INFLUENCE OF TREEFALL GAPS ON DISTRIBUTIONS OF BREEDING BIRDS WITHIN INTERIOR OLD-GROWTH STANDS IN BIAŁOWIEŻA FOREST, POLAND[1]

ROBERT J. FULLER

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK, e-mail: rob.fuller@bto.org

Abstract. Breeding birds were counted using point counts at 50 treefall gaps and 50 closed-canopy sites within one of the largest tracts of old-growth forest in Europe. Numbers of species and individuals were slightly, but significantly, higher at gaps. Overall bird species composition differed substantially at gaps and non-gaps. Dunnock (*Prunella modularis*), Blackcap (*Sylvia atricapilla*), and Chiffchaff (*Phylloscopus collybita*) were significantly more abundant at gaps. Wood Warbler (*Phylloscopus sibilatrix*) and Red-breasted Flycatcher (*Ficedula parva*) were significantly more abundant at non-gaps. Warblers (Sylviidae), ground insectivores, ground nesters, and short-distance migrants were significantly more abundant at gaps, but no species groups were more abundant at non-gaps. Eight species breeding in forest edges and young plantations in eastern Poland were not recorded in natural treefall gaps. The proportion of tropical migrant passerines was considerably higher in closed-canopy stands (0.47) than at gaps (0.29), which contrasts with the situation in most managed European forests where the highest proportions of tropical migrants typically occur in young-growth forests.

Key words: Białowieża Forest, community structure, forest dynamics, old-growth, treefall gaps.

INTRODUCTION

Resources used by some forest birds, including food and preferred habitat structures, can be localized within treefall gaps (Blake and Hoppes 1986, Martin and Karr 1986, Levey 1988). I examine how treefall gaps in Białowieża National Park, Poland, affected spatial variation in the composition of bird assemblages within old-growth stands. This was done by comparing bird numbers and habitat attributes at 50 treefall gaps and 50 closed-canopy locations in 1988. I also examine whether the bird species that use edges or the young-growth stages of managed European forests also use natural gaps.

This appears to be the first study of its kind for a European temperate forest. Many previous studies have considered responses of birds to young-growth in managed forests, most commonly the early stages of tree growth after felling (Głowaciński 1975, Ferry and Frochot 1990, Fuller and Henderson 1992), but not to natural treefalls. Historical destruction of forests and intensive management of the surviving fragments have eliminated opportunities for research on natural forest dynamics throughout most of Europe. The old-growth stands of Białowieża Na-

tional Park remain a singular exception (Falinski 1986, Tomiałojć and Wesołowski 1990, Peterken 1996). These stands have never been systematically cut but they do have a history of human activity, including sporadic felling and overgrazing by artificially high numbers of deer and cattle in the early twentieth century. Natural processes have been the only source of disturbance within the National Park since 1921. The mosaic of deciduous, coniferous, and mixed stands contains gaps of varying sizes caused by storms.

METHODS

STUDY AREA

Białowieża National Park covers an area of 47 km^2 positioned at the core of a much larger area of lowland managed forest (> 1,000 km^2) extending over a plain straddling the Polish-Belarus border. Approximately 20% of the boundary of the National Park is formed by an agricultural clearing; the remaining boundary lies adjacent to managed forest or swampy river valleys. The climate is subcontinental with average temperatures of −4.3°C in January and 17.6°C in July with up to 92 days snow cover (Wesołowski and Tomiałojć 1997). Tree communities include deciduous and coniferous stands (see Falinski 1986, Peterken 1996 for details). On the better drained soils, deciduous stands are dominated by

