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Winter abundance of hole-nesting birds in natural- versus managed woods in Zealand (Denmark)

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Abstract. Foraging observations (1 observation/bird) of tits and associated species were recorded during four winter months in two natural old-growth and two managed forests. The number of daily foraging observations was used as an index of bird abundance. The daily mean number of foraging observations for *Parus major*, *P. caeruleus*, *P. palustris*, *Sitta europea*, *Certhia familiaris* and *Dendrocopos major* was significantly higher in natural old-growth vs managed forest (ratio 4.8 : 1 for all six species pooled and 3.1 : 1, 3.2 : 1, 4.7 : 1, 5.7 : 1, 7.4 : 1 and 4.7 : 1 for the above-mentioned species, respectively). As the larger dominant species has an advantage in competition for nest holes, we would expect these to exhibit the smallest abundance ratio skews. This was not, however, the case and consequently, the results of this study do not support the hypothesis that a lack of nest holes should be the primary limiting factor for hole nesting species in managed forests. It was found that the species showing the strongest preference for foraging on dead wood were the same that had the most pronounced density skew between forest types. This could indicate that the lack of food resulting from silvicultural practice could be very important as a limiting factor in managed forests. Analyses of the use of dead wood of different diameter and from different tree species indicate that forest birds exploit diverse types of dead wood. Partially decayed standing dead wood was the most important substrate for the majority of species.

Key words: hole-nesting birds, natural forest, abundance of birds, foraging of birds, forest microhabitats, dead wood

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INTRODUCTION

Intensively managed forests are characterised by the lack of forest continuity, lower structural diversity, lack of old trees and dead wood — especially in large diameters. Furthermore, lowered ground water levels due to extensive drainage, heavily disturbed soils and impoverished floristic and faunal diversity are factors that differentiate silvicultural forests from primeval and natural old-growth forests (Sandström 1992).

Several studies have demonstrated that bird densities in the breeding season are higher in unmanaged than in managed forests (Joensen 1965, Nilsson 1979, 1984, Boström 1988, Brøgger-Jensen 1992, 1996, Sandström 1992), where densities of primary and secondary hole-nesters correlate positive-

ly with the frequency of dead wood in the habitat. Measurements of stand age and structural diversity such as foilage height, tree species and crown height diversity indices have equally been shown to correlate positively with densities (Joensen 1965). Comparative density studies of hole-nesters in different temperate forest habitats have almost exclusively been based on counts from the breeding period (Hübertz 1979, Brøgger-Jensen 1996).

It is a well-known fact that the guild of hole-nesters is strongly dependent on dead wood for breeding and foraging purposes. Hence it has been argued that higher densities of these species are promoted by the presence of this vital microhabitat (Jensen 1996). But few studies, if any, have quantified the importance of different categories of dead wood as foraging substrates.

This work, based on the number of foraging observations, is aimed to give an index of winter abundance of Great Tit *Parus major*, Blue Tit *P. caeruleus*, Marsh Tit *P. palustris*, Nuthatch *Sitta europea*, Treecreeper *Certhia familiaris* and Great Spotted Woodpecker *Dendrocopos major* in intensively managed woods (henceforth "man") compared with natural old-growth woods (henceforth "nat"). Furthermore it is attempted to quantify the importance of dead wood as foraging substrates for the six hole-nesters in unmanaged natural old-growth woods.

STUDY AREAS

The fieldwork was conducted in four deciduous woods on the island of Zealand in Denmark. They were all dominated by beech *Fagus sylvatica*:

1) Suserup Wood (nat-Sus, 19 ha) is an isolated unmanaged natural old-growth forest, containing all stages of succession. Apart from beech there were quite a few oaks *Quercus robur*, ashes *Fraxinus excelsior* and alders *Alnus glutinosa*.

2) Næsbyholm Forest, "Enemærket" (man-Ncs, 32 ha) comprises 32 ha of straight-stemmed beech forest without understorey. The greater part of this wood was indigenous but intensively managed. Additionally, it contained stands of ash and maple *Acer pseudoplatanus*. The census area was part of the 1760 ha Sorø Sønderskov-Næsbyholm forest complex.

