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Feeding habitat and nest-site selection of breeding Great Spotted Woodpeckers *Dendrocopos major*

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We studied within-territory habitat and nest-site selection of breeding Great Spotted Woodpeckers *Dendrocopos major*, by means of radio-telemetry, to test the general notion that this woodpecker is able to utilize a variety of forest habitats. The birds (4 males and 3 females) were monitored in the Varaldskogen study area, a managed, boreal forest of south-central Scandinavia. An 85% home-range estimate averaged 20 ha (range 7–43 ha, n = 4 birds) and breeding pairs lived in separate territories with extensive intersexual overlap of home-ranges. The habitats being used for feeding varied considerably from dry, open clearcuts to moist old-forest stands. When feeding observations were combined for all birds (n = 85 observations), older stands and wet vegetation types were preferred, whereas clearcuts and middle-aged stands were used according to their availability. The birds spent about equal time arboreal and ground feeding. Surface feeding in Scots pine canopies and swamp vegetation constituted half of the observations. Nest sites (n = 36) were preferentially located in older stands of deciduous and spruce trees. In general, our findings confirm the notion that Great Spotted Woodpeckers are flexible in their choice of feeding habitat during breeding. However, the results indicate a certain preference for older forest stands and swamp vegetation types, which we suggest is linked to the availability of important insect prey groups.

1. Introduction

The Great Spotted Woodpecker *Dendrocopos major* is a medium-sized woodpecker distributed throughout the Palearctic and eastern Oriental faunal regions. Being one of the most omnivorous woodpeckers it occupies a wide range of habitats throughout boreal and temperate forests (Glutz von Blotzheim & Bauer 1980, Cramp 1985). In boreal Fennoscandia the Great Spotted Woodpecker is the most common woodpecker occurring sympatrically with five other true woodpeckers. Whereas, the Great Spotted Woodpecker seems to have remained stable or even increased in number, most of the others have decreased during the last decades (Järvinen et al. 1977, Järvinen & Väisänen 1979, Hildén 1987), except perhaps the Black Woodpecker *Dryocopus* *martius* (Nilsson et al. 1992, Majewski & Rolstad 1993). Several reasons have been offered to explain this, including habitat alteration by means of modern forestry (Nilsson 1979, Angelstam & Mikusinski 1994). It has also been suggested that the adaptive and general aggressive behavior of the Great Spotted Woodpecker may have contributed to the negative population trends in the other more specialized woodpeckers (Aulén 1988, Gjerde et al. 1992, but see Virkkunen 1967 and Scherzinger 1990).

Numerous studies have documented diet and feeding habits of the Great Spotted Woodpecker in different parts of its range (reviewed by Cramp 1985). According to Pynnönen (1939), the omnivorous feeding habits suggest a habitat and food selection largely dictated by availability. Durango (1945) concludes that high individual variation and adaptivity enables the Great Spotted Woodpecker to effectively utilize a great variety of habitat types. However, no study has considered selectivity, that is, compared habitat and resource use with availability (but see Aulén 1988 and Hansson 1992).

As part of a larger woodpecker study, in south-central boreal Scandinavia (Rolstad et al. 1992), we radio-monitored a few pairs of Great Spotted Woodpeckers during the breeding season of 1993. The objective of this work was to document feeding behavior, within-territory habitat use and nest-site selection during the nestling period, in order to critically evaluate the above-mentioned general notion that habitats are used according to availability.

2. Study area, material and methods

The birds were monitored at the Varaldskogen study area (15 000 ha), situated on both sides of the Norwegian-Swedish border in Hedmark and Värmland counties (60°10′N, 12°30′E). Topography is gentle, climate is moderate continental, and the tract belongs to the middle boreal zone (Ahti et al. 1968). Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* constitute the main tree species, but forest stands are scattered with deciduous trees of birches *Betula* spp., aspen *Populus tremula*, grey alder *Alnus incana*, and rowan *Sorbus aucuparia*. The forest has been managed by stand replacement practices since 1950, giving rise to a mosaic landscape of clearcuts, even-aged plantations (< 50 yr), and older stands of "semi-natural" forests managed by selective cutting measures. In many clearcuts, dead trees and living deciduous trees have been left after the logging. A more comprehensive description of the study area is given by Rolstad and Wegge (1989a, 1989b).

