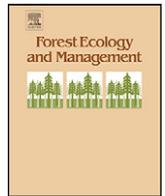




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Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Habitat prediction model for three-toed woodpecker and its implications for the conservation of biologically valuable forests

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ARTICLE INFO

Article history:

Received 22 December 2008

Received in revised form 5 May 2009

Accepted 8 May 2009

Keywords:

Three-toed woodpecker

Habitat selection

Forest management

Biologically Important Forests

Maxent model

ABSTRACT

We studied habitat selection of three-toed woodpecker (TTW) in relation to forest structural variables, habitat types and hydrological conditions in north-eastern Poland. Based on known locations of 34 breeding pairs and the data on location of forest areas with high conservation value (referred to as Biologically Important Forests), we created a habitat prediction model for TTW using a Maxent algorithm. We found that this species most often selected breeding sites characterized by high contribution of old-growth stands with uneven vertical structure and considerable amount of very old trees of previous generations, as well as boreal spruce-dominated bogs and riverine forests. Such sites were preferred regardless of their actual protection status, which leads to the following conclusion: although existing forest reserves are very important to three-toed woodpecker, suitable habitats with similar characteristics can still be found outside protected areas and are also utilized by the species. However, such sites outside reserves are threatened by fragmentation due to timber extraction. Therefore it is recommended to protect these sites by either including them into existing reserves or putting them under special management schemes.

The presented model can be applied in similar environmental conditions across lowland Europe, allowing for identification of representative habitat network for future conservation planning at landscape scale.

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1. Introduction

The three-toed woodpecker (TTW) *Picoides tridactylus* is widely recognized as a prey specialist, strongly dependent on habitats where the sufficient amount of insects living on recently dead conifers can be found (Mikusiński and Angelstam, 1998; Mikusiński et al., 2001; Angelstam et al., 2003; Roberge et al., 2008). The occurrence of TTW can be positively related with forest disturbances such as fire or wind falls (Fayt, 2003a), as well as with presence of old-growth stands with their natural dynamics. TTW is regarded as an indicator species for a guild of organisms dependent on dead wood (Roberge and Angelstam, 2006). Additionally, like other woodpecker species, it has a keystone value as a provider of cavities for secondary users. Finally, TTW plays particularly important role while considering economical aspects of forest management, due to its ability to control and limit bark beetle populations under epidemic levels (Fayt et al., 2005).

According to available literature, both TTW subspecies (*P.t. tridactylus*: Pakkala et al., 2002; Fayt, 2003a,b; Bütler et al., 2004a and *P.t. alpinus*: Bütler et al., 2004a; Pechacek and d'Oleire-Oltmanns, 2004; Pechacek, 2006) have been thoroughly studied, providing wide knowledge about species' habitat preferences. However, broader studies on the ecology of TTW population from the European lowland have been performed only in the unique conditions of Białowieża Primeval Forest, which cannot be compared to any other area in lowland part of Europe (Wesołowski and Tomiałojć, 1986; Wesołowski et al., 2005).

TTW, like other indicator species, is particularly suitable for habitat models due to its specific and well-defined requirements (Angelstam et al., 2004; Edenius and Mikusiński, 2006; Romero-Calcerrada and Luque, 2006). The TTW occurrence is correlated with presence of potentially valuable forest habitats; thus using it as a model-species provides efficient planning tool for management of such biologically important areas.

In this study we focus on two related aspects: (1) how to use the geographically oriented data on forest areas with high biological value in habitat prediction models for specialized woodpecker species, and (2) whether such models can be applied in practice as

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a basis for setting conservation targets in managed forest landscapes. The research was carried out in the Knyszyńska Forest (NE Poland), which represents an area of high biological value, but also a commercial forest with all aspects related to its productive functions; therefore our results can be implemented to other similar areas in lowland Europe.

2. Material and methods

2.1. Study area

Research was carried out in the Knyszyńska Forest (1260 km²) located in north-eastern Poland, a valuable breeding area of TTW, designated as an Important Bird Area and NATURA 2000 Special Protection Area (Sidło et al., 2004) (Fig. 1).

