Studies on Hole-Nesting Birds in Natural Nest Sites

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STUDIES ON HOLE-NESTING BIRDS IN NATURAL NEST SITES

1. AVAILABILITY AND OCCUPATION OF NATURAL NEST SITES

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1. INTRODUCTION

Since their introduction, nest-boxes have become increasingly popular as research tools for the study of breeding biology and population dynamics. Because several species (*e.g.*, the Great Tit *Parus major,* Pied Flycatcher *Ficedula hypoleuca,* Starling *Sturnus vulgaris,* and Tree Sparrow *Passer montanus*) can be readily induced to breed in nest-boxes, our knowledge of these species is much more complete than that of most other passerines. However, reliance on nest-boxes as the only source of breeding data involves risks of several kinds.

A number of authors (see Von Haartman 1971) have shown that the breeding density of hole-nesting birds increases as a result of the introduction of nest-boxes. Although this increase is probably due partially to the decreased availability of natural nest sites in woodlands as managed at present (*cf.* Haapanen 1965), the possibility that nest-box populations are unnaturally dense cannot be excluded.

The species composition of populations nesting in nest-boxes may also differ from that in more natural situations. Nest-boxes tend to be uniform, permitting use by only a few species, whereas natural holes differ as to dimensions, size of the entrance, and height above the ground, which allows many species to nest. A limited number of natural holes can, however, reduce the number of occupying species to those most successful in the competition for nest-sites. In nest-box populations the abundance of boxes suitable for the species under study usually precludes competition.

Furthermore, the fact that some species show a distinct preference for boxes of specific dimensions (Löhrl 1970, 1977, Nilsson 1975) means that some caution must be exercised in interpreting the results of studies done with uniform nest-boxes.

In recent years it has become apparent that properties of nesting holes can affect several breeding parameters of tits. The size of nesting holes influences the date of egg-laying (Van Balen 1972) and the number of eggs laid (Ludescher 1973 for *Parus montanus* and *P. palustris;* Löhrl 1973 and Van Balen 1972 for *Parus major*; Karlsson & Nilsson 1977 for *Parus major* and, in some years, *Ficedula hypoleuca*). Moreover, Mertens and Van Balen found (see Mertens 1977, p. 49) in experiments with normal-sized (9 × 12 × 23 cm) and smaller (6 × 6 × 22 cm) nest-boxes at different temperatures, that considerable mortality among Great Tit broods occurred in the narrower boxes, especially at high temperatures. At high ambient temperatures the nestlings evidently need to keep space between them; unless they can avoid contact they will suffer from hyperthermia. In this way the dimensions of the nesting cavity may become important for nestling survival.

Another way in which properties of the nesting hole may affect nestling survival is the size of the entrance hole, on which entry of predators may depend.

These considerations suggest that populations of hole-nesting birds that make use of nest-boxes may deviate from more natural populations in breeding density, composition of the participating species, clutch size, and nesting success. Differences in reproductive output might influence the density in later periods. A comparative study on hole occupation and breeding biology should give information on the relevance of the results obtained with nest-boxes, such as those of Van Balen (1973) on the Great Tit. Information about the breeding biology of hole-nesting birds in natural situations is very fragmentary. The only systematic study on hole-nesting birds in natural cavities is the one done by Nilsson (1975), whose results indicate that both the clutch size and the breeding success of several tit species can differ from the situation in nest-boxes. However, it would be wrong to generalize from these results without further study, because the dimensions of natural holes are extremely variable (see 4.1). It was therefore decided to collect information on hole occupation and breeding biology in natural nest sites in areas close to our main nest-box study area in the Hoge Veluwe region.

In this paper the results on hole occupancy and interspecific competition will be presented.

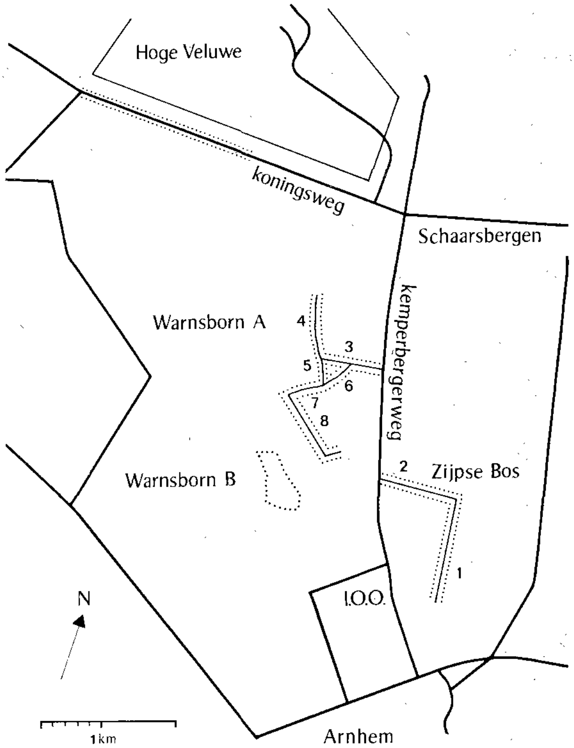

Fig. 1. Location of the various parts of the study area, indicated by dotted lines. Roads 1 and 2 form the Zijpse Bos area, 3 = Rustwatlaan, 4 = Campinglaan, 5 = Dwarslaan, 6 = Berkenlaan, 7 = Verbindingslaan, 8 = Heidelaan.

2. STUDY AREA

To increase efficiency, a study area was chosen in which tree holes were abundant and relatively close together. This situation was found north of Arnhem, where many roads and paths are bordered with old deciduous trees, mainly beeches (*Fagus sylvatica*) and oaks (*Quercus rubra* and *Q. robur*). Between these roads are larger complexes of young deciduous or coniferous plantations (Fig. 1). The old trees have many holes.

In 1975, the study area had three parts: Warnsborn A, Zijpse Bos, and Koningsweg. In 1976 a fourth area, 9 ha of old mixed woodland called Warnsborn B, was added. This area was also inspected in 1977, when the Zijpse Bos was extended and Warnsborn A was used for experiments on competition (see below). In each year additional observations were made on nest-holes scattered throughout the surrounding area.

Table 1 gives data on the number of trees of various species and their size, expressed as the trunk circumference at chest height. The vegetation bordering the roads is highly uniform as to species composition and tree age. Warnsborn B shows more variation in both species composition and tree size. The mean trunk circumference in Warnsborn B is similar to that in the other areas (except for Oak), but this area is richer in both small and very large trees (circumference < 100 and > 150 cm, respectively).

3. METHODS

Starting in March 1975, all trees were examined systematically to locate holes. During the breeding season all suitable holes (as defined below) were inspected weekly with a dentist mirror on which a small lamp had been mounted. This method made it possible to establish and collect breeding data. Occupation was determined primarily for the main breeding season, *i.e.* from early April to 20 May, to avoid inclusion of repeat and second clutches. To make sure that no occupied holes were missed, attention was paid to birds engaged in nest building and in feeding nestlings.

Holes situated higher than *ca.* 7 m above the ground could not be inspected. These holes were only located by observations of building or feeding birds, which means that a proportion of them were not found.

In each hole found, several measurements were made. All holes were considered to have the shape shown in Fig. 2, which was the most common shape. The parameters measured are indicated in this figure. From the inner dimensions of the cavity, the bottom area and the volume could be estimated: these estimates may be biased, because of the irregular shape of some cavities. Besides volume and bottom area, the entrance size and the height of the entrance above ground level were thought to be important for hole selection. Further, the direction of exposure of the entrance, the

Table 1. Vegetation characteristics of the study area. Number of trees of different species and trunk circumference at breast height (mean ± SD, in cm). Very small trees (circumference < 60 cm) were omitted

Part of study area	Zijpse Bos		Koningsweg		Warnsborn A		Warnsborn B	
Dimensions (m)	780×23		1200×17		2005×21			
Area (ha)	1.8		2.0		4.1		9.0	
	No. of trees	trunk circumference	No. of trees	trunk circumference	No. of trees	trunk circumference	No. of trees	trunk circumference
Beech, *Fagus sylvatica*	188	130 ± 26	392	133 ± 25	876	123 ± 26	671	124 ± 39
Red Oak, *Quercus rubra*	200	95 ± 20	138	144 ± 27	15	90 ± 19	403	115 ± 34
Oak, *Quercus robur*	—	—	—	—	1	—	249	131 ± 58
Silver Birch, *Betula verrucosa*	—	—	—	—	52	89 ± 18	33	102 ± 21
Other deciduous species[1]	—	—	—	—	—	—	197	117 ± 47
Conifers[2]	—	—	—	—	—	—	477	116 ± 37

[1] Mainly Horse Chestnut (*Aesculus hippocastaneum*), Spanish Chestnut (*Castanea sativa*), Sycamore (*Acer pseudoplatanus*), Lime (*Tilia europaea*), and Locust (*Robinia pseudoacacia*).
[2] Spruce (*Picea abies*), Douglas Fir (*Pseudotsuga menziesii*), Larch (*Larix decidua*), and Scots Pine (*Pinus sylvestris*).

tree species in which the hole was situated and the circumference of the trunk at chest height were noted.

As the diameter of the entrance, the smallest of the two measurements (a and b) was taken. The bottom area was estimated from the two diameters (x and y) measured at entrance height or (preferably) at nest height, with the equation for the area of an ellipse $\pi \times \frac{1}{2}y \times \frac{1}{2}x$. The volume of the cavity was estimated by multiplying the bottom area by the total height (th = d + a + hae, up to a maximum of 30 cm). For cavities, that became appreciably narrower above the entrance, the value of hae was multiplied by ½.

The following conditions had to be fulfilled for a cavity to be considered suitable for breeding purposes:

1. The bottom area should measure at least 25 cm², and the smallest diameter at least 4 cm. The distance bottom-top should be at least 10 cm.
2. The entrance should have a diameter of at least 23 mm (if circular), or a width of at least 18 mm (if slit-like).
3. The entrance should not be so large that the nest is exposed.
4. The hole should be closed at the bottom.
5. There should not be a substantial amount of water in the hole.

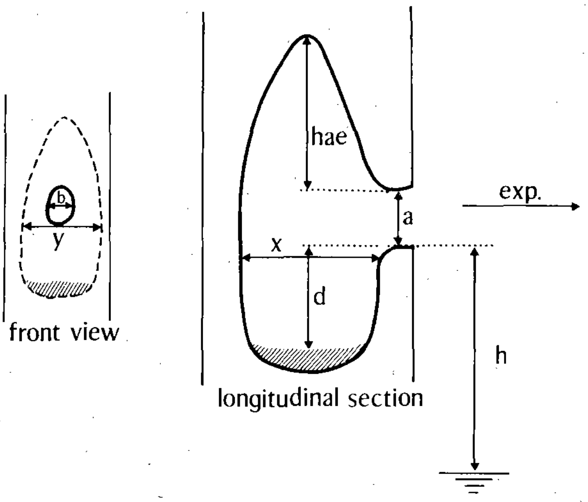

Fig. 2. Schematic representation of a natural hole, indicating the parameters measured. h: height above the ground, exp: direction of exposure, a: height of entrance hole, b: width of entrance hole, d: hole depth, hae: height above entrance, x: distance to rear wall, y: width of hole.