3) The Strødam forest reserves (nat-Strø, 11 ha), "Strødam II" plus contiguous forest of which 7 ha is virtually "primeval-like". The beeches were mixed with oak, ash and forest elm *Ulmus glabra*.

4) Strøgårdsvang (man-Strø, 24.5 ha) non-indigenous, managed and sprinkled with a few oaks. This forest is like nat-Strø part of the 5500 ha Grib Forest complex.

In pairs, the forests were "sister forests", i.e. situated close to one another and almost "identical" except for differences caused by modern forestry practices. Suserup and Næsbyholm are situated in southern Zealand. Strødam and Strøgårdsvang are situated in northern Zealand.

METHODS

Collection of data took place from 17 Nov. 1997 to 19 March 1998 with a total of 72 field observation days evenly distributed over the period. The observations took place during 7 daylight hours, irre-

spective of the weather. Daily periods of observation comprised 3" hours in the morning and 3" hours in the afternoon. The two daily observation periods were spread symmetrically on each side of midday which was defined as halfway between sunrise and sunset. So, the day was divided into 4 periods of each 1 hour and 45 minutes: two of them during the morning and two periods during the afternoon. The fieldwork took place in alternate weeks with 2 × 2 days at Suserup/Næsbyholm and 2 × 2 days at Strødam/Strøgårdsvang.

In order to ensure even coverage of the study sites, the observations took place along random transects chosen by pulling random compass directions from a bag. For every 100 metres' walk at about 2 km/h, an observation stop was made. The surroundings were scanned until the first foraging bird was spotted and identified. Observations were commenced when the first "feeding peck" or "gleaning movement" was seen. Data were recorded on a dictaphone as long as possible (max. 2 minutes). For every individual, microhabitat, tree species and the estimated foraging height were noted. Non-foraging birds or individuals that appeared to be affected by the presence of the observer were not recorded. In order to minimise pseudoreplication (Hurlbert 1984) only the first observation of each individual (henceforth "1st obs.") was used in statistics and other calculations.

Microhabitats were divided into: 1) forest floor, 2) dead wood, 3) trunks (> 30 cm), 4) large branches (8–30 cm), 5) branches (4–8 cm), 6) small branches (0.8–4 cm), 7) twigs (< 0.8 cm) and 8) herbs.

Dead wood was additionally categorised in the diameter groups 3–7 as above. Moreover, the degree of decay was ranked on the following ordinal scale: 1) fresh, the wood hard, bark intact, unchanged cross section; 2) superficially soft, bark loose or partly detached, unchanged cross section; 3) wood soft several centimetres down, bark gone; 4) rotten throughout and full of holes, breaks easily, oval cross section; 5) partly or nearly wholly decomposed. The trees were divided into beech, oak, ash, alder and "other species".

If the bird changed substrate or foraging height during the observation period, this was recorded. If the bird did not make at least one feeding peck, gleaning movement or "searching movement" (clear visual exploration of the substrate) approximately every 10 seconds as a minimum, the observation period was discontinued. Only one sequence of observation was made for every individual. In order to define the available niche space (see below), foraging records were done on all species of forag-

ing birds. The transect was continued, when all birds at the observation post had been observed only once. If no birds were spotted at the observation post, it was abandoned after approx. 2 minutes. When the edge of the observation area was reached, a new random transect direction was pulled. The new direction had to be at least 40 degrees different from the direction of the last route.

Tapes were played back and converted into continuous time successions on changing substrates, which were subsequently converted into scanning observations: 15 sec. intervals (n = 13484), each scanning observation linked separately to the above-mentioned set of substrate categories and other recordings.