The forest landscape embraces broad river valleys, raised bogs and slight elevations. The dominant tree species are Scots pine *Pinus silvestris* and Norway spruce *Picea abies*; however, besides coniferous forest communities, broad-leaf and mixed stands are also present. In the past the Knyszyńska Forest was well connected to other large north-eastern European forests, but since the turn of the 18th–19th centuries the area has lost its linkages (Czerwiński, 1995). The best preserved fragments are located in 25 reserves totalling 49.7 km² (3.9% of Knyszyńska Forest area). However, only one of them (3.1 km²) is under strict protection. Outside protected areas, natural forest communities have been mostly replaced by planted stands revealing a simplified structure and altered tree species composition (Sokołowski, 2006). Clearcuts and intensive salvage cutting of spruce infested by the bark beetle *Ips typographus* are commonplace. Salvage cutting and sanitary measures are also practiced to some extent in nature reserves. Forest operations extend far into the bird breeding season.

2.2. Bird data

Data on TTW distribution was divided into two parts: (1) breeding pairs census within studied area carried out in years 2005–2007 (base locations), and (2) repeated census during verification of the model predictions in 2008 (new locations). Both censuses were done using the same method, in which census points were located inside potentially suitable TTW habitats, identified on the basis of known species' requirements. Woodpeckers were located using the playback stimuli during April and May. As many as 52 field visits were made, each one 6 h long on average. A single playback consists of 3–5 min of stimulation and 2 min of waiting for the response. Hearing points were located at least 500 m away from each other, in order to avoid double-counting the same individuals (Wesołowski et al., 2005; Tumił, 2008). Feeding sites and other signs of woodpeckers' presence (spontaneous calling or drumming) were also recorded and checked. The breeding pair was defined according to the Polish Ornithological Atlas (PAO) criteria (PAO, 1986). To ensure that each site was occupied by a breeding pair, 2–4 control visits were conducted during one season. Each breeding pair was located on topographic map (1:25 000 scale) and the coordinates were imported into ArcGIS 9.x software.

2.3. Environmental predictors

The data on the forest age and structure was taken from Belarusian-Polish Forest Mapping (BPFM) database (Yermokhin et al., 2007). The BPFM project is a part of the wider mapping programme, Biologically Important Forests (BIF) Mapping, aimed to identify and map European forests revealing a high concentration of habitats valuable for biological diversity. BIFs can be represented by forest patches of any size, partially overlapping existing legally protected areas, designated NATURA 2000 sites and

other valuable areas identified by various conservation initiatives, but also including forests selected on the basis of the project's specific criteria (Birdlife European FTF, 2008).

The information on BIFs was obtained mainly through the filtering of forest inventory database. The results were then associated with digital maps and transformed into generalized 25 ha grid (Yermokhin et al., 2007). For each 25 ha cell, the contribution of forest area meeting individual criteria was calculated (Table 1).

2.4. Statistical analysis

2.4.1. Habitat selectivity

We tested the model of habitat selection by woodpeckers based on comparison between the existing and randomly simulated populations. In this model TTW artificial locations were generated in random sequences within the study area with the average nearest distance between locations based on the data from existing populations ($N = 34$, mean = 1876 ± SE = 198 m). Random locations were generated using Hawth's Tools extension (Beyer, 2004) for ArcGIS 9.x. Data on forest parameters from the BPFM database was assigned both to existing and randomly generated locations. The differences between existing and simulated population were tested using a non-parametric Mann–Whitney *U*-test with Monte-Carlo exact test as a correction for random data (confidence level = 99%, number of resamples = 10 000). All statistics were performed with SPSS 16.0 for Windows.

2.4.2. Prediction model

In the model we used 25 ha grid cells by following reasons: (1) we focus on the habitat in the neighbourhood of nest hole, since, as it was observed in the field, this core area is mainly used by foraging individuals and has the highest probability of encountering woodpeckers; (2) the spatial resolution of BPFM database used in this study amounts to 25 ha, which is a trade-off between the analysis efficiency and the accuracy appropriate for regional scale analysis; and (3) producing more coarse resolution from source data can reduce explanatory power of predicted model (Luoto et al., 2007).

Table 1

Environmental predictors used for the model design.

