POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	60	4	805–814	2012

Regular research paper

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QUANTIFICATION OF ECOLOGICAL PREFERENCES OF THE CAPERCAILLIE *TETRAO UROGALLUS* BY MEANS OF THE HABITAT SUITABILITY INDEX: A CASE STUDY IN THE AUGUSTÓW FOREST (NE POLAND)

ABSTRACT: Habitat structure and selection by the Capercaillie *Tetrao urogallus* were assessed in the Augustów Forest (NE Poland), where a population of 50–80 birds and 11 active leks existed. Habitat preferences in the local scale were studied, based on measurements of total 1952 circular sample plots with radius of 15 m. On plots, in total, 10 variables describing forest structure (*e.g.* successional stage, canopy cover, vertical stand structure, share of Scots pine *Pinus sylvestris*, shrub layer cover, bilberry *Vaccinium myrtillus* cover, average height of ground vegetation, occurrence of feeding and roosting trees), as well as signs of Capercaillie presence, were assessed. Then, the model of Habitat Suitability Index (HSI) was constructed. Plots with high HSI scores were used by Capercaillie more often than expected in a case of a random choice, and those with low scores – less than expected. Capercaillie in the Augustów Forest prefers relatively old, one-layered stands, dominated by Scot pine with a sparsely developed shrub layer. The most important differences between abandoned and active leks were related to shrub cover in ground vegetation and height of ground vegetation and share of bilberry.

KEY WORDS: Augustów Forest, Capercaillie, forest structure, habitat suitability index, lek, *Tetrao urogallus*

1. INTRODUCTION

The population of Capercaillie *Tetrao urogallus*, a large, boreal bird species of Eurasia, has been strongly decreasing during the last decades, especially, in the western part of its natural range. The species is red listed in most of European countries, yet several local extinctions from Europe were reported (Storch 2000, 2001, 2007). A good knowledge of the habitat requirements of Capercaillie could help to actively protect this species. Its habitat preferences were evaluated by an analysis of stand structure on the display grounds in Norway and Slovakia (Rolstad and Wegge 1987, Saniga 1996). A detailed method of assessing habitat conditions for Capercaillie was developed in Scotland (Picozzi *et al.* 1992). Summers *et al.* (2004) assessed winter habitat preferences, based on feeding trees characteristics. Storch (1993) precisely described habitat used by telemetry-studied birds in the Bavarian Alps (Germany). During the last decade, in many mountainous areas of Central Europe, analysis of habitat structure and its key elements at different spatial scales were performed (Bollmann *et al.* 2005, Graf *et al.* 2005, 2006, Quevedo *et al.* 2006, Braunisch and Suchant 2007).

Storch (2002) applied for Capercaillie the Habitat Suitability Index (HSI) model, which is commonly used as a wildlife management tool in North America (see Verner *et al.*1986, van Horne and Wiens 1991). The HSI defines optimal habitat conditions, based on elements important for ecological requirements of the species (Storch 2002). The high HSI values describe habitat, which enables maximal density of a given species.

The aim of this study was to find a tool for effective protection of Capercaillie in the Augustów Forest (NE Poland), which harboured 50–80 birds and 11 active leks (displaying ground). This population has been steadily declining in the recent decades (Zawadzka and Zawadzki 2008). Detailed aims concerned: (1) to assess the applicability of the HSI model developed in Alps in the lowland forest in Poland, and (2) to assess differences in habitats between areas with active *versus* abandoned Capercaillie leks in order to test the hypothesis that changes in habitat occupancy were habitat-related. Habitat characteristics were measured on 9 active leks and 9 leks abandoned by Capercaillie during the last 25 years. We expected that the HSI will attain higher values on active leks than on abandoned ones. Furthermore, we expected to obtain information, which elements of forest habitats on abandoned leks had changed to make them unsuitable for Capercaillie.

Fig. 1. Study area in the Augustów Forest (NE Poland) for testing the Habitat Suitability Index of Capercaillie *Tetrao urogallus*. Black points – active leks, open points – abandoned leks.