Table 1. List of birds, number of locations, and home-range size of Great Spotted Woodpeckers at the Varaldskogen study area in south-central Scandinavia in 1993. Nest letters refers to the locations in Fig.1.

Nest	Bird	No. locations	No. independent feeding locations	No. visual feeding observations	HR ha	85% HR ha	Notes
A	Male 020	42	32	34	46	17	
	Female 270	40	31	32	84	43	
B	Male 182	20	9	9	15	7	
	Female 280	20	9	4	37	13	
C	Male 310	—	—	—	—	—	Lost contact
	Female 060	5	2	2	—	—	
D	Male 057	5	2		—	—	
	Female	—	—	—	—	—	Unmarked
E	Male	—	—	—	—	—	Unmarked
	Female	—	—	—	—	—	Unmarked
	Σ	132	85	84			

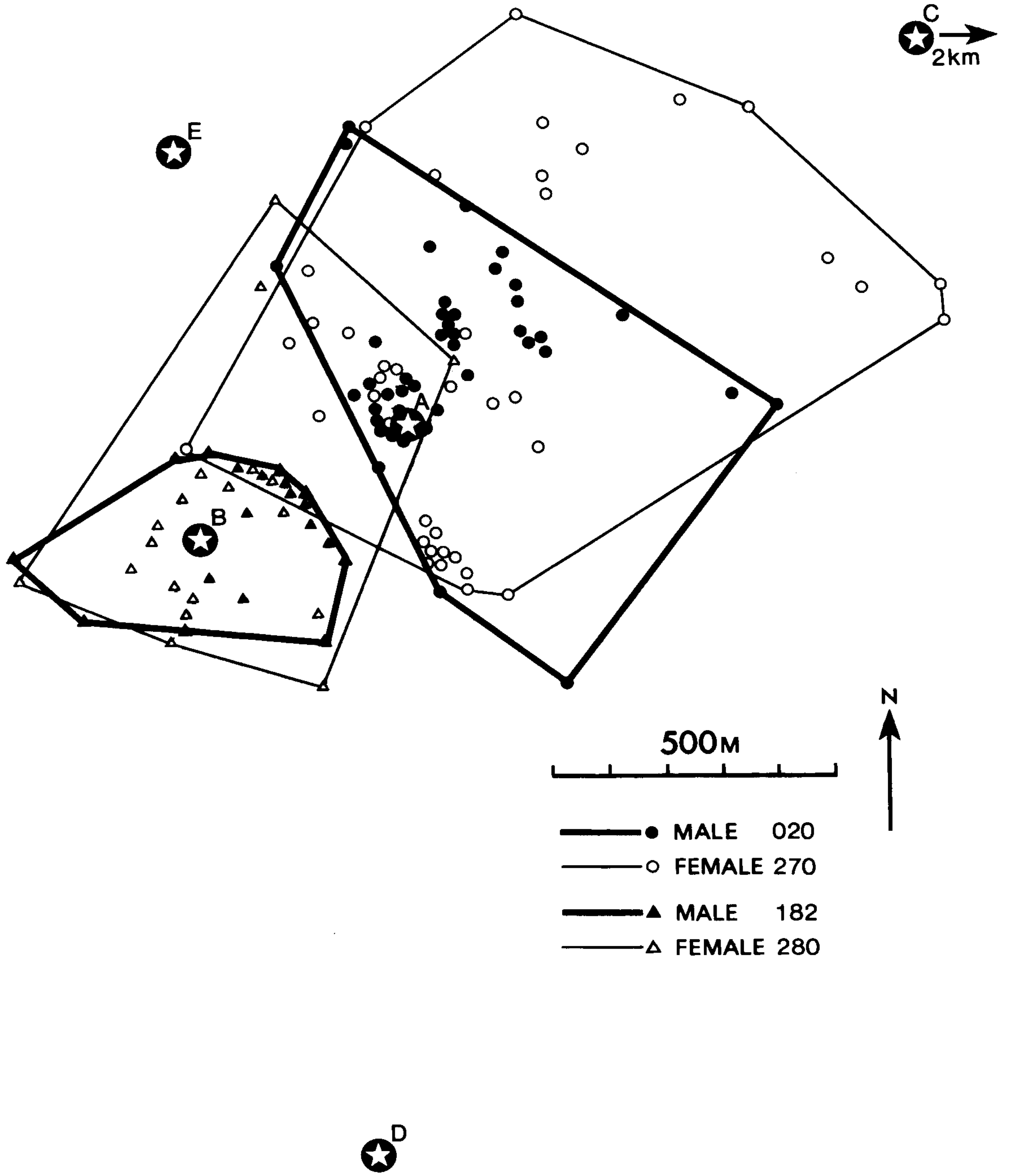

Fig. 1. Spatial pattern of home-ranges and radio-locations of two pairs of Great Spotted Woodpeckers at the Varaldskogen study area in June 1993. The letters denote the nest-sites of the radio-tagged pairs and unmarked neighbouring pairs. (Confer Table 1).

Four males and three females in four breeding pairs (A–D) were fitted with radio-transmitters in the summer of 1993 (Table 1, Fig. 1). Two radio-tagged pairs (A and B) and an unmarked pair (E) were neighbours. The birds were captured at the nest-holes with a hoop net on a telescope pole and fitted with a 5 gram (inclusive harness) SS-2 type, backpack transmitter

(Biotrack, UK), attached with a nylon harness enclosed in silicon rubber (Brander 1968). The radio-gear constituted 4.8–5.6% of the body mass and we could not observe any negative effects on the feeding behavior. However, the tags did hamper some birds when passing through the entrance hole of the nest. This probably caused two pairs to desert the nest (pairs A and C), and another pair (B) to enlarge the entrance hole slightly. Pair A adopted a nearby (50 m) old hole and successfully bred there. These problems did not invalidate the interpretation of the present results, and a discussion of the effect of the radio mounting is presented elsewhere (Rolstad & Rolstad in press).