Variable code	Description
Forest structural dataset (Yermokhin et al., 2007)	
NOACT	Limited forestry actions; no timber extraction except for occasional and sanitary cuts; areas designated as forest reserves
OG	Old-growth stands: stands over certain age (specific age limit was set for each dominant species, generally the stand was assumed as OG if it was 20 years older than cutting age)
STR1	Uneven age structure: age of trees in stand varies more than 30 years and average stand age is more than 80 years
STR2	Uneven canopy structure: presence of five or more species in dominant canopy layer, at least 50 years old (excluding understory)
STR3	Very old trees present: presence of single trees over 20 years of age limits set in criterion (OG)
Forest habitat and hydrological dataset (Czerwiński, 1995)	
BORBAG	Raised pine-bogs <i>Vaccinio uliginosi</i> - <i>Pinetum</i> , <i>Ledo-sphagnetum</i>
BORMECH	Pine bogs <i>Carici chordorrhizae</i> - <i>Pinetum</i>
BORPODM	Wet and bog conifer-dominated communities on sandy or dusty soils <i>Myceli-Piceetum</i> , <i>Quercu-Piceetum</i>
BORSWIER	Boreal spruce-dominated bogs <i>Sphagno-piceetum</i>
BRZEZINA	Bog forests with birch <i>Thelypteri-Betuletum</i>
GRUD	Mixed forests with spruce <i>Tilio-Piceetum</i>
LEG	Riverine forests <i>Circaeo-Alnetum</i> , <i>Fraxino-Ulmetum</i> , <i>Piceo-Alnetum</i>
OLS	Alder bogs <i>Carici elongatae</i> - <i>Alnetum</i>
HYDRO	Hydrogenic area

We used Maxent 3.2.1 algorithm which has been recently adapted to the modelling of species distribution (Phillips, 2005, 2008; Phillips et al., 2006; Phillips and Dudík, 2008). This approach allows to find the probability distribution of maximum entropy (closest to the uniform) subject to the constraints imposed by the information available regarding the observed distribution of the species and the environmental conditions across the study area (Phillips et al., 2006). The method assigns an occurrence probability to each grid cell within the study area. The input data includes a set of grid layers with environmental variables for a geographical region and a set of species presence data within that region. Maxent assumes *a priori* an uniform distribution and performs a number of iterations in which the weights are adjusted to maximize the average probability of the point localities, expressed as the training gain (Phillips, 2005). These weights are then used to compute the Maxent distribution over the entire studied geographic space. Maxent can be applied to presence-only data to produce habitat suitability predictions as a function of corresponding environmental variables. Higher function values indicate more suitable conditions for the given species (Phillips, 2005). In this study we used logistic function to describe the habitat prediction model for the TTW within Knyszyńska Forest. The highest function value (close to 1) indicates the most suitable habitat conditions for studied species, in contradiction to unsuitable habitat indicated by the lowest value (close to 0). Being aware of the fact that environmental variables are usually correlated with each other, we used jackknife analysis (based on the area under the curve (AUC) of a receiver operating characteristic (ROC) plot for each environmental layer) to evaluate their significance as predictors in this model. Occurrence locations (the dependent variable) were randomly partitioned into two subsamples: 75% used as training dataset and the remaining 25% reserved for testing the resulting (partitioned) models. This can be interpreted as the probability that a presence site will be ranked above a random background site (Phillips et al., 2006; Phillips, 2008; Phillips and Dudík, 2008). A random ranking has a value of around 0.5, while a perfect ranking achieves the maximum possible AUC of 1.0. Rankings with the AUC value above 0.75 are considered as potentially useful (Elith et al., 2006).

3. Results

3.1. Habitat selection model

While analysing the entire dataset for existing and simulated three-toed woodpecker populations, we found significant differences in almost all environmental predictors, except STR2, BORBAG, BORMECH and GRUD variables, that describe quite unique conditions, mostly limited to the reserves in the studied area. The greatest differences were observed between such environmental predictors as: limited forestry actions, presence of old-growth stands and flooded areas with riverine forest types (Table 2). We found no significant differences in all environmental predictors that characterized TTW breeding sites inside and outside forest reserves (Table 3). Based on direct observations, we observed that all of the TTW locations from existing population were associated with dead and/or decaying spruce trees and snags present in the field.

3.2. Habitat prediction model

The data used for preparing and testing of the prediction model for TTW appeared suitable and useful for Maxent analysis. The training AUC (0.976) and test AUC (0.955) were significantly different from random AUC (0.5) at a level of $p < 0.001$. The performance of logistic output was significantly better than raw

Table 2

Comparison of forest structure variables between existing (TTW-N, $N = 34$) and random locations (TTW-R, $N = 34$) of three-toed woodpecker. Significant values are given in bold. See Table 1 for the variable definitions.