RESULTS

Differences between the forests — abundance index

It was assumed that the number of foraging observations serves as a good measurement of bird abundance in the forests (Table 1). Based on this assumption an abundance index was calculated as the average number of 1st obs./day. The number of foraging observations was generally much higher in the natural old-growth forests than in the intensively managed ones. Daily mean number of observations in nat-woods were 76.9 ± 22.3 compared with 24.9 ± 16.3 in man-woods. The abundance indices in the forests for all species pooled was found to be significantly different (Repeated measures ANOVA based on



Fig. 1. Abundance index (all species/day) in the four forests. Identical letters indicate no significant difference between indices based on pairwise Turkey-Kramer Tests at p > 0.05 significance level. Sig-nificant differences at p < 0.001

square root transformed data, $F_{3,51} = 40.189$, $p < 0.0001$, $n = 18$; Fig. 1). The same trend was significant in all cases for single species data, ($F_{3,51} = 20.51-55.16$, $p < 0.0001$, $n = 18$; Fig. 2).

When pooling the six species into the two forest types, the factor of difference between density indices in the two forest types was found to be $4.8 \pm 1.84 : 1$ (nat : man).

The use of dead wood

Dead wood was practically absent in the man-woods. In the nat-forest, observations on dead wood were plentiful (N = 655 of 1st obs.).

As there was no significant difference in the use of dead wood between the nat-Sus and nat-Str ($\chi^2 = 0.2$, $df = 1$, ns), the dead wood data was

Table. 1 Total numbers of observations – total (1st obs./day) and mean factor of difference between particular woods (x – nat : man) and wood types (xx – nat : man, pooled ratio).

Species	nat-Sus	x	man-Nas	nat-Str	x	man-Stro	xx
<i>P. major</i>	367 (20.4)	2.4	153 (8.5)	221 (12.3)	3.8	58 (3.2)	3.1
<i>P. caeruleus</i>	194 (10.8)	2	97 (5.4)	333 (18.5)	4.4	75 (4.2)	3.2
<i>P. palustris</i>	178 (9.9)	4.7	36 (2)	105 (5.8)	4.5	23 (1.3)	4.7
<i>S. europea</i>	165 (9.2)	5.1	32 (1.8)	148 (8.2)	6.3	23 (1.3)	5.7
<i>C. familiaris</i>	171 (9.5)	8.6	20 (1.1)	100 (5.6)	6.2	15 (0.9)	7.4
<i>D. major</i>	65 (3.6)	6	11 (0.6)	62 (3.4)	3.4	18 (1)	4.7
All species	1140		349	969		212	

Table 2: Percentage of foraging observations (1st obs.) on dead wood an preferences in relation to availability. N in parenthesis (), * – p < 0.05, ** – p < 0.01, *** – p < 0.001, neg. – negative prefer-ences.

	Total	<i>P. major</i>	<i>P. caeruleus</i>	<i>P. palustris</i>	<i>S. europea</i>	<i>C. familiaris</i>	<i>D. major</i>
% dead wood	25.5	25.2 (588)	21.3 (527)	13.1 (283)	34.2 (313)	27.7 (271)	45.7 (127)
Preferences	*	ns	ns	neg***	***	*	***

