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The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland

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The White-backed Woodpecker (WbW) and the Three-toed Woodpecker (TtW) are rare woodpecker species that inhabit natural old-growth forests with abundant dead wood in Eurasia. We studied stand-related environmental factors subject to forest management (stand structure, tree-species composition, accessibility by humans) in determining the distribution of these two species in mountainous forests of the Polish Carpathians. Data were collected during 2007–2009 at the Beskid Wyspowy Mountains. WbWs preferred multispecies deciduous over pure beech forests, whereas TtWs were most frequently found in spruce-dominated forests. The thresholds of dead and dying wood for WbW presence in managed forests were approximately 50 m^{3}ha^{-1} and 35 m^{3}ha^{-1}, respectively, and for TtW were approximately 30 m^3 ha^{-1} and 115 m^{3}ha^{-1}, respectively. These were 5–8 times higher than in randomly-selected control plots with no woodpeckers. In both cases, lower logging intensity on difficult-to-access slopes and higher amount of dead and dying wood correlated with increasing occupancy probability of the woodpeckers. These results help develop classification criteria for the monitoring of woodpecker habitats over the Natura 2000 network and improve the ecological soundness of forest management guidelines.

1. Introduction

European forests have been exploited for hundreds of years by humans, and this has led to the impoverishment of forest biodiversity (Thirgood 1989). The only areas that remain close to their natural state are those in which logging has not been economically feasible (Angelstam *et al*. 1997). These areas are often situated in swampy lowlands, deep foothill valleys and steep, rocky mountain slopes. Because of the pristine nature of these sites, some are protected as reserves or national parks. However, many old-growth forest patches still exist without protection, especially in mountainous regions. They are mostly small in size and isolated from each other. In comparison with natural forest remnants, managed forests typically lack over-mature and dead trees that are necessary for the maintenance of a large number of forest species (Hansen *et al*. 1991).

Woodpeckers (Picidae) are commonly used as indicators of forest naturalness as they typically search for food and excavate cavity nests in old, dying and dead trees (Mikusiński & Angelstam 1997, Mikusiński *et al*. 2001, Roberge *et al*. 2008a). White-backed (WbW) and Three-toed Woodpeckers (TtW) are the most specialized in their feeding micro-habitats among European Picidae, and prey almost exclusively on saproxylic beetles that colonize weakened and dead trees. This specialization makes them vulnerable to modern forestry, as old and dead trees are commonly removed in logging operations (Conner 1979, Nilsson 1992, Angelstam & Mikusinski 1994, Tucker & Heath 1994, Mikusinski 2006, Roberge *et al*. 2008b). Although both species rely on old trees for their survival, they rarely interfere with each other, as they mostly forage on different tree species (but see Nowak 2003). The WbW is associated with deciduous and the TtW with coniferous trees (Winkler *et al*. 1995). Both species feed on larvae of longhorn beetles (Cerambycidae), and the TtW shows a marked preference for bark beetles (Scolytidae; Winkler *et al*. 1995, Fayt *et al.* 2005). The availability of dead wood in their territories is therefore crucial for their survival (Aulén & Lundberg 1991, Bütler & Schlaepfer 2003).

As these two woodpeckers have specific habitat preferences, they have been suggested as being 'umbrella' species (Bütler *et al*. 2004a, 2004b, Romero-Calcerrada & Luque 2006, Roberge *et al*. 2008a). Both species require a continuous supply of saproxylic (dead-wood dependent) beetles in old and decaying trees over large areas, and so are affected by alterations of habitat conditions. The protection of woodpeckers is assumed to be beneficial for numerous other (inconspicuous) species within the same habitat but with smaller home ranges. Examples include saproxylic beetles and secondary cavity nesters (e.g., Pygmy Owl *Glaucidium passerinum*, Boreal Owl *Aegolius funereus*, Edible Dormouse *Glis glis* and Forest Dormouse *Dryomys nitedula*). Protecting WbW or TtW territories may thus, at least theoretically, protect the entire old-growth forest-species assemblage (Martikainen *et al*. 1998, Mikusiński *et al*. 2001, Angelstam *et al*. 2003, Roberge *et al*. 2008b).

WbW and TtW are listed in the Annex 1 of the Birds Directive of the European Union, and Special Protection Areas in the Natura 2000 network have been designated for these species (Directive 2009/147/EC of the European Parliament and of the Council). The Carpathian Mountains host some of the largest populations of WbW and TtW in Europe. Several Carpathian ranges in Poland, Slovakia and Romania have special areas designated for the protection of the WbW and/or TtW in the Natura 2000 network. These two species are the rarest woodpeckers in Poland (approximately 500 pairs of each, about half of which is in Carpathians, Piotrowska & Wesołowski 2007a, 2007b), The WbW is classified as near threatened and the TtW is classified as vulnerable in the Polish Red List (Głowaciński & Wesołowski 2001, Wasilewski 2001). Their populations are mostly found in nature-protection areas of the north-eastern lowlands and the Carpathian Mountains in Poland.

Efficient protection of these woodpeckers requires information about the number of individuals and their distribution, and about specific habitat preferences in particular parts of their ranges. Bütler *et al*. (2004a) found that the probability of presence of TtW increases sharply once a certain number of dead standing trees are available. Deadwood threshold conditions may vary between geographic regions, site productivity and forest management, but such information would help draw management recommendations at different spatial scales. The present study follows the approaches of Bütler *et al*. (2004a) and Garmendia *et al*. (2006). Our study area consists of a mosaic of coniferous and deciduous forests located within a recently-designated Important Bird Area (IBA) in the Beskid Wyspowy Mountains in south-eastern Poland. Most of these forests are being extensively exploited, and those that remain untouched or only little exploited are usually situated on protected land or on remote, steep slopes with limited accessibility (http://rdlpkrakow.gis-net.pl/, authors' pers. obs.).

The aim of the present study was to evaluate the role of certain local factors in explaining woodpecker occurrence at the territory level, with special attention to possible threshold conditions in dead wood. Such factors have sometimes been overlooked in landscape-level habitat-prediction modeling (Stachura-Skierczynska *et al*. 2009, Edman *et al*. 2011). Information about forest structure, tree-species composition and accessibility was compared between plots occupied by WbW or TtW and unoccupied plots. For the WbW, data from territories located in protected areas (small nature reserves) were added to demonstrate possible differences between managed and unmanaged stands as well as the effects of timber harvesting on the distribution of WbW. Besides advancing basic knowledge about the ecology of the woodpeckers, our data will be a useful resource for the conservation of these birds and their habitats.

2. Material and methods

2.1. Study area

The Beskid Wyspowy range is situated in the central part of the Polish Western Carpathians (49°41' N, 20°14' E; 1,000 km^2 of which 40% is forested) and consists of several independent forested peaks spanning between 500 and 1,170 m a.s.l. (Kondracki 2000). Forests are mostly located in the lower mountain-forest zone and consist of a few main tree species (mainly beech *Fagus silvatica*, Norway spruce *Picea abies*, fir *Abies alba* and sycamore *Acer pseudoplatanus*) either in pure stands or mixed with other species (Matuszkiewicz 2008).

The forested areas consist of a mosaic of wooded patches, i.e., stands of the same type of forest. Each patch was distinguished on the basis of features which characterized a particular forest stand (age and species composition), and differed from other patches with respect to at least one of these features. Fourty percent of the forests are deciduous (beech and sycamore) and 60% are coniferous (with a considerable share of spruce, fir and mixed spruce-fir) (http://rdlpkrakow.gis-net.pl/). The forests vary considerably in age (most patches are 30–80 years and occasionally 80–150 years old) and condition, as approximately 80% are extensively and 20% are slightly managed due to the difficulties in logging on steep slopes. Less than 1.5% is protected in six small deciduous reserves. Most forests are semi-natural with only a few recently-planted coniferous patches (http://rdlpkrakow.gis-net.pl/).

2.2. Woodpecker inventories

The occurrence of WbW and TtW was recorded during 2007–2008 (cf. Kajtoch 2009). The presence of these species in the study area had been a priori confirmed during 2001–2006 (Kajtoch & Piestrzyńska-Kajtoch 2006). The inventories were conducted over the entire study area in spring (from March to early May) and autumn (September–October) each year. Play-back (drumming and calls) was used to increase the efficiency of woodpecker detection (Wesołowski *et al*. 2005, Czeszczewik & Walankiewicz 2006).

The inventories were carried out according to the following protocol: 2 min of play-back followed by 5 min of listening at points 200–500 m apart (depending on topography) along forest roads and boundaries between forest sub-compartments. Throughout the study, all old-growth forest patches were checked at least four times in spring and two times in autumn. In other forest patches, play-backs were used at least twice in spring. Foraging signs, especially fresh ones, made by the studied woodpeckers were geo-referenced using a hand-held GPS unit. A plot (territory) was considered occupied if pairs and/or drumming individuals had been detected at least twice during the breeding period, and/or if young birds or nests had been found there.

As almost every territory was over 1 km from the nearest other occupied plot (often one territory per mountain peak), double recording of the same individual was not an issue. Plots with only single birds detected (mostly in autumn) were excluded from the randomly-selected plots (not occupied by woodpeckers). The occurrence of woodpeckers was also systematically verified each time during habitat-data collection (play-backing and foraging signs), especially in plots assigned as unoccupied, in order to rule out the existence of undetected territories. Occurrence was rejected if the verification failed.

2.3. Plot selection

Twelve territories (occupied plots) of both TtW and WbW in managed forests and six WbW territories in nature reserves were used in the analysis. Twelve additional plots were randomly assigned

Table 1. Variables used in the analysis.