Variable	TTW-N (Mean \pm SE)	TTW-R (Mean \pm SE)	Z	P value	P value*
NOACT	36.7 \pm 8.0	0.2 \pm 0.2	-3.858	<0.001	<0.001
OG	16.3 \pm 3.7	3.1 \pm 2.0	-3.813	<0.001	<0.001
STR1	15.3 \pm 4.0	4.9 \pm 2.6	-2.806	0.005	0.005
STR2	3.8 \pm 1.5	3.7 \pm 1.9	-0.823	0.411	0.494
STR3	11.9 \pm 3.8	3.4 \pm 2.0	-2.500	0.012	0.011
BORBAG	0.4 \pm 0.4	0.0 \pm 0.0	-1.000	0.317	1.000
BORMECH	2.8 \pm 2.8	0.0 \pm 0.0	-1.000	0.317	1.000
BORPODM	4.3 \pm 1.7	1.2 \pm 1.2	-2.277	0.023	0.029
BORSWIER	7.9 \pm 3.1	0.8 \pm 0.8	-3.129	0.002	0.002
BRZEZINA	3.9 \pm 2.0	0.0 \pm 0.0	-2.767	0.006	0.011
GRUD	1.3 \pm 1.2	0.0 \pm 0.0	-1.425	0.154	0.490
LEG	14.1 \pm 3.7	2.2 \pm 1.3	-2.928	0.003	0.002
OLS	22.0 \pm 4.7	0.0 \pm 0.0	-5.691	<0.001	<0.001
HYDRO	54.6 \pm 6.7	16.5 \pm 5.3	-4.228	<0.001	<0.001

* Monte-Carlo exact test.

Table 3

Comparison of forest structure variables between three-toed woodpecker locations inside (TTW-IN, $N = 14$) and outside (TTW-OUT, $N = 20$) reserves. See Table 1 for the variable definitions.

Variable	TTW-IN (Mean \pm SE)	TTW-OUT (Mean \pm SE)	Z	P value	P value*
OG	19.7 \pm 7.7	13.9 \pm 3.3	-0.110	0.913	0.931
STR1	22.5 \pm 8.1	10.3 \pm 3.6	-1.001	0.317	0.377
STR2	2.3 \pm 1.8	4.9 \pm 2.3	-0.792	0.428	0.592
STR3	20.0 \pm 7.9	6.2 \pm 2.8	-1.441	0.150	0.217
BORBAG	0.9 \pm 0.9	0.0 \pm 0.0	-1.195	0.232	0.743
BORMECH	6.7 \pm 6.7	0.0 \pm 0.0	-1.195	0.232	0.743
BORPODM	1.8 \pm 1.4	6.3 \pm 2.7	-0.811	0.417	0.545
BORSWIER	9.5 \pm 6.1	6.7 \pm 3.3	-0.295	0.768	0.823
BRZEZINA	7.7 \pm 4.6	1.3 \pm 1.0	-1.782	0.075	0.217
GRUD	3.1 \pm 2.9	0.0 \pm 0.0	-1.716	0.086	0.500
LEG	14.5 \pm 5.1	13.9 \pm 5.3	-0.760	0.447	0.522
OLS	18.5 \pm 6.9	24.4 \pm 6.4	-1.032	0.302	0.323
HYDRO	63.5 \pm 11.0	48.4 \pm 8.3	-1.267	0.205	0.217

* Monte-Carlo exact test.

output when using random background ($Z = -13.318$, $p < 0.001$, two-tailed Wilcoxon signed-rank test). The PCA analysis showed that environmental variables explained 71.7% of variance in the prediction model. A heuristic estimate of relative variable contributions implemented in Maxent, showed that the most important predictors were OLS (38.1%), NOACT (24.2%), BORSWIER (12.2%) and OG (9.6%) with cumulative 84.1% of share. As for the other predictors, the individual contribution in each case did not exceed 5%. The jackknife analysis showed that the most important variables were BORSWIER, OLS and OG which represented the highest ACU values for the TTW habitat prediction (Fig. 2).

Considering the above facts, we created the predictive habitat map for TTW. According to the model, the optimal habitat was found in 256 cells of studied area (Fig. 3) and showed the highest probability for encountering TTW, varying from 0.31 to 0.98. The suboptimal habitat was represented by 771 cells and showed lower probability of encountering TTW, varying from 0.11 to 0.30 (Fig. 3). Optimal habitats covered 3.9% of Knyszyńska Forest, while the existing population utilizes merely 0.5% of the total forest area (34 cells).