small-leaved lime (*Tilia cordata*) and hornbeam (*Carpinus betulus*), with variable amounts of Norway maple (*Acer platanoides*), pedunculate oak (*Quercus robur*), and Norway spruce (*Picea abies*). Deciduous stands in wet areas are mostly of alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*). Coniferous stands tend to occur in the more acid and peaty areas, with spruce more abundant on damper, organic soils, and pine (*Pinus sylvestris*) on dry sand. The period of heavy grazing in the late 1800s and early 1900s appeared to favor spruce regeneration, and the forest now seems to be in a recovery phase whereby spruce is being replaced by lime, hornbeam, and Norway maple (Peterken 1996). Numbers of red deer (*Cervus elaphus*) increased during the 1980s but this does not appear to have greatly inhibited regeneration (L. Tomiałojć, pers. comm.). Canopy gaps occur in many sizes, from single fallen trees to blowdowns covering several hectares. Many of the present treefalls in Białowieża National Park occur where there has been considerable blowdown of mature spruce.

GAP DEFINITIONS AND SELECTION OF STUDY LOCATIONS

All treefall gaps examined were created by blowdown. Gaps contained at least three fallen trees and were at least 40 m across their longest dimension (gaps were frequently asymmetrical). Hence, small gaps created by isolated fallen trees and gaps containing only standing dead trees and no fallen trees were excluded. Edges of the gaps were usually clearly defined. Gaps typically contained substantial numbers of standing as well as fallen trees. Exact ages of the gaps were unknown but they were all thought to be 2–10 years old, with the exception of four cases known to be less than 2 years old. Tree regeneration was highly variable, and typically of lime and hornbeam, but was generally no taller than 2 m. Even where tree regeneration was sparse, there was often a dense field layer of raspberry (*Rubus idaeus*). All the gaps studied were in dry areas, the majority (*n* = 44) being in lime-hornbeam stands where broadleaves formed at least 50% of the trees. Even in the lime-hornbeam, the majority of fallen trees within the gaps were spruces.

A total of 50 treefall gaps were located and, as far as possible, these were matched with closed-canopy locations. Criteria for matching were that pairs of locations should be in close proximity (200–400 m) and be of similar stand type with respect to soil type and tree species composition. At each location a point was chosen at which birds were counted (see below); in the case of gaps, this point was as close to the center of the gap as possible. For 9 of the 50 gaps, it proved impossible to match them with nearby closed-canopy locations and in these cases an equivalent number of closed-canopy locations in similar stand types were selected some distance away (0.6–3.0 km). All closed-canopy locations were a minimum of 80 m from the edge of any treefall gap, excluding small canopy gaps created by the collapse of individual trees. All 100 points (i.e., 50 gaps and 50 closed-canopy) were at least 400 m inside the National Park so they were not influenced by edge effects. A minimum spacing of 200 m between points was achieved.

COUNTING BIRDS

Five-minute point counts were undertaken on three occasions at each of the 100 locations. Each point received one morning count in each of the three periods: 11–17 May, 20–25 May, 3–7 June 1988. Counts commenced at dawn and were completed before 11:15. The sequence changed between the three counts so that all points received at least one count in the very early morning. Paired points were always counted within 30 min of one another. Birds were recorded in two distance bands: 0–30 m ("near") and 30–50 m ("far"). The data were treated as fixed distance counts with radii of 50 m (Hutto 1986). This helped ensure that gap counts did not include large numbers of records from beyond the edge of the gap. Detectability of territorial singing birds of most forest species is good at distances up to 50 m (Schieck 1997).

It was important to be sure that comparisons of bird communities between gaps and non-gaps were not confounded by differences in detectability which could be associated with the large differences in vegetation structure. *G*-tests (Zar 1996) were used to assess whether the relative numbers of near to far records differed between the gaps and non-gaps.

The main seasonal song periods of most species in Białowieża Forest were covered by the count period. The main exceptions were Hazel Grouse (*Bonasa bonasia*), most woodpeckers, and possibly Marsh Tit (*Parus palustris*). These species are most vocal in April and early May,

so they are probably under-represented in the counts.

