as in two larger (>200 ha) forests. Most study areas were dominated by well-developed oak stands. We found no differences in reproductive parameters between fragments and the two large forests, nor any relationship with the size or degree of isolation of individual fragments. Failed nests more often were taken over by nest competitors (particularly starlings) in fragments, but this did not seem to affect overall success rates. Pairs nesting in parks had a lower chance to produce recruits than pairs in similar-sized oak fragments, and early broods recruited more offspring than late broods. We conclude that fragmentation does not affect the suitability of mature oak stands for reproduction of nuthatches within the size range of oak stands frequented by this species. *Received 14 July 1997, accepted 12 March 1998.*

FRAGMENTATION OF NATURAL HABITATS is a potential threat to the persistence of animal and plant populations in many different kinds of landscapes and habitat types (Saunders et al. 1991, Andrén 1992, Robinson et al. 1995). Many studies have demonstrated a lower diversity and/or abundance of various organisms in habitat fragments compared with larger habitat tracts (e.g. Soulé 1986, Opdam 1991, Matthysen et al. 1995b). Two major groups of hypotheses to explain these patterns involve changes in population structure and habitat quality, respectively. Changes in population structure include a reduction in population size, diminishing dispersal between patches or between local populations within a metapopulation, and loss of genetic variation (Gilpin and Hanski 1991). Changes in habitat quality may result from the increasing influence of abiotic and biotic elements from the surrounding landscape (the matrix) on the habitat remnant, or from changes in community structure within the habitat (e.g. abundance of prey, parasites, predators, competitors; Soulé 1986, Saunders et al. 1991). Consequently, fitness parameters and ultimately population growth may be negatively (or positively) related to the nature of adjacent habitats as well as the size, shape, and degree of isolation of the remaining patches.

Relatively few studies have documented the

effects of habitat fragmentation on fitness parameters. The prominent exception is the reproductive success of open-nesting birds, which generally decreases in smaller fragments and/or near habitat edges owing to increased predation or brood parasitism (Gates and Gysel 1978, Brittingham and Temple 1983, Møller 1988, Kurki and Lindén 1995, Robinson et al. 1995). This pattern has been verified experimentally by the use of artificial nests in a wide variety of habitats (Andrén 1992, Santos and Telleria 1992, Burkey 1993, Nour et al. 1993). However, nest predation and brood parasitism are unlikely to provide a general explanation for the effects of habitat fragmentation on bird species that nest in more protected sites such as tree cavities. Reproductive success of cavity-nesting birds may be influenced by other factors such as changes in competition for nest sites or in food availability, but very few studies have addressed reproductive success in forest fragments (Kuitunen and Helle 1988, Tjernberg et al. 1993, Nour et al. 1998).

The Eurasian Nuthatch (*Sitta europaea*) appears ideally suited to test whether forest fragmentation affects reproductive success of a cavity-nesting bird species. The effects of fragmentation are well documented at the population level, but the underlying causes are not resolved. Nuthatches have been shown to be less abundant in small and isolated forest fragments and in that respect are among the most

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fragmentation-sensitive forest bird species (Opdam and Schotman 1987, van Dorp and Opdam 1987, Enoksson et al. 1995, Matthysen unpubl. data). These negative effects have generally been attributed to lack of dispersal, or to higher mortality during dispersal among fragments (Verboom et al. 1991, Enoksson et al. 1995, Matthysen et al. 1995a, Matthysen and Currie 1996), but effects of resource availability (nest sites and/or food) have not been studied. In the breeding season, nuthatches are generalist insectivores that mainly glean and probe for arthropods on bark and leaves. They are obligate secondary cavity nesters, and competition for suitable nest sites is well documented (e.g. Nilsson 1984). Here, we report on reproductive success of nuthatches in a set of forest and parkland fragments of varying sizes, as well as in two larger forests.