3.3. Model evaluation

In 2008 another TTW census was conducted. We found 11 additional locations, including eight described as new locations (territorial birds observation) and three described as possible

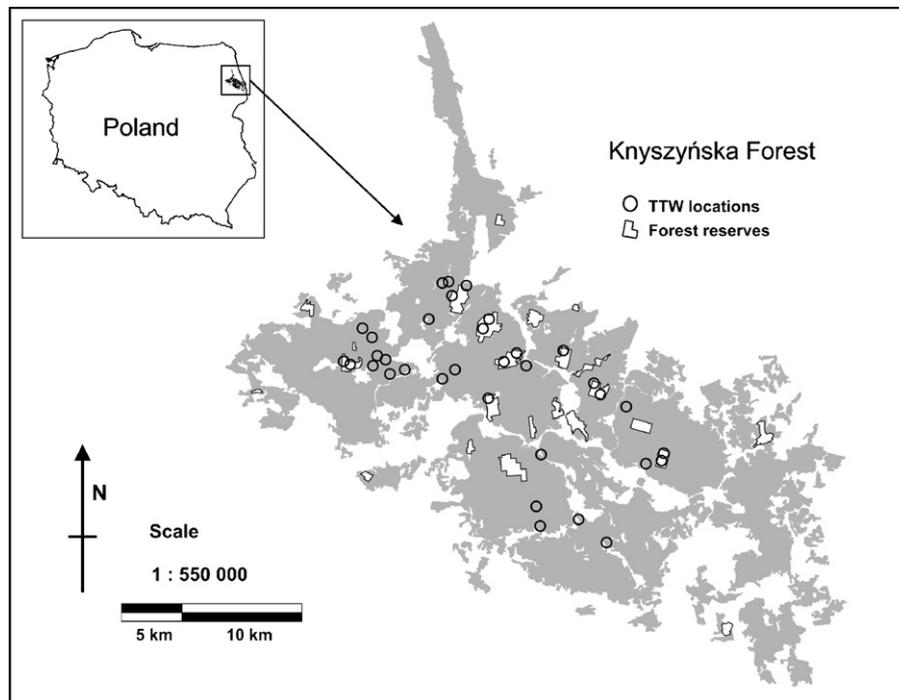


Fig. 1. Locations of studied three-toed woodpecker (TTW) population within Knyszyńska Forest and its reserves.

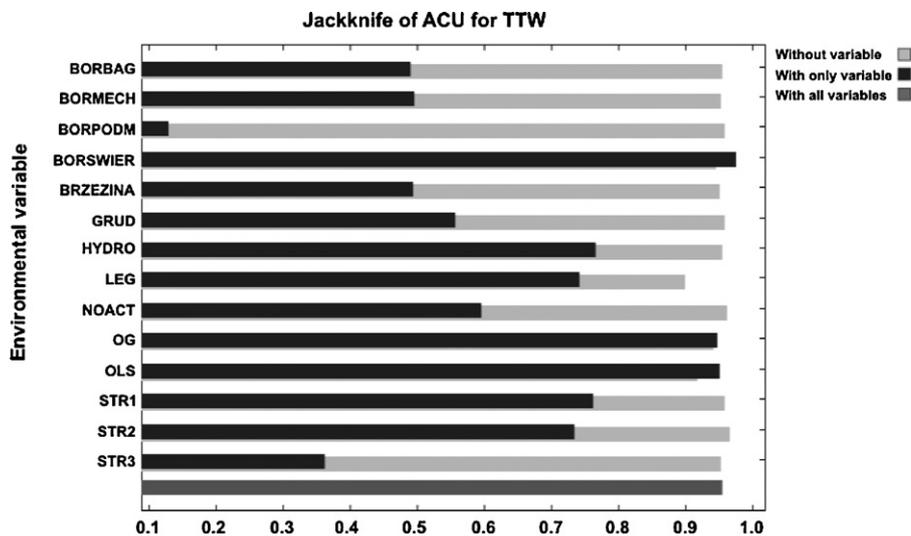


Fig. 2. The jackknife analysis of variable significance as a predictors in TTW model. TTW – three-toed woodpecker, AUC – the area under the curve of a receiver operating characteristic (ROC) plot.

locations (feeding sites, solitary birds without territorial behaviour). All these TTW locations were found in optimal ($N = 7$) and suboptimal ($N = 4$) habitats (Fig. 3). It seems worth noticing that the majority of best predicted habitats for TTW (suitable and optimal) is located outside existing reserves: 51.4% (36 cells), 75.8% (138 cells) for suitable and optimal habitats respectively and 68.8% (176 cells) for both classes together (Table 4). To sum up, the area of best habitats remaining outside reserves makes 2.7% of total area of Knyszyńska Forest (Fig. 4).