Abbreviation	Descriptions of variables
Spruce trees *	% of all standing trees
Beech trees **	% of all standing trees
Deciduous trees *	% of all standing trees
Dead branches **	Volume of living trees with at least one >10 cm thick dead branch (m^3 ha^{-1}; class 1a)
Dying trees	Volume of dying trees (m^3 ha^{-1}; class 2***)
Dead trees	Volume of dead trees (m^3 ha^{-1}; class 3***)
Fallen-off bark	Volume of dead trees with dropping bark (m^3 ha^{-1}; class 4***)
Without bark	Volume of dead trees without bark (m^3 ha^{-1}; class 5***)
Proportion of snags	% of all standing trunks
Snags	Volume of snags (m^3 ha^{-1}; classes 3–5***)
Broken trees	Volume of broken trees (m^3 ha^{-1}; classes 6–7***)
Logs	Volume of fallen logs (m^3 ha^{-1})
Dead wood volume	Total dead wood volume (m^3 ha^{-1})
Recent harvesting	Number of 0–2-yrs old stumps/ha
Past harvesting	Number of >2 yrs old stumps/ha
Veteran trees	Number of trees with diameter at breast height > 40 cm per ha
Thick snags	Number of snags with diameter at breast height > 20 cm per ha
Slope	Slope inclination (degrees)
Exposure	Exposure of sampling plots
Shannon	Diversity index of tree species
Roads	Road density within 0.5 km from the center of a study plot (km km^{-2})

* Calculated for the Three-toed Woodpecker only
** Calculated for the White-backed Woodpecker only
*** According to Maser *et al.* (1979)

to deciduous and another twelve to coniferous forests, determined on the basis of forest GIS maps (http://rdlpkrakow.gis-net.pl/). For the former, forest cover was 100%, beeches and/or sycamores constituted at least 70% of stands aged over 60 years, and altitude varied between 500 and 1,000 m a.s.l., i.e., these have a higher-than-average probability of WbW occurrence in the study area (Kajtoch 2009). For the latter, forest cover was also 100%, but spruce constituted at least 60% and coniferous trees altogether made up more than 80% of stands aged over 60 years; altitude varied between 700 and 1,200 m a.s.l., i.e., such forests have a higher-than-average probability of TtW occurrence in the study area (Kajtoch 2009).

Additional WbW territories in reserves were chosen for comparison with WbW territories located in managed patches. Similar analysis could not be performed for TtW as the study area contained no protected coniferous forests. As territories in reserves represented a distinctive category of unmanaged forest, inclusion of them into analyses together with territories located in managed stands could lead to an overestimation of thresholds for WbW in managed stands. To rule out this problem, reserve-WbW territories were analyzed separately.

Each study plot consisted of two subplots that were placed within each of the occupied (woodpecker territories) and unoccupied plots (no woodpecker observations). Each subplot was a 50 m × 50 m (2,500 m^2) square, located within a 500-m radius from the midpoint of the study plot (see below). Subplots were placed by randomly choosing one of the four cardinal directions and subsequently randomly selecting an up-to-500-m distance from the midpoint of each subplot. The midpoint of an occupied plot (territory) was defined as being a cavity-nest tree or the midpoint within an area delimited by lines that connect bird observations. In unoccupied plots, the midpoint was determined by a random choice further than 1 km from the nearest known woodpecker territory. The subplots within a given study plot were at least 250 m apart. Occupied plots were labeled as “reserve-WbW plot” (6; “reserve” refers to a plot located within the protected area; no TtW territories were found within reserves), “WbW plot” (12) and “TtW plot” (12), and unoccupied plots were labeled as “non-WbW plot” (12) and “non-TtW plot" (12). Average values for each subplot pair, within a given plot, were used for habitat variables, i.e., the two subplots were considered a single sample to avoid pseudo-replication.

2.4. Environmental variables (habitat data)

Data about forest type and structure in each subplot were collected during the autumn of 2008 (TtW and random coniferous plots) and summer of 2009 (WbW and random deciduous plots; Table 1). Previous studies on WbW and TtW habitat preferences suggest certain habitat variables that can be important for these species at the local scale (Hogstad & Stenberg 1994, Pechacek & D'oleire-Oltmanns 2004, Bütler *et al*. 2004a, Wesołowski *et al*. 2005, Gjerde *et al*. 2005, Czeszczewik & Walankiewicz 2006, Garmedia *et al*. 2006, Czeszczewik 2009). The set of variables was chosen on the basis of this knowledge, and included basic information about forest type, tree-species diversity, and the abundance of dead and dying trees. Other characteristics (slope, exposure, roads, etc.) were chosen to account for their impact on the accessibility and the likelihood of logging at a given plot.

In each subplot, the number of trees of each species was recorded and the following characters were measured: diameter at breast height (for all trees ≥ 7 cm), height, condition (living, dying or dead), snags, broken stems and logs (these were classified to decay classes according to Maser *et al*. 1979 and Gutowski *et al*. 2004). With reference to WbW, the classification of decay classes by Maser *et al*. (1979) was modified by adding another class, which was named "1a" (Table 1). Moreover, the number of stumps and their state (new, cut down within the last two years, or older), the presence of broken and dying branches (with bark falling off) in deciduous trees, signs of woodpecker foraging, and tree cavities were recorded. Data about forest age, slope inclination and forest-road density (total length of roads within a 0.5-km radius of each subplot [km km^{-2}]) were obtained from forestry and topographic maps. The exposure of sampling subplots, measured in the field with a compass, were transformed into numerical values following Beers *et al*. (1966). Tree-species diversity was computed using the Shannon-Wiener index (Krebs 1989).

Dead-wood volume (m^3/ha) of all standing trees (living, dying and dead) was based on data on diameter at breast height and height, and obtained from tables of Czuraj (1991). For broken stems, the following formula was used:

$$V = 1 / [3\, \pi\, h\, (R^2 + Rr + r^2)] \qquad (1)$$

where h is trunk height/length, and R and r are lower- and upper-end diameters of the trunk. The volume of lying trunks with a diameter of at least 10 cm was calculated using the formula (Bruchwald 1999):

$$V = l * g\, ½\, l \qquad (2)$$

where l = length of the trunk and g = diameter in the middle part of the trunk.

2.5. Statistical analyses

For each occupied and unoccupied study plot, averages of environmental variables for each subplot pair were calculated. Statistical analyses were performed for these data based on the 12 TtW, 12 non-TtW, 6 reserve-WbW, 12 WbW and 12 non-WbW plots. The similarity between occupied and unoccupied plots, and for the occupied plots of WbW between managed and reserve forests, among the habitat variables was assessed using Mann-Whitney U test. Additionally, the similarity in stand diversity (Shannon-Wiener index) was evaluated using a t test (Hutcheson 1970). Logistic regression was used to detect variables crucial for TtW and WbW occurrence (Hosmer & Lemeshow 1999, Menard 2002, Stanisz 2006). This method was used due to the dichotomous nature of the dependent variable (occupied/unoccupied plots).

Three separate analyses were run: (1) occupied vs unoccupied TtW plots; (2) occupied vs unoccupied WbW plots; and (3) occupied managed-forest vs occupied reserve WbW plots. Akaike's information criterion was used for model selection (Burnham & Anderson 2004). Generally, predictors included in the model selection process were assumed to be independent. Only variables not correlated with each other were considered, and possible multicollinearity was checked with Spearman correlation test (results not presented). For highly correlated predictors – such as variables describing dead-wood supply – the strongest

Table 2. Proportions of the number of trees and wood volume in managed forest plots (i.e., reserve plots excluded). Nr% = proportion of the number and Vol% = proportion of the volume of each tree species (standardized to $m^3 ha^{-1}$); WbW = White-backed Woodpecker; TtW = Three-toed Woodpecker; "non-" indicates a random plot with no woodpecker territory (others represent occupied plots).

Species tree	Nr%/WbW	Nr%/non-WbW	Nr%/TtW	Nr%/non-TtW	Vol%/WbW	Vol%/non-WbW	Vol%/TtW	Vol%/non-TtW
Spruce *Picea abies*	10.5	1.8	62.6	64.0	8.3	0.9	66.7	57.8
Fir *Abies alba*	11.2	16.7	23.9	25.3	8	17.8	23.9	29
Other coniferous	0.6	0.3	1.0	4.3	0.6	0.2	1.8	8.1
Beech *Fagus silvatica*	66.2	81.1	6.8	3.8	72.4	81.1	2.9	3.1
Sycamore *Acer pseudoplatanus*	5.4	0.0	0.2	0.3	4.6	0.0	0.1	0.1
Other deciduous	6.1	0.1	5.5	2.3	6.1	0.0	4.6	1.9
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

determinants in a univariate logistic regression (performed for all predictors) were selected based on literature and authors' knowledge.

As the number of study plots (sample size) in each modeling approach was relatively small (n/K ratio <40), a small-sample version of AIC with bias adjustment (AICc) was applied (Hurvich & Tsai 1989, 1991). AIC values adjusted for small samples were also corrected for overdispersion with the help of variance-inflation factor (quasi-likelihood parameter >1, indicating some overdispersion) and resulted in QAICc used in the final model selection (Lebreton *et al*. 1992, Burnham & Anderson 2002, Lehikoinen *et al*. 2011). Before model building, numbers of the estimated parameters were presumed to be lower than the root of the number of observations multiplied by 2 (Kornacki & Sokołowska 2010).