#### METHODS

*Study species and areas.*—In western Europe, Eurasian Nuthatches typically occur at relatively low densities (one to five pairs per 10 ha) in mature deciduous woodland. They normally raise a single brood per year in a natural cavity or old woodpecker nest. Pairs defend the same territory year-round (Matthysen 1990). Most of the data were collected from 1990 to 1994 in a 200-km<sup>2</sup> study area close to Antwerp, northern Belgium. The study area contained scattered forest patches or parkland areas with extensive wooded cover (henceforth "fragments") that together covered only 1.5% of the area (see Matthysen et al. 1995a). Additional data were collected in two study plots within large forests (>200 ha; see below). For this study, fragments were defined as discrete patches of a single habitat type ("oak forest" or "park") separated from similar habitat patches by at least 100 m (typically  $\geq 500$  m). Using this definition, we never observed color-banded individuals to include more than one fragment in their home range. A few patches with nuthatches but belonging to other forest types were not considered in this study. All oak forest fragments were well-developed stands (>20m canopy height) of common oak (*Quercus robur*), with at most 10% other trees such as European beech (*Fagus sylvatica*), birch (*Betula* spp.), and red oak (*Quercus rubra*). Park areas were mostly old private estates, often turned into public parks, with a mixture of woodland, ponds, lawns and paved areas. The wooded vegetation in these parks consisted of large old trees, often  $\geq 30$  m tall, mainly oak and beech but also ornamental trees such as lime (*Tilia platyphyllos*), horse chestnut (*Aesculus hippocastanum*), and some conifers. All of the oak fragments and about half of the parks were to a

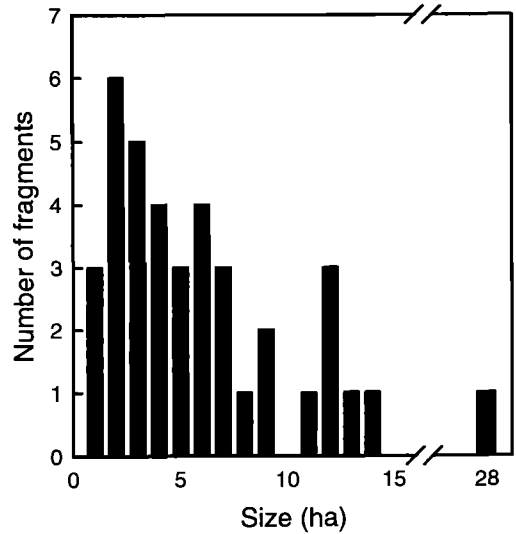


FIG. 1. Size distribution of forest fragments with at least one observation of Eurasian Nuthatches ( $n = 38$ ), excluding one large (30 ha) fragment with 16 observations (see text).

large degree surrounded by agricultural land, whereas the other half of the parks were largely surrounded by residential areas. Only a few fragments were connected by hedgerows, and these were usually only one tree-width wide. Nest boxes of various types and sizes were present in only a few areas.

Fragment sizes as measured from aerial photographs varied from 0.8 to 30 ha (Fig. 1). Adjacent gardens with scattered trees were not incorporated in this measure, and lanes connected to a woodlot were only incorporated if at least three or four trees wide. Because most fragments were small (Fig. 1), sizes were logarithmically transformed to obtain a normal distribution for statistical analysis (Kolmogorov-Smirnov test, untransformed  $P = 0.02$ , transformed  $P > 0.9$ ). On average, parks were somewhat smaller ( $\bar{x} = 4.6$  ha, range 1.5 to 14 ha) than oak stands ( $\bar{x} = 6.9$  ha, range 0.8 to 28 ha), but the difference was not significant (Mann-Whitney  $U$ -test,  $z = -0.97$ ,  $P > 0.3$ ). The degree of isolation ( $I$ ) from other nuthatch habitat was calculated by a modified version of Whitcomb et al.'s (1981) gravitation index, calculated for each fragment as:

$$I = -\log \sum_i (T_i / d_i^2), \quad (1)$$

where  $d$  = distance from the focal fragment to the  $i$ th fragment (including all fragments within the 200-km<sup>2</sup> study area and the 2-km zone around it), and  $T$  = the maximum number of nuthatch territories in the  $i$ th fragment during the study. We used number of territories rather than size because this allowed us to integrate different types of habitat supporting dif-

ferent population densities. In particular, densities in parks were 50% higher than those in oak fragments (Matthysen unpubl. data), which may be explained by differences in canopy volume, tree-species diversity, or other factors. The number of territories in both habitat types was a simple linear function of size and was not related to isolation (Matthysen unpubl. data). Logarithmic transformation was used to obtain a normal distribution (Kolmogorov-Smirnov test, untransformed  $P < 0.001$ , transformed  $P > 0.5$ ).

In addition to the fragments, we studied two plots of about 28 ha within larger forests: Peerdsbos (PB; >200 ha, data collected 1991 through 1994), and Meerdaalbos (MB; ca. 1,500 ha, data collected 1992 through 1994). These forests are located 15 km north and 40 km southeast from the fragments, respectively. Both study plots were situated near the edge of the forest bordering on agricultural land. The plots were dominated by oaks (>80%), and only nests within oak stands were studied.

In all oak forests we measured trunk circumference at breast height of 20 common oaks and converted this to diameter as an index of habitat quality. This measurement was chosen both for ease of measurement and because oak stands were very similar in other respects such as canopy cover, tree-species composition, and understory. Trees were chosen arbitrarily by tossing a pencil in the air at roughly equidistant intervals along an arbitrary transect, and measuring the nearest tree at about 15 m in the indicated direction that had a circumference of at least 50 cm. Mean trunk diameters were larger in large forests than in fragments ( $\bar{x} = 55$  vs. 46 cm;  $F = 4.7$ ,  $df = 1$  and 14,  $P = 0.047$ ), but the ranges overlapped completely (large forests, 53 to 58 cm; fragments, 37 to 60 cm). Habitat quality was not estimated in parks because of the large variation in tree species, tree size, and other characteristics that were difficult to assess (i.e. disturbance, degree of canopy cover, paved areas, lawns, etc.).

*Nest observations.*—Each spring we located as many nests as possible. Nests were found by following females during nest building and males who were provisioning their incubating mates. A few nests were found during the nestling stage. Including renesting attempts, we found 8 nests in 1990, 61 to 68 from 1991 to 1993, and 43 in 1994 (253 nests total). There were no second broods. Only 16% of the nests were in nest boxes. When we detected a nest failure, based on nest inspection or lack of parent attendance on successive observations, we searched the territory again for renesting attempts. We could not search all fragments for renesting attempts, but we conducted such searches without bias as to fragment characteristics. Causes of failure were not established, but we noted whether the nest was taken over by another species at the first observation following failure. We studied from 1 to 12 (median = 3) nesting attempts

per fragment, with the exception of the largest fragment ZR. In this 30-ha fragment, of which 16 ha were studied, 28 nesting attempts were monitored; ZR was treated separately in all analyses.

Most nests were observed only from a distance. Breeding stage was inferred at least every 10 days based on parental behavior (i.e. nest building, incubation, feeding nestlings and fledglings). Nests were scored as successful if they produced large nestlings or fledglings, or unsuccessful if they failed before producing large nestlings. For each successful nest, the range of possible fledging dates was estimated using the following assumptions (Matthysen 1998): incubation or brooding (on eggs or small young) occurred until the young were at most 10 days old; nestlings were fed for a maximum of 25 days, and were not seen in the nest entrance until 3 days before fledging; and fledged young stayed with their parents for no more than 20 days. If this range could be narrowed down to 10 days or less, the midpoint was taken as the best estimate of fledging date ( $n = 57$ ).