Transmitting distance varied between 0.3 and 2 km depending on the local topography. Birds were localized with a portable receiver and a hand-held antenna. Home ranges were obtained by continously tracking the birds for 3-hour periods, during five days randomly chosen within the three weeks of nestling feeding. To obtain reliable data it was neccessary for two persons to communicate with portable radios. One was situated close to the nest to monitor nest visits and the direction of feeding activity. The other person established visual contact with the birds to ascertain the type of feeding substrate and habitat characteristics.

Home ranges (n = 4) were delineated by drawing a polygon among the successive outermost locations, the convex polygon method (Mohr 1965). We included all locations of visual contact and cross-bearings closer than 50 m (n = 132). For non-visual locations (n = 48) we assumed feeding activity when birds were active (highly variable radio-signals) more than one minute (n = 16). We assessed habitat selection by comparing habitat use with availability. To avoid dependency between successive feeding locations the analysis was based only on the first location during feeding after a nest visit (n = 85), which usually lasted 5–15 min. The results did not significantly change if the analysis was based on the second or third feeding location.

We recorded age of the forest stand, tree species composition and vegetation type at each independent feeding site (n = 85), and we distinguished between ground and arboreal feeding for visual contacts ($n_{total} = 84$, $n_{independent} = 69$). To allow for statistical analyses, forest stand age was categorized into clearcuts (0–10 yrs), middle-aged stands (11–50 yrs) and older stands (> 50 yrs). Within the area of radio-monitoring (250 ha), no stands were available in the age category 50–90 yrs and the oldest stand was 150 yrs. Tree species composition was categorized into three classes (pine, spruce and

Table 2. Distribution of Great Spotted Woodpecker feeding observations categorized on feeding substrate and behavioral technique. Median distance from nest to feeding locations is shown for categories with > 5 observations. Varaldskogen, June 1993.