The resulting models were subsequently ranked in an order of increasing QAICc. The model with lowest QAICc explains most variance with fewest parameters. Differences in these values between models (QAICc), indicating the relative support for each model, were also presented. Models with QAICc < 2 compared to the model with the lowest QAICc were assumed to have high strength-of-evidence, while models with QAICc >10 have essentially no support (Burnham & Anderson 2004). Model likelihoods were normalized according to Akaike weights (w) to illustrate the weight of evidence of each model: the higher the weight, the higher the explanatory power of the selected model (cf. Freckleton 2011).

A multimodel inference for all candidate models was applied to evaluate the importance of each model predictor. QAICc weights were summed for models containing given variables. The predictor with largest weight was considered the most important. This method essentially produces a probability that of the variables considered, a given variable would be in the best approximating model were the data collected again under identical circumstances (Burnham & Anderson 2002, 2004, Freckleton 2011). This procedure is superior to making inferences concerning the relative importance of variables based only on the best model, which is particularly important when the second- or third-best model is nearly as well supported as the best model (Burnham & Anderson 2004).

A univariate logistic regression for selected variables known to be crucial for woodpeckers presence (see above) was run to detect threshold values of dying and dead wood in determining woodpecker presence. For the TtW, a logistic regression using the explanatory variables Dying trees and Total standing volume of dead wood (Snags+Broken trees) is presented, and for the WbW, Dying trees and Total volume of dead wood (Snags+Broken trees+Logs) is presented. We included the variable Logs only for WbW as this species frequently feeds on fallen dead trees (e.g. Wesołowski 1995, authors' pers. obs.), whereas TtW only rarely forages on fallen dead spruce, at least in managed forests of the Carpathians (authors' pers. obs.). Moreover, fallen

Table 3. Descriptive statistics and Mann-Whitney test results for all variables calculated for the White-backed (WbW) and Three-toed (TtW) Woodpeckers. Reserve = protected forest reserves (only occupied WbW plots); M-Occ = occupied managed-forest plots; M-Unocc = unoccupied managed-forest plots. Values for these columns show mean ± SD.

Variable	Reserve WbW (A)	M-Occ WbW (B)	M-Unocc WbW (C)	M-Occ TtW (D)	M-Unocc TtW (E)	B vs C		A vs B		D vs E	
						U	*p*	*U*	*p*	*U*	*p*
Beech trees	68.9±33.8	66.1±26.6	81.1±14.5	–	–	46	0.133	32	0.708	–	–
Spruce trees	–	–	–	62.56±18.9	64.0±16.0	–	–	–	–	70	0.908
Dead branches	294.5±82.8	234.7±151.2	102.1±43.1	–	–	24	0.006	19	0.111	–	–
Deciduous trees	–	–	–	12.6±11.6	6.4±5.9	–	–	–	–	54.5	0.312
Dying trees	18.0±27.5	20.9±24.2	3.9±8.8	64.7±54.9	19.00±13.34	34	0.028	31	0.640	25	0.007
Dead trees	8.7±6.7	4.5±12.5	3.9±11.7	19.5±18.4	1.5±3.0	55	0.326	14	0.039	26	0.008
Fallen-off bark	6.7±15.4	3.6±5.9	0	26.7±26.7	0.1±0.2	36	0.038	33	0.778	7.5	0.000
Without bark	0	1.0±3.5	0	1.2±2.5	0	60	0.488	30	0.574	54	0.299
Proportion of snags	5.2±5.3	4.2±5.9	0.6±1.2	13.8±10.6	2.4±2.1	41.5	0.078	28	0.453	13.5	0.001
Snags	15.4±14.6	9.0±15.7	3.9±11.7	47.3±38.8	1.6±3.0	46.5	0.141	24.5	0.281	6.00	0.000
Broken trees	6.2±7.1	5.2±8.7	3.4±11.7	8.2±7.7	0.9±1.7	25	0.007	29	0.512	18.5	0.002
Logs	34.9±33.8	19.0±27.6	2.0±3.8	13.1±11.2	2.1±2.6	31.5	0.019	25	0.303	15	0.001
Dead wood volume	56.5±45.9	33.2±43.2	9.4±23.3	68.7±42.5	4.6±3.9	32	0.021	27	0.399	2	0.000
Recent harvesting	16±39.2	12±25.2	24±24.36	10.7±23.2	40.0±43.2	50.5	0.215	29.5	0.543	26.5	0.009
Past harvesting	58.7±55.4	84.7±	190.7±117.1	74±70.3	163.3±129.7	26	0.008	30.5	0.606	46	0.133
Veteran trees	125.3±38.1	82±48.6	60.7±39.7	43.3±45.3	4.7±8.9	54.5	0.312	18.5	0.101	38.5	0.053
Thick snags	20±17.3	13.3±24.4	2±4.9	6.3±5.3	8.8±3.2	52	0.248	21.5	0.174	13.50	0.001
Slope	18.5±4.7	13.4±2.7	8.3±2.4	11.3±5.6.0	8.8±3.2	10	0.000	13.5	0.035	49	0.184
Exposure	1.3±0.7	1.3±0.5	1.1±0.5	1.3±0.8	0.9±0.6	62.5	0.583	32.5	0.743	49.5	0.194
Shannon	0.7±0.6	0.76±0.4	0.5±0.3	0.8±0.2	0.9±0.3	40	0.065	33	0.779	62.5	0.584
Roads	1.0±0.4	1.5±0.3	2.3±0.7	1.2±0.4	1.9±0.4	15.5	0.001	12	0.025	13	0.001

spruce trees are routinely removed by foresters in the study area (authors' pers. obs.), so their number is limited.

The proportion of dead trees between diameter at breast height classes was compared with the proportions of dead trees with signs of TtW foraging using χ^2 test. The χ^2 test was also used to compare the distribution of the amount of fallen logs among decay classes between occupied and unoccupied WbW plots.

All calculations were performed using Statistica 7.0 software.

3. Results

3.1. General patterns

A total of 19 WbW territories and 16 TtW territories were found. Six WbW territories were located in nature reserves, whereas managed forests hosted 13 WbW and all TtW territories; however, some were in the vicinity of the reserves. In managed forests, twelve of the 13 WbW territories and 12 of the 16 TtW territories were selected for further analysis due to difficulties in obtaining measurements at localities with rocky slopes and an inclination of >60°. The number of studied territories was determined by the scarcity of breeding pairs of the two species in the managed forests (Kajtoch 2009, Matysek & Kajtoch 2010).

Variation in tree-species composition, based on the number and volume of trees, is presented in Table 2. Occupied TtW plots were dominated by spruce (63%) and fir (24%), with only a small portion of deciduous trees (<13%; mainly beech). By contrast, occupied WbW plots were dominated by beech (66%) and other deciduous trees (11%; mostly sycamore), although coniferous trees were also common (23%).

3.2. White-backed Woodpecker

Total volume of dead wood was significantly higher (over three times) in occupied than in unoccupied managed-forest plots. In addition, total vol-

Table 4. Sets of candidate models explaining the occurrence of Three-toed (TtW) and White-backed (WbW) Woodpeckers (for variables, see Table 1). The number of variables (k), Akaike's information criterion (QAICc), difference between the given model and the most parsimonious model (Δ) and Akaike weight (w) are reported for each model. Models with ΔQAICc ≤2 compared to the model with the lowest QAICc are in bold.

Nr.	Model variables	k	QAICc	Δ	w
TtW occurrence in managed forests (occupied vs unoccupied plots)					
1	**Past harvesting+Roads**	**2**	**11.642**	**0.000**	**0.229**
2	**Dead trees+Roads**	**2**	**12.565**	**0.923**	**0.144**
3	**Dying trees+Roads**	**2**	**12.852**	**1.210**	**0.125**
4	**Veteran trees+Roads**	**2**	**12.87**	**1.228**	**0.124**
5	Dead trees+Veteran trees	2	13.924	2.282	0.073
6	Dying trees+Dead trees	2	13.970	2.328	0.071
7	Dead tree+Past harvesting+Roads	3	14.222	2.580	0.063
8	Past harvesting+Veteran trees+Roads	3	14.521	2.879	0.054
9	Dying trees+Veteran trees	2	14.932	3.290	0.044
10	Dying trees+Dead trees+Roads	3	15.47	3.828	0.034
11	Dying trees+Dead trees+Veteran trees	3	16.728	5.086	0.018
12	Dying trees+Dead trees+Past harvesting+Roads	4	17.448	5.806	0.013
13	Dying trees+Dead trees+Veteran trees+Roads	4	18.692	7.050	0.007
14	Dying trees+Dead trees+Past harvesting+Veteran trees+Roads	5	20.976	9.334	0.002
					1.000
WbW occurrence in managed forests (occupied vs unoccupied plots)					
1	**Dying trees+Roads**	**2**	**11.178**	**0.000**	**0.203**
2	**Logs+Roads**	**2**	**11.511**	**0.333**	**0.172**
3	**Dead branches+Roads**	**2**	**11.58**	**0.402**	**0.166**
4	**Dead branches+Recent harvesting**	**2**	**12.097**	**0.919**	**0.128**
5	**Dead branches+Recent harvesting+Roads**	**3**	**12.445**	**1.267**	**0.108**
6	Dead branches+Dying trees+Roads	3	13.554	2.376	0.062
7	Logs+Shannon+Roads	3	13.692	2.514	0.058
8	Dying trees+Recent harvesting+Roads	3	13.947	2.769	0.051
9	Dead branches+Logs+Recent harvesting+Roads	3	15.381	4.203	0.025
10	Dead branches+Dying trees+Recent harvesting+Roads	4	15.457	4.279	0.024
11	Dead branches+Dying trees+Logs+Shannon+Roads	5	19.873	8.695	0.003
12	Dead branches+Dying trees+Recent harvesting+Shannon+Roads	5	20.114	8.936	0.002
13	Dead branches+Logs+Dying trees+Recent harvesting+Shannon+Roads	6	23.009	11.831	0.001
					1.000
Occupied WbW plots, a comparison between reserve and managed-forest plots					
1	**Veterans+Roads**	**2**	**10.425**	**0.000**	**0.430**
2	**Dead total+Roads**	**2**	**11.694**	**1.269**	**0.228**
3	**Dead total+Veteran trees**	**2**	**11.989**	**1.564**	**0.197**
4	Dead total+Veteran trees+Roads	3	13.223	2.798	0.106
5	Dying trees+Dead total+Veteran trees+Roads	4	16.715	6.290	0.019
6	Dead total+Veteran trees+Shannon+Roads	4	16.739	6.314	0.018
7	Dying trees+Dead total+Veteran trees+Shannon+Roads	5	20.713	10.288	0.003
					1.000

ume of dead wood was on average six times higher in occupied reserve than in unoccupied managed-forest plots but only marginally (less than two times) higher in reserves than in occupied managed-forest plots (Table 3). However, in terms of the latter comparison, the volume of recently-dead trees (class 3 according to Maser *et al.* 1979) was significantly higher in the reserve plots. The reserve plots also differed significantly from the other compared plots in terms of slope inclination and roads. Dead wood accounted for 10.8% of the total wood biomass in reserve plots (all occupied),