A subsample of nests ( $n = 88$ ) was inspected when the young were suspected to be between 10 and 18 days of age. Nestlings were counted (i.e. brood size), aged (Winkel 1970), individually color banded, and weighed (in 1993 and 1994 only). In 11 broods an exact count was not possible. Young were assumed to fledge at 23 days (Matthysen 1998) unless fledging was observed directly. Each spring and summer most fragments were searched for color-banded nestlings (Matthysen et al. 1995a). Recruitment was defined as the probability that at least one nestling from a successful nest was observed again at least one month after fledging, i.e. after the dispersal period had begun.

*Data analysis.*—Variation in reproductive parameters was studied on two levels. On the first level, we analyzed variation among five categories of study area: oak fragments, park fragments, the 30-ha fragment (ZR), and the two large forests. Because of the small samples for brood size and fledgling mass, the three largest forests were pooled for analysis of these variables. On the second level, we related reproductive parameters to characteristics of individual fragments, excluding the 30-ha fragment. These characteristics were habitat type (oak or park), fragment size (log transformed), and isolation as defined above. For oak and park fragments where sample sizes were sufficiently large, additional analyses compared the variables trunk diameter (measured in oak fragments only) or matrix type (agricultural or residential in park fragments only, because all oak fragments belonged to the former type). For the analysis of recruitment, we also included the distance between the fragment center and the center of the entire study area, because birds born in the periphery are less likely to be found within the study area (Matthysen et al. 1995a). We assumed that nests within fragments provide independent information relative

TABLE 1. Reproductive parameters of Eurasian Nuthatches in oak fragments, parks, and oak stands within larger forests (i.e. ZR, PB, MB). Values between brackets are sample sizes (in the two top rows, number of pairs or broods/number of fragments).

Area	Proportion of pairs successful	Standardized fledging date <sup>a</sup>	Brood size	Fledgling mass (g)	Proportion of broods with recruits
Oak fragments	0.69 (52/12)	0.8 (34/11)	7.2 (20/8)	24.6 (10/5)	0.35 (17/8)
Parks	0.84 (25/5)	-1.6 (51/16)	6.0 (35/15)	24.4 (9/4)	0.14 (37/16)
ZR (30 ha)	0.79 (24)	0.03 (19)	6.2 (4)	— <sup>b</sup>	—
PB (300 ha)	0.86 (35)	0.9 (29)	6.8 (13)	23.4 (10)	—
MB (1,500 ha)	0.61 (23)	3.3 (16)	6.8 (5)	— <sup>b</sup>	—
Total	0.75 (159)	—	6.5 (77)	24.1 (29)	0.20 (54)

<sup>a</sup> Relative to overall yearly mean.

<sup>b</sup> Pooled with PB.

to the investigated fragment variables. Also, we could not check for independence of nests by the same individuals because only a sample of them was banded. However, because the total number of nests per fragment was rather low (median = 3, different years combined), violation of these assumptions would have only a limited effect.

Breeding success, nest-site takeover, and recruitment were analyzed as 0/1 response variables in logistic regression models using GLIM (Crawley 1993). For analyses involving only one independent variable, we calculated Fisher exact probabilities with STATXACT. Breeding success was analyzed as success (0/1) of a pair, either from a first or a repeat nest. For this analysis we omitted a number of areas where we did not systematically search for repeat nests. Fledging date, brood size, and mean fledgling mass were analyzed with PROC GLM using type III sum of squares (SAS 1994), or with ANOVA if all independent variables were factorial. Fledging dates were standardized per year (see Results). In both logistic regression and GLM, model selection was performed by backward elimination of least significant terms starting from a model including all interactions, unless specified otherwise. In particular, interactions between habitat parameters and year were not tested in analyses of brood size, fledging mass, or recruitment where annual sample sizes were small. Lower-order terms were not eliminated as long as they were incorporated in higher-order terms still in the model. All test parameters refer to the last model that included the parameter or interaction before it was removed. All final logistic models were checked for overdispersion (Crawley 1993). Chi-square tests have one degree of freedom unless indicated otherwise.