VEGETATION SAMPLING

Vegetation was measured at all locations, centered on the point. Canopy cover was estimated to the nearest 5% through a 28-mm camera lens. Canopy height was estimated as the mean of the height to the nearest 2.5 m, of the two tallest trees within 30 m using a clinometer. The species of the nearest 20 trees that were >20 cm diameter at breast height (dbh) were recorded and the proportion of broadleaved trees calculated. Any other species of trees or woody shrubs within 10 m were also listed and together with the data from the 20 large trees used to calculate tree and shrub richness. The density of the understory (shrub layer foliage plus fallen trees) was estimated using a checkered sighting board (Fuller and Henderson 1992). The distance at which the board was obscured by vegetation at eye height was estimated to the nearest 10 m on NE, SE, SW, NW bearings. An index of shrub density was then derived from the reciprocal of the mean × 1,000. All trees of dbh > 20 cm were counted that were lying on or close to the ground and for which any part lay within 10 m of the point. Toppled, but supported, trees were counted as fallen. All snags within 10 m were counted. A snag was defined as a standing dead tree or stump at least 2 m tall and ≥20 cm dbh. Vertical root plates >2 m tall and within 10 m of the point were counted. Minimum and maximum dimensions of the gaps were estimated to the nearest 10 m.

DATA ANALYSIS

For each point, a single abundance value was derived for each species by taking the highest count recorded within 50 m of the point from any of the three visits. The resulting species abundances were compared between gaps and non-gaps using chi-square goodness-of-fit tests with the Yates' correction with the expectation that individuals should be equally abundant in gaps and non-gaps. Detrended correspondence analysis (DCA) was used, without downweighting for rare species (Jongman et al. 1995) to determine whether overall bird species composition at gaps differed from non-gaps. This ordination approach arranges samples in multidimensional space defined by axes that represent gradients of bird species composition. Scores at-

tained by each location on axis 1, the main gradient, were treated as indices of bird species composition. Forward stepwise multiple regression was used to relate the number of bird species, the number of individuals, and scores on DCA axis 1 to vegetation variables. The vegetation variables were those listed in Table 1 with two exceptions. First, the number of root plates was excluded because of a large number of zeros. Second, in the case of gaps, two additional variables were used: the minimum and maximum gap dimensions. Canopy cover and % broadleaved trees were arcsine transformed and tree height, understory density, snags, and fallen trees were log transformed. Results from stepwise regression were compared with those from all possible combinations of variables (PROC RSQUARE; SAS Institute 1996). This confirmed that in all cases the stepwise regression had selected the optimum combination of variables in terms of maximizing R^2.

Analyses were conducted separately for the 41 pairs of matched points, but in all cases the patterns and conclusions drawn were the same as for the full data set. Therefore, results are only presented for analyses of all 100 points.

RESULTS

VEGETATION

Gaps and non-gaps differed greatly in structural aspects of habitat but did not differ in the broad composition of tree communities (Table 1). Canopy openness, understory density, and numbers of fallen trees, snags, and root plates were far higher at gaps than non-gaps. Tree height was slightly lower and tree and shrub richness slightly higher at gaps than non-gaps. There was no difference in the ratio of standing broadleaved trees between gaps and non-gaps.

DETECTABILITY AT GAPS AND NON-GAPS

For all species combined, the total number of near and far individuals recorded at gaps were 307 and 606 (ratio 0.51) and at closed-canopy points 262 and 546 (ratio 0.48), respectively (G_1 = 0.26, P > 0.50). This calculation also was made for all families of birds with at least three species recorded: Picidae, Turdidae, Sylviidae, Muscicapidae, Paridae, Fringillidae (all G_1 ≤ 1.8, all P > 0.10). Samples sizes were adequate in both gaps and at closed-canopy locations to test for differences in relative numbers of near to far counts in 16 species. Only for Wood War-

TABLE 1. Vegetation at gaps and non-gaps. Median values, with 25% and 75% quartiles in parentheses, are shown. Differences between gaps and non-gaps were tested by Mann-Whitney U-tests.