Feeding substrate	Behavior	% of locations			Distance from nest (m)	
		All birds	Male 020	Female 270	median	range
Ground feeding		48	38	56	260	40–810
Bilberry	Gleaning	12	6	16	260	40–810
Swamp vegetation	Gleaning	20	29	9	340	100–610
Grass	Gleaning	4	0	3	–	–
Stumps	Scaling and pecking	12	3	28	260	70–319
Arboreal feeding		52	62	44	170	20–970
Pine canopy	Gleaning	31	53	16	170	20–550
Spruce canopy	Gleaning	4	0	9	–	–
Deciduous canopy	Gleaning	12	6	13	120	50–770
Trunk	Scaling and pecking	5	3	6	–	–
		% = 100	100	100	Median = 230	20–970
		N = 84	34	32	N = 84	

deciduous) based on the dominant species. Vegetation was divided into wet (forested bogs and swamp forests) and dry sites. Availability was recorded using a detailed forest company map and aerial photos, checked in the field to correct for recent logging activity. Use of feeding substrate was not analyzed with respect to selectivity. Hence, we included all visual contacts separated by more than 10 min in time or 10 m in space (n = 84) and categorized them according to Table 2.

The number of locations decreased with increasing distance from the nest (Fig. 2). To obtain a relevant picture of habitat selection, we, therefore, weighted available habitats according to the number of independent observations in successive 300 m circles from the nest. When data were pooled among birds, we also weighted the availability according to the number of locations for each bird.

During 1991 to 1993, we found 36 nests within the study area. The nests were randomly distributed across the area, and we are confident that the detection rate was fairly similar among different habitat types. The Great Spotted Woodpecker is known as an aggressive woodpecker (Hurme & Sarkanen 1975), and the birds usually responded vocally within a 50 m radius or more from the nest. If there is a bias in the sample, it should be that detectability may have been slightly lower in old forest and dense stands.

At each nest we recorded age of the forest stand, dominant tree species and type of nest-tree. Selectivity was calculated with respect to stand age and dominant tree species. We also weighted the habitats according to the availability of potential nest-trees. All nests were in deciduous trees with a diameter at breast height larger than 20 cm. Hence, we defined a potential nest-tree as any deciduous tree, alive or dead, with a diameter at breast height of more than 20 cm (see also Aulén 1988 and Hansson 1992). The availability of these trees was calculated from detailed records in the forest owners files.

Throughout we use the terms preference and avoidance for significantly greater or smaller use of habitats than would be expected on the basis of statistical comparisons with availability ($P < 0.05$). We use χ^2-test, with Bonferroni's adjustments of significance level, in multiple comparisons, and Fisher's exact probability-test to analyse 2 × 2 tables.

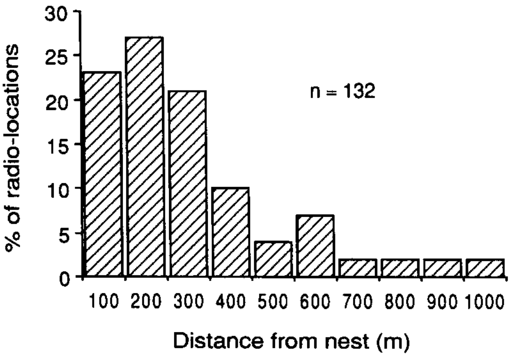

Fig. 2. The percentage distribution of Great Spotted Woodpecker radio-locations according to the distance from nest. Varaldskogen study area, June 1993.

3. Results

3.1. Habitat selection, feeding behavior and spacing

The two pairs at nests A and B were monitored long enough to estimate home-range size. Male home-ranges were 15 and 46 ha, and the female home-ranges were 37 and 84 ha, respectively (Table 1). Within the pairs, male and female home-ranges overlapped almost completely (Fig. 1). The nests were spaced 450 m apart and there was no overlap between the male home-ranges. Female home-ranges overlapped, but this resulted from two locations, one for each female. When 15% of the outermost locations were excluded, home-range sizes more than halved, resulting in 85% home-ranges of 7 and 17 ha for the males, and 13 and 43 ha for the females, respectively, with no intrasexual overlap. The average 85% home-range size, all 4 birds combined, was 20 ha. A third nest (nest E, with unmarked birds) was a neighbour of nests A and B, 600 m to the north (Fig. 1). Nest D was located 1 150 m south of nest B, probably with an unmarked pair nesting in between. Nest C was 2 km east of nest A, with several unmarked pairs occuring in between.