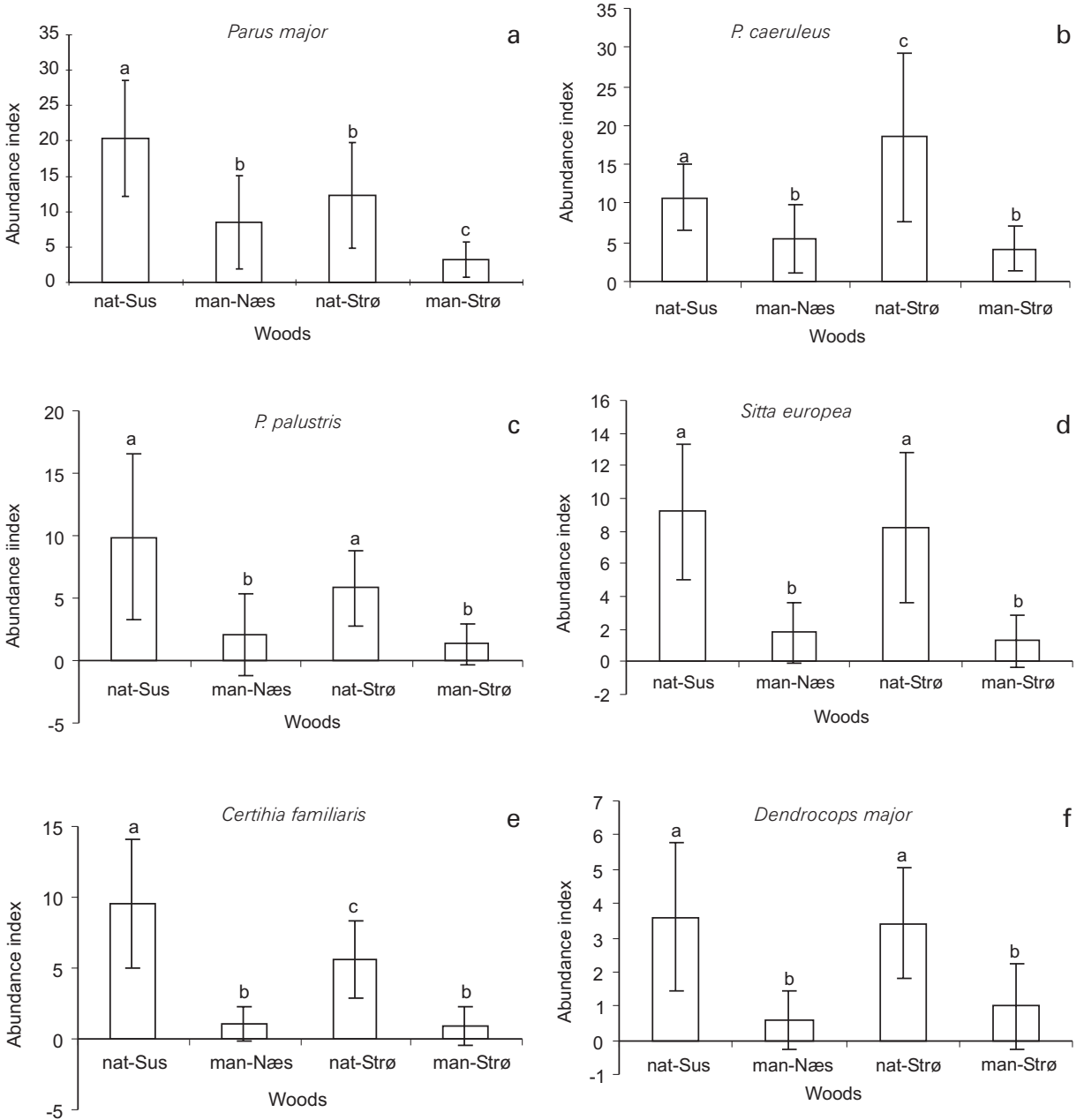


Fig. 2. Abundance indices of six species studied. Identical letters indicate no significant difference between indices based on pairwise Turkey-Kramer Tests at $p > 0.05$ significance level.

pooled. All species, except Marsh Tit which had a negative preference for dead wood ($p < 0.0001$), foraged more than 25% of the time on dead wood. One-sample χ^2 -tests were performed to reveal preferences in relation to available niche space in the habitat (Table 2). Expected values were calculated as 1st obs. of all species on dead wood per 1st obs. of all species on all microhabitats \times 1st obs. of the species in the habitat.

It appears (Table 3) that the six species explore different niches when foraging on dead wood ($\chi^2 = 172.08$, $df = 15$, $p < 0.0001$). A Bonferroni correction was used to adjust the significance level to $p > 0.008$ ($0.05/6$) when testing for departure from homogeneity at species level. Expected values were calculated as explained above. All species except the Great Tit ($p = 0.54$) showed significant preferences for selected diameters when foraging

Table 3. The use of dead wood in nat-forests (% 1 st obs.). Dead wood: T – trunk, Lb – large branches, Br – branches, S – small branches and twigs. Tree species: B – beech, O – oak, ash and other species, D – median degree of decay \pm SD, H: average foraging height \pm SD. Bonferroni corrected significans level: * $p < 0.0125$, ** $p < 0.0025$, *** $p < 0.00025$.