Table 5. QAICc weights for each variable used in the model selection procedure (compare Table 4). Values are probabilities for a given predictor to be in the best approximating model. TtW = Three-toed Woodpeckers, WbW = White-backed Woodpeckers.

Variable	Managed-forest TtW, occupied vs unoccupied	Managed-forest WbW, occupied vs unoccupied	Occupied WbW plots, reserve vs managed
Roads	0.794	0.872	0.803
Dying trees	0.313	0.345	0.022
Dead trees	0.424		
Past harvesting	0.361		
Veteran trees	0.322		0.772
Dead branches		0.517	
Logs		0.295	
Recent harvesting		0.337	
Shannon		0.064	0.021
Dead wood volume			0.570

7.6% in occupied and 2.9% in unoccupied managed-forest plots. Inclination and road density also differed significantly between occupied and unoccupied managed-forest plots. Road density and inclination correlated negatively with each other ($R = -0.77$, $p < 0.001$). Road density was 1.5 times lower and inclination was 1.6 times steeper in occupied than in unoccupied managed-forest plots. Living trees with dead branches significantly differed between occupied and unoccupied managed-forest plots. Certain variables that may have affected the volume of dead and dying trees within a given decay class (dying trees, trees with bark falling off, broken trees, and fallen logs) were significantly higher in occupied than in unoccupied plots (Table 3). The occupied plots in general – both reserve and managed-forest plots – had 1.6 times higher tree-species diversity than the unoccupied plots ($t = 6.87$, $p = 0.05$).

Occupied and unoccupied WbW plots were compared using 13 models with combinations of Dead branches, Logs, Dying trees, Recent harvesting, Shannon and Roads, and reserve vs occupied managed-forest plots were compared using 7 models with a combination of Dying trees, Dead total, Veteran trees, Shannon and Roads. Five combinations with QAICc < 2 were selected for further examination (Table 4). A subsequent comparison of QAICc weights showed that the variables Roads and Dead branches best explained WbW occurrence (Table 5).

For occupied WbW plots, relative differences between reserve and managed-forest plots were low: most variables were non-significant in the regression modeling. A few variables indicated some discrimination, however. Hence, seven models were built with variables Dying trees, Dead wood volume, Veteran trees, Shannon and Roads. Three of these were in the three best models (Table 4). The importance of these variables was determined by QAICc weights (Table 5), which indicated that the most important variable was Roads, followed by Veteran trees and Dead wood volume. The other two variables, which were non-significant also in the univariate modeling, did not increase the informative value of models.

According to the univariate logistic regression, the probability of WbW occurrence in managed forests reached 100% when the dead wood volume was ≥ 50 m^3 ha^{-1} and the volume of dying trees was ≥ 35 m^3 ha^{-1} (Fig. 1). The distribution of the volume of logs among decay classes differed significantly between occupied and unoccupied plots ($\chi^2 = 17.50$, $p = 0.003$), and also between occupied reserve and managed-forest plots ($\chi^2 = 14.62$, $p = 0.012$). In the reserve forests, fallen wood frequently represented advanced decay stages (mostly class 4) whereas in the managed forests they were mostly in class 2 (Fig. 2). Unoccupied plots had little fallen dead wood (Table 3).

3.3. Three-toed Woodpecker

The total volume of dead wood was nearly 15 times higher in occupied than in unoccupied TtW

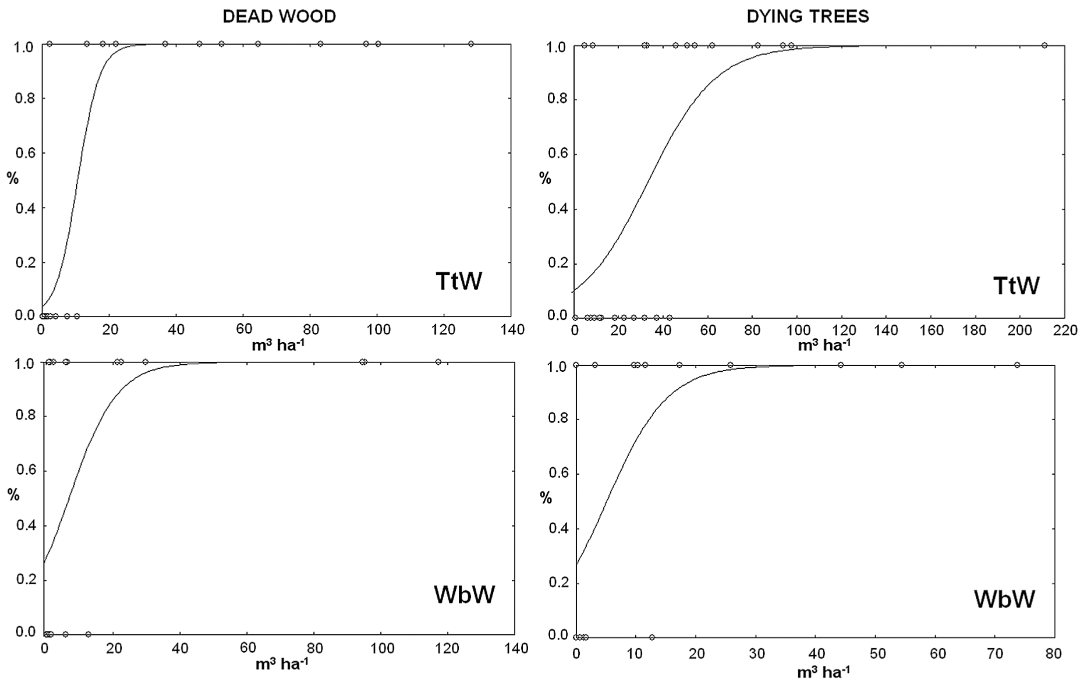

Fig. 1. Logistic regression models for the volume of dead wood (snags and broken trees for the Three-toed Woodpecker [TtW]; snags, broken trees and logs for the White-backed Woodpecker [WbW]) and for dying trees in managed forests.

plots (Table 3). The values of all variables concerning the amount of dead and dying wood in each decay class were significantly higher in the former. The largest relative differences were found for dead trees, trees with bark falling off, and snags (Table 3). About 95% of the total wood volume and 92% of the quantity of dying and dead trees were attributed to spruce. These values apply to 62% of the living, and 63% of the dying and dead, trees in the study plots. Plots occupied by TtW had a significantly higher proportion of snags among their standing trunks than the unoccupied

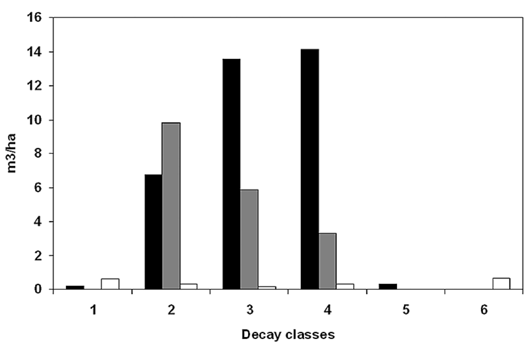

Fig. 2. Log-volume distribution among decay classes (Maser *et al.* 1979) for the White-backed Woodpecker (black columns = reserve plots, grey columns = managed-forest plots, white columns = unoccupied by the species).

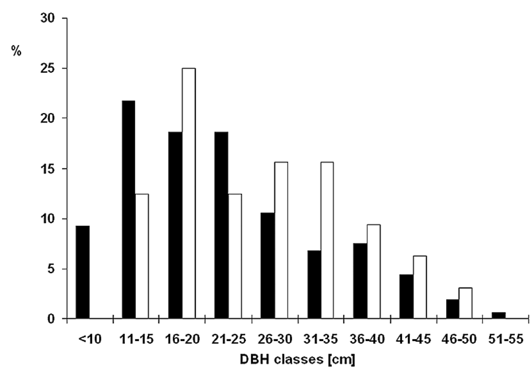

Fig. 3. Proportion of the total number of dead trees (black columns; N = 1288) and dead trees used by Three-toed Woodpeckers for foraging (white columns; N = 256) arranged to different diameter at breast height (DBH) classes.

plots (Table 3). The percentages of spruce and deciduous trees did not significantly differ between the two plot categories (Table 3). TtW plots had a marginally lower tree-species diversity ($t = 2.61$, $p = 0.05$). The proportion of total dead-wood biomass amounted to 19% in the occupied but only 1.7% in the unoccupied TtW plots.