Use of forest age categories differed between the sexes at nest A. Because availability was not the same in the two home-ranges, they could not be compared directly. However, when available

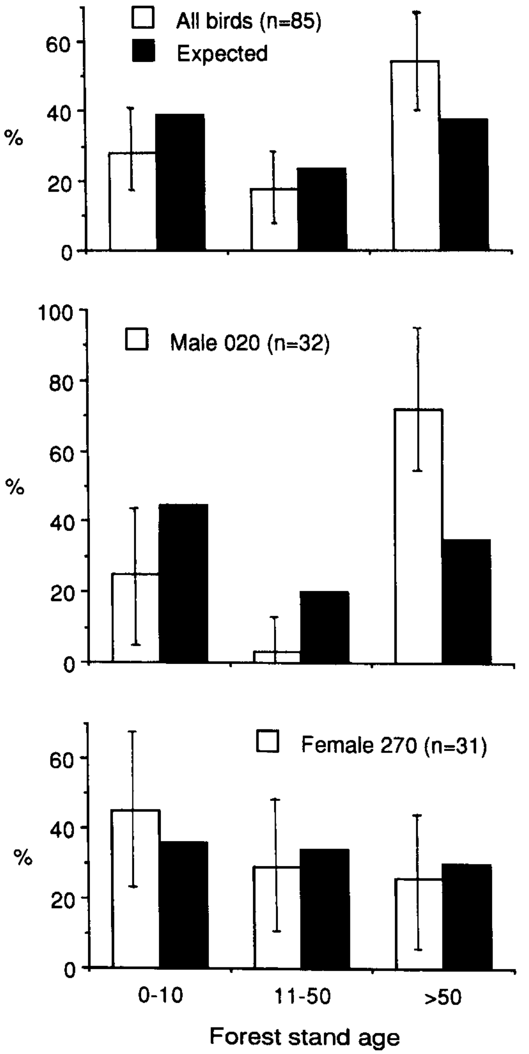

Fig. 3. Observed and expected distribution of 85 independent feeding locations of Great Spotted Woodpeckers in relation to forest standage. Bars denote Bonferroni 95% family confidence intervals. Varaldskogen study area, June 1993.

age categories were controlled for, the male preferred older forest stands and avoided clearcuts and middle-aged stands (Fig. 3). The female used age categories according to their availability. When feeding observations were combined for all birds, older stands were preferred, whereas clearcuts and middle-aged stands were used according to their availability (Fig. 3). Birds preferred wet vegetation types ($\chi^2 = 5.9$, df = 1, P = 0.02, n = 85). This presumably was due to a preponderance of ground feeding observations in this type (36%) compared with availability (20%), although this difference was not statistically significant (Fisher's exact test, P = 0.13, n = 36). When the birds foraged on trees, vegetation types were used according to their availability (P = 1.0, n = 33).

Feeding locations were about equally distributed in pine and spruce dominant stands ($\chi^2 = 0.12$, df = 1, P = 0.73, n = 70). (Deciduous dominant stands were not available within the home-ranges). However, within stands, birds used pine canopies more often than spruce. Of 19 canopy feeding observations in pine dominant stands, all were in pine trees. In spruce dominant stands, 7 of 10 canopy observations also were in pine trees. When feeding in pine canopies the birds searched for prey on the outermost twigs.

The dominant feeding behavior was surface feeding in canopies (47%). Surface feeding in ground vegetation constituted 36%, and bark scaling and pecking in stumps and trees were recorded in 17% of the cases (Table 2). Males were observed more often surface feeding (94%) than females (69%) (Fisher's exact test, P = 0.004, n = 84), but this may be due to individual variation and small sample size (Table 2).

Birds were more often observed feeding in the vicinity of the nest than at more distant sites (Fig. 2). We were not able to record the time spent at different feeding substrates, but we noted the distance from nest (Table 2). Feeding sites in pine canopies were located significantly closer to the nest (median 170 m) than other feeding sites (median 260 m) (Mann-Whitney U = 224, P = 0.005, $n_1 = 19$, $n_2 = 43$).