These conditions mean that a suitable hole, as defined here, can be used for breeding by at least the smallest species of hole-nesting birds, such as the Blue Tit *Parus caeruleus,* Marsh Tit *Parus palustris,* and Coal Tit *Parus ater.* Larger species require larger holes. Holes that did not satisfy the above conditions were sometimes used by species like the Tree Creeper *Certhia brachydactyla,* Spotted Flycatcher *Muscicapa striata,* and Redstart *Phoenicurus phoenicurus,* which are not reckoned among the obligatory hole-nesters.

In 1977 a special study was undertaken to determine the relation between the numbers of potential and actual breeding Great Tits. For this purpose, territorial activity was recorded during March and April in the Zijpse Bos and Koningsweg, and territory maps were drawn. In the Koningsweg area the identity of many territory owners could be established by the use of coloured rings. Non-territorial pairs were ignored.

The interspecific competition for nesting holes was studied in 1977 in Warnsborn A by means of two experiments:

1. In one part of Warnsborn A (Rustwatlaan and surroundings) almost all large entrances were narrowed (in March) to a diameter of *ca.* 30 mm. Hole occupation in 1977 was compared with that in 1975 and 1976.
2. In another part of Warnsborn A (Heidelaan) twenty large nestboxes were put up, ten with a 50 mm entrance (accessible to Starlings) and ten with a 30 mm entrance. In early May, when breeding attempts by Starlings and Great Tits were well under way, the 50-mm entrances were exchanged for 30-mm entrances and vice versa, after which the behaviour of the birds was studied.

4. RESULTS

4.1. AVAILABILITY

The first question to be answered here is how many nesting sites are available to hole-nesting birds. The availability of nesting holes can be

Table 2. Density of suitable tree holes in various parts of the study area

	Area (ha)	No. of trees	No. of holes	No. of holes /100 trees	No. of holes /ha
Zijpse Bos	1.8	388	17	4.4	9.4
Koningsweg	2.0	530	60	11.3	30.0
Warnsborn A	4.1	944	72	7.6	17.6
Warnsborn B	9.0	2030	56	2.8	6.2
Warnsborn B*	7.9	1553	54	3.5	6.8

* without conifers.

expressed most adequately as the number of suitable holes per unit area (ha). For our study this led to difficulties because of the linear arrangement of the trees in most of the areas. Therefore, hole density was expressed as the number per 100 trees as well as number per ha (Table 2). For the calculation of numbers per 100 trees, all young trees (trunk circumference < 0.6 m) were omitted, because no holes were found in them.

The number of available holes was roughly the same in the three years. Between the breeding seasons some holes became unsuitable and a few new holes appeared, for instance due to woodpecker activity. Within each year hole availability varied slightly, *e.g.*, due to wet holes drying up in the course of the breeding season.

Hole availability (Table 2) varied from 4.4 to 11.3 per 100 trees along the roads, and in Warnsborn B amounted to 2.8 per 100 trees. When expressed in numbers per area, the "linear" areas too have much higher values than Warnsborn B. However, caution must be exercised in comparing these values with data from literature, because the "linear" areas are not representative of larger uniform areas of the same vegetation. For example, woodpeckers, which are important producers of tree holes, probably do not make as many holes in large uniform areas with suitable trees, as they do in tree rows situated in areas otherwise unsuitable for nesting.

A density of 6—7 holes/ha, as found for Warnsborn B, corresponds well with the hole densities given in the literature, where values from 1—2 up to 15/ha are mentioned (Edington & Edington 1972, Kneitz 1961, Löhrl 1958, Ludescher 1973, Schiermann 1934). Most authors point out that hole density depends on tree species composition as well as on the age and degree of management of the forest (Haapanen 1965, Kneitz 1961). Such differences in hole density were also found in our study area. The most striking observation is that only two holes were found in nearly 500 conifers. This is in contrast with the high density of holes found by Schiermann in 175—200 year old coniferous woodland (Schiermann 1934). Kneitz (1961), however, found no woodpecker holes in young coniferous woodland (up to 60 years old), whereas older conifers showed a density of *ca.* 0.7 holes/ha. Addition of holes made by other agents (than woodpeckers) increased the density to 1—1.5 holes/ha. In a climax coniferous forest with a slight admixture of deciduous trees, Haapanen (1965) found most of the holes to be situated in the deciduous trees.

Deciduous forests may show rather high tree-hole densities. The values recorded in the literature range from *ca.* 5/ha (Ludescher 1973) to 15.5/ha (Edington & Edington 1972) or locally to 17 holes/ha (Kneitz 1961). In this type of woodland the number of holes also increases with the age of the trees (Kneitz 1961).

The differences in hole density in our study area (see Table 2) may be partly due to the different shapes of the areas, and partly to such factors as species composition and the age and condition of the trees. Data on the number of holes in various tree species are given in Table 3; the data for all areas consisting of tree rows along roads were pooled, and those for Warnsborn B given separately. In the combined "linear" areas Beeches seem to have more holes than Red Oaks and Birches, but the differences are not significant according to the G-test. (Sokal & Rohlf 1969). In Warnsborn B the percentage of trees carrying holes differs among the tree species or groups of species ($G = 14.930$, d.f. $= 5$, $p = 0.011$) but within the group of de-

Table 3. Frequency of holes in different tree species

	No. of trees	% with holes	No. of holes	No. of holes /100 trees	No. of holes per hole-tree	Mean trunk circumference (cm)
			Roads=Zijpse Bos + Koningsweg + Warnsborn A			
Beech	1456	6.8	123	8.4	1.24	126.8
Red Oak	353	5.4	22	6.2	1.16	108.8
Birch	52	3.8	2	3.8	—	89.2
			Warnsborn B			
Beech	671	1.6	20	3.0	1.8	123.7
Red Oak	403	2.7	16	4.0	1.5	114.7
Oak	249	2.8	9	3.6	1.3	130.9
Birch	33	6.1	3	9.1	1.5	102.3
Other deciduous	197	3.6	8	4.1	1.1	117.0
Conifers	477	0.4	2	0.4	1.0	115.9

ciduous trees no differences were found (G = 4.509, d.f. = 4, p = 0.479). This implies that conifers have fewer holes than deciduous trees.

Table 3 also shows that the Beeches and Red Oaks along the roads carry more holes than those in Warnsborn B, but this difference is due to the linear *versus* circular shape of the areas which can lead to high densities of woodpeckers in the "linear" areas. Further analysis of the data shows that the Koningsweg and Rustwatlaan areas (part of Warnsborn A), in which cars use the roads, have higher hole densities than the other "linear" areas. For Beech the percentages of trees with holes amount to 9.4, 10.1, and 5.1, respectively (G = 11.096, d.f. = 2, p = 0.004). Presumably, this difference is due to a decline in the condition of trees along roads with car traffic.

Another source of variability may be sought in the age of the trees. In this study the trunk circumference at chest height was used as a measure of age. In areas that do not differ considerably as to soil conditions, this procedure is probably justified. As already mentioned, no holes were found in trees with a trunk circumference up to 60 cm. Above this limit differences in hole frequency occurred. In the "linear" areas, where the age of the trees is rather similar, there was no clear relationship between the trunk circumference and the frequency of holes. This is apparent from the data presented in Table 4, in which the frequency of hole occurrence in various size classes is given for all deciduous trees together. However, in Warnsborn B the distribution of trees with holes differed significantly among the size classes. Presumably, this is due to the wide range of tree-size classes available for hole excavation. In principle, one would expect an increase in hole occurrence with increasing age of the trees. It is

Table 4. Frequence of holes in relation to size of the tree; pooled data for deciduous trees

Trunk circumference (cm)	Roads			Warnsborn B		
	No. of trees	No. with holes	% with holes	No. of trees	No. with holes	% with holes
60 — 80	137	5	3.6	252	1	0.4
85 — 105	472	25	5.3	412	7	1.7
110 — 130	624	46	7.4	404	5	1.2
135 — 155	427	33	7.7	229	8	3.5
160 — 180	151	9	6.0	116	8	7.0
> 180	35	2	5.7	137	9	6.6
	G = 5.217; p = 0.390			G = 25.044; p < 0.001		

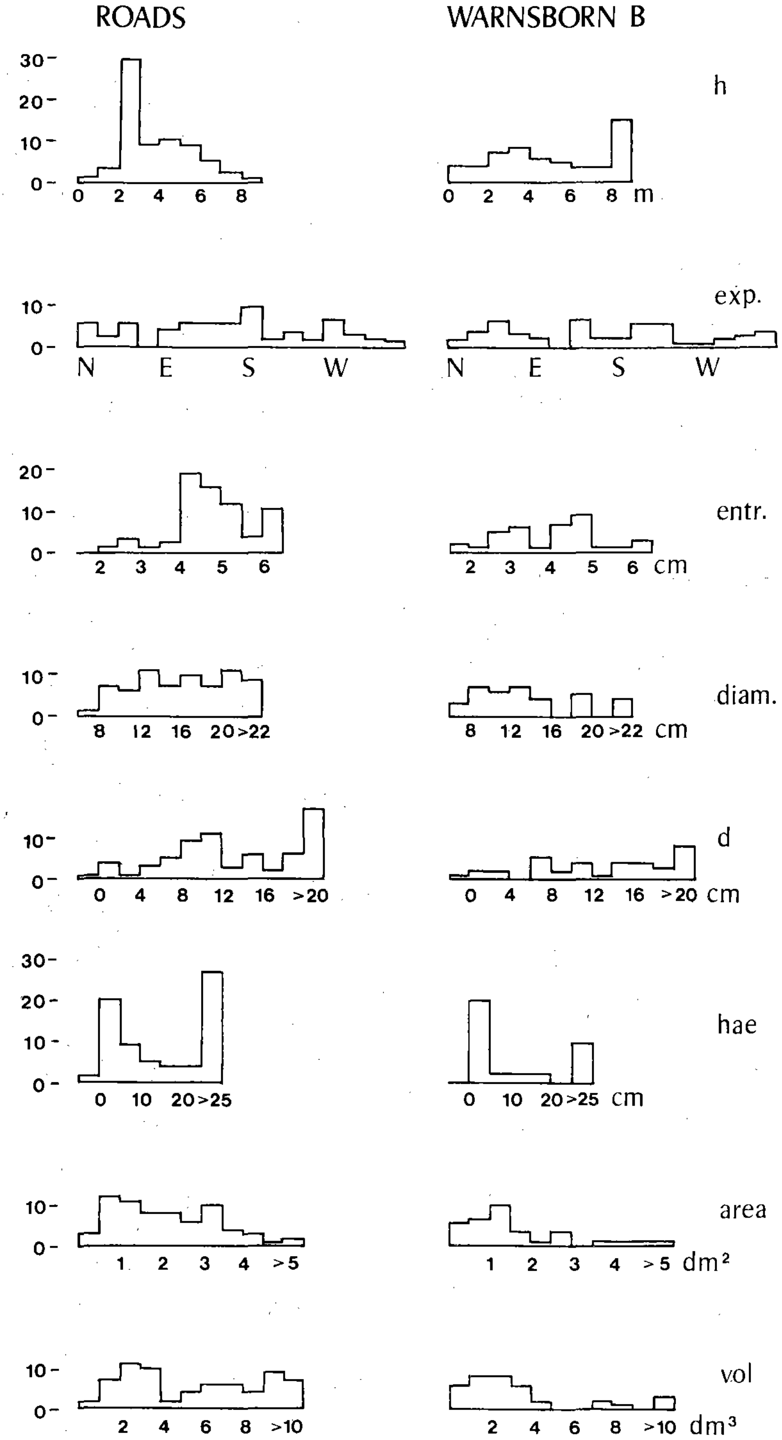

Fig. 3. Frequency distribution of important properties of tree holes in 1977. All areas along roads (except experimental area) were taken together and compared with Warnsborn B. For explanation of symbols, see Section 4.1.

evident that such a trend will be expressed most distinctly in an area with a wide availability of trees of different age classes.