4. Discussion

According to our research it can be concluded that TTW in north-eastern Poland prefers natural and seminatural old-growth stands with considerable amount of snags rather than managed,

human altered forest habitats. Similar preferences were described for this species in another biologically important area in the region – the Białowieża Forest (Walankiewicz et al., 2002; Wesołowski et al., 2005) and also reported from a scope of various European TTW populations (Fayt, 2003a; Büttler et al., 2004a,b; Hanski and Walsh, 2004; Pechacek and d'Oleire-Oltmanns, 2004; Roberge et al., 2008).

TTW population in the Knyszyńska Forest was recently estimated by Tumiel (2008) at the level of 34 breeding pairs. Our results suggest that TTW population in studied area can be larger than what has been originally estimated. Considering the predicted amount of optimal habitat we estimate potential TTW population at the level of 50–60 breeding pairs. However, more research on TTW breeding success in optimal and suboptimal forest patches is needed. As far as we are concerned, there is no

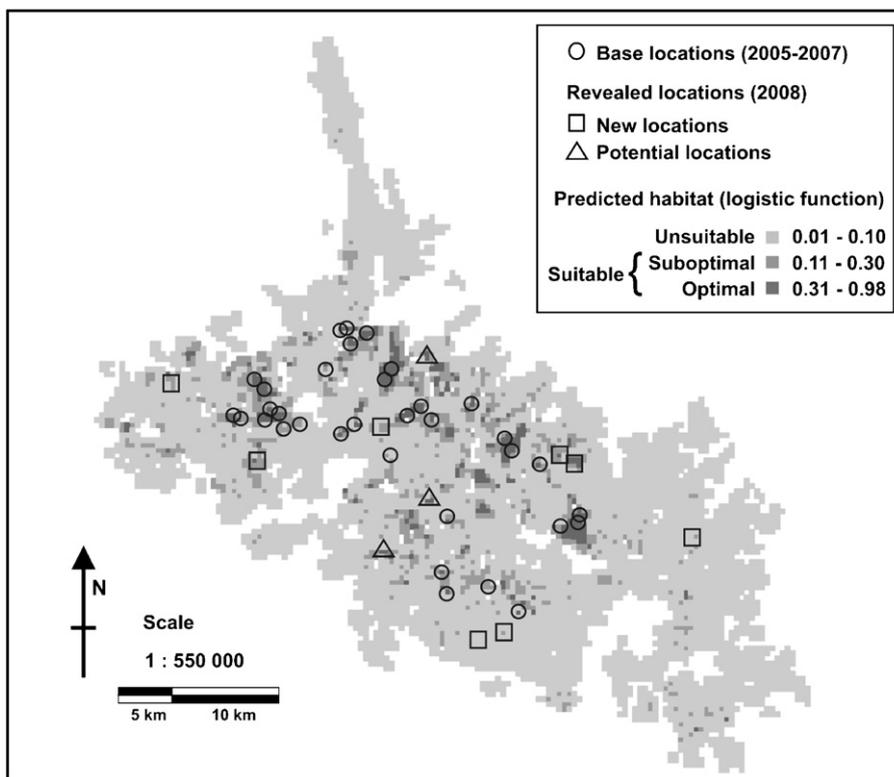


Fig. 3. Habitat prediction model for three-toed woodpecker in Knyszyńska Forest including TTW base and revealed locations. For description of base and revealed location see Section 2.2.