## RESULTS

**Breeding success.**—Overall, 120 of 159 of nuthatch pairs (75%) successfully raised large nestlings or fledglings. Breeding success did

not vary between years or areas (logistic regression, year effect:  $\chi^2 = 2.4$ ,  $df = 3$ ,  $P > 0.3$ ; area effect:  $\chi^2 = 8.0$ ,  $df = 4$ ,  $P = 0.09$ ). Pairs in oak fragments had an intermediate success rate between those in the two largest forests (Table 1).

We analyzed breeding success in relation to fragment characteristics for oak fragments only, because for park areas both the number of failures ( $n = 4$ ) and the number of different fragments ( $n = 5$ ) was small. The initial model for oak fragments included year, three habitat parameters (size, isolation, trunk diameter), and two-way interactions among the three habitat parameters only. None of the variables explained a significant amount of variation in breeding success ( $P_s > 0.1$ ). Because the effect of isolation was rejected at  $P = 0.06$  ( $\chi^2 = 3.6$  in a model also containing size, diameter, and their interaction), we reentered this variable in each successive step of the model selection, but it never came close to significance (all  $P_s > 0.2$ ). The final model was slightly overdispersed ( $\chi^2 = 64.2$ ,  $df = 51$ ) but this does not affect the conclusions.

**Nest-site takeover.**—Failed nesting cavities were taken over by European Starlings (*Sturnus vulgaris*) in 11 cases and Great Spotted Woodpeckers (*Dendrocopos major*) in 9 cases (Table 2). Because of the small number of failed nests in parks (see above), the analysis was restricted to oak fragments and large forests. Takeover by starlings was more common in fragments than in the three large forests combined (29% vs. 6%, respectively; Fisher exact test,  $P = 0.01$ ; Table 2). Takeover by woodpeckers followed the same trend, but the difference was not significant (19% vs. 9%;  $P = 0.3$ ; Table 2). Within the

TABLE 2. Proportion of failed Eurasian Nuthatch nests (%) that were taken over by European Starlings or Great Spotted Woodpeckers;  $n$  = number of failures, with number of fragments in parentheses for oak fragments and parks.

Area	Takeover species			$n$
	Starling	Woodpecker	None	
Oak fragments	29	19	52	31 (12)
Parks	0	0	100	4 (4)
ZR (30 ha)	13	13	75	8
PB (300 ha)	0	10	90	10
MB (1,500 ha)	7	7	87	15
Total	16	13	71	68

oak fragments, takeover by starlings was not related to fragment size, isolation, or trunk diameter (logistic regression, all  $P$ s > 0.1; year effects not tested). Takeover by woodpeckers was influenced by a size  $\times$  diameter interaction term ( $\chi^2 = 7.0$ ,  $P < 0.01$ ). Inspection of the data parameter estimates suggested that takeovers occurred more often in large fragments if trees were large. However, this effect was not very robust because it disappeared when a single nest in a very small fragment (0.8 ha) was removed ( $\chi^2 = 2.1$ ,  $P > 0.1$ ).

**Fledging dates.**—Because area MB was not studied in 1991, we first verified that no area  $\times$  year interaction was present in the 1992 to 1994 data (two-way ANOVA,  $F = 0.7$ ,  $df = 8$  and  $84$ ,  $P > 0.5$ ). A second test, without an interaction term, on the four years of data showed that fledging dates varied between years ( $F = 13.7$ ,  $df = 3$  and  $130$ ,  $P < 0.001$ ) but not between areas ( $F = 1.8$ ,  $df = 4$  and  $130$ ,  $P > 0.1$ ). For further analysis, we recalculated fledging dates as differences from the overall yearly means. These varied from 25 May (1993 and 1994) to 1 June (1992). Mean standardized fledging dates per area are shown in Table 1.