So far, all holes considered suitable according to the criteria given in Section 3 have been discussed together. However, the available tree holes differed widely in dimensions and, consequently, in suitability for different species. Not only is it impossible for large species to enter many of the small tree holes, but, presumably, there are preferences for holes of a certain size class. Experiments with nest-boxes have shown that Great Tits prefer large and deep holes, Nuthatches (*Sitta europaea*) large and shallow holes, Blue Tits small and shallow holes, and Coal Tits shallow holes with a slit-like entrance (Löhrl 1970, 1977; see also Henze 1964). Some of Löhrl's results were confirmed by Van Balen (1972) and Nilsson (1975). Löhrl (1977) also obtained some evidence indicating a preference of Great Tits for small (30 mm) over large (40 mm) entrance sizes, but his results are not statistically significant. Another feature for which different species show differences in preference, or at least in distribution, is that of the height of the nest-hole above the ground (Löhrl 1970).

The conclusions derived from the literature led us to analyse the distribution of the properties of suitable holes. The following properties will be discussed (see Fig. 2):

— height above ground (h), in m;
— entrance exposure (exp);
— entrance diameter (entr), in cm;
— mean hole diameter (diam. = $\frac{x + y}{2}$), in cm;
— hole depth (d), in cm;
— height above entrance (hae), in cm;
— bottom area (area), in dm^2;
— volume (vol), in dm^3.

Fig. 3 gives, as an example, the distribution of the properties of all suitable holes in 1977. The data for the areas along the roads (Warnsborn A, Koningsweg, Zijpse Bos) were pooled. Warnsborn B was considered separately.

The height above the ground shows a peak at 2—3 m along the roads and an additional peak at large heights in Warnsborn B. In the latter area, where the trees are taller than in the "linear" areas, the number of very high cavities ($\geq$ 8 m) is certainly underestimated, for at such height only the occupied holes were found by watching the behaviour of the occupants.

The direction of exposure of the hole entrances is fairly evenly distributed. In both cases the distribution was homogeneous.

The minimal entrance diameter (usually the width) has a very uneven distribution. The lower limit (1.8 cm) is set by suitability condition 2. Entrance diameters up to 4 cm are rather scarce, and values between 4 and 5 cm are the most common. A large proportion of such holes are excavated by Great Spotted Woodpeckers (*Dendrocopos major*). A second peak (> 6 cm) includes holes made by Black Woodpeckers (*Dryocopus martius*).

The hole diameter varies from about 6 to about 25 cm, and does not show a distinct peak. Diameters below 8 cm are decidedly rare.

The depth of the holes often shows a bimodal distribution, with a peak at about 10 cm and a second peak above 20 cm. This is connected with the age of the holes and with the different ways in which the holes originate, *i.e.*, by the actions of woodpeckers or by decay.

The same applies to the height above the entrance, which is often close to zero (*e.g.*, in fresh woodpecker holes), but in many other cases is considerable, *i.e.* up to *ca.* 100 cm, in decaying trunks and branches.

The bottom area has by definition a minimum value of 0.25 dm^2, and has a maximum of nearly 7 dm^2. Within this range the classes between 0.5 and 2 dm^2 are better represented than the others.

The volume of the tree holes ranges from about 0.35 to 20 dm^3, the majority lying between 1 and 6 dm^3.

In sum, it is clear that the available tree holes vary considerably in all of the examined properties. This enables the different species to choose their preferred type of hole, provided that inter-and intraspecific competition do not hinder such a choice.

4.2. OCCUPATION

4.2.1. GENERAL PICTURE OF HOLE OCCUPATION

The numbers of holes occupied by different species, in terms of first clutches, as defined in Section 3, are given in Table 5. It should be kept in mind that the actual numbers of clutches found are slightly higher, because data in this table do not include:

1. a few clutches found in holes defined as "unsuitable",
2. clutches in holes that became available dur-

Table 5. Occupation of natural holes by different species, on the basis of first clutches

Part of study area	Zijpse Bos			Koningsweg			Warnsborn A			Warnsborn B	
Years	75	76	77	75	76	77	75	76	77	76	77
Number of suitable holes	15	13	14	42	47	53	56	61	61*	44	52
Great Tit	2	3	3	3	—	2	10	6	19	5	11
Blue Tit	—	—	1	3	1	5	3	2	8	4	9
Marsh Tit	—	—	—	1	1	—	—	—	1	1	1
Coal Tit	—	1	—	—	1	—	1	—	—	—	—
Nuthatch	—	—	—	2	—	2	1	1	3	2	3
Treecreeper	—	—	—	—	—	—	—	—	3	—	—
Redstart	—	—	—	—	—	—	1	3	—	—	—
Robin	—	—	—	—	—	—	—	1	—	—	—
Starling	8	7	9	26	24	33	24	20	9	14	20
Great Spotted Woodpecker	1	1	—	—	—	—	—	—	—	1	—
Green Woodpecker	—	—	—	—	—	1	—	—	—	—	—
Jackdaw	—	—	—	1	2	2	—	—	—	—	—
Stock Dove	—	—	—	1	1	—	—	—	—	—	1
Total holes occupied	11	11	13	37	30	45	40	33	43	27	45
% occupied	73	85	93	88	64	85	71	54	70	61	87

* The entrance of 21 holes was narrowed to *ca.* 30 mm; in part of the area nest-boxes were provided (see Section 3).

ing the main laying season, chiefly in freshly excavated woodpecker holes,

3. a few clutches laid in holes already occupied by other birds within the main laying season, and
4. clutches laid after the main laying season.

Even without these "extra" clutches the occupation percentages are high, ranging from 54 to 93% in different areas and years. Several authors (Edington & Edington 1972, Schiermann 1934) have published much lower percentages, but these were found in areas with old deciduous trees probably very rich in tree holes. Moreover, the "linear" arrangement of the trees in many of our areas promotes high occupation rates. In such a situation the population of a large adjacent area will concentrate its breeding attempts in the small strip where tree holes are abundant. In addition, occupation by Starlings can be high because of the presence of suitable foraging grounds in the vicinity.

As suggested in the Introduction, natural holes may harbour a more variable breeding avifauna than nest-boxes. The species composition of the occupants of the tree holes inspected during this study is given in Table 6, where all breeding attempts recorded during the main laying periods in 1975—1977 are pooled. For comparison, similar figures are presented for two neighbouring nestbox areas with a similar vegetation, *i.e.*, Hoge Veluwe (165 ha, *ca.* 370 boxes) and Warnsborn (17 ha, *ca.* 75 boxes).

The species composition of the birds nesting in tree holes and in nest-boxes differs appreciably. The most obvious and self-evident difference is the absence in the latter of Starling, woodpeckers, Jackdaw and Stock Dove, none of which can enter through a 3-cm entrance hole. But apart from this factor the remaining species also show large differences. The absence of the Pied Flycatcher and the Tree Sparrow in tree holes is striking. For the Tree Sparrow, a species that in this region occurs mainly near farms, the scarcity of farms in the study area may explain this finding. The absence of the Pied Flycatcher as a breeding bird using natural holes, in a region where the species is very common in nestboxes, is rather puzzling. The heavy competition for tree holes (section 4.2.3) could be a possible cause of this species' absence. If this were the case one would have expected at least some breeding attempts in 1976, when the populations of the competing species were rather low. The failure of the species to establish itself in the part of Warnsborn A where some of the tree holes were provided with narrower entrance holes in 1977 (see Section 3), is also not in favour of nest-site competition as the decisive

Table 6. Species composition for breeding attempts in tree holes in 1975—1977 and in nest-boxes in two neighbouring areas. Numbers in tree holes are slightly larger than totals from Table 5, because "extra" clutches (see text) were included. The percentage composition is given in parentheses for the most common species. The inner dimensions of the nest-boxes were 9 × 12 × 23 cm and the entrance was 3 cm in diameter

Species	Zijpse Bos, Koningsweg, Warnsborn A and B	Hoge Veluwe (nest-boxes)	Warnsborn (nest-boxes)
Great Tit, *Parus major*	66 (19)	503 (56)	123 (75)
Blue Tit, *P. caeruleus*	37 (10)	102 (11)	14 (9)
Marsh Tit, *P. palustris*	5	9	—
Coal Tit, *P. ater*	4	10	—
Crested Tit, *P. cristatus*	1	—	—
Nuthatch, *Sitta europaea*	14	5	2
Short-toed Treecreeper, *Certhia brachydactyla*	7	3	—
Redstart, *Phoenicurus phoenicurus*	4	2	—
Pied Flycatcher, *Ficedula hypoleuca*	— (0)	174 (19)	23 (14)
Spotted Flycatcher, *Muscicapa striata*	1	—	—
Robin, *Erithacus rubecula*	1	—	—
Tree Sparrow, *Passer montanus*	— (0)	85 (10)	2 (1)
Starling, *Sturnus vulgaris*	195 (55)	— (0)	— (0)
Jackdaw, *Corvus monedula*	5	—	—
Stock Dove, *Columba oenas*	3	—	—
Great Spotted Woodpecker, *Dendrocopos major*	8	—	—
Green Woodpecker, *Picus viridis*	2	—	—
Black Woodpecker, *Dryocopus martius*	2	—	—
	355	893	164

factor. Clutches of Pied Flycatchers in natural sites seem to be extremely rare, at least in The Netherlands. An explanation of this phenomenon cannot be given yet.

When the remaining species (the top eight in Table 6) are considered separately, there are still differences between the tree-hole and the nest-box populations. The Great Tit is more abundant in the boxes, whereas the other tits, Nuthatch, Treecreeper, and Redstart occur more frequently in the tree holes (20% of the clutches) than in the boxes (15 and 10%). This is probably connected with the large range of dimensions of the tree holes, which permits a wide rang of species to nest.

The occupation percentages show considerable annual fluctuations. In most areas more holes were occupied in 1975 and 1977 than in 1976. When all areas inspected in both years (and not affected by experiments) are combined, the percentages are as follows: 78 to 61 from 1975 to 1976, and 65 to 87 from 1976 to 1977. Both the decrease and the increase were significant ($p < 0.01$). The same procedure can be followed for the individual species or groups of species, and shows that (see Table 7) Great Tit, Blue Tit, and Nuthatch decreased considerably from 1975 to 1976 and increased even more from 1976 to 1977. The number of Starling clutches fluctuated similarly, but to a smaller extent. The few clutches of the smaller tit species (Marsh, Coal) tend to fluctuate inversely. Possibly, the decrease in numbers of the dominant species, especially Starling and Great Tit, reduced the competition for nest sites and also provided some sites for the subordinate Marsh and Coal Tits. This may also hold for the Redstart (see Warnsborn A in Table 5).