The slope inclination was 1.3 times steeper in occupied than in unoccupied TtW plots, though this difference was not significant. The density of forest roads was 1.6 times lower in occupied than in unoccupied TtW plots, and this factor was negatively correlated to the amount of dead wood and the slope inclination ($R = –0.66$, $p < 0.001$ and $R = –0.53$, $p = 0.008$, respectively).

For TtW, 14 candidate models with combinations of Dying trees, Dead trees, Past harvesting, Veteran trees and Roads were compared with QAICc. Variable combinations in the competing models were expected to have the strongest effect on TtW occurrence. The four best models (QAICc <2) included all five predictors and indicated that all variables appeared informative for TtW occurrence (Table 4). To detect the most important factors, summarized QAICc weights were applied (Table 5). This approach indicated that the predictor Roads appeared the single most important factor in explaining TtW occurrence. The remaining four variables had approximately two times lower weights. According to the univariate logistic regression, the occurrence probability of TtW reached 100% when the volume of dead wood was ≥ 30 m^3 ha^{-1} and that of dying trees was ≥ 115 m^3 ha^{-1} (Fig. 1). Signs of foraging TtW were mainly found on dead spruce and only occasionally on fir. The proportion of dead trees varied significantly among the diameter at breast height classes, and the distribution significantly differed from that of TtW foraging trees ($\chi^2 = 34.03$, df $= 9$, $p = 0.0001$; Fig. 3). On average, dead trees used by woodpeckers were larger than those available in the study area (Fig. 3).

4. Discussion

Our data collected from the Western Carpathians showed that both WbW and TtW prefer semi-natural old-growth forest patches with a significant volume of dead and dying trees. Such high-quality patches were usually on difficult-to-access slopes. WbW territories were also frequently found in unmanaged beech-sycamore nature reserves. These results corroborate previous studies conducted in lowland boreal forests of Scandinavia (Carlson 2000, Pakkala *et al*. 2002, Roberge *et al*. 2008b) and in temperate primeval forests of north-eastern Poland (Wesołowski *et al*. 2005, Czeszczewik & Walankiewicz 2006, Czeszczewik 2009, Lõhmus *et al*. 2010). The relationship between the occurrence of TtW and forest quality in mountainous habitats has previously only been studied in semi-natural spruce forests of the Alps and the Juras (Bütler *et al*. 2004a, 2004b, Pechacek & d'Oleire-Ottmanns 2004, Pechacek 2006), and similar studies on WbW have only been conducted in the Pyrenees (Garmedia *et al*. 2006; subspecies *D. l. lilfordi*). Thus, before the present study there has been little information from other mountain ranges, including the Carpathians, which are inhabited by a significant part of the European population (but see Pavlik 1996).

4.1. Forest structure affects the occurrence of the White-backed Woodpecker

The occurrence of WbW was strongly determined by the degree of forest exploitation. The best models describing WbW occurrence in managed forests included road density – which was roughly two times higher in unoccupied than in occupied plots – signs of recent logging activity, and certain variables related to dead wood. Thus, in managed forests WbW was associated more with plots only slightly harvested that contained abundant dead and dying trees and older trees with dying and dead branches. In managed stands, trees with dying and dead branches (mainly beeches and sycamores) are more common than dying and dead trees (Kajtoch 2009, this study). Forest managers often remove dead and dying trees to decrease the likelihood of tree-pest insect infestations (e.g., Barnes *et al.* 1997) but may retain living trees with dead branches, as such trees still represent valuable timber. In such intensively-managed forests, WbW may be forced to forage on, and excavate nest cavities, in large dead branches (instead of decaying tree trunks). This may limit the breeding success and survival of WbW, as individuals have to invest more time and energy for finding food. Indeed, WbW was frequently observed foraging on such dead branches in managed stands, whereas in reserves they fed on more diverse kinds of dying and dead wood (authors' pers. obs.). Apart from tree trunks, such thicker branches also serve as important nesting places for this species (Matsuoka 1979, Aulén 1988, Hogvar *et al*. 1990, Bernoni 1994, Wesolowski 1995, Grangé *et al*. 2002).

Differences between WbW territories in reserves and in managed plots were best explained by the model containing road density and old (veteran) trees, whereas a model also including volume of dead wood was only slightly worse. This suggests that reserves represent important unmanaged habitat for the species, similar to populations of WbW in northern Poland (Sikora & Ryś 2004). According to the present data, the reserve plots also contained considerably more very old trees and dead wood in general than the managed-forest plots. Thus, the most important WbW occurrence predictors seem to generally suggest primeval conditions that are often absent from managed stands. Interestingly, in reserves the second-most important variable was the abundance of very old trees, whereas in managed stands the occupied WbW plots were characterised by the abundance of trees with dead and dying branches. Hence, merchantable trees with dead branches may, to some degree, substitute very old trees in managed forests.

White-backed Woodpecker prefers variable deciduous or mixed forests over pure beech forests (Kajtoch 2009). The species is more common in the eastern Carpathians where forests largely consist of several deciduous tree species with similar proportions (Hordowski 1999). These tree species include beech, sycamore, lime *Tilia* spp., poplar *Populus* spp., willow *Salix* spp., cherry *Prunus* spp., ash *Fraxinus* spp. and elm *Ulmus* spp. Also the Carpathian Foothills host up to 30% of the Polish Carpathian population of WbW (Ł. Kajtoch, unpubl. data) where forests harbor diverse tree species (Kajtoch 2009). In typical managed patches, WbW is commonly found in beech woods, but apparently due to a deficiency of other deciduous trees rather than an actual preference for beech (Kajtoch 2009).

4.2. The importance of forest structure for the Tree-toed Woodpecker

The occurrence of TtW in managed forests was strongly and negatively affected by road density, a surrogate measure for forest exploitation. Moreover, the best model included signs of past harvesting, as the occupied TtW plots showed over two times fewer signs of intense forestry than the unoccupied plots. The importance of these two variables can be explained through an avoidance of highly utilized forest patches by the woodpeckers.

Amount of dead and dying and very old trees also positively affected the occurrence probability of TtW. Occupied plots contained nine times more very old (veteran) trees, three times more dying trees, and 13 times more dead spruce trees. Clearly, TtW appears strongly dependent on dying and dead spruce trees through requirements for bark beetles for food (cf. Fayt *et al.* 2005) and sufficiently large weakened or dead trees for cavity excavation. Patches characterized by large numbers and amounts of dead and dying trees were exclusively limited to steeper slopes where logging is not feasible. Interestingly, TtW preferred patches with lower tree diversity. Apart from the strong dependence of this species on spruce trees, this finding can be interpreted through the fact that spruce monocultures are prone to wind-caused and other smaller-scale disturbances (cf. Kuuluvainen 2009) which increase the amount of dying and dead wood.

The present results might be affected by the exclusion of difficult-to-access territories, but this issue concerns only TtW, as about 25% of its territories could not be considered in this work. An inclusion of these territories could have affected the present dead-wood estimates differently in occupied and unoccupied plots.

4.3. Thresholds of dead wood and dying trees

Environmental factors related to the number and volume of dead and dying wood turned out to be significant predictors for the occurrence of woodpeckers at the Beskid Wyspowy Mountains, Western Carpathians. Dead and dying wood were considerably more numerous and abundant in occupied than in unoccupied plots for both species, suggesting threshold conditions for woodpecker occurrence and territory formation in managed forests. The thresholds for TtW in managed forests were approximately 30 m^3 ha^{-1} of dead wood and 115 m^3 ha^{-1} of dying trees, preferably spruce trees with bark falling off. The thresholds for WbW in managed-forests had approximately 50 m^3 ha^{-1} of dead and 35 m^3 ha^{-1} of dying trees, mainly older beeches and sycamores. Similar amounts of dead and dying wood were found in occupied WbW plots of reserves, which can be considered additional evidence that these numbers represent threshold conditions. These numbers of dead wood correspond with those obtained in lowland and mountain forests of Europe (Nilsson *et al.* 2002). Between 10 and 58 m^3 ha^{-1} of dead wood should be present in WbW territories (Angelstam 2002, Frank 2002, Czeszczewik & Walankiewicz 2006, Roberge *et al.* 2008a), and for TtW, between 11 m^3 ha^{-1} and >100 m^3 ha^{-1} (Penttilä *et al.* 2004, Pechacek & d'Oleire-Ottmanns 2004, Bütler *et al.* 2004a, Kratzer 2008). For efficient conservation of WbW and TtW, at least 10–20 m^3 ha^{-1} of dead wood over areas larger than 100 ha should be retained (Angelstam *et al.* 2003, Bütler *et al.* 2004b). But thresholds of these values for 100% probability of occurrence in the Carpathian forests should be at least two times higher for both species. These values of dead and dying trees in unoccupied plots were from five to eight times lower than what is required by these species (see above).