Variable	Gap $(n = 50)$	Non-gap $(n = 50)$	z	P
Canopy cover (%)	15 (10–35)	90 (85–95)	8.54	<0.001
Tree height (m)	28 (25–30)	30 (28–33)	3.71	<0.001
Number of tree and shrub species	7 (6–8)	6 (5–6)	3.23	<0.01
Broadleaved trees (%)	73 (60–85)	70 (35–85)	1.16	ns
Understory density (index)	67 (50–77)	26 (22–30)	8.11	<0.001
Number of fallen trees	10 (8–14)	3.5 (2–5)	7.95	<0.001
Number of standing dead trees	4 (2–7)	2 (1–3)	4.75	<0.001
Number of upturned root plates	2 (1–3)	0 (0–0)	6.51	<0.001

bler (*Phylloscopus sibilatrix*) was there a significant result (G_1 = 11.8, P < 0.001). At gaps, the number of near and far individual Wood Warblers was 13 and 57 (ratio 0.23), respectively, but at non-gaps the respective numbers were 57 and 84 (ratio = 0.68). The relatively low number of near records from gaps was almost certainly a consequence of the fact that Wood Warblers avoid areas of dense understory. In conclusion, there was no evidence that detectability was a serious confounding factor in this study.

COMPARISONS OF BIRD ASSEMBLAGES AT GAPS AND NON-GAPS

More species and more individuals were recorded at gaps than non-gaps. Median numbers of species (± SD) were 10.6 ± 2.3 at gaps and 8.7 ± 2.7 at non-gaps (Mann-Whitney U-test, z = 3.71, P < 0.001) and of individuals 12.5 ± 2.6 and 10.7 ± 3.1, respectively (z = 3.03, P < 0.01). The fact that differences were slightly

stronger for the number of species than for individuals suggests that the higher species richness at gaps was not simply a consequence of a larger number of individuals being recorded there.

Gaps and non-gaps differed substantially in overall bird species composition, showing marked separation on DCA axis 1. The axis had an eigenvalue of 0.244. Scores of gaps and non-gaps were significantly different on axis 1 (Mann-Whitney U-test, z = 6.26, P < 0.001), but were not significantly different on axis 2. Hence, axis 1 represented a clear gradient in species composition from gaps to non-gaps.

Across all 100 points, the number of species was positively related to understory density and tree species richness, whereas number of individuals increased with tree richness and the proportion of broadleaved trees (Table 2). The regression model explaining overall bird species composition (as indexed by DCA axis-1 scores)

TABLE 2. Regression models accounting for variation in number of species, number of individuals, and bird species composition, the latter as shown by sample scores on axis 1 of detrended correspondence analyses. Variables used were those listed in Table 1 together with minimum and maximum gap dimension for the analyses of gaps. Variables are listed in the order they were entered in the models with cumulative R^2 and the sign indicating direction of the relationship in parentheses. All variables listed are significant at least at P < 0.05.

Number of species	
All sites[a]	understory density (0.15+), number of tree species (0.20+)
Gaps	no variables significant
Non-gaps	number of tree species (0.21+)
Number of individuals	
All sites	number of tree species (0.09+), broadleaved trees (0.15+)
Gaps	no variables significant
Non-gaps	number of tree species (0.17+), broadleaved trees (0.24+)
Bird species composition	
All sites	canopy cover (0.36−), broadleaved trees (0.40+), number of fallen trees (0.45+)
Gaps	minimum gap dimension (0.31−)
Non-gaps	Broadleaved trees (0.27−), understory density (0.39−)

[a] All sites; n = 100, Gaps: n = 50, Non-gaps: n = 50.

TABLE 3. Abundance of birds within selected groups defined by taxonomy, feeding habits, nest site, and migratory status. Chi-square goodness-of-fit tests with the Yates' correction were used to assess probability of no difference between gaps and closed-canopy locations with an expectation of equal numbers in both. Groups are defined following Tomiałojć and Wesołowski (1990).