The question arises whether the annual numerical fluctuations found for the tree holes are representative of the overall fluctuations in population size. The population size is approximated by the number of first clutches in areas with plenty of nest-boxes, and for species that find suitable nesting sites in those boxes. In

Table 7. Population fluctuations of selected species during 1975—1977. Values are numbers of first clutches in areas inspected in both years and not affected by experiments

	1975	1976	1976	1977
Great Tit	15	9	8	16
Blue Tit	6	3	5	15
Other Tits	2	3	4	2
Nuthatch	3	1	2	5
Starling	58	51	45	62

practice, this only applies to the Great Tit and Blue Tit, since the smaller species are too scarce, and the Starling is too large to enter the boxes. Table 8 gives the breeding population of

Table 8. Number of breeding pairs of Great Tit and Blue Tit in four nest-box areas during 1975—1977

	Great Tit			Blue Tit		
	1975	1976	1977	1975	1976	1977
Hoge Veluwe	169	133	201	30	29	43
Warnsborn	41	15	53	5	5	4
Oosterhout	22	16	30	21	14	18
Liesbos	31	27	51	19	18	29
Total	263	191	335	75	66	94
in % of 1975	100	73	127	100	88	125

the two tit species in four nestbox areas, two of which are quite near the study area. These data show that both Great and Blue Tits decreased in numbers from 1975 to 1976 and increased from 1976 to 1977, with the Great Tit fluctuating most strongly. The fluctations in the nest-box populations are reflected in the occupation of the natural holes by these species (see above). The fact that the numbers of Great Tit clutches in tree holes in 1977 did not exceed the number of 1975, despite the larger breeding population in the nestboxes, suggests that in 1977 the tree holes were maximally occupied. The occupation rate did not reach 100%, but this is probably due to incompleteness of our suitability criteria. In Section 4.2.3 it will be shown that in 1977 many Great Tits dit not succeed in laying a clutch in their territories and were compelled to search for a vacant nest-site elsewhere.

4.2.2. HOLE OCCUPATION IN RELATION TO HOLE PROPERTIES

The fact that some holes were not occupied each year enables us to examine hole occupation in relation to the properties of the holes. This can be done for the total population of hole-nesting species and for the most frequent species separately. The results of this study will be discussed in terms of preference and competition, processes that can rarely be studied separately in nature.

The combined data for the areas along the roads (Warnsborn A, Koningsweg, Zijpse Bos) were analysed separately from those for Warnsborn B. The experimental areas (1977) were excluded from the calculations. Fig. 4 summarizes the results. At first glance, there are a number of cases in which the distribution of the occupied and unoccupied holes differs, *e.g.*, as to hole diameter, area, and volume in 1976. In other cases differences appear to be less pronounced or even absent. G-tests were applied to the data presented in Fig. 4. It appeared that the relationship between occupation rate and hole properties did not differ from year to year, which justified pooling of the data for the separate years. Table 9 gives the results of the G-tests for the pooled data. In the areas along the roads the distribution of occupied and unoccupied holes differed significantly for six out of eight properties.

From the combined results of Fig. 4 and Table 9 we conclude that in the areas along the roads large holes (large diameter, depth, bottom area, and volume) were more frequently occupied than small holes, and that holes exposed towards the east (between N and SSE)

Table 9. Frequency distribution of hole properties of occupied and unoccupied holes. Results of G-tests. n.s. = not significant

Property	Part of study area					
	Roads			Warnsborn B		
	G	d.f.	P	G	d.f.	P
Height above ground (h)	10.661	9	n.s.	5.700	6	n.s.
Exposure (exp)	17.254	9	0.045	4.915	6	n.s.
Entrance diameter (entr)	8.812	6	n.s.	3.450	6	n.s.
Hole diameter (diam)	23.154	9	0.006	8.286	6	n.s.
Depth (d)	27.132	9	0.001	10.008	6	n.s.
Height above entrance (hae)	11.115	9	n.s.	10.586	6	n.s.
Bottom area (area)	21.582	12	0.042	15.334	8	0.053
Volume (vol)	24.946	12	0.015	17.844	8	0.022

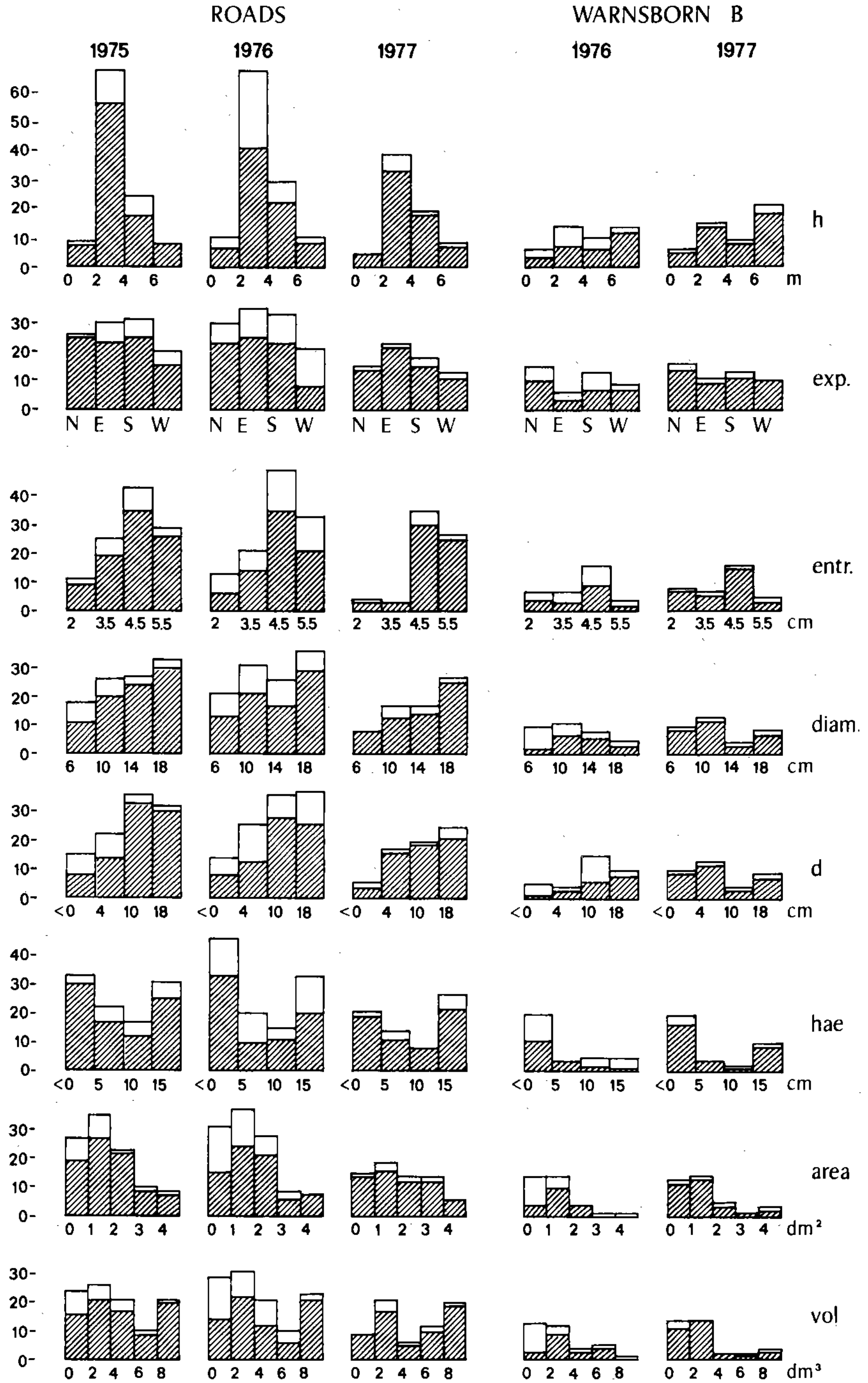

Fig. 4. Frequency distributions of properties of tree holes, whether occupied by any species (hatched) or unoccupied (open). All areas along roads were taken together, but experimental areas (1977) were excluded. For explanation of symbols, see Section 4.1. Data divided into broader classes than in Fig. 3 for statistical purposes. For each class the smallest value is indicated (*cf.* Table 11).

were occupied more often than those with a western exposure (S-NNW). Moreover, holes with small entrances were less often occupied than those with a medium or large entrance. No significant differences were found as to the height of the holes above the ground and the internal height above the entrance.

In Warnsborn B, for which area far fewer data were available, only two significant results were obtained. However, closer examination of Fig. 4 and calculation of occupation percentages in different classes of holes makes it clear that for quite a number of hole properties the trends found in the "road" areas are also present in Warnsborn B: height above ground, hole diameter, height above entrance, bottom area, and volume.

Starling. This species, the most numerous among the occupants of the natural holes, is the most obvious candidate for a study of hole occupancy in relation to hole properties. For this purpose, the pooled data for the areas along the roads were studied separately for 1976 and 1977. G-tests were performed for the same eight parameters as in the analysis of total occupancy. Since the relationship between occupation rate and hole properties was similar for the two years, the data for 1976 and 1977 were pooled. As the next step, all holes with an entrance diameter smaller than 3.5 cm were excluded, since these appeared to be inaccessible to Starlings. The remaining data were then divided into three or four classes, according to dimension, and G-tests were applied. The results are shown in Table 10. When appropriate, the classes were further pooled and χ^2-tests applied.

For the height above the ground the G-value

Table 10. Occupation by Starlings in relation to hole properties. Pooled data for 1976 and 1977, collected in Warnsborn A, Koningsweg, and Zijpse Bos. Holes with entrance < 3.5 cm excluded. n.s. = not significant

Property	Classes	No. available	No. occupied	% occupied	G	P
Height above ground	0—2 m	6	1	17	5.983	n.s.
	2—4 m	93	54	58		
	4—6 m	43	29	67		
	> 6 m	18	10	56		
Exposure	N-ENE	41	27	66	5.020	n.s.
	E-SSE	54	33	61		
	S-WSW	34	22	65		
	W-NNW	31	13	42		
Entrance diameter	3.5—4.4 cm	55	36	65	6.750	0.034
	4.5—5.4 cm	69	44	64		
	> 5.4 cm	33	13	39		
Hole diameter	6—9 cm	19	3	16	20.158	< 0.001
	10—13 cm	39	24	62		
	14—17 cm	34	20	59		
	> 17 cm	62	45	73		
Depth	< 0—3 cm	12	8	67	3.064	n.s.
	4—9 cm	32	17	53		
	10—15 cm	50	34	68		
	> 15 cm	61	33	54		
Height above entrance	< 0—5 cm	60	32	53	3.741	n.s.
	5—15 cm	27	14	52		
	15—24 cm	19	12	63		
	> 24 cm	49	34	69		
Bottom area	0—1 dm²	35	12	34	12.916	0.005
	1—2 dm²	44	28	64		
	2—3 dm²	38	25	66		
	> 3 dm²	37	27	73		
Volume	0—3 dm³	51	19	37	17.927	< 0.001
	3—6 dm³	40	29	73		
	6—9 dm³	35	22	63		
	> 9 dm³	28	22	79		

was not significant which indicates that the occupation rate did not differ among the height classes. The low occupation rate in the 0—2 m category suggests that low heights are avoided, but the sample size is too small to permit conclusions.