Within the fragments ( $n = 85$  broods), fledging date was related in a complex way to habitat, isolation, and fragment size (three-way interaction,  $F = 11.3$ ,  $df = 1$  and  $77$ ,  $P = 0.001$ ). When the analysis was repeated for each habitat type (including extra variables, see Methods), we found significant size  $\times$  isolation interactions both in oak and park fragments, but with opposite signs for the parameter estimates (oak:  $F = 15.8$ ,  $df = 1$  and  $28$ ,  $P < 0.001$ ; park:  $F = 4.7$ ,  $df = 1$  and  $46$ ,  $P = 0.03$ ). Inspection of the predicted response surfaces (details

not shown) revealed that in oak fragments, nesting was earlier in small, nonisolated fragments and in large isolated fragments, whereas in park fragments the reverse was true. In addition, we found an interaction between fragment size and trunk diameter in oak fragments ( $F = 5.2$ ,  $df = 1$  and  $28$ ,  $P = 0.03$ ). Broods fledged earliest in small fragments with small trees and in large fragments with large trees. It should be noted that when the interaction terms were deleted from the previous models, none of the main effects of habitat type, isolation, fragment size, or trunk diameter were significant (all  $P$ s > 0.1). In the park fragments, however, there was an additional effect of matrix type on fledging date ( $F = 7.0$ ,  $df = 2$  and  $46$ ,  $P < 0.01$ ). Broods in parks within residential areas fledged an average of 5.3 days earlier than those in parks surrounded by agricultural land. This effect remained significant even in a model without interactions.

**Brood size.**—Brood size varied from 2 to 10 ( $\bar{x} = 6.5$ ,  $n = 77$ ). The three largest forests were lumped in the analysis. Brood size varied among areas ( $F = 4.2$ ,  $df = 2$  and  $73$ ,  $P = 0.02$ ) and with fledging date ( $F = 5.0$ ,  $df = 1$  and  $73$ ,  $P = 0.03$ ) but not among years ( $P > 0.5$ ). Brood size was largest in oak fragments, followed by larger forests and parks (Table 1), and it decreased with time by  $0.08 \pm$  SE of  $0.03$  fledglings per day. Mean brood size differed between oak and park fragments, but neither differed from brood size in large forests (Tukey test,  $\alpha = 0.05$ ).

An analysis on brood size in relation to fragment characteristics (not including the three large forests) confirmed the effects of habitat type ( $F = 7.7$ ,  $df = 1$  and  $52$ ,  $P < 0.001$ ) and date ( $F = 6.2$ ,  $df = 1$  and  $52$ ,  $P = 0.02$ ) but revealed no effects of year, fragment size, or isolation (all  $P$ s > 0.1). According to this analysis, successful broods fledged 1.5 more young in oak fragments than in parks when we controlled for the effects of fledging date. The seasonal decline in brood size was similar to that in the complete data set (0.09 per day). In the following analyses based on habitat type, year effects were no longer tested.

In the sample of oak fragments used to study brood size, the three habitat parameters (size, isolation, trunk diameter) were significantly correlated ( $r^2$  between 0.22 and 0.7, all  $P$ s < 0.05) and were therefore entered one by one in

separate models. None of these three parameters had a significant effect on brood size (all  $P$ s > 0.1), but the effect of fledging date remained ( $P < 0.05$ ). In the park fragments there was also a date effect ( $F = 6.1$ ,  $df = 1$  and  $32$ ,  $P = 0.02$ ) and a significant effect of matrix type ( $F = 6.2$ ,  $df = 1$  and  $32$ ,  $P = 0.02$ ); nests in parks surrounded by agricultural land contained an average of 1.8 more nestlings (corrected for date) than those in residential areas. Again, we found no effects of fragment size or isolation ( $P > 0.2$ ). Note that in this analysis, no higher-order interactions were included in the initial model.

*Mass at fledging.*—Mean nestling mass was recorded for 29 broods in 1993 and 1994 at estimated ages of 14 to 17 days. Body mass did not vary with age between days 14 and 17 ( $F = 6.2$ ,  $df = 3$  and  $25$ ,  $P = 0.09$ ) and thus is considered to represent mass at fledging ( $\bar{x} = 24.1$  g).