	Gaps ($n = 50$)	Non-gaps ($n = 50$)	χ^2	P
Families				
Picidae	30	19	2.0	ns
Turdidae	81	81	0	ns
Sylviidae	159	111	8.2	<0.01
Muscicapidae	62	79	1.8	ns
Paridae	70	54	1.8	ns
Fringillidae	112	108	0.1	ns
Feeding groups				
Ground insectivores	205	146	9.6	<0.01
Foliage insectivores	327	307	0.6	ns
Bark insectivores	48	33	2.4	ns
Nest site				
Hole nesters	202	176	1.7	ns
Ground nesters	229	160	11.9	<0.001
Crown nesters	184	193	0.2	ns
Migratory status				
Tropical migrants	138	166	2.4	ns
Short-distance migrants	313	220	15.9	<0.001
Residents	178	150	2.2	ns

accounted for more than twice as much variation as those for numbers of species and individuals (Table 2). The main gradient in bird species composition was explained in terms of canopy cover, proportion of broadleaves, and number of fallen trees. Canopy cover and fallen trees both differed strongly between gaps and non-gaps, but the proportion of broadleaved trees did not (Table 1). This suggests that much of the main variation in bird species composition was accounted for by whether points were gaps or non-gaps, but that an additional element of variation was accounted for by tree species composition.

Despite the general difference in bird species composition at gaps and non-gaps, few species differed significantly in frequency or abundance between gaps and non-gaps. For 25 species it was possible to test the null hypothesis that numbers were equal at gaps and non-gaps with chi-squared goodness-of-fit tests. Blackcap (*Sylvia atricapilla*) and Chiffchaff (*Phylloscopus collybita*) were strongly more abundant (χ^2_1 = 16.2, P < 0.001 and χ^2_1 = 32.7, P < 0.001, respectively), and Dunnock (*Prunella modularis*) weakly more abundant (χ^2_1 = 5.3, P < 0.05), at gaps than non-gaps. Several scarcer species were recorded solely at gaps, but sample sizes were too small to draw conclusions: Hazel Grouse, Stock Dove (*Columba oenas*), Lesser

Spotted Woodpecker (*Dendrocopos minor*), Three-toed Woodpecker (*Picoides tridactylus*), Tree Pipit (*Anthus trivialis*), and Bullfinch (*Pyrrhula pyrrhula*). Two species were more abundant at closed-canopy locations: Wood Warbler (χ^2_1 = 8.8, P < 0.01) and Red-breasted Flycatcher (*Ficedula parva*) (χ^2_1 = 10.3, P < 0.001).

Broader patterns in bird community composition of gaps and non-gaps were examined with respect to groups of species defined by taxonomy (families), feeding habits, nest site, and migratory status (Table 3). To ensure that species were appropriately classified and weighted by groups, I followed the information in Table 1 of Tomiałojć and Wesołowski (1990). Warblers (Sylviidae), ground insectivores, ground nesters, and short-distance migrants were more abundant at gaps than expected. No groups were more abundant than expected at non-gaps. More flycatchers (Muscicapidae), crown nesters, and long-distance migrants were counted at non-gaps than gaps but the differences were not significant.

VARIATION IN BIRD ASSEMBLAGES AT GAPS AND NON-GAPS

Within gaps, numbers of species and individuals could not be related to variation in vegetation or

gap size. However, the main gradient in bird species composition, as indexed by DCA axis-1 scores, was solely related to minimum gap dimension (Table 2). Effect of gap size was examined further by classifying gaps according to size and calculating frequency of occurrence within each size class for the 12 species recorded most frequently at gaps. Exact sizes of gaps were not obtained, so gaps were classified by minimum dimension as small ($<$ 50 m, n = 17), medium (50–90 m, n = 18), and large ($>$ 90 m, n = 15). Two species, Dunnock and Chiffchaff, appeared to avoid small gaps or to select large gaps, whereas five species appeared to avoid large gaps or to prefer small gaps: Winter Wren (*Troglodytes troglodytes*), Blackbird (*Turdus merula*), Wood Warbler, Great Tit (*Parus major*), and Nuthatch (*Sitta europaea*). There was no evidence, however, that any of these species occurred more or less frequently in particular gap size classes than one would expect by chance (all chi-square tests P > 0.10, except Dunnock, Wood Warbler and Nuthatch where 0.10 > P > 0.05). At non-gaps, the number of species recorded was related to tree species richness and number of individuals to tree species richness and to proportion of broadleaves (Table 2). Variation in bird species composition at non-gaps was related to proportion of broadleaves and to understory density (Table 2).