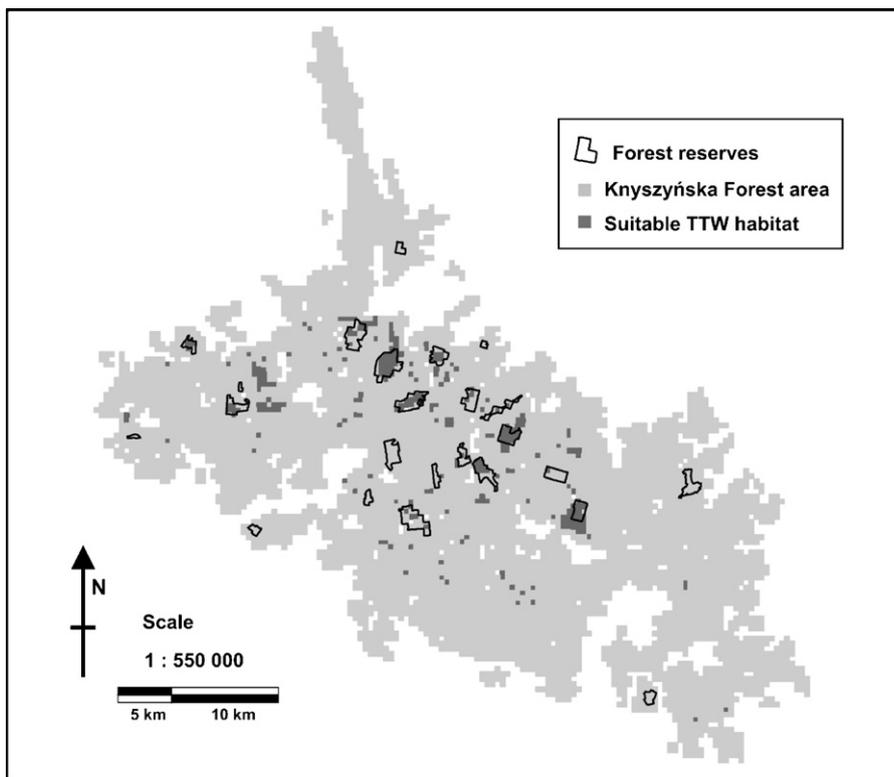


Fig. 4. Suitable and optimal TTW habitat inside and outside existing reserves within studied area.

sufficient data referring to the ability of studied Polish TTW populations to colonize new habitats that occur due to natural disturbances. On the contrary, such behavioural responses have been observed in North America, where TTW is able to recognize

disturbed forests (i.e. burned areas) and colonize new habitats quite rapidly (Villard, 1994; Murphy and Lenhasuen, 1998; Hoyt and Hannon, 2002). This can also be true for western and northern European populations which are characterized by quite good natal

dispersal patterns (Fayt, 2003b; Pechacek, 2006). On the other hand, while there are no suitable disturbances around, the species remains in old growths as well (Pakkala et al., 2002; Bütler et al., 2004a,b).

Another important fact is that 65% of TTW locations (22 out of 34) were situated close to the European beaver *Castor fiber* settlements or areas flooded by beavers, especially riverine stands with alder and spruce (Tumiel, 2008). Therefore, we presume that the presence of beavers and their settlements can positively influence the long-term survival of TTW population, due to continuous supply of snags and dead wood and maintenance of suitable habitats. Those suggestions were also supported by our results, where we found that the presence of hydrogenic areas with riverine and alder bog forests was positively correlated with TTW occurrence. Such coexistence of TTW and beavers was also recorded in Finland (Gorman, 2004) and North America (Short, 1974).

The relationship with stand vertical structure discovered in our study could be explained by the fact that the only remaining patches of suitable, dead wood-rich habitat were in natural stands, characterized by such diversified structure. No differences found in the STR2 structural variable can be explained by the feeding habits of TTW. This woodpecker is a prey specialist, searching for insects on snags of few tree species i.e. Norway spruce (Fayt, 1999, 2003a,b; Bütler et al., 2004b), therefore it does not depend on the stand species richness (an attribute described by the variable STR2).

Many of sites containing suitable TTW habitats remain unprotected at the moment. Clearcuts and sanitary felling practiced by the forest service contribute to the gradual loss of old-growth patches outside protected areas. Nevertheless, even the legal protection status of forest reserves does not prevent from removal of dying spruces. The importance of forest reserves for TTW in studied area is underlined by the fact that despite making up only 3.9% of total forest area they contained 41% of all TTW breeding pairs recorded during the study and similar findings were reported from this region of Poland also by Angelstam et al. (2002). However, only one of these reserves is strictly protected and the rest can be subjected to 'active protection' with all its consequences, i.e. sanitary cuttings. The lack of differences in forest structural variables between TTW nesting sites inside and outside reserves suggests two important conclusions: first, there are still sites characterized by similar features as nearly natural forests in reserves, but not protected at all; second, current conservation approach does not guarantee the preservation of all features typical for pristine, undisturbed forests. Nevertheless, it should be noticed that: (1) suitable habitats for TTW outside reserves are still quite rare, and not likely to be found by chance (see Table 2 for comparison), (2)

moreover, suitable sites outside reserves are threatened by fragmentation due to commercial use for timber extraction.