Because of the small sample sizes, the three largest forests were again lumped for analysis (total  $n = 10$  broods), and no higher-order interactions were tested. Fledging mass did not differ among areas ( $F = 2.6$ ,  $df = 2$  and  $25$ ,  $P = 0.1$ ) or years ( $F = 2.0$ ,  $df = 1$  and  $21$ ,  $P > 0.1$ ) and was not related to fledging date ( $F = 0.3$ ,  $df = 1$  and  $24$ ,  $P > 0.3$ ) or brood size ( $F = 2.3$ ,  $df = 1$  and  $27$ ,  $P > 0.1$ ). Within the fragments (19 broods in 9 fragments), there was no relationship with year, habitat type, fragment size or isolation, fledging date, or brood size (all  $P$ s > 0.1). No further tests were done on parks and oak fragments separately.

*Recruitment.*—Within the fragment areas (excluding the 30-ha fragment), 15 recruits were found from 11 different broods (Matthysen et al. 1995a). We performed a logistic regression on the probability that a brood produced at least one recruit, with the independent variables habitat type, log fragment size, isolation, distance from the center of the study area, fledging date, and number of young banded per brood. Because of the small sample, we only included four two-way interactions, chosen *a priori* in the initial model (habitat  $\times$  size, habitat  $\times$  isolation, habitat  $\times$  fledging date, size  $\times$  isolation).

Surprisingly, brood size and distance from the center were dropped in the early stages of model selection (both  $\chi^2 < 0.2$ ,  $P > 0.5$ ) and remained nonsignificant even when reentered in

the later stages of model selection. Fragment size and isolation also had no effect (both  $\chi^2 < 0.3$ ,  $P > 0.5$ ). The final model contained only fledging date ( $\chi^2 = 9.9$ ,  $P < 0.01$ ) and habitat type ( $\chi^2 = 6.3$ ,  $P = 0.01$ ). Broods in oak fragments were more than twice as likely to produce recruits than were those in parks (Table 1), and broods with recruits fledged an average of 5.5 days earlier than those without recruits.

## DISCUSSION

Our main objective was to test the hypothesis that habitat fragmentation reduces the reproductive success of a cavity-nesting bird. We found no evidence for reduced reproductive output in fragments versus large forests, nor for relationships with fragment size or isolation. Nuthatches in oak fragments had an intermediate success rate compared with those in the two larger forests and had relatively high brood sizes and fledgling masses, but no significant differences were found. The mean number of young per pair was very similar in oak fragments and parks (5.0 young/pair) and large forests (5.1 young/pair; three largest forests pooled). Fragmentation had no effect on fledging date, which is important given the effect of date on the chance of recruitment within the study area. A premium on early fledging had been predicted based on the severe competition for summer territories very soon after fledging (Matthysen 1987, 1990) but is confirmed here for the first time. The complex statistical interactions among the effects of fragment size, isolation, and habitat type on fledging date are difficult to interpret, but they do not suggest a consistent effect of fragmentation.

One could argue that breeding performance is not a good indicator of habitat quality because birds may follow an "ideal free" distribution among territories of different quality within and between habitats (Fretwell 1972, Matthysen 1990) such that expected fitness does not vary with the average quality of a habitat. According to this reasoning, the combination of high breeding success and low density in oak fragments might imply that on average, territories are poorer, but that only the best territories are occupied. However, observations on dispersal and territory establishment suggest that the best territories are not al-

ways selected (Matthysen and Currie 1996). Furthermore, the fact that nuthatch densities are not correlated with the size or isolation of individual fragments (Matthysen unpubl. data) rules out any "ideal free" explanation for the lack of a relationship between breeding success and fragment characteristics.