DISCUSSION

Previous multi-species studies of use of treefall gaps in temperate forests have focused on migrating birds and have found that some species, particularly foliage insectivores and frugivores, are more abundant in gaps (Blake and Hoppes 1986, Martin and Karr 1986). To my knowledge, this paper is the first study to provide evidence that treefall gaps also influence the spatial patterning of bird communities during the breeding season. Nonetheless, there was considerable overlap in the bird species composition at gaps and non-gaps, with only a handful of species showing strong preferences for gaps or for closed-canopy areas. This contrasts with European managed forests where many species are confined to one particular stage of growth. Examples include the studies of Głowaciński (1975), Smith et al. (1985), and Ferry and Frochot (1990) which show that hole-nesting species can be largely absent from early stages of growth in managed forests.

In terms of vegetation structure, natural treefalls typically differ from many young managed stands in several respects. Treefalls usually contain a substantial number of live standing trees, many of which may have damaged limbs which rapidly become sources of dead wood and nest cavities. Young managed stands rarely retain such high densities of standing trees. Dead wood is typically a scarce resource in managed forests at all stages of growth (Kirby et al. 1991, 1998), whereas natural treefalls offer concentrations of standing and fallen dead wood. The floor of a treefall is a dense tangle of fallen trees and exposed root plates and may even exhibit an "instant shrub layer" formed by the canopies of fallen trees. Natural treefalls will tend, therefore, to offer more niches for forest bird species than will most managed young-growth. The difference in bird assemblage structure between treefall gaps and adjacent closed old-growth forest is, therefore, likely to be less marked than in the case of young and old stands in managed forest.

It appears that several species using forest edges or young-growth habitats within modern European forests do not occur in, or are rare in, the interior treefall gaps in Białowieża National Park. All of the gap specialists identified in this study also used stands at the edge of the National Park and man-made gaps in the surrounding managed forest. Several species occur in edge habitats at Białowieża that I did not record in interior gaps including Redwing (*Turdus iliacus*), Icterine Warbler (*Hippolais icterina*), Barred Warbler (*Sylvia nisoria*), and Rosefinch (*Carpodacus erythrinus*) (Tomiałojć and Wesołowski 1990). Species occurring in young plantations in the surrounding forest, but not in the natural treefall gaps, were Whitethroat (*Sylvia communis*), Red-backed Shrike (*Lanius collurio*), Linnet (*Carduelis cannabina*), and Yellowhammer (*Emberiza citrinella*). Some other species are more abundant at edges or in managed stands than in treefall gaps. Chiffchaff, although strongly associated with gaps within the natural forest, attains even higher densities in the managed forests and appears to have benefitted from forest management (Piotrowska and Wesołowski 1989). Thrush Nightingale (*Luscinia luscinia*) was recorded in just two treefall gaps but was far more abundant at the forest edge (pers. observ.). Willow Warblers (*Phylloscopus trochilus*) were recorded in only two treefall gaps which was surprising given the

ubiquity of the species in young-growth forests throughout central and western Europe.

Previous work on the composition of European forest passerine assemblages has shown that tropical migrants contribute a higher proportion of individuals in young-growth habitats than in later stages of forest growth (Helle and Fuller 1988). One would expect, therefore, that the proportion of tropical migrants should be higher at gaps than non-gaps. This was not the case. The proportion of tropical migrant passerines in gaps was 0.29 compared with 0.47 at closed-canopy points. This was largely due to the high abundance of flycatchers (Muscicapidae) and Wood Warblers in closed-canopy forest. Previous studies of habitat distribution patterns of tropical migrants in Europe have been based mainly on managed plantations which seldom contain stands of old trees with large numbers of suitable hole nesting sites for flycatchers. Fuller and Crick (1992) also reported that mature western oakwoods in upland Britain support high ratios of migrants to residents. I suggest that the apparent association of tropical migrants in Europe with young-growth habitats may be partly a consequence of forest management which tends to remove habitats favored by hole-nesting tropical migrants.