3.2. Nest-sites

Nest-trees were not distributed randomly with respect to forest stand age classes ($\chi^2 = 18.0$, df = 3, P < 0.001). Most were situated in forest stands older than 50 years and very few were in stands 10–50 years of age (Table 3). Older forest stands also had the highest density of potential nest-trees. Deciduous trees were ten times more abundant compared with the age class 20–50 years. Taking into account the density of potential nest-trees the distribution of observed nests did not differ from their availability (Table 3). With respect to type of forest, nest-trees were located in spruce and deciduous stands more often than expected from their areal distribution (Table 4) (Fisher´s exact test, P = 0.003, deciduous and spruce stands combined). However, after taking the density of potential trees into account, nest-trees were randomly distributed (P = 0.30). All 36 nests were in deciduous trees, with half of them in live aspen (Table 5). Because the forest company files did not specify the availability of different species of deciduous trees nor their condition, we were not able to test for selectivity.

4. Discussion

The Great Spotted Woodpeckers in our study area utilized a variety of different feeding habitats. By and large the results conform to the

Table 3. Observed and expected distribution of nest-sites of Great Spotted Woodpeckers according to age classes of forest stands and the densities of potential nest-trees.

Forest stand age class	Available area		Avail. trees per		Avail. trees		Observed nest trees		Expected no. nest trees based on	
	ha	(%)	ha	20 ha [1]	no.	(%)	no.	(%)	Area	Avail. trees
0-10 yr	1560	(13)	0.5	10	780	(16)	8	(22)[2]	5	6
10-20 yr	1560	(13)	0.2	4	320	(6)	1	(3)[3]	5	2
20-50 yr	5520	(46)	0.1	2	552	(11)	3	(8)[4]	16	4
>50 yr	3360	(28)	1.0	20	3 360	(67)	24	(67)[5]	10	24
	12000	(100)	0.4	8	5012	(100)	36	(100)	36	36

[1] Average 85% home-range estimate for radio-monitored birds (n = 4).
[2] Bonferroni Z-test comparing the distribution of observed nest-trees against expected values based on area: Z = 1.2, P > 0.50
[3] Z = 4.1, P < 0.001
[4] Z = 7.8, P < 0.001
[5] Z = 4.9, P < 0.001

Table 4. Observed and expected distribution of nest-sites of Great Spotted Woodpeckers according to the dominant tree species in forest stands older than 50 years and the densities of potential nest-trees.

Dominant tree species	Available area		Avail. trees per		Avail. trees		Observed nest trees		Expected no. nest trees based on	
	ha	(%)	ha	20 ha [1]	no.	(%)	no.	(%)	Area	Avail. trees
Spruce forest	1575	(46.9)	1.2	24	1890	(56)	17	(71)	11	14
Pine forest	1777	(52.9)	0.5	10	889	(26)	3	(12)	13	6
Deciduous forest	8	(0.2)	75.0	—	600	(18)	4	(17)	0	4
3360	(100)	1.0	20	3379	(100)	24	(100)	24	24	

[1] Average 85% home-range estimate for radio-monitored birds (n = 4).

general notion that high individual variation and adaptivity enables the Great Spotted Woodpecker to effectively utilize a great variety of habitat types (Pynnönen 1939, Durango 1945, Glutz von Blotzheim & Bauer 1980, Cramp 1985).

Surface feeding on foliage in tree canopies was the dominant behavior, constituting half of the feeding observations. Of these observations, two-thirds were in pine canopies, all located in older forest stands. From what we could see at the nest, and from a few twig samples, the prey items were aphids. A similar situation was reported by Pynnönen (1939, 1943) from Finnish Karelia, where he captured an adult with 38 aphids in the bill. He observed frequent feeding visits to rowan foliage, which was heavily infected by aphids. The second most important behavior was ground feeding among bilberry and swamp vegetation, where we observed different Lepidoptera larvae taken as prey, along with a variety of other insect prey. From Poland, Steinfatt (1937) reported that Lepidoptera larvae of *Lymantria monacha* constituted 94% of a total of 2 347 identified prey items. This occurred during a plague year of the moth. Similarly, Korol'kova (1954) recorded 137 and 886 Lepidoptera larvae of the species *Malacosome neustria* and *L. dispar*, respectively, as prey items in an oak forest in southern Russia. In a Swiss oak forest, Jenni (1983) found Lepidoptera larvae to constitute 85% of the biomass given to the nestlings. Third in importance at Varaldskogen was bark scaling on recently logged stumps which contained Cerambycid larvae. Sielmann (1959) reported that Great Spotted Woodpeckers chiseled holes up to 10 cm deep to expose wood-boring beetle larvae. We conclude that this flexibility in diet and feeding behavior most probably is the underlying explanation for the large variation in the use of habitats and feeding substrates.