Managed mountain forests of the Polish Carpathians host 220–270 m^3 ha^{-1} of deciduous and 270–320 m^3 ha^{-1} of coniferous wood (Central Statistical Office – Forestry 2009). Given these values, the dead wood threshold for WbW translates to retention of 20% of the total volume of wood in a given forest patch and to 10% for TtW. However, in many semi-natural forests in the Carpathians where logging is not feasible, or in reserves, the total wood volume is much higher – up to 1,000 m^3 ha^{-1} (Holeksa *et al.* 2009) and the volume of dead wood can be 130–140 m^3 ha^{-1} (Christensen *et al.* 2005, Svoboda & Pouska 2008). These values demonstrate that, in terms of dead wood, the occupied managed-forest plots were 3–4 times poorer than semi-natural (mostly protected) forests. These differences obviously have a strong influence on populations of the two focal species, as their home ranges encompass a few dozen ha in unmanaged and managed semi-natural and a few hundred ha in managed forests (Hogstad & Stenberg 1994, Wesołowski 1995, Amcoff & Ericsson 1996, Głowaciński & Wesołowski 2001, Pechacek 2004). The observed dead-wood biomass, necessary for the survival of TtW and WbW, is similar to reported dead-wood percentages in natural forests but higher than those found in managed forests (10–37% and 1–7%, respectively; Bobiec 2002, Siitonen 2001, Holeksa 2001). Unmanaged forests of high conservation value cover about 15% of the forested area in the Western Carpathians, mostly on steep, rocky slopes and in swampy areas (Stachura-Skierczyńska 2007). However, sanitary logging may be carried out even in these patches. Refraining from logging in these patches would support woodpecker populations, but FSC-certified forests in Poland are subject to regulations requiring that dead wood account for at least 5% of the total wood volume. The present data show that even this is 2–4 times less than the minimum requirements by woodpeckers: consequently, WbW and TtW are scarce in managed forests, even in mountains (e.g., Kajtoch 2009, Matysek & Kajtoch 2010).

4.4. Influence of forest management on woodpeckers

The "standing crop" of dead wood at a given time is a result of the balance between the processes of generation and loss (Friedman & Walheim 2000). This balance appears crucial for dead-wood dependent organisms, such as woodpeckers. In Europe, WbW and TtW are probably the woodpecker species most negatively affected by forestry (Wesołowski *et al.* 2005, Czeszczewik & Walankiewicz 2006). Forest quality and management methods are pivotal for the occurrence of these species (Wesołowski *et al.* 2005, Czeszczewik & Walankiewicz 2006), and as sedentary specialists, these species are extremely sensitive to habitat loss (Opdam 1990). The local declines of WbW and TtW populations in Poland can often be explained by habitat destruction due to intensive sanitary logging (Wesołowski *et al.* 2005, Czeszczewik & Walankiewicz 2006). This seems to be the case also in the Beskid Wyspowy Mountains, where extensive logging especially in spruce stands during 2009–2011 caused the loss of five TtW territories and two WbW territories in the present study area (Ł. Kajtoch, unpubl. data).

Although WbW and TtW are sometimes considered old-growth forest species (Mikusiński & Angelstam 1997, Mikusiński *et al*. 2001, Roberge *et al*. 2008a), they are probably evolutionarily adapted to natural disturbance dynamics, driven by, e.g., wildfire, windfalls and insect outbreaks (cf. Kuuluvainen 2009). Logging, however, would prevent the accumulation of dead wood, even if these events occurred in unmanaged patches (Pakkala *et al*. 2002). In the present managed forests, these woodpeckers were mostly found in patches with little or no management, but also patches recently affected by wind storms and subsequent bark beetle infestations support at least TtW (Kajtoch 2009, Matysek & Kajtoch 2010).

We show that timber harvesting and the consequent removal of old, dying and dead trees strongly and negatively affected the two focal woodpecker species, which supports conclusions of Mikusiński and Angelstam (1997). Accordingly, woodpecker territories were often at sites with limited access to logging vehicles (i.e., on steep slopes with few roads in the vicinity). Slope inclinations were 1.3–1.6 times steeper, and road densities were 1.5 times lower, in occupied than in unoccupied woodpecker plots. Dead and dying wood may be more abundant on steeper slopes, which makes them suitable for woodpeckers. Similar "unintentional conservation" of woodpeckers occurred also in remote post-fire forests in Canada (Schmiegelow *et al.* 2006, Koivula & Schmiegelow 2007). In accordance with these patterns, road density was negatively correlated with the volume of dead wood, and was indirectly associated with the spatial distribution of TtW in the Swiss mountains (Bütler *et al*. 2004a). Not surprisingly, intensive logging and associated removal of dead wood resulted in a WbW decline in the managed parts of the Bialowieża Forest (Czeszczewik & Walankiewicz 2006). On the other hand, the occurrence of WbW and TtW in managed mountain forests may be beneficial for forestry due to their role in controlling bark-beetle populations (Bütler & Schlaepfer 2003, Fayt *et al*. 2005).

4.5. Implications for conservation

The protection of WbW and TtW populations requires the protection of their habitats. This would in turn support several other rare species dependent on natural and semi-natural forests, such as secondary cavity-nesting birds and mammals, and insects living in dead wood (Fleishman *et al*. 2000, Mikusiński *et al*. 2001, Angelstam *et al*. 2003, Roberge *et al*. 2008b).

Critical values of dead wood for the occurrence of WbW and TtW in managed mountain forests provide useful guidelines for conservation strategies for these two species. The ecological requirements of WbW and TtW (in terms of dead wood and associated supply of dead-wood dependent beetles) are hardly compatible with the classic clear-cut based forestry (Mikusiński & Angelstam 1997). To counteract the negative impacts of forestry, the present data have already been used to define criteria for the monitoring of WbW and TtW habitat in Special Protection Areas for birds in the Polish mountains as part of the Natura 2000 network (Rejt *et al.*, in press). These criteria may also help prepare guidelines for management and conservation officials commissioned by the General Directorate for Environmental Protection in Poland.

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Metsän rakenteen vaikutus kahden erikoistuneen tikkalajin esiintymiseen Puolan Karpaateilla

Valkoselkä- (*Dendrocopos leucotos*) ja pohjantikka (*Picoides tridactylus*) ovat harvinaisia lajeja, jotka asuttavat Euroopassa luonnontilaisen kaltaisia, runsaslahopuustoisia vanhoja metsiä. Selvitimme metsikkörakenteen, puulajisuhteen ja vaikeapääsyisyyden suhdetta näiden kahden lajin esiintymiseen. Nämä ovat metsikkökohtaisia ympäristötekijöitä, joihin metsätaloudella voidaan vaikuttaa. Aineisto kerättiin 2007–2009 Beskid Wyspowyn vuorilla.

Valkoselkätikka suosi usean puulajin metsiä ennemmin kuin puhtaita pyökkimetsiä, kun taas pohjantikkaa löytyi ainoastaan kuusivaltaisista metsistä. Kynnysarvot valkoselkätikan esiintyvyydelle olivat noin 50 m^3/ha kuollutta ja 35 m^3/ha kuolevaa puuta, ja pohjantikalle vastaavasti noin 30 ja 115 m^3/ha. Nämä arvot olivat 5–8 kertaa korkeampia kuin satunnaispisteissä, joissa tikkoja ei tavattu. Molemmilla tikkalajeilla alempi hakkuuintensiteetti vaikeapääsyisillä rinteillä sekä korkeampi kuolleen ja kuolevan puun määrä olivat yhteydessä suurempaan esiintymisen todennäköisyyteen. Tulokset auttavat kehittämään tikkojen elinympäristöjen luokitteluperusteita Natura 2000 -verkostossa sekä kohentamaan metsänkäsittelyn ohjeiden ekologista kestävyyttä.

References

Amcoff, M. & Eriksson, P. 1996: Occurrence of Three-toed Woodpecker *Picoides tridactylus* at the scales of forest stand and landscape. — Ornis Svecica 6: 107–119.

Angelstam, P. & Mikusinski, G. 1994: Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. — Annales Zoologici Fennici 31: 157–172.

Angelstam, P.K., Anufriev, V.M., Balciauskas, L., Blagovidov, A.K., BorgegÍrd, S-O, Hodge, S.J., Majewski, P., Ponomarenko, S.V., Shvarts, E.A., Tishkov, A.A., Tomialojc, L. & Wesolowski, T. 1997: Biodiversity and sustainable forestry in European forests – how west and east can learn from each other. — Wildlife Society Bulletin 25: 38–48.

Angelstam, P. 2002: Reconciling land management with natural disturbance regimes in European boreal forests. — In Landscape ecology and resource management: linking theory with practices (eds. Bissonette J. & Storch, I.): 193–226. Island Press.

Angelstam, P., Bütler, R., Lazdinis, M., Mikusiński, G. & Roberge, J.-M. 2003: Habitat thresholds for focal species at multiple scales and forest biodiversity conservation – dead wood as an example. — Annales Zoologici Fennici 40: 473–482.

Aulén, G. 1988: Ecology and distribution history of the White-backed Woodpecker *Dendrocopos leucotos* in Sweden. — Swedish University of Agricultural Sciences, Department of Wildlife Ecology Report No. 14, Uppsala.

Aulén, G. & Lundberg, A. 1991: Sexual dimorphism and patterns of territory use by the Whitebacked Woodpecker *Dendrocopos leucotos*. — Ornis Scandinavica 22: 60–64.

Barnes, B.V., Zak, D.R., Denton, S.R. & Spurr, S.H. 1997: Forest ecology. Fourth edition. — John Viley & Sons.

Beers, T.W., Dress, P.W. & Wensel, L.C. 1966: Aspect transformation in site productivity research. — Journal of Forestry 64: 691–692.

Bernoni, M. 1994: The White-backed Woodpecker in the Abruzzo National Park. Contributi Scientifici Alla Conoscenza del Parco Nazionale d'Abruzzo 46: 1–68. (In Italian with English summary)

Bobiec, A. 2002: Living stands and dead wood in the Bialowieza Forest: suggestions for restoration management. — Forest Ecology and Management 165: 125–140.

Bruchwald, A. 1999: Dendrometria [Dendrometry]. SGGW. Warszawa. [in Polish]

Burnham, K. P. & Anderson, D. R. 2002: Model selection and multi-model inference: a practical information-theoretic approach. — Springer-Verlag, New York.