Treefall gaps provide concentrations of fruit and insects associated with dense low foliage that are heavily exploited by migrant birds (Blake and Hoppes 1986, Martin and Karr 1986). During the breeding season, gaps also are likely to provide important localized resources for birds. These resources may be food, especially invertebrates, or preferred habitat structures. The relatively dense understory foliage is probably an important factor influencing use of gaps by Dunnock, Blackcap, Garden Warbler (Sylvia borin), and Chiffchaff. Selection of gaps by these insectivorous species is consistent with their habitat preferences in managed forests where they are associated with early stages of forest growth with low dense regeneration (Ferry and Frochot 1990, Fuller and Henderson 1992). Tree Pipit (Anthus trivialis) is probably the first breeding bird species to colonize newly formed gaps, a pattern of habitat selection consistent with that in managed forest (Fuller and Moreton 1987).

Gaps probably offer concentrations of two main types of invertebrate food resources for birds: low-foliage invertebrates and dead-wood invertebrates. The higher abundance of ground insectivores at gaps was probably a response to the former resource. These species included ones that forage on the ground (e.g., Tree Pipit and Dunnock) and ones that forage in the field layer or low shrub layer (e.g., Garden Warbler, Blackcap, Winter Wren). There was no evidence that bark insectivores, the group most likely to benefit from an abundance of dead wood, were more abundant at gaps. These species include the woodpeckers, Nuthatch, and Treecreeper (Certhia familiaris). Angelstam and Mikusiński (1994) have argued that the spatial dynamics of several woodpecker species in natural forests will be closely linked with the availability of dead wood created through natural disturbances, both fire and blowdown. The failure to detect relationships between gaps and woodpecker distribution in Białowieża may be partly methodological—studies of foraging ecology, including ranging behavior are more appropriate for ascertaining the importance of gaps to these species. It also is likely that gaps will be more heavily used in winter than in the breeding season by woodpeckers. During the breeding season, several species feed mainly by surface gleaning but in winter become more dependent on excavating insects from dead wood (Snow and Perrins 1998). Another possibility that merits further investigation is that there may be rapid succession of bark insect communities following tree death and that gaps may offer a rather short-lived food resource for some bark insectivores.

Gaps may be more significant to breeding birds than suggested by the results of this paper. Inevitably, breeding season counts in forest are biased towards vocal individuals, especially singing birds, and hence can reveal only the broadest patterns of habitat use. Counts tend to produce little information about nonvocal foraging individuals. It is very likely, therefore, that important patterns of habitat use will have gone undetected by the present study. For example, gaps could act as resource centers for insectivorous species nesting in the surrounding closed-canopy forest. If this is the case, territories close to gaps could be of higher quality than territories farther away with consequences for reproductive success, site fidelity, and spatial patterns of age structure. Smith and Dallman (1996) described a situation where breeding Black-throated Green Warblers Dendroica virens used mosaics of gaps

and closed-canopy forest but spent more time foraging within gaps than in contiguous forest. Studies involving radio tracked individuals are highly desirable to gain a more realistic appraisal of the role of patchiness within forests in determining habitat quality for insectivorous birds. Such work is needed across a wider range of gap sizes than examined in the present study. Even small gaps, created by single treefalls, may create important feeding habitats in the context of individual territories.

ACKNOWLEDGMENTS

LITERATURE CITED

ANGELSTAM, P., AND G. MIKUSIŃSKI. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest—a review. Ann. Zool. Fennici 31:157–172.