	Foraging sites				Tree species		D	H	Height of 1st obs.		
	T	Lb	Br	S	B	O			0	0-2	> 2
All species (n = 645)	13.8	10.1	41.7	34.4	74.3	25.7	2.3 \pm 0.6	8.0 \pm 6.5	10.4	17.7	71.9
P. major (n = 148)	14.9	10.1	45.9	29	81.8*	18.2	2.3 \pm 0.2	7.5 \pm 6.3	8.1	18.9	73
P. caeruleus (n = 112)	6.3	2.7	32.1	58.8***	83*	17	2.0 \pm 0.1	8.6 \pm 6.4	5.4	22.3	72.3
P. palustris (n = 37)	0.3	0.3	16.2	78.4***	64.9	35.1	2.1 \pm 0.2	6.2 \pm 6.7	18.9	21.6	59.5
S. europaea (n = 107)	14	20.6**	56.1***	9.4	81.3	18.7	2.4 \pm 0.4	9.5 \pm 6.2	5.6	9.3	85.1
C. familiaris (n = 75)	24*	12	61.3**	2.6	38.7	61.3***	2.0 \pm 0.1	8.2 \pm 5.2	2.6	13.3	84.1
D. major (n = 58)	10.3	17.2	69***	3.4	77.6	22.4	2.2 \pm 0.4	13.7 \pm 5.8	5.2	0	94.8

on dead wood (χ^2 -test, $df = 3$, $p < 0.0001$). When identifying preferences at species level by means of one-sample χ^2 tests (Table 3), the Bonferroni corrected significance level was set to $p > 0.0125$ (0.05/4). Tree species preferences (dead wood) were tested with one-sample χ^2 -test without Bonferroni correction of the significance level. Non significant tendencies ($p < 0.02$) is marked with (x) in Table 3.

Differences in median degree of decay on dead wood substrates used by the six species (Table 3) were significant (Kruskal-Wallis ANOVA, $H = 18.757$, $p = 0.0021$). At species level significant differences were found only between Great Tit/Blue Tit and Blue Tit/Nuthatch (Dunn's Multiple Comparisons Test, $p < 0.05$).

DISCUSSION

The abundance indices based on this data set confirm earlier findings which found higher densities of hole-nesters in natural old-growth forests compared with intensively managed forests (see Introduction). In the early nineties, Brøgger-Jensen (1996) conducted a comparative density study in the same census areas. As the densities found by Brøgger-Jensen were based on breeding counts (line transects), the species' composition is different from the present study. Consequently, they cannot be compared directly with the abundance index ratios found in this study. Comparisons were made only for the six selected species in the hole-nesting guild (raw data supplied by S. Brøgger-Jensen). When pooling all six species in the two forest categories, a abundance ratio in nat- vs man-forest — 5.2 : 1 \pm 4.26 was found in Brøgger-Jensen's data. So, abundance of the selected hole-nesters were in both cases approximately 5 times

higher both in breeding and winter time in nat-compared with man-woods.

The true winter abundance difference between nat- and man-woods could conceivably have been even more distinct caused by the following conservative biases:

1) a higher structural diversity in the nat-forest (Jensen 1992) makes the birds a bit harder to discover in the first place (pers. obs.).

2) Densities were higher in nat-forests. Consequently, more time was spent observing and less time spent searching, leading to an underestimation of the density ratio between the two forest types. The ratio in observing time was 2.5 : 1.

3) The majority of Danish forest stands are non-indigenous coniferous stands dominated by Norway Spruce *Picea abies* or relatively young deciduous stands. As densities of hole-nesters are known to be lower in these forest types (Joensen 1965, Hübertz 1979, Brøgger-Jensen 1996) the abundance indices found in this study in a broad perspective tend to underestimate the abundance ratio skew considerably.