In general, the occupation rate was not related to the direction of exposure. As Verheijen (1969) found some effect of exposure on occupation rate, further examination of the data seemed justified. Then it was found that holes exposed toward directions W-NNW were occupied significantly less frequently than the other holes were ($\chi^2 = 4.848$, $p = 0.028$).

The diameter of the entrance appeared to have a marked influence on the occupation rate. Entrance holes larger than 5.5 cm in diameter were significantly avoided ($\chi^2 = 6.812$, $p = 0.009$).

The occupation rate was significantly related to hole diameter and, as expected, also to the calculated bottom area and volume. For all of these parameters the smallest class has a significantly lower occupation rate than the remaining classes, which do not differ significantly from each other. The χ^2-values amount to 17.410, 12.202, and 16.029, respectively, which is significant at $p < 0.001$.

The remaining hole properties (depth and height above the entrance) appear to be unrelated to the occupation rate. Holes are occupied by nesting Starlings even when the bottom is at the level of the entrance, and, alternatively, when the roof is at the level of the entrance. There was no relation between the total height of the holes and the occupation rate, but the total height was often quite large, 30 cm or more, and was seldom less than 16 cm. The smallest total height recorded for occupied holes amounted to 14 cm.

In sum, it appears that Starlings occupy natural tree-holes less frequently when these are exposed toward W-NNW directions, have an unnecessarily large entrance, and a small diameter, bottom area, and volume.

Verheijen (1969) showed that Starlings occupy nestboxes exposed E-SE most frequently, at least in situations with little shelter. Moreover, he found that in choice experiments boxes hanging at greater heights were preferred to those hanging lower. A certain avoidance of low-hanging boxes was also found by Coleman (1974). The findings of both authors agree with the results presented here.

Lumsden (1976) established that boxes with a "small" entrance (in his case 7.5 × 6 cm) were more frequently occupied than those with a larger entrance. A similar result was obtained by McGilvrey & Dawson (1971) who compared horizontal nest boxes with 3 × 4 inch (7.5 × 10 cm) elliptic and 4 × 11 inch (10 × 28 cm) semicircular entrances.

The avoidance of nest sites with a large entrance may be due partly to competition with larger species which can enter holes with large entrances, such as, in the present study, Jackdaw (*Corvus monedula*) and Stock Dove (*Columba oenas*). Another factor in the avoidance of holes with large entrances may be the risk of predation.

Most of the relations between hole parameters and occupation rate can be explained as the avoidance of holes that do not lie in the preferred range of hole properties. With respect to the influence of hole size, there is some experimental evidence on the nest-box preferences of Starlings. Karlsson (1978) offered boxes with a bottom area of 120, 144, or 225 cm² to a small population of Starlings in southern Sweden, and found no relation between bottom area and clutch size. From the data given in his Table 2 it can be concluded that there was also no preference for boxes of a certain size, as judged from the number of clutches and the mean laying dates. These results are not in contradiction with our findings, since the box sizes used by Karlsson fall within the range of bottom areas (1 dm² and larger) in which the occupation rate for the different size classes did not differ significantly (see Table 10). Mooed & Dawson (1979) studied the occupation of (among others) wooden boxes with a bottom area of 180, 250, 310, 520, or 775 cm², and found that boxes with a 310 cm² bottom area were more frequently occupied in the first five days of the laying season than both larger and smaller boxes. Their conclusion, *i.e.*, that the area of the "ideal nest site" should be about 300 cm², is not fully confirmed by our data since in the present study tree holes with a bottom area of more than 400

cm^2 were occupied just as often as smaller holes (bottom areas down to 100 cm^2).

Great Tit. This species also provided a sufficient number of data to permit an analysis of occupancy in relation to hole properties. As for the Starling, all data from the areas along the roads were used, in this case for all three years. Because the relationships between occupation rate and the various hole properties apparently did not differ in the three years, the data for 1975—1977 were pooled. Table 11a gives the results of the G-tests applied to the pooled data. Since it was evident that the results were strongly affected by interspecific competition, all data of holes occupied by species assumed to be dominant over Great Tits (Nuthatch, Starling, Jackdaw, Stock Dove, woodpeckers) were excluded. The remaining data were were analysed with G-tests and, when necessary, χ^2-tests. The results are given in Table 11b.

There is a highly significant relationship between occupation rate and the height above the ground (Table 11a), with the highest occupation

Table 11. Occupation by Great Tits in relation to hole properties, in the presence (a) and absence (b) of interspecific competition. For b all holes occupied by species with large body size were excluded. Pooled data for 1975—1977, collected in Warnsborn A, Koningsweg, and Zijpse Bos. In all cases d.f.=3. *** : $p < 0.001$; n.s.=not significant

Property	a	b					
	G	Classes	No. available	No. occupied	% occupied	G	p
Height above ground (h)	19.293***	0—2 m	23	9	39	11.213	0.01
		2—4 m	75	22	29		
		4—6 m	25	2	8		
		> 6 m	6	0	0		
Exposure (exp)	4.899 n.s.	N-ENE	17	6	17	4.111	n.s.
		E-SSE	35	8	35		
		S-WSW	48	15	48		
		W-NNW	29	4	29		
Entrance diameter (entr)	30.265***	2.0—3.4 cm	46	18	39	7.709	0.052
		3.5—4.4 cm	31	4	13		
		4.5—5.4 cm	35	7	20		
		> 5.4 cm	17	4	24		
Hole diameter (diam)	16.482***	6— 9 cm	42	7	17	3.798	n.s.
		10—13 cm	36	10	28		
		14—17 cm	37	13	35		
		> 17 cm	14	3	21		
Depth (d)	7.761 n.s.	< 0—3 cm	25	4	16	2.670	n.s.
		4—9 cm	42	14	33		
		10—15 cm	32	8	25		
		> 15 cm	30	7	23		
Height above entrance (hae)	1.589 n.s.	< 0—4 cm	45	10	22	1.574	n.s.
		5—14 cm	26	6	23		
		15—24 cm	16	6	38		
		> 24 cm	40	9	23		
Bottom area (area)	18.548***	0—1 dm^2	55	12	22	5.722	n.s.
		1—2 dm^2	49	15	31		
		2—3 dm^2	18	6	33		
		> 3 dm^2	7	0	0		
Volume (vol)	16.572***	0—3 dm^3	72	18	25	3.114	n.s.
		3—6 dm^3	41	12	29		
		6—9 dm^3	13	3	23		
		> 9 dm^3	3	0	0		

rate in the class of 0—2 m. After exclusion of the data for the holes occupied by dominant species, a similar relationship is found. Division of the data in Table 11b into two classes (0—4 and > 4 m) results in a significantly higher occupation rate for the holes in the 0—4 m class ($\chi^2 = 7.844$, $p = 0.005$). This means that the Great Tits occupied tree holes at low heights preferentially.

The occupation rate was not related to direction of exposure, either for the total data set, or for the more limited data. In the total material holes with small entrances were significantly more frequently occupied than holes with large entrances. This is due partly to the competition with larger species. When this competition is excluded, the occupation rates of the four classes differ almost significantly (Table 11b; $p = 0.052$). Regrouping of the data into two classes (2.0—3.4 and > 3.4 cm) results, however, in a significant difference ($\chi^2 = 6.894$, $p = 0.009$). Hence it is evident that Great Tits prefer to nest in holes with small entrances.

No consistent evidence indicating a preference for holes of a certain diameter was obtained. Although the occupation rates in the total material differed significantly, this difference could be ascribed wholly to the effects of interspecific competition, the dominant species avoiding holes with small diameters. When the effect of competition is excluded (Table 11b), no differences are found. However, the results of the experiment carried out in 1977 in part of Warnsborn A (see 4.2.3) indicate that there is some preference for holes with large diameters. In this situation, in which competition by larger species was excluded by narrowing the entrance, the occupation rate was positively correlated with hole diameter.

With respect to the influence of hole depth on the occupation rate, the situation is rather complex. In the total data set we found a relation which is just not significant (Table 11a, $p = 0.051$), but regrouping of the data showed that holes in the depth class of 4—9 cm had a significantly higher occupation rate than the holes in the remaining classes. After exclusion of the data for the dominant species (Table 11b), no significant differences in hole occupation were found. Thus, it seems that Great Tits are scarcely affected by hole depth when selecting a nest site.

The heigh above the entrance appeared to be unrelated to hole occupation. This also holds for the total height of the holes, *i.e.*, the sum of depth, entrance diameter, and height above the entrance. Total height varied from 8 to over 100 cm. The smallest holes occupied by Great Tits had a total height of 13 cm. Above this height no differences in occupation rate between different height classes were found.

Both bottom area and volume were significantly correlated with the occupation rate in the presence of interspecific competition (Table 11a), large holes being occupied much less frequently than small holes. When the effect of interspecific competition is excluded, no significant differences are found. However, just as for the diameter of the holes, the results of the 1977 experiment seem to suggest that large holes (> 2 dm^2 bottom area, > 6 dm^3 volume) are preferred to holes with smaller dimensions.

In sum, the Great Tit prefers to nest in holes at rather low heights and with small entrance holes, and there is some evidence for a preference for holes with large diameter, bottom area, and volume.

There is some evidence in the literature that the Great Tit prefers nest holes with certain properties. All of these studies were performed by varying the size of one of the properties of nest-boxes. Usually, equal numbers of boxes in the various classes were offered, a situation which is quite different from that in the present study. This may hamper comparison of the results of both types of study. Another difference is that in the present study holes usually differed not only as to the property under study, but also as to other properties, *i.e.*, properties are correlated.

Concerning the height above the ground, Löhrl (1970) observed that, in a choice experiment, boxes placed at a height of 3.5 and 7.0 m were occupied more frequently than boxes at 1.75 m and 15.0 m. In our study, holes situated at 0—4 m were preferred to holes at greater heights. The high occupation rate in the lowest height class (0—2 m, see Table 11) might be due to a combination with other (favourable) hole properties, such as a small entrance size. In fact, many of the holes in the lowest height-class had long slit-like entrances; the smallest diameter of the entrance was usually less than 3.5 m and the volume was larger than average. These favourable properties could explain the high occupation rate.

Hublé (1964) studied the relation between nest-box orientation and occupation by Great and Blue Tits. His results, pooled for the two species, show that these species do not prefer boxes with a certain orientation, which is in agreement with our findings.

Experiments performed by Löhrl (1977) with nest boxes having entrance sizes ranging from 30 to 40 mm did not give statistically significant results, but his findings suggest that boxes with a 32 mm entrance are preferred to those with a 38 or 40 mm entrance, which corresponds with our results for tree holes.