Burnham, K.P. & Anderson, D.R. 2004: Multimodel Inference. Understanding AIC and BIC in Model Selection. — Sociological Methods & Research 33: 261–304.

Bütler, R. & Schlaepfer, R. 2003: Three-toed woodpeckers as an alternative to bark beetle control by traps? — In International Woodpecker Symposium (eds. Pechacek, P. & d'Oleire-Oltmanns, W.): 13–26. Forschungsbericht 48, Nationalparkverwaltung Berchtesgaden.

Bütler, R., Angelstam, P., Ekelund, P. & Schlaepfer, R. 2004a: Dead wood threshold values for the Tree-toed woodpecker presence in boreal and sub-Alpine forest. — Biological Conservation 119: 305–318.

Bütler, R., Angelstam, P. & Schlaepfer, R. 2004b: Quantitative snag targets for the three toed woodpecker *Picoides tridactylus*. — Ecological Bulletin 51: 219–232.

Carlson, A. 1998: Territory quality and feather growth in the White-backed Woodpecker *Dendrocopos leucotos*. — Journal of Avian Biology 29: 205–207.

Christensen, M., Hahn, K., Mountford, E.P., O'dor, P., Standova'r, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrśka, T. 2005: Dead wood in European beech (Fagus sylvatica) forest reserves. — Forest Ecology and Management 210: 267–282.

Conner, R. 1979: Seasonal changes in woodpecker foraging methods: Strategies for winter survival. — In The role of insectivorous birds in forest ecosystems (eds. Dickson, J.G., Conner, R.N., Fleet, R.R., Kroll, J.C. & Jackson, J.A.): 95–105. Academic Press, NY.

Czeszczewik, D. & Walankiewicz, W. 2006: Logging and distribution of the White backed Woodpecker *Dendrocopos leucotos* in the Białowieża Forest. — Annales Zoologici Fennini 43: 221–227.

Czeszczewik, D. 2009: Marginal differences between random plots and plots used by foraging White-backed Woodpeckers demonstrate supreme primeval utility of the Bialowieża National Park. — Ornis Fennica 86: 30–37.

Czuraj, M. 1991: Tablice miąższości kłód odziomkowych i drzew stojących. [Tables of logs and standing trees volumes] — Państowe Wydawnictwo.Rolnicze i Leśne, Warszawa. (In Polish)

Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. Official Journal of the EU, L 20, 26.1.2010

Edman, T.H.E., Angelstam, P., Mikusinski, G., Roberge, J.M. & Sikora, A. 2011: Spatial planning for biodiversity conservation: assessment of forest landscapes' conservation value using umbrella species requirements in Poland. Landscape and Urban Planning 102: 16–23.

Elling, W., Dittmar, Ch., Pfaffelmoser, K. & Rotzer, T. 2009: Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. — Forest Ecology and Management 257: 1175–1187.

Fayt, P. 1999: Available insect prey in bark patches selected by the Three-toed Woodpecker *Picoides tridactylus* prior to reproduction. — Ornis Fennica 76: 135–140.

Fayt, P., Machmer, M.M. & Steeger, C. 2005: Regulation of spruce bark beetles by woodpeckers-a literature review. —Forest Ecology and Management 206: 1–14.

Fleishman, E., Jonsson, B.G. & Sjagren-Gulve, P. 2000: Focal species modeling for biodiversity conservation. — Ecological Bulletins 48: 85–99.

Frank, G. 2002: Brutzeitliche Einnischung des Weißrückenspechtes *Dendrocopos leucotos* im Vergleich zum Buntspecht Dendrocopos major in montanen Mischwäldern der nördlichen Kalkalpen. — Die Vogelwelt 123: 225–239. (In German)

Freckleton, R.P. 2011: Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. Behavioral Ecology and Sociobiology 65: 91–101.

Fridman, J. & Walheim, M. 2000: Amount, structure, and dynamics of dead wood on managed forestland in Sweden. — Forest Ecology and Management 131: 23–36.

Garmendia, A., Ca'rcamo, D. & Schwendtner, O. 2006: Forest management considerations for conservation of Black Woodpecker *Dryocopus martius* and White-backed Woodpecker *Dendrocopos leucotos* populations in Quinto Real (Spanish Western Pyrenees). — Biodiversity and Conservation 15: 1399–1415

Gjerde, I., Sćtersdal, M. & Nielsen, T. 2005: Abundance of two threatened woodpecker species in relation to the proportion of spruce plantations in native pine forests of western Norway. — Biodiversity and Conservation 1514: 377–393

Głowaciński, Z. & Wesołowski, T. 2001: Dzięcioł białogrzbiety [White-backed Woodpecker]. — In Polska Czerwona Księga Zwierząt [Polish Red Data Book of Animals] (ed. Głowaciński, Z.): 248–250. — PWRiL Warszawa. (In Polish with English summary)

Grangé, J.-L., Auria, J.-C., André, C. & Navarre, P. 2002: Biologie de reproduction du Pic ŕ dos blanc Dendrocopos leucotos lilfordi dans les Pyrénées occidentales (France). — Nos Oiseaux 49: 199–212.

Gutowski, J.M., Bobiec, A., Pawlaczyk, P. & Zub, K. 2004: Second life of tree. — WWF Polska: 30–41.

Hansen, A. J., Spies, T. A., Swanson, F. J. & Ohmann, J. L. 1991: Conserving biodiversity in managed forests. — BioScience 41: 382–392

Hogstad, O. & Stenberg, I. 1994: Habitat selection of a viable population of White-backed Woodpeckers *Dendrocopos leucotos*. — Fauna Norvegica Ser. C 17: 75–94.

Hogstad, O. & Stenberg, I. 1997: Breeding success, nestling diet and parental care in the White-backed Woodpecker *Dendrocopos leucotos*. — Journal of Ornithology 138: 25–38.

Hogvar, S., Hogvar, G. & Monness, E. 1990: Nest site selection in Norwegian woodpeckers. — Holarctic Ecology 13: 156–165.

Holeksa, J., Saniga, M., Szwagrzyk, J., Czerniak, M., Staszyńska, K. & Kapusta, P. 2009: A giant tree stand in the West Carpathians – an exception or a relic of formerly widespread mountain European forests? — Forest Ecology and Management 257: 1577–1585.

Holeksa, J. 2001: Coarse woody debris in a Carpathian subalpine spruce forest. — Forstwissenschaftliches Centralblatt 120: 256–270.

Hordowski, J. 1999: Ptaki Polskich Karpat Wschodnich i Podkarpacia [Birds of Polish Estern Carpathians and Podkarpacie]. T. I Pteroclidiformes Passeriformes. — Badania nad ornitofauną Ziemi Przemyskiej. 7: 1–186. (In Polish)

Hosmer, D.W. & Lemeshow, S. 1989: Applied logistic regression. — Wiley. New York.

Hurvich, C.M. & Tsai, C-L. 1989: Regression and time series model selection in small samples. — Biometrika 76: 297–307.

Hurvich, C.M. & Tsai C-L. 1991: Bias of the corrected AIC criterion for underfitted regression and time series models. — Biometrika 78: 499–509.

Hutcheson, T.P. 1970: A test for comparing diversities based on the Shannon formula. — Journal of Theoretical Biology 29: 151–154.

Imbeau, L. & Desrochers, A. 2002: Area sensitivity and edge avoidance: the case study of the Three-toed Woodpecker *Picoides tridactylus* in a managed forest. — Forest Ecology and Management 164: 249–256.

Kajtoch, Ł. & Piestrzyńska-Kajtoch, A. 2006: Awifauna środkowej części Beskidu Wyspowego – propozycje ochrony [Birds of central part of Beskid Wyspowy Mts. – proposition of protection]. — Chrońmy Przyrodę Ojczystą 62: 33–46. (In Polish with English summary)

Kajtoch, Ł. 2009: Występowanie dzięciołów: trójpalczastego *Picoides tridactylus* i białogrzbietego *Dendroco-*

pos leucotos w Beskidzie Wyspowym [Occurrence of the Three-toed woodpecker *Picoides tridactylus* and White-backed woodpecker *Dendrocopos leucotos* in Beskid Wyspowy Mts. (SE Poland)]. — Notatki Ornitologiczne 50: 85–96. (In Polish with English summary)

Kajtoch, Ł. 2010: Beskid Wyspowy. — In Ostoje ptaków o znaczeniu międzynarodowym w Polsce [Important Bird areas of international importance in Poland]. (eds. Wilk, T., Jujka, M., Krogulec, J. & Chylarecki, P.): 378–380. OTOP, Bogucki Wyd. Nauk., Poznań. (In Polish with English summary)

Koivula, M.J. & Schmiegelow, F.K.A. 2007: Boreal woodpecker assemblages in recently burned forested landscapes in Alberta, Canada: effects of post-fire harvesting and burn severity. — Forest Ecology and Management 242: 606–618.

Kondracki, J. 2000: Geografia regionalna Polski. [Regional geography of Poland]. PWN, Warszawa. (In Polish)

Kornacki, A. & Sokołowska, E. 2010: The estimation of smooth operation time until failure with the application of the Akaike Information Criterion (AIC). — Maintenance and Reliability 45: 69–76.

Kratzer, R. 2008: Totholzschwellenwertanalyse für die Habitate des Dreizehenspechts (*Picoides tridactylus alpinus*) im Schwarzwald.Diploma, Fakultät für Forst- und Umweltwissenschaften. — University Freiburg, Freiburg.

Krebs, C.H. 1989: Ecological methodology. — Harper Collins, New York.