4) Suserup forest was isolated and Strødam was lying at the edge of a large forest complex. Consequently, the edge/forest interior quotient is larger in the two nat-forests compared with the managed stands (nat-Sus = 0.11 km edge/ha, man-Næs = 0.03 km edge/ha, nat-Strø = 0.11 km edge/ha, man-Strø = 0.01 km edge/ha). It is well documented that ecotones usually have a higher diversity and density of birds (Joensen 1965). An edge effect could therefore be suspected to give rise to an overestimation of density indices in the nat-forests. As empirical evidence has demonstrated that densities of hole-nesters in the edges of deciduous forests roughly correspond to the densities in the forest interior (Brøgger-Jensen

1996), a potential bias caused by an edge effect is considered insignificant.

Differences in abundance ratios–species

Species showing significant preferences for foraging on dead wood (Table 2) were the same which exhibited the most skewed density ratio between nat- and man-forests (Table 1). This result could be a response to the lack of preferred foraging substrates. As Treecreepers have a strong preference for dead oak wood (Table 3) and oak in general (own data, Cramp 1993), the lack of suitable foraging substrates in this case also refers to tree species.

Great Tit and Blue Tit used the dead wood to a large extent (Table 2) but less than the birds in the bark foraging guild. As the Great and Blue tits preferred the dominant tree species in the census areas (beech) (authors data), it is hardly surprising that the density ratio was not quite as skewed as observed in the latter guild. Marsh Tits prefer moist patches with alder, oak (Cramp 1988) or ash (authors data). The fact that the density skew is more pronounced in Marsh Tits compared with the other *Parus* species could be explained by the fact that moist patches are becoming increasingly rare with modern silvicultural practices such as drainage. Another explanation could be that the Marsh Tits are lowest in the dominance hierarchy of *Parus* tits in deciduous forests (Cramp 1988), resulting in a low probability of getting their share of suitable nest-holes and roosting sites. As very little mast was available in the census areas during the fieldwork (data of the Danish Tree Improvement Station), it is probable that the abundance difference between nat- and man-forests for species depending on this food resource, i.e. all species except Treecreeper and Great Spotted Woodpecker (Gensbröl 1991, Harrap 1996) might have been less pronounced in most years.

The exploitation of different dead wood categories in nat-forests

Great Tit differed in microhabitat choice from Blue Tit in having a significant preference for more decayed wood than the latter (Table 3). Blue and Marsh tits both showed a preference for small dead branches but as Blue Tits showed a significant preference for beech and tended to forage more on dead branches, the exploitation of microhabitats seems to differ to some extent. Furthermore, Blue Tit preferred less decayed wood significantly more than Nuthatch (Table 3). Marsh Tits forage slightly lower and have a tendency to prefer dead ash wood (Table 3) corresponding to its general habitat choice (see above).

Furthermore, the overlap with Blue Tit would be expected to be lower in most years because Marsh Tit is known to be hoarding extensively in autumn and winter (Harrap 1996). Treecreepers, Nuthatches and Great Spotted Woodpeckers showed a preference for dead branches and trunks. As Nuthatches in this study tended to forage more on dead beech wood as compared with the Treecreepers' preference for oak (Table 3), the overlap seems to be small. Nuthatches and Great Spotted Woodpeckers preferred almost the same diameters and breakdown categories of dead wood on beech but as Nuthatches are hoarders (Harrap 1996), this overlap may be smaller in most years. Furthermore, Great Spotted Woodpeckers tended to forage higher (Table 3).

All six species of hole-nesters most often used standing dead wood as foraging substrate (Table 3). This tendency was most distinct for Great Spotted Woodpecker, Nuthatch and Treecreeper and less pronounced for Marsh Tit. Based on these data, it appears to be evident that practically all types of dead wood are exploited by the hole-nesting birds in winter, with standing dead wood of all diameters (breakdown category 2–3) being by far the most important foraging substrate for the six hole-nesters.

Limiting factors in intensively managed forests

It has been demonstrated that the number of cavities suitable for nesting correlate positively with the amount of dead wood and that nat-forests contain almost 4 times as many cavities as man-forests (Sandström 1992).