Löhrl (1970) found a distinct effect of hole depth on the occupation by Great Tits, boxes with d = 10 cm being preferred over boxes with d = 14 cm, and the latter preferred to boxes with d = 8.5 cm. The depth was measured from the entrance to the bottom of the box, whereas in the present study d was measured from the entrance to the surface of the nest. This technical difference cannot, however, explain why

Table 12. Occupation by Blue Tits in relation to hole properties. Pooled data for 1975—1977, collected in Warnsborn A, Koningsweg, and Zijpse Bos

Property	Classes	No. available	No. occupied	% occupied	G	p
Height above ground	0—2 m	23	4	17	8.661	0.034
	2—4 m	184	7	4		
	4—6 m	75	5	7		
	> 6 m	24	4	17		
Exposure	N-ENE	72	1	1	5.610	n.s.
	E-ESE	88	7	8		
	S-WSW	89	8	9		
	W-NNW	56	4	7		
Entrance diameter	2.0—3.4 cm	49	8	16	8.750	0.033
	3.5—4.4 cm	96	5	5		
	4.5—5.4 cm	104	3	3		
	> 5.4 cm	55	4	7		
Hole diameter	6—9 cm	49	13	27	29.088	< 0.001
	10—13 cm	79	4	5		
	14—17 cm	73	2	3		
	> 17 cm	99	1	1		
Depth	< 0—3 cm	41	3	7	6.010	n.s.
	4—9 cm	71	9	13		
	10—15 cm	91	5	5		
	> 15 cm	97	3	3		
Height above entrance	< 0—4 cm	105	11	10	4.100	n.s.
	5—14 cm	58	3	5		
	15—24 cm	40	1	3		
	> 24 cm	95	5	5		
Bottom area	0—1 dm^2	80	15	19	25.121	< 0.001
	1—2 dm^2	96	3	3		
	2—3 dm^2	66	2	3		
	> 3 dm^2	58	0	0		
Volume	0—3 dm^3	109	16	15	19.592	< 0.001
	3—6 dm^3	90	2	2		
	6—9 dm^3	56	2	4		
	> 9 dm^3	45	0	0		

hole depth did not affect occupation in the present study.

Several authors concluded that Great Tits prefer to nest in boxes with a large diameter or a large bottom area. This seems to hold for a wide range of sizes. Henze (1964) reported that boxes with a 182 cm² bottom area were preferred to boxes with a 132 cm² bottom area. Nilsson (1975) found a difference in occupation rate between boxes having a bottom area of 87 and 57 cm², and Van Balen (1972) obtained similar results with boxes of 108 and 36 cm² area. Löhrl (1970) offered boxes with a diameter of 11.5, 14, or 20 cm (bottom area 104, 154 and 314 cm², respectively) and showed that the widest boxes were most frequently occupied. The present results do not fully support the conclusion drawn by these authors from the nest-box experiments. This could be due to disturbing influences exerted by other hole properties. Wide tree holes often have a large entrance and might therefore be avoided by Great Tits. The results of the experimental narrowing of the entrances, referred to above, suggest that when most of the entrances have a favourable size (*ca.* 3 cm), large tree holes are preferred to small ones.

Blue Tit. The relationship between hole properties and occupation was also studied for the Blue Tit. Because only 7 per cent of the tree holes were occupied by this species, insufficient data were obtained to allow division into subsets for different years or for holes not occupied by dominant species. Some very distinct relationships were found in the total material for 1975—1977, as shown in Table 12. Blue Tit nests were predominantly found either at very small or at great heights and most of the holes had a very small entrance and (especially) a small diameter, bottom area, and volume. The relationship between entrance size, bottom area, and occupation rate was such that the few occupied holes with a large entrance had a small bottom area, and *vice versa.* This is clearly demonstrated by the data in Table 13. With only one exception, the occupied holes had either an entrance hole smaller than 2.8 cm or a bottom area of less than 100 cm². This strongly suggests that interspecific competition forces the Blue Tit to nest in tree holes that are inaccessible to or offer inadequate space for larger species. Several observations have shown that Blue Tits are often evicted from tree holes by larger species.

Table 13. Frequency of occurrence of different combinations of entrance diameter and bottom area for all Blue Tit nests found in 1975—1977. Pooled data for all areas

Bottom area (cm²)	Entrance diameter (cm)		
	1.5—2.7	2.8—3.9	> 3.9
0— 49	2	6	6
50— 99	7	4	3
100—199	3	0	0
200—299	3	0	1
> 299	0	0	0

Other species. The data for the remaining species are scanty. All data on occupied holes in the areas inspected in all three years are given in Table 14. For comparison, the relevant data for Starling, Great Tit, and Blue Tit are added. The species are ranked according to the mean value of the hole property concerned. The results can be compared with Fig. 3 which shows the frequency distribution of the properties in all holes studied in 1977. In spite of the small samples some provisional conclusions can be drawn, but the results do not permit any conclusions about preferences for certain hole properties.

Coal Tits were found nesting at low heights, in holes with a small entrance, and a rather small diameter and bottom area. Marsh Tits nested in extremely narrow holes, also with a small entrance hole, but at about average height above the ground. The Nuthatch was one of the species that nested at greater heights. This species used holes with an average entrance size or larger, but the birds had narrowed the entrances by plastering to a very uniform size (2.7 to 3.0 cm). The hole diameter and bottom area were about average, but varied considerably.

The Nuthatch is the only small passerine that is found nesting in relatively large tree holes with a bottom area of more than 3 dm³. Its habit of narrowing the entrance by plastering in the early stages of nesting enables it to withstand the competition by Starlings. The other possible

Table 14. Properties of tree holes occupied by uncommom species. Pooled data of all areas and years, for species with n > 2. For comparison, mean and standard deviation are given for all holes occupied by Great Tit, Blue Tit, and Starling. Same data as in Tables 10, 11 and 12

Property (unit)	Species	No. of observations	Mean	S.D.	Minimum	Maximum
Height above ground (m)	Coal Tit	4	1.7	0.9	0.4	2.4
	Redstart	4	1.9	1.0	0.4	2.5
	Great Tit	33	2.6	0.9	—	—
	Stock Dove	5	3.1	0.3	2.8	3.5
	Marsh Tit	6	3.4	1.1	1.6	4.7
	Starling	94	3.9	1.6	—	—
	Blue Tit	20	4.0	2.4	—	—
	Great Spotted Woodpecker	3	4.5	1.7	2.6	5.5
	Nuthatch	12	4.7	1.5	2.3	7.2
	Jackdaw	6	5.0	1.2	3.5	6.5
Entrance diameter (cm)	Nuthatch[1]	10	2.8	0.1	2.7	3.0
	Coal Tit	4	3.4	0.6	2.5	4.0
	Marsh Tit	6	3.6	0.8	2.8	4.8
	Great Tit	33	3.9	1.4	—	—
	Blue Tit	20	4.0	1.6	—	—
	Great Spotted Woodpecker	3	4.3	0.3	4.0	4.5
	Starling	93	4.7	0.7	—	—
	Nuthatch	10	5.5	1.6	4.0	8.0
	Redstart	4	7.6	4.9	4.5	15.0
	Jackdaw	6	8.4	1.8	7.5	12.0
	Stock Dove	5	8.6	1.5	7.0	10.0
Hole diameter (cm)	Marsh Tit	6	7.3	0.5	7	8
	Blue Tit	20	9.8	3.5	—	—
	Great Spotted Woodpecker	3	10.3	2.1	8	12
	Redstart	4	10.8	2.2	9	14
	Coal Tit	4	12.3	2.9	8	14
	Great Tit	33	13.0	3.4	—	—
	Nuthatch	12	16.2	4.7	10	24
	Starling	92	16.9	4.4	—	—
	Jackdaw	6	21.8	5.2	18	30
	Stock Dove	5	22.4	3.7	19	28
Bottom area (cm^2)	Marsh Tit	6	38.7	4.5	33	44
	Great Spotted Woodpecker	3	85.7	32.3	50	113
	Blue Tit	20	88.5	66.4	—	—
	Redstart	4	93.0	39.4	63	151
	Coal Tit	4	120.5	52.0	44	153
	Great Tit	33	139.2	64.3	—	—
	Nuthatch	12	212.3	130.6	75	491
	Starling	92	239.2	121.3	—	—
	Jackdaw	6	389.0	165.0	254	679
	Stock Dove	5	427.4	137.8	283	589

[1] Entrance size reduced by plastering.

competitors (Jackdaw, Stock Dove, etc.) need a larger hole than those used by the Nuthatch.

The main features of the holes that were used by Redstarts are a low height and a large and variable entrance size. Diameter and bottom area were below average.

The holes that were used by the Great Spotted Woodpecker were usually freshly excavated by the birds. They were found at average height, and had a uniform entrance size of 4.0—4.5 cm in diameter. Hole diameter and bottom area were small, but further excavation in subsequent breeding seasons (or perhaps in the winter) and decay may widen them appreciably. Generally, however, these holes are used by the excavator for only one season, and become

Table 15. Constancy and change of occupation in different years. Frequency of occupation by different species in 1975 v. 1976, 1976 v. 1977, or 1975 v. 1977 (if not occupied in 1976). Pooled data for all regularly inspected areas. Constancy percentages calculated for the totals of columns and rows

Species in first year	Species in second year												
	Black Woodpecker	Jackdaw	Stock Dove	Green Woodpecker	Great Spotted Woodpecker	Starling	Nuthatch	Redstart	Great Tit	Blue Tit	Coal Tit	Marsh Tit	Tree Creeper
Black Woodpecker	—	1	—	—	—	—	—	—	—	—	—	—	—
Jackdaw	—	2	—	—	—	—	1	—	—	—	—	—	—
Stock Dove	—	1	3	—	—	—	—	—	—	—	—	—	—
Green Woodpecker	—	—	—	—	—	1	—	—	—	—	—	—	—
Great Spotted Woodpecker	—	—	—	—	—	4	—	—	—	—	—	—	—
Starling	—	—	—	1	—	90	3	1	8	—	—	—	—
Nuthatch	—	—	—	—	—	3	3	—	—	—	—	—	—
Redstart	—	—	—	—	—	—	—	1	—	1	—	—	—
Great Tit	—	—	—	—	—	4	—	—	15	3	—	—	—
Blue Tit	—	—	—	—	—	—	—	—	2	11	—	—	1
Coal Tit	—	—	—	—	—	—	—	—	1	1	1	—	—
Marsh Tit	—	—	—	—	—	—	—	—	—	1	1	1	—
Tree Creeper	—	—	—	—	—	—	—	—	—	—	—	—	—
Total no. of cases	1	5	4	2	4	115	10	3	33	20	4	3	1
Constancy percentages	—	40	75	0	0	78	30	33	45	55	25	33	—

available for other species in the following year. The woodpecker's habit of excavating a nest hole each year contributes strongly to the stock of available holes.

Nests of the Stock Dove were found at medium height, those of the Jackdaw often at great heights. Both species nested in wide holes with a large entrance, often originally excavated by the Black Woodpecker.

So far, the properties of tree holes occupied by different species have been discussed separately. The findings lead to the conclusion that interspecific competition plays a major role in determining the occupation of holes by different species. Another way of studying the roles of interspecific competition and preference for certain hole properties is to compare hole occupation in different years. Table 15 shows that many holes had different occupants in the three years of our study. For most species, the occupying species differed between the years in more than half of the cases. Woodpecker holes were always used by another species (often the Starling) in the year after excavation. This implies that the distribution of Starling nests is to a large extent determined by the distribution of woodpecker holes. Holes used by Starlings often did not change as to the species of the occupant between the years. When a change occurred, the second species was usually a smaller one (Nuthatch, Great Tit). Presumably, the accumulation of nest material renders such holes unsuitable for Starlings in the long run.