Kuuluvainen, T. 2009: Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. — Ambio 38: 309–315.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson D.R. 1992: Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. — Ecological Monographs 62: 67–118.

Lehikoinen, A., Lehikoinen, P., Lindén, A. & Laine, T. 2011: Population trend and status of the endangered White-backed Woodpecker *Dendrocopos leucotos* in Finland. — Ornis Fennica 88: 195–207.

Lőhmus, A., Kinks, R. & Soon, M. 2010: The importance of dead-wood supply for woodpeckers in Estonia. — Baltic Forestry 16: 76–86.

Martikainen, P., Kaila, L. & Haila, Y. 1998: Threatened beetles in White-backed Woodpecker habitats. — Conservation Biology 12: 293–301.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T. & Martin, R.E. 1979: Dead and down woody material. In Wildlife habitats in managed forests (ed. Thomas, J.W.): 78–95. The Blue Mountains of Oregon and Washington, USDA Forest Service, Agriculture Handbook No. 553, Portland–Washington DC.

Matsuoka, S. 1979: Ecological significance of the early breeding in White-backed Woodpeckers *Dendrocopos leucotos.* — Tori 28: 63–75.

Matuszkiewicz, J.M. 2008: Zespoły leśne Polski. [Forest assemblages of Poland]. PWN, Warszawa. (In Polish)

Matysek, M. & Kajtoch, Ł. 2010: Dzięcioł bialogrzbiety *Dendrocopos leucotos* i dzięcioł trójpalczasty *Picoides tridactylus* w Beskidzie Średnim [White-backed woodpecker *Dendrocopos leucotos* and Three-toed woodpecker *Picoides tridactylus* in Beskid Średni Mountains (SE Poland)]. — Ornis Polonica 3: 231–234. (In Polish with English summary)

Menard, S. 2002: Applied Logistic Regression Analysis. — Thousand Oaks, CA: Sage.

Mikusiński, G.& Angelstam, P. 1997: European woodpeckers and anthropogenic habitat change: a review. – Die Vogelwelt 118: 277–283.

Mikusiński, G. & Angelstam, P. 1998: Economic geography, forest distribution, and woodpeckers diversity in Central Europe. — Conservation Biology 12: 200–208.

Mikusiński, G., Gromadzki, M. & Chylarecki, P. 2001: Woodpeckers as indicators of forest bird diversity. — Conservation Biology 15: 208–217.

Mikusinski, G. 2006: Woodpeckers (Picidae) – distribution, conservation and research in a global perspective. — Annales Zoologici Fennici 43: 86–95.

Nilsson, S.G. 1992: Population trends and fluctuations in Swedish woodpeckers. — Ornis Svecica 2: 13 – 21.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G. & Ranius, T. 2002: Densities of large living and dead trees in old-growth temperate and boreal forests. — Forest Ecology and Management 161: 189–204.

Nowak, D. 2003: Agresywne zachowania dzięcioła dużego *Dendrocopos major* i dzięcioła białogrzbietego *D. leucotos* wobec dzięcioła trójpalczastego *Picoides tridactylus*. [Aggresive behaviour of Great Spotted Woodpeckers *Dendrocopos major* and White-backed Woodpeckers *D. leucotos* towards Three-toed Woodpeckers *Picoides tridactylus*.] — Notatki Ornitologiczne 44: 57.

Opdam, P. 1990: Dispersal in fragmented populations: the key to survival. In: Species Dispersal in Agricultural Habitats (eds. Bunce, R.G.H. & Howard, D.C.): 3–17. Belhaven Press, London.

Paine, R.T. 1966: Food web complexity and species diversity. — American Naturalist 100: 65– 75.

Pakkala, T., Hanski, I. & Tomppo, E. 2002: Spatial ecology of the three-toed woodpecker in managed forest landscapes. — Silva Fennica 36: 279–288.

Pavlik, S. 1996: Habitat distribution of woodpeckers (Aves, Picidae): Beech and oak forests. — Biologia 51: 213–217.

Pechacek, P. 2004: Spacing behaviour of Eurasian Three-toed Woodpeckers (*Piciodes tridactylus*) during the breeding season in Germany. — Auk 121: 58–67.

Pechacek, P. & D'oleire-Oltmanns, W. 2004: Habitat use of the Three-toed Woodpecker in central Europe during the breeding period. — Biological Conservation 116: 333–341.

Pechacek, P. 2006: Breeding performance, natal dispersal and nest site fidelity of the Three-toed Woodpecker in the German Alps. — Annales Zoologici Fennici 43: 165–176.

Penttilä, R., Siitonen, J. & Kuusinen, M. 2004: Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. — Biological Conservation 117: 271–283

Piotrowska, M.& Wesołowski, T. 2007a: Dzięcioł białogrzbiety *Dendrocopos leucotos*. — In Atlas rozmieszczenia ptaków lęgowych Polski 1985–2004. [The atlas of breeding birds od Poland 1985–2004] (eds. Sikora, A., Rohde, Z., Gromadzki, M., Neubauer, G. & Chylarecki, P.): 308–309. Bogucki Wyd. Nauk., Poznań. (In Polish with English summary)

Piotrowska, M. & Wesołowski, T. 2007b: Dzięcioł trójpalczasty *Picoides tridactylus* [Three-toed Woodpecker *Picoides tridactylus*]. — In Atlas rozmieszczenia ptaków lęgowych Polski 1985–2004 [The atlas of breeding birds of Poland 1985–2004] (eds. Sikora, A., Rohde, Z., Gromadzki, M., Neubauer, G. & Chylarecki, P.): 312–313. Bogucki Wyd. Nauk., Poznań. (In Polish with English summary)

Rejt, Ł. Figarski, T., Kajtoch, Ł., Zawadzka, D., Ciach, M. (eds.) (in press): Metody wyznaczania i monitorowania stanu zachowania siedlisk ptaków. [Methods for designation and monitoring of bird's habitats quality]. — General Directorate for Environmental Protection, Warszawa. (In Polish)

Roberge, J.M., Mikusinski, G. & Svensson, S. 2008a: The white-backed woodpecker: umbrella species for forest conservation planning? — Biodiversity & Conservation 17: 2479–2494.

Roberge, J.-M., Angelstam, P. & Villard, M.-A. 2008b: Specialised woodpeckers and naturalness in hemiboreal forests—deriving quantitative targets for conservation planning. — Biological Conservation 141: 997–1012.

Romero-Calcerrada, R. & Luque, S. 2006: Habitat quality assessment using weights-of-evidence based GIS modelling: The case of *Picoides tridactylus* as species indicator of the biodiversity value of the Finnish forest. — Ecological Modelling 196: 62–76.

Schmiegelow, F.K.A., Stepnisky, D.P., Stambaugh, C.A. & Koivula, M. 2006: Reconciling salvage logging of boreal forests with a natural-disturbance management model. — Conservation Biology 20: 971–983.

Siitonen, J. 2001: Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. — Ecological Bulletins 49: 11–41.

Sikora, A., Ryś, A. 2004: Rozmieszczenie, liczebność i siedliska dzięcioła białogrzbietego *Dendrocopos leucotos* na Warmii i Mazurach. [Distribution, abundance and habitat preferences of White-backed Woodpecker *Dendrocopos leucotos* in the regions of Warmia and Mazuria]. — Notatki Ornitologiczne 45: 150–160. (In Polish with English summary)

Smith, K.W. 2007: The utilization of dead wood resources by woodpeckers in Britain. — Ibis 149: 183–192.

Stachura–Skierczyńska, K. 2007: Ocena wartości biologicznej lasów w Polsce [Estimation of biological value of Polish forests]. — OTOP, Warszawa. (In Polish)

Stachura–Skierczyńska, K., Tumiel, T. & Skierczyński, M. 2009: Habitat prediction model for three-toed woodpecker and its implications for the conservation of biologically valuable forests. — Forest Ecology and Management 258: 697–703.

Stanisz, A. 2006: Accessible course in statistics in basing for the STATISTICA PL program on examples from medicine. Vol. 1: Basic statistics. — StatSoft Polska, Krakow (In Polish).

Svoboda, M.& Pouska, V. 2008: Structure of a Central-European mountain spruce old-growth forest with respect to historical development. — Forest Ecology and Management 255: 2177–2188.

Thirgood, J.V. 1989: Man's impact on the forests of Europe. —Journal World Forests Resources Management 4: 127–167.

Tucker, G.M. & Heath, M.F. (eds.) 1994: Birds in Europe – their conservation status. — BirdLife International, Conservation Series No. 3, Cambridge.

Wasilewski, J. 2001: Dzięcioł trójpalczasty [Tree-toed Woodpecker]. — In Polska Czerwona Księga Zwierząt [Polish Red Data Book of Animals] (ed. Głowaciński, Z.): 250–252. PWRiL Warszawa. (In Polish with English summary)

Wesołowski, T. 1995: Ecology and behaviour of White-backed Woodpecker (*Dendrocopos leucotos*) in a primaeval temperate forest (Białowieża National Park, Poland). — Vogelwarte 38: 61–75.

Wesołowski, T., Czeszczewik, D. & Rowiński, P. 2005: Effects of forest management on Three-toed woodpecker Picoides tridactylus distribution in the Białowieża Forest (E Poland): conservation implications. — Acta Ornithologica 40: 53–60.

Winkler, H., Christie, D. & Nurney, D. 1995: Woodpeckers: a guide to the woodpeckers, piculets and wrynecks of the World. — Pica Press, Sussex.

Vrška, T., Adam, D., Hort, L., Kola, R.T. & Jani, K.D. 2009: European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians – a developmental cycle or a linear trend induced by man. — Forest Ecology and Management 258: 347–356.