We estimated the amount of most suitable TTW habitat remaining outside reserves as 2.7% of total area of Knyszyńska Forest. It is strongly recommended that biologically valuable sites occupied by TTW in managed forest are also preserved in the future. Moreover, in order to prevent the effects of fragmentation into small, isolated patches of protected forest unable to maintain the viable populations at the regional scale, these 'key habitats' should be surrounded by functional buffers and connectors. Forest management in these zones should be focused on maintaining continuous forest cover and preserving the presence of over-mature trees and snags (Hanski and Walsh, 2004).

Despite the fact that unoccupied suitable habitats are still present, during field investigations we observed that they were subjected to regular sanitary cutting. As a result, the lack of key factor – old spruces, infested by bark beetle – prevents TTW from colonizing these sites. The conflict between biological and commercial values is a common problem in managed forest (see i.e. Wesolowski, 2005). Virkkala (2006) proposes the holistic approach: instead of costly and inefficient removal of infested trees, old-growth forests (preferred by i.e. three-toed woodpeckers) should be maintained and preserved in large enough quantities. Maintenance of viable populations of specific predators is an efficient way to solve the problem of pest control (Fayt et al., 2005). Allowing for natural processes in managed forests makes it possible to benefit from both timber extraction and nature protection (Virkkala, 2006).

5. Conclusions

The model presented above can be applied in other lowland European forests with similar environmental conditions, where data on TTW presence and location of Biologically Important Forests is available. What is more important, by applying models created for specialized forest-dwelling species, we are able to assess representative habitat networks for future direct conservation planning at landscape scale (Angelstam et al., 2004). As a result, we obtain a predictive map of new suitable habitat for considered species. In the next step, the locations of identified species-specific habitats should be compared with borders of existing protected areas (such as reserves). Such analysis enables to identify potential habitats that should be sustained in order to maintain the amount necessary for the survival of species population (Cowley et al., 2000) in that case for TTW.

Acknowledgements

We thank Marcus Walsh and Andrzej Bobiec for comments on the earlier draft of this manuscript and linguistic corrections. The Belarusian-Polish Forest Mapping (BPFM) was sponsored by Aage V. Jensens Fonde and conducted under supervision of Birdlife European Forest Task Force in 2005–2007.

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Table 4

Comparison of best predicted forest patches (suitable and optimal) inside (Forest-IN, $N = 40$) and outside (Forest-OUT, $N = 40$) reserves. Significant values are given in bold. See Table 1 for the variable definitions.

Variable	Forest-IN (Mean ± SE)	Forest-OUT (Mean ± SE)	Z	P value	P value*
OG	16.6 ± 3.3	34.4 ± 4.9	-2.839	0.005	0.002
STR1	15.7 ± 4.0	28.3 ± 5.5	-1.581	0.114	0.107
STR2	1.4 ± 0.6	3.5 ± 1.0	-1.574	0.116	0.109
STR3	18.4 ± 4.6	6.1 ± 1.4	-1.342	0.180	0.177
BORBAG	0.4 ± 0.4	0.1 ± 0.1	-0.018	0.986	1.100
BORMECH	3.7 ± 2.6	0.0 ± 0.0	-1.754	0.079	0.245
BORPODM	1.2 ± 0.5	5.2 ± 1.7	-1.940	0.052	0.048
BORSWIWER	3.6 ± 1.7	6.4 ± 2.4	-0.639	0.523	0.524
BRZEZINA	12.6 ± 4.0	0.7 ± 0.7	-3.509	<0.001	<0.001
GRUD	8.3 ± 2.7	2.1 ± 1.4	-2.082	0.037	0.045
LEG	10.3 ± 2.9	8.2 ± 2.6	-0.141	0.888	0.887
OLS	17.8 ± 3.6	10.7 ± 2.5	-1.065	0.287	0.289
HYDRO	58.3 ± 6.6	50.8 ± 7.0	-0.483	0.629	0.631

* Monte-Carlo exact test.

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