The fact that the species occupying tree holes often changes between years indicates that there is ample opportunity for interspecific competition. Some observations and experiments on competition, particularly within one breeding season, are presented in the next section.

4.2.3. OBSERVATIONS AND EXPERIMENTS ON NEST-HOLE COMPETITION

Since several cases of inter- and intraspecific competition for nest-holes were established in 1975 and 1976, special attention was paid to these phenomena in 1977. Nest-hole competition in the Great Tit was studied in Zijpse Bos and Koningsweg, by mapping the territorial males in March and April and comparing the number of males and their locations with clutches found in the tree holes.

The Zijpse Bos area consisted (in 1977) of two forest roads, with a total length of 1360 m, bordered by Beeches and Red Oaks. In March and April, 18 territories of Great Tits were mapped, but the tits succeeded in laying a clutch in only five of these territories (= 28%). Two clutches were succesful. Many breeding attempts failed because of occupation by Starlings. In all cases this occurred at an early stage, before the tits had laid eggs. In this respect 1977 may have been an aberrant year, because the Starlings laid unusually early; in other years there was an interval of 10—14 days between the laying dates of Great Tits and Starlings. Most of the unsuccessful tits stayed in the area for the rest of the breeding season. A few moved to the surrounding forest, where the occurrence of breeding could not be established. Clearly, the situation in 1977 was such that only a fourth of the Great Tits present in April succeeded in laying a clutch in their territories.

Similar observations were done along the Koningsweg; here, there was the additional advantage that part of the population could be identified because they had been given coloured rings while visiting the neighbouring study area Hoge Veluwe. This enabled us to record some movements into and out of the study area. Along the Koningsweg, in an area of 1750 × *ca.* 50 m, 20 territorial pairs were present in late March-April. The fate of these pairs can be summarized as follows:

7 pairs obtained a nest-hole along the road and laid eggs, three of them being successful in fledging at least one young;

7 pairs nested outside the study area: 3 in the immediate surroundings and 4 in nest-boxes in the Hoge Veluwe at a distance of 50—200 m from their territories;

a few (0—2) pairs stayed in the area without nesting;

3—5 pairs left the territory, moving up to 800 m away but did not nest; and 1 pair left the area in mid-April.

This summary means that only seven out of 20 territorial pairs (35%) were successful in building a nest and laying eggs in their spring territory. Many pairs were compelled to search for a nest site outside their territory. This tendency may be promoted by the availability of nest-boxes at a short distance.

The relationship between the number of territorial Great Tits and the number of clutches was also studied in part of Warnsborn A (Rustwat-gebied). Here the availability of nest-holes for Great Tits was changed in March 1977 by narrowing the entrances of 21 tree holes to a diameter of 2.5—3.5 cm. The number of Great Tit territories amounted to 25, at least 18 of them belonging to pairs. Twenty breeding attempts were recorded, 17 of which concerned pairs with territories along the roads and the other three from outside pairs. These results show that in an area with tree holes that are inaccessible to Starlings, the majority of the territorial Great Tits are able to nest successfully, and that such an area attracts tits from surrounding areas that are unsuitable for nesting.

Table 16. Effect of narrowing the entrance on nest-hole occupation by Great Tits. Rustwat-gebied = experimental area (1977). Koningsweg and Zijpse Bos=control area

	Rustwat-gebied		Koningsweg + Zijpse Bos	
Year	No of suitable holes	No. occupied	No. of suitable holes	No. occupied
1975	39	8 (21%)	59	5 (9%)
1976	42	6 (14%)	63	6 (10%)
1977	43	20 (47%)	71	9 (13%)

Table 16 shows the occupation of holes by Great Tits in the experimental area and a control area. Whereas in the control area the percentage of occupied holes hardly differed in the three years, the occupancy in the experimental area increased about threefold from 1976 to 1977. The accompanying decrease in the number of Starling clutches is evident from Table 5 (see under Warnsborn A).

The occupation of the tree holes in the Zijpse Bos area was followed closely (see above). In many cases holes occupied by Great Tits and other tits were taken over by Starlings in the nest-building or laying stage but not in the incubation stage; this might have been due to the earliness of the Starling's breeding season. The interactions between Great Tits and Starlings were also studied experimentally in the Heidelaan area (see Fig. 1). On May 2nd, the entrance holes of seven nest-boxes occupied by Great Tits were enlarged. Six of these contained incomplete clutches, the seventh a nest without eggs. At the same time, the entrance holes of six boxes with incubated Starling clutches were narrowed, thus creating a small population of nest-prospecting Starlings.

Within 1—2 days, five of the seven boxes occupied by Great Tits were taken over by Starlings, and the first Starling eggs were laid after 3, 6, 6, 7 and 26 days, respectively. In these five boxes the tits had laid only a few (0—4) eggs before the experiment. In the remaining two boxes, which contained 4 and 5 tit eggs on May 2nd, the Starlings only took over after 2—3 weeks. In one of these boxes the female tit incubated persistently after laying the 6th egg (May 4). These findings suggest that Starlings are capable of occupying nest-holes with Great Tit clutches in the early laying stages without any difficulty, and have more trouble in evicting incubating tits. When the shortage of nest holes available to Starlings is not very serious, incubating tits may be relatively safe from eviction.

5. DISCUSSION

From the foregoing sections it may be concluded that most species of hole-nesting birds show differences in the average values of some properties of the occupied holes, and several species display distinct preferences. On the other hand, there is a large overlap in most of the hole properties studied so far. The distribution of the species over the available tree holes is the result of specific preferences for holes with certain properties and of intra- and interspecific competition. Both processes are strongly affected by the availability of holes, *i.e.*, both the numbers available and the suitability of the holes for the species concerned. Under the conditions of the present study, where high occupation percentages (54—93%) were found, competition is likely to be clearly expressed. Numerous cases of interspecific competition were indeed found, and an experiment showed that Starlings can evict Great Tits when holes are in short supply. Furthermore, the observations on territorial behaviour showed that only about 30 per cent of the Great Tits pairs present in March 1977, succeeded in occupying a tree hole for breeding. Hence it is clear that, at least for the Great Tit, suitable holes were in short supply. This may apply to several other small passerine species as well.

The unsuccessful Great Tit pairs either stayed in their territories without nesting or moved to surrounding areas. At least some of the latter pairs succeeded in obtaining a nest-box and nested successfully. Drent (1978) observed that in the neighbouring nest-box area (Hoge Veluwe) late immigrant pairs — called guest pairs — entered occupied territories and nested successfully, unharassed by the owners.

Edington & Edington (1972) studied the breeding birds of an old neglected deciduous wood in Wales with an abundance of tree holes. The authors counted 62 holes in 4 ha, only 13 of which (21%) were occupied in 1970. Even in their situation there was a large overlap in the properties of holes used by different species, *e.g.*, entrance size and height from the ground. The authors' conclusion that the hole nesters in general did not select holes of a particular size seems unjustified, because only the entrance dimensions were measured. Their results concerning the height of nest holes from the ground correspond roughly with the results of the present study. Among the five species common to both studies, the Redstart nested at the smallest heights, the Great Tit at intermediate heights, and Blue Tit, Nuthatch and Starling at the greatest heights.

Preferences for certain hole parameters were most pronounced in studies with nest-boxes (*e.g.*, Löhrl 1970, 1977), were the provision of widely differing types of box forces the birds to make a distinct choice.

The introduction of nest-boxes into an area has a favourable effect not only on the species that inhabit these boxes but also on the other local species, by reducing interspecific competition for nest sites.

The question whether populations in areas with many nest-boxes have an "unnaturally" high breeding density cannot be answered properly except by population studies in primeval forests, which are urgently needed.

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7. SUMMARY

The scarcity of studies on hole-nesting birds in natural nest sites prompted us to undertake such a study, and to compare the results with those obtained with nest-boxes. The study was performed in 1975—1977 in a wooded area north of Arnhem, where many roads are bordered with old deciduous trees, rich in tree holes. The study area consisted of three sets of roads and a 9 ha plot of deciduous woodland (Warnborn B, see Fig. 1). From the suitable holes found several measures were taken (Fig. 2).

Suitable holes occurred in densities of 6—30 per ha, or 3—11 per 100 trees. High densities were found along the roads (Table 2), presumably because the surrounding forest was rather young and unsuitable for hole excavation. Conifers had very few holes (Tale 3), but the various deciduous tree species did not differ in hole density. Young trees (trunk circumference smaller than 60 cm) had no holes at all and there was a general tendency for hole density to increase with the age of the trees (Table 4).

All measured hole parameters showed considerable variability (Fig. 3), enabling a wide selection of species to nest. Many species were found indeed, but Starling and Great Tit predominated (Table 5). Occupation percentages were high (54—93%), especially in 1975 and 1977. The species composition differed appreciably from that in neighbouring nest-box areas (Table 6). These differences can be understood from the differences in size and entrance diameter between nest-boxes and tree holes. Only the striking absence of the Pied Flycatcher in the tree holes could not be explained in this way.

The annual fluctuations in the numbers of clutches of the most common species (Table 7) corresponded with the fluctuations found in several nest-box areas (Table 8).

The properties of occupied and unoccupied holes were compared for all species together and for the most common species separately, in order to study preferences and interspecific competition. In general, holes with a large diameter, depth, bottom area, and volume were occupied most frequently, as well as holes exposed to eastern directions (Fig. 4 and Table 9).

Starlings did not occupy holes with an entrance diameter of less than 3.5 cm. For the remaining holes it was found that those at small heights and those exposed to W-NNW directions were avoided. This also holds for holes with a wide entrance (diameter > 5.5 cm), and for holes with a small diameter, bottom area and volume (Table 10).

For the Great Tit we made separate calculations for those holes that were left unoccupied by larger-sized (dominant) species (Table 11b), to enable conclusions about preferences to be drawn. Initially no significant differences were found, but by further pooling of classes it was found that holes at low heights (0—4 m) and holes with a small entrance (< 3.5 cm) were preferred. An experiment, in which the entrance of tree holes were reduced to *ca.* 3 cm to exclude larger species, showed that in this situation the Great Tits preferred to nest in holes with a large diameter, bottom area and volume.

Blue Tit clutches were predominantly found at very small or at great heights, and most of their holes had either a very small entrance or a small hole diameter (Tables 12 and 13). These findings were evidently due to interspecific competition.

Data for the other species were scanty (Table 14). Coal Tits nested at low heights, in holes with a small entrance and a rather small bottom area. Marsh Tits nested in extremely narrow holes, also with a small entrance. The Nuthatch nested at greater heights than most of the tits. The entrances, often rather large, were narrowed by plastering to a uniform size (2.7—3.0 cm). The bottom area was usually rather large. The habit of narrowing the entrance increased its success in the competition with larger species. Redstart holes were situated at small heights and had a large and rather variable entrance size.

The fact that many holes were used by different species in successive years (Table 15) suggests that the preferences of these species overlap each other considerably and that there is ample opportunity for interspecific competition.

Comparison of the numbers and locations of territorial male Great Tits and the numbers of clutches found in the tree holes showed that in 1977 only about 30% of the pairs succeeded in laying a clutch in a hole inside their territory. Competition with Starlings was the main cause of this low success rate. The other tits either stayed without nesting or moved several hundred of metres in order to nest outside their territories.