2. STUDY AREA

The Polish part of the Augustów Forest (the AF) (NE Poland, 23°15'E, 54°N, Fig. 1) covers 1140 km^2. Forests, interspersed with marshes and lakes, cover fairly flat area. Climate has continental features. The mean annual temperature is 6.2°C. Vegetation period lasts for 135 days, and snow cover persists for about 100 days. The mean annual precipitation amounts to 547 mm. Forests cover 93% of the total area, and lakes 6%. Tree stands are dominated by the Scots pine *Pinus sylvestris* (78%), Norway spruce *Picea abies* (8%), black alder *Alnus glutinosa* (9%), birches *Betula pendula* and *Betula pubescens* (5%), and oak *Quercus robur* (1%). The mean age of tree stands is about 60 years. Most of the Augustów Forest are commercial stands managed by six forest districts of the Polish State Forests. The whole area of the AF is enlisted as the NATURA 2000 Birds Special Protection Area Puszcza Augustowska PLB200002.

Population of Capercaillie living in the AF is one of four isolated Polish populations of the species (Głowaciński and Profus 2001). We used data about localization of active and abandoned leks from our own field searches performed in 1996–2005 as well as from literature, questionnaires, personal communication with foresters and hunters (Zawadzka and Zawadzki 2008).

3. MATERIAL AND METHODS

3.1. Field work

Field work was carried out in July-August 2005 and July-September 2006 in the areas of 9 active and 9 abandoned leks. Habitat measurements were conducted in the area surrounding the leks, on circular plots, located in a 200 × 200 m grid (Fig. 2). Each plot had a radius of 15 m and covered 706 m^2 (see Storch 2002). The number of study plots per one lek area varied from 53 to 133 (depending on local conditions), on average 98, spread over 4 km^2. Nine active leks were represented by a total of 1032 plots and 9 abandoned leks by 747 circular plots. We assessed scores of 10 habitat features used to HSI construction in all the plots. In addition, Capercaillie signs (tracks, feathers, dustbaths, droppings) were searched in each plot in a smaller area of 5-m radius around the plot centre.

3.2. Habitat Suitability Index

Construction of the HSI model is based on a list of habitat variables, important for given species, combined in a simple equation. The equation takes values from 0 (unsuitable habitat) to 1 (excellent habitat). Based on knowledge about habitat requirements and preferences of Capercaillie, collected from publications, expert opinions, and direct field observations, we selected 10 habitats variables (comp. Morrison *et al.* 1992, Storch 2002). Range of variation of each parameter was divided into classes to which scores of Suitability Index (SI) from 0 to 1 were attributed (Tab. 1). In order to estimate the scores, we used data from a forest numerical map, providing the characteristics of stands growing on active and abandoned lek area. We took into account the successional stage of trees in the stand (age), share of Scots pine, canopy closure of the upper tree layer, canopy closure of the second tree layer, percentage cover of shrubs and bushes. The scores for height of the ground vegetation cover and percentage share of bilberries in the ground cover were adopted after Storch (1993, 2002). Presence of feeding trees, rotten trees, and ant hills was added based on our experience and Capercaillie habitat preferences described by Klaus *et al.* (1989) and (Graf *et al.* 2005). while scoring of the distance from road, we took into account the study by Summers *et al.* (2007) and personal observations.

The Habitat Suitability Index was calculated after Storch (2002), with some modification:

$$HSI = 0.2 *((SI_{suc} * SI_{can} * SI_{II\,lay}) + (2SI_{bil} * SI_{shr}) + SI_{veg} + SI_{elem}) * (SI_{pine} * SI_{stru}{}^{1/2})) * SI_{road} \quad (1)$$

where: abbreviations mean the following variables: SI_{suc} – successional stage (age) of tree stand, SI_{can} – canopy cover of the upper layer of trees, SI_{IIlay} – canopy cover of the second layer of trees, SI_{bil} – percentage share of bilberry in ground vegatation, SI_{shr} – percentage cover of bushes and shrubs, SI_{veg} – the height of ground vegetation, SI_{ele} – presence of structural elements, SI_{road} – the distance from road.

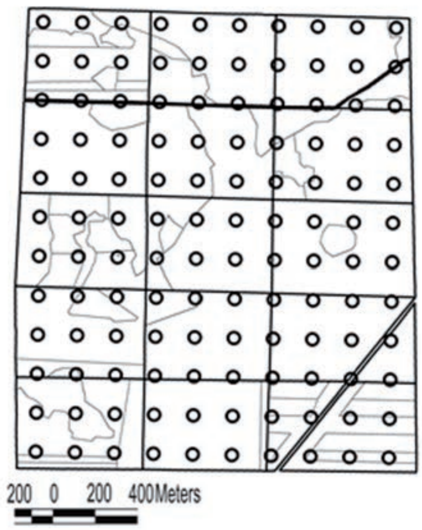

Fig. 2. Methodical design for field measurements of 10 habitat features in active and abandoned leks of Capercaillie. The whole rectangle – the area of lek and its surroundings (4 km^2). Measurements were conducted in small circular plots (15 m radius, located in 200 × 200 m grid). Thick lines – borders limits of forest compartments and roads, thin lines – borders limits of subcompartments (tree stands of different age or species composition).