The only parameter that differed between fragments and large forests was the probability of nest takeover by other species. Aggressive takeover by European Starlings is a common cause of nest failure in Eurasian Nuthatches (Löhrl 1956, 1958; Nilsson 1984) and other cavity nesters (e.g. Troetschler 1976, Kerpez and Smith 1990). Our observations are not sufficiently detailed to distinguish between active evictions that cause brood failure, and takeovers of previously abandoned nests. Even though it did not seem to affect the overall success rate in fragments, the frequent occurrence of takeovers suggests that competition for nest sites was intense. Indeed, starlings were very abundant in some fragments but rather scarce in the large forest plots. In a very different habitat, Kerpez and Smith (1990) found that proximity to agricultural land increased the competition for nest sites between starlings and woodpeckers.

The differences in reproductive parameters between oak fragments and parks, although unrelated to habitat fragmentation, revealed that our study is sufficiently powerful to detect effects of habitat quality. Broods in parks were significantly smaller by 1.5 nestlings, which is probably not caused by variation in clutch size. In similar habitats, Dhondt et al. (1990) found considerable between-area differences in brood sizes (but not clutch sizes) of Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*). Food availability might be lower in parks, where insect populations on exotic trees can be expected to be less diverse (Kennedy and Southwood 1984), but this was not reflected in lower nestling masses. Broods in parks also were less likely to produce recruits. Again, food could be an explanation through effects on predispersal mortality or on predispersal condition affecting future survival. Another possibility is predation on young nuthatches by corvids, which were more abundant in parks than in oak fragments (Matthysen unpubl. data). A final result is that parks surrounded by residential areas had earlier fledging dates than those in rural

areas. Dhondt et al. (1984) found a similar pattern in Great Tits but not Blue Tits, and suggested an effect of anthropogenic food (i.e. seeds, bread, fat) that is more readily taken by Great Tits, and also by nuthatches.

Our conclusion that forest fragmentation does not affect the quality of oak forest as breeding habitat agrees with the few published studies of other cavity nesters. Kuitunen and Helle (1988) found no relationship between distance to forest edge and nesting success, clutch size, or laying date of Eurasian Treecreepers (*Certhia familiaris*). Although they did not consider fragment size, any change in this parameter necessarily leads to closer proximity to edges. Nour et al. (1998) found no consistent effects of fragment size on reproductive parameters of Great Tits and Blue Tits in forests similar to those in our study. Tjernberg et al. (1993) found no difference in breeding success or laying date of Black Woodpeckers (*Dryocopus martius*) in a large forest and those in an agricultural area where each territory encompassed many small fragments. However, none of these studies investigated the effects of size or isolation of a large number of fragments.

The contrast between the results for cavity nesters and open-nesting birds is not entirely unexpected, because cavities are better protected from predators and brood parasites. A potential cost of cavity nesting is increased competition for nest sites, and our study suggests that such competition increases with fragmentation, even though the effect on breeding success appears to be limited. The above-cited studies on cavity nesters could not address this issue, either because customized boxes were provided (treecreeper, tits) or because the focal species was a dominant competitor (woodpecker). Food availability does not appear to be lower in smaller or more isolated fragments, as shown by large brood size and high nestling body mass. This result agrees with studies on food provisioning and breeding success in tits in similar areas (Nour et al. 1998). Previous studies have reached divergent conclusions on the effects of forest fragmentation on arthropod populations. Some found reductions in abundance or species diversity (Faeth and Kane 1978, Nilsson and Ebenmann 1981), whereas others found no effects (Morse 1977, Middleton and Merriam 1983, Nilsson et al. 1985).

The lower breeding densities of nuthatches in fragments compared with large forests are unlikely to be explained by reduced habitat quality, a conclusion that is further supported by relatively high survival rates (Matthysen unpubl. data). This reinforces our earlier conclusion (Matthysen and Currie 1996) that the vital demographic parameter affected by forest fragmentation is survival during or shortly after dispersal, rather than reproductive performance of established birds.

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