BLAKE, J. G., AND W. G. HOPPES. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103:328–340.

FALINSKI, J. B. 1986. Vegetation dynamics in temperate lowland primeval forests. Ecological studies in Białowieża Forest. W. Junk Publishers, Dordrecht, Netherlands.

FERRY, C., AND B. FROCHOT. 1990. Bird communities of the forests of Burgundy and the Jura (eastern France), p. 183–195. In A. Keast [ED.], Biogeography and ecology of forest bird communities. SPB Academic Publishing, The Hague, Netherlands.

FULLER, R. J., AND H. Q. P. CRICK. 1992. Broad-scale patterns in geographical and habitat distribution of migrant and resident passerines in Britain and Ireland. Ibis 134(suppl.):14–20.

FULLER, R. J., AND A. C. B. HENDERSON. 1992. Distribution of breeding songbirds in Bradfield Woods, Suffolk, in relation to vegetation and coppice management. Bird Study 39:73–88.

FULLER, R. J., AND B. D. MORETON. 1987. Breeding bird populations of Kentish sweet chestnut (Castanea sativa) coppice in relation to age and structure of the coppice. J. Appl. Ecol. 24:13–27.

GŁOWACIŃSKI, Z. 1975. Succession of bird communities in the Niepolomice Forest (southern Poland). Ekol. Polska 23:231–264.

HELLE, P., AND R. J. FULLER. 1988. Migrant passerine birds in European forest successions in relation to vegetation height and geographical position. J. Anim. Ecol. 57:565–579.

HUTTO, R. L., S. M. PLETSCHET, AND P. HENDRICKS. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593–602.

JONGMAN, R. H. G., C. J. F. TER BRAAK, AND O. F. R. VAN TONGEREN. 1995. Data analysis in community and landscape ecology. Cambridge Univ. Press, Cambridge.

KIRBY, K. J., C. M. REID, R. C. THOMAS, AND F. B. GOLDSMITH. 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. J. Appl. Ecol. 35:148–155.

KIRBY, K. J., S. D. WEBSTER, AND A. ANCTZAK. 1991. Effects of forest management on stand structure and the quantity of fallen dead wood: some British and Polish examples. For. Ecol. Manage. 43:167–174.

LEVEY, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69:1076–1089.

MARTIN, T. E., AND J. R. KARR. 1986. Patch utilization by migrating birds: resource oriented? Ornis Scand. 17:165–174.

PETERKEN, G. F. 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge Univ. Press, Cambridge.

PIOTROWSKA, M., AND T. WESOŁOWSKI. 1989. The breeding ecology and behaviour of the Chiffchaff Phylloscopus collybita in primaeval and managed stands of Białowieża Forest (Poland). Acta Ornithol. 25:25–76.

SAS INSTITUTE. 1996. SAS/STAT user's guide. Version 6.1. SAS Institute Inc., Cary, NC.

SCHIECK, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. Condor 99:179–190.

SMITH, K. W., B. AVERIS, AND J. MARTIN. 1985. The breeding bird community of oak plantations in the Forest of Dean, southern England. Acta Oecologia/Oecologia Generalis 8:209–217.

SMITH, R., AND M. DALLMAN. 1996. Forest gap use by breeding Black-throated Green Warblers. Wilson Bull. 108:588–591.

SNOW, D., AND C. M. PERRINS. 1998. The birds of the Western Palearctic. Concise ed. Oxford Univ. Press, Oxford.

TOMIAŁOJĆ, L., AND T. WESOŁOWSKI. 1990. Bird communities of the primaeval temperate forest of Białowieża, Poland, p. 141–165. In A. Keast [ED.], Biogeography and ecology of forest bird communities. SPB Academic Publishing, The Hague, Netherlands.

WESOŁOWSKI, T., AND L. TOMIAŁOJĆ. 1997. Breeding bird dynamics in a primaeval temperate forest: long-term trends in Białowieża National Park (Poland). Ecography 20:432–453.

ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Upper Saddle River, NJ.