Pine canopies were the most frequently visited feeding substrate. However, due to the sampling method, that is, the number of feeding observations or independent radio-locations, we may have over-estimated the importance of pine. Pine trees were often visited during short feeding trips in close vicinity of the nest, whereas ground feeding in swamp vegetation and bilberry were associated with longer feeding trips. Presumably pine canopies contained abundant but small prey items, for example, aphids, whereas bigger, energetically more favorable prey items, like Lepidoptera and Coleoptera larvae, were patchily distributed at more distant locations.

Although the birds used a variety of habitats and feeding substrates, the data indicate a certain preference for older forest when feeding in trees and for wet swamp vegetation when feeding on the ground. This is in accordance with Scherzinger (1982) reporting a higher density of breeding pairs in German natural old forest areas (4.5 pairs/100 ha) compared with younger managed forests (0.6/100 ha) (see also Virkkala et al. 1994). It is known that swamp vegetation types contain higher numbers of invertebrates than dryer sites (Atlegrim 1991), especially Lepidoptera larvae, which constitutes an important prey group for insectivorous birds (Royama 1970, Kastdalen & Wegge 1985, Holmes & Schultz 1988). To conclude, the Great Spotted Woodpecker seems to be able to inhabit and reproduce in a great variety of habitats, ranging from old natural forests to suburban villages (Hansson 1992). On the other hand, the affinity for older stands of spruce and

Table 5. The distribution of Great Spotted Woodpecker nests according to tree species and condition of the tree. Varaldskogen, 1991–94.

	Live	Rotten	Dead	Σ	
Aspen *Populus tremula*	18	7	1	26	72%
Birch *Betula* spp.	2	3	3	8	22%
Rowan *Sorbus aucuparia*	2	0	0	2	6%
Σ	22	10	4	36	
	61%	28%	11%		100%

deciduous forest and swamp vegetation types indicates that these productive sites are preferred feeding habitats (Nilsson 1979, Scherzinger 1982).

Based on the areal frequencies of habitats, the nest-trees were preferentially located in older spruce and deciduous stands. This agrees well with Aulén (1988) who found that the Great Spotted Woodpecker nested twice as often in old forest compared with the White-backed Woodpecker *Dendrocopos leucotos*. In his central Swedish area, 70% (n = 66) of the Great Spotted Woodpecker nests were in old forest. However, taking into account the differential densities of potential trees at Varaldskogen, nest-trees were distributed at random. Old forest contained ten times more potential nest-trees than middle-aged forest, and twice as many as recent cutover areas. Thus, the apparent preference for old forest could be a consequence of a random use of available nest-trees. The same pattern also holds for the apparent preference for spruce and deciduous stands. After correcting for densities of potential trees, nest-trees were distributed according to their availability.

Although the distribution of nest-trees could be dictated by the availability of potential trees, it is tempting to explain the affinity for older forest as a consequence of preferred feeding habitat. That is, birds locate their nests in those habitats which contain the most food. The Great Spotted Woodpecker carries food items in the bill to the nestlings, in contrast to ant-specialized woodpeckers, like the Black Woodpecker and the Green Woodpecker *Picus viridis*, which regurgitate the food. Thus, the Great Spotted Woodpecker needs to find the food close to the nest. Our birds found 70% of their prey within 300 m from the nest. Consequently, depending on the resolution of the forest landscape mosaic, and presupposing that potential trees are available, nests will preferentially be located in older, productive forest stands.

In this study, we have focused on the habitat selection within breeding territories. Among the Scandinavian woodpeckers the Great Spotted Woodpecker holds a special position due to its marked seasonal shift in diet, from invertebrate summer food to conifer seeds in winter. Thus, on a landscape level it may well be that Great Spotted Woodpeckers chose territories based on the availability of conifer seeds, as they are crucial for winter survival. However, this does not invalidate our conclusion that Great Spotted Woodpeckers are flexible in their choice of feeding habitats within their breeding territories.

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