Several studies have hypothesised that a scarcity of suitable nest hole building substrates, available nests and roosting sites are the chief limiting factors for most species of hole-nesting birds (reviewed by Newton 1994, Waters et al. 1995). On the other hand other researchers has shown that scarcity of suitable nest sites/holes is not necessarily the chief limiting factor on populations of hole-nesters (Walankiewicz 1991, Sandström 1992, Welsh & Capen 1992). The results of this study support the latter hypothesis:

The interspecific dominance hierarchy is as follows: Great Spotted Woodpecker > Nuthatch > Great Tit > Blue Tit > Marsh Tit (Morse 1978, Cramp 1988). Assuming hole availability to be the main limiting factor in man-forests, we would expect the sub-ordinate hole-nesters to exhibit the most skewed abundance ratio, because they have more problems obtaining suitable cavities in the managed forests as a result of harder competition

with larger and more dominant species. This seemed only to be the case for Marsh Tit compared with the dominant Great Tit and Blue Tit. In most cases — Blue Tit vs Great Tit, the *Parus* species vs Nuthatch and Great plus Blue tits vs Great Spotted Woodpecker — dominant species exhibited the most skewed abundance ratio. Treecreepers normally nest under flaps of loose bark or in small crevices (Harrap 1996) and must be assumed to compete relatively little with the other birds in the guild which prefer more regular cavities.

Nilsson (1979) suggests that most hole-nesting species are probably limited by winter food availability. This study has demonstrated that the abundance of hole-nesters were higher in the nat-forests compared with the man-forests, and that the dead wood constituted a very important winter foraging substrate for the above-mentioned bird species. Animal densities are considered to be positively correlated with food supply (Lack 1954). As standing dead wood, and the fauna of saproxylic invertebrates it supports, is practically non-existent in the managed forests (Speight 1989), it seems reasonable to suspect that the lack of this foraging substrate, in interplay with other food related factors such as inter-habitat differences in structural- and tree species diversity, may have been the main limiting factor in the managed forests of this study. However — this does not exclud the possibility, that lack of suitable nest holes and roosting sites also acts as a limiting factor on the density of hole-nesters in intensively managed forests.

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STRESZCZENIE

[Częstość występowania dziuplaków w naturalnych i zagospodarowanych lasach Zelandii (Dania) w okresie zimowym]

Badania prowadzono ciągu zimy 1997/8 w czterech lasach na duńskiej wyspie Zelandia. Dwie pary: las zagospodarowany (man) i naturalny (nat), położone były blisko siebie tworząc w parach lasy „siostrzane”, różniące się tylko intensywnością gospodarki leśnej.

Na losowo wybranych transektach co 100 m wybierano punkty obserwacyjne, w których poszukiwano żerujących ptaków. Do analizy wyników tylko pierwsza obserwacja każdego zaobserwowanego ptaka była używana. Liczba tych obserwacji używana była jako miara liczebności ptaków. Dla sześciu badanych gatunków dziuplaków: bogatki, modraszki, sikory ubogiej, kowalika, pełzacza leśnego i dzięcioła dużego oszacowana w ten sposób liczebność ptaków była znacznie wyższa w lasach naturalnych niż zagospodarowanych, tak gdy liczono ją dla całego zespołu (4.8:1), jak i dla poszczególnych gatun-

ków (zakres 3.1-7.4 : 1) (Tab. 1, Fig. 1). W lasach naturalnych wszystkie obserwowane gatunki (prócz sikory ubogiej) preferowały martwe drzewa i ich fragmenty jako miejsca żerowania (Tab. 2 i 3), zaś im chętniej dany gatunek wykorzystywał martwe drewno, tym większe były różnice liczebności między lasami naturalnymi a zagospodarowanymi.

Na podstawie uzyskanych wyników wydaje się, że brak odpowiednich miejsc żerowiskowych, a nie dostępność dziupli może być główną przyczyną zaobserwowanych różnic w liczebnościach dziuplaków.