Narrowing the entrances in part of the area resulted in reduced occupation by Starlings and increased occupation by Great Tits (Table 16). In another experiment the entrance of nest-boxes occupied by Great Tits were enlarged during the laying period; this resulted in a rapid take-over by Starlings.

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9. SAMENVATTING

De biologie van holenbroedende vogels wordt gewoonlijk onderzocht met behulp van nestkasten. Verschillende overwegingen maken het duidelijk dat de met nestkasten gevonden resultaten niet zonder meer gegeneraliseerd mogen worden. Populaties van holenbroeders, die in natuurlijke holten (vooral boomholten) broeden, kunnen afwijken in dichtheid, soortsamenstelling, legselgrootte en broedresultaten. Deze overwegingen waren aanleiding om het broeden van holenbroeders in semi-natuurlijke omstandigheden te onderzoeken, en de resultaten te vergelijken met de met behulp van nestkasten behaalde resultaten. In dit artikel komen de beschikbaarheid en de bezetting van boomholten ter sprake, alsmede de concurrentie om nestplaatsen tussen verschillende soorten.

Het proefgebied (Fig. 1) lag ten noorden van Arnhem en bestond uit een aantal oude loofhoutlanen omgeven door jonger naald- en loofbos (Warnsborn A, Zijpse Bos en Koningsweg) en een 9 ha groot perceel gemengd loofbos (Warnsborn B). Dit laatste was variabeler voor wat betreft het aantal boomsoorten en de grootte van de bomen. In het broedseizoen werden alle bomen tot op ca. 7 m hoogte op holten onderzocht, en werden alle geschikte holten eens per week met behulp van een spiegel en een lamp gecontroleerd. Van alle holten werden verschillende afmetingen bepaald, zoals in Fig. 2 is aangegeven. Uit de maten werden bodemoppervlak en inhoud berekend.

Het aantal beschikbare boomholten bedroeg in Warnsborn B 6—7 per ha, en in de lanen 9—39 per ha, of (een betere maat) 4—11 per 100 bomen (zie Tabel 2). De holen waren sterk geconcentreerd in de lanen, vermoedelijk omdat het omringende gebied ongeschikt was voor nestbouw door spechten. In naaldbomen werden zeer zelden holen gevonden (Tabel 3); de verschillende loofhoutsoorten verschilden niet in het aantal holten per boom. Loofbomen langs verkeerswegen hadden meer holten dan bomen langs wegen zonder verkeer. Dit zou door een verschil in conditie van de bomen verklaard kunnen worden. Jonge bomen, met een stamomvang van minder dan 60 cm, bevatten geen holten. In Warnsborn B nam het aantal bomen met holten toe met toenemende leeftijd, gemeten aan de stamomvang (Tabel 4).

Fig. 3 geeft een voorbeeld van de gevonden verdelingen van de verschillende holte-eigenschappen. Het is duidelijk dat alle eigenschappen grote variabiliteit vertonen. Vele holten lagen 2—3 m hoog, terwijl soms bij grote hoogten (> 8 m) een tweede piek in het aantal optrad. De holten waren gelijkelijk verdeeld over de verschillende kompasrichtingen. De meest voorkomende grootte van het vlieggat lag tussen 4 en 5 cm. Vele van deze holten waren door Grote Bonte Spechten uitgehakt. De inwendige doorsnede van de holten varieerde sterk, van ca. 6 tot ca. 25 cm. De gemeten diepte was tweetoppig verdeeld, met toppen bij ca. 10 en bij groter dan 20 cm. Hetzelfde geldt voor de hoogte boven het vlieggat, die in veel gevallen zeer klein was, maar in andere gevallen zeer groot, tot ca. 100 cm. Hierbij speelt de ouderdom van de holten ongetwijfeld een grote rol.

Het berekende bodemoppervlak en de inhoud van de holten waren zeer variabel. De klassen 0.5—2 dm^2 (opp.) en 1—6 dm^3 (inhoud) kwamen het meest frequent voor.

Tabel 5 geeft een overzicht van de gevonden aantallen eerste legsels. In vele gevallen, vooral in 1977, lagen de bezettingspercentages erg hoog. De soortsamenstelling was veel variabeler dan die van naburige terreinen met nestkasten (Tabel 6). In de boomholten ontbraken Ringmus en Bonte Vliegenvanger, maar in de nestkasten ontbraken de grotere soorten (vlieggat te klein) en waren de kleinere mezensoorten, Boomklever, Boomkruiper en Gekraagde Roodstaart slechter vertegenwoordigd dan in de boomholten. De uniformiteit van de nestkasten in deze terreinen leidde ertoe dat alleen Koolmees, Bonte Vliegenvanger en Ringmus er talrijker in broedden dan in de boomholten.

In 1976 was een kleiner percentage van de boomholten bezet dan in 1975 en 1977. Dit werd veroorzaakt door schommelingen in het aantal legsels van Koolmees, Pimpel-

mees, Boomklever en Spreeuw (Tabel 7), die deels ook in terreinen met nestkasten optraden (Tabel 8). In 1977 was het aantal koolmeeslegsels in de boomholten lager dan op grond van de nestkastgegevens verwacht kon worden. De boomholten waren toen praktisch maximaal bezet.

Fig. 4 geeft de verdelingen van de eigenschappen van bezette en onbezette holten in de drie jaren. Deze gegevens zijn getoetst met behulp van de G-toets. Dan blijkt (Tabel 9) dat holten met een grote diameter, diepte, oppervlak en inhoud frequenter bezet waren dan kleine holten, en dat holten met naar het oosten gerichte vliegopening vaker bezet waren dan naar het westen gerichte holten.

De bezetting door Spreeuwen van holten met verschillende eigenschappen werd bestudeerd. Hieruit bleek dat, zoals verwacht, holten met een vlieggat van kleiner dan 3.5 cm niet bezet werden. Vervolgens werden de holten met een vlieggat van tenminste 3.5 cm opnieuw bekeken, en de resultaten met een G-toets getoetst (Tabel 10). Voor de meeste eigenschappen werden significante verschillen gevonden. Holten, die lager dan 2 m boven de grond lagen, werden vermoedelijk gemeden. Holten met een expositie naar het W-NNW werden minder vaak bezet dan de overige holten. Holten met grote vlieggaten (> 5.5 cm) werden gemeden. Holten met een kleine diameter, bodemoppervlak en inhoud werden minder frequent door Spreeuwen bezet dan holten met grotere afmetingen. Er bestaat dus een voorkeur voor ruime boomholten met een vliegopening van 3.5—5.4 cm. De meeste van deze resultaten komen overeen met de resultaten van reeds gepubliceerde proeven met nestkasten.

De resultaten van het onderzoek naar de bezetting door Koolmezen van holten met verschillende eigenschappen staan in Tabel 11 vermeld. Holten, die door vermoedelijk dominante soorten (Spreeuw, Boomklever, Kauw, Holenduif, Spechten) waren bezet, zijn in Tabel 11a wel, in Tabel 11b niet meegerekend. Alleen in het laatste geval kan iets gezegd worden over de voorkeur van de Koolmees met betrekking tot holte-eigenschappen. Het bleek dat (in afwezigheid van de dominante soorten) holten, die 0—4 m hoog gelegen waren, vaker bezet waren dan de hoger gelegen holten. Verder kon een voorkeur voor holten met een kleine vliegopening (< 3.5 cm) vastgesteld worden, en werden aanwijzingen verkregen voor een voorkeur voor ruime holten (bodemoppervlak > 2 dm^2, inhoud > 6 dm^3). De meeste van deze resultaten zijn ook verkregen bij proeven met nestkasten.

Legsels van de Pimpelmees werden vooral gelegd (zie Tabel 12) in holten die zeer laag of zeer hoog gelegen waren, in holten met een zeer klein vlieggat, en een zeer kleine doorsnede, bodemoppervlak en inhoud. In vrijwel alle gevallen was óf het vlieggat, óf het bodemoppervlak zeer klein (Tabel 13). Dit suggereert dat concurrentie met andere, meer dominante soorten de Pimpelmees doet uitwijken naar holten die voor de concurrenten ongeschikt zijn.

Tabel 14 geeft een overzicht van de eigenschappen van de door diverse soorten bezette holten. Zwarte Mezen broedden in kleine laag gelegen holten met een klein vlieggat. Glanskoppen nestelden vooral in zeer nauwe holten, ook met een klein vlieggat. Legsels van Boomklevers werden vaak op vrij grote hoogte aangetroffen. De vliegopening was door metselwerk tot 2.7—3.0 cm verkleind. Hierdoor is deze soort in staat de concurrentie met o.a. de Spreeuw het hoofd te bieden. De overige afmetingen van door deze twee soorten bezette holten komen goed overeen. De Gekraagde Roodstaart broedde vooral in laag gelegen holten met een groot en variabel vlieggat. De door Grote Bonte Spechten uitgehakte holten hadden een vlieggat met uniforme afmetingen (4.0—4.5 cm doorsnede); de holten waren aanvankelijk vrij nauw.

Vele holten werden in opeenvolgende jaren door verschillende soorten bewoond (Tabel 15). Spechtenholten werden gewoonlijk later door Spreeuwen gebruikt. De laatste soort was het meest constant in het holtegebruik.

Het optreden van concurrentie om holten tussen de Koolmees en andere soorten werd onderzocht met behulp van het karteren van koolmeesterritoria in maart—april. Het bleek dat in 1977 in twee complexen van lanen slechts 28% resp. 35% van de territoriale paren er in slaagden om een legsel in een boomholte te produceren. Concurrentie met Spreeuwen was de belangrijkste oorzaak van de mislukkingen. Langs de Koningsweg broedden sommige Koolmezen buiten hun territorium, op 50—200 m afstand; andere bleven ter plaatse, maar broedden niet, of verplaatsten zich tot op 800 m afstand zonder te broeden.

Het verkleinen (tot *ca.* 3 cm) van vlieggaten van boomholten in een deel van het gebied in 1977 had tot resultaat dat daar vrijwel alle territoriale Koolmezen in deze holten tot broeden kwamen, in tegenstelling tot elders. Het bezettingspercentage van de Koolmees was daar 3—4 maal zo hoog als op andere plaatsen (Tabel 16). In een ander terrein (Heidelaan) werd in een proef met nestkasten in de legtijd de grootte van de vliegopeningen veranderd. Kasten met koolmeeslegsels, die een grotere vliegopening kregen, werden vaak reeds binnen een week door Spreeuwen bezet. Bebroede koolmeeslegsels lopen slechts een gering risico om door interspecifieke concurrentie verloren te gaan.

Hoewel vele soorten holenbroeders duidelijk verschillende voorkeuren voor holten met bepaalde eigenschappen hebben, overlappen de waarden van deze eigenschappen voor de verschillende soorten toch sterk. Dit geeft de mogelijkheid tot interspecifieke concurrentie. Het ophangen van nestkasten in een dergelijke situatie verschaft niet alleen broedgelegenheid aan de soorten die deze kasten gebruiken, maar reduceert gelijktijdig de concurrentie om nestholten, zodat indirect ook andere soorten hiervan profiteren.

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