When the HSI was constructed, we assumed that four elements of this index have compensatory effect (comp. Storch 2002). They were: successional stage of stands (age), canopy cover of the upper tree layer, canopy cover of the second tree layer ($SI_{suc} * SI_{can} * SI_{II\,lay}$), cover of the shrub layer, bilberry cover ($2SI_{bil} * SI_{shr}$), the height of ground vegetation (SI_{veg}), and presence of structural elements (old trees, rooten trees, and ant hills) (SI_{ele}). Among the four main components of HSI, the limiting factors can be successional stage of stand and canopy cover (both in the main and the second layer) on one hand, and the share of bilberries and shrub cover on the other hand. Ecological importance of bilberries was emphasized by giving this parameter double weight in comparison with other variables. Factors that may limit suitability of habitat for Capercaillie are also the share of pine in tree stand and stand vertical structure. We assumed that those factors may be partly compensatory and we used the geometric mean. Scores of those features are bigger than

Table 1. Values of suitability indices for 10 features of the forest habitat used for calculation of Habitat Suitability Index of Capercaillie. See text for further details.

Parameter	Value of Suitability Index (SI)								
	0	0.1	0.2	0.3	0.4	0.6	0.7	0.8	1
Age of tree stands (years)		0	1–10		11–30	31–60		>100	61–100
Tree stand structure			Two-layered	Multi-layered					Single-layered
Share of pine (%)			<20		20–50	50–70		70–90	>90
Canopy closure of upper layer	Absent			Full	Loose, medium				Discontinuous
Canopy closure of second layer			Full		Medium	Discontinuous		Loose	Absent
Cover of shrubs (%)			>60		40–60	20–40			0–20
Ground vegetation height (cm)	>80		70–80		60–70	<10, 50–60		10–20, 40–50	20–40
Cover of bilberries (%)					<10	10–20		21–30	>30
Presence of structural elements[1]				1 type present			2 types present		3 types present
Distance from roads (m)			<50			50–100		101–150	>150

[1] Three types of structural elements: old trees with horizontal branches good for perching, dead fallen trees, anthills.

zero, therefore, they cannot strictly limit Capercaillie occurrence. Similarly, in the case of the distance from road, scores were > 0.

3.3. HSI calculation and validation

HSI was calculated for each circular plot. Next, plots were sorted into 10 classes, depending on the HSI score, with 0–1 being unsuitable habitats and 9–10 being optimal habitats. For all plots in each class (1–10) we calculated mean HSI score, the relative frequency of all study plots in a given class, and the relative frequency of plots with a record of Capercaillie signs. Then, by using Ivlev's electivity index (Krebs 1989, after Storch 2002) we checked whether plots with higher HSI values were indeed preferred habitats for Capercaillie. The Ivlev's index is:

$$I = (U - A) / (U + A) \quad (2)$$

where: U is a fraction of plots with the Capercaillie signs in a given class of HSI, and A is a fraction of all plot in a given class of HSI index. I varies from -1 (completely avoided habitat) to 1 (maximal positive selection of habitat).

In order to check whether the differences between the mean value of HSI index of the active and the abandoned leks are significant, we performed a one-way analysis of variance with the non-parametric Kruskal-Wallis test, using the program STATGRAPHICS Plus. The relationship between Capercaillie traces and the score of HSI was obtained by analysis of regression in the STATGRAPHICS Plus program. Frequency distributions of the 10 habitat variables in active *versus* abandoned leks were compared with G-test for goodness of fit (calculated on percentages).

4. RESULTS

4.1. Habitat Suitability Index verified by Capercaillie occurrence on active leks

Traces of Capercaillie were recorded on 11.1% of plots surveyed in active leks (SE 2.7, range 2.5–23.7%) compared to only 0.4% plots in abandoned leks (SE 0.2, range 0–1.6%). The difference was highly significant (Mann-Whitney U-test, U = 81, P <0.0005). Moreover, the percentage of plots with Capercaillie signs positively correlated with the number of displaying cocks recorded on those leks in spring, which varied from 0 to 7 (n = 18 leks, Spearman's r = 0.867, P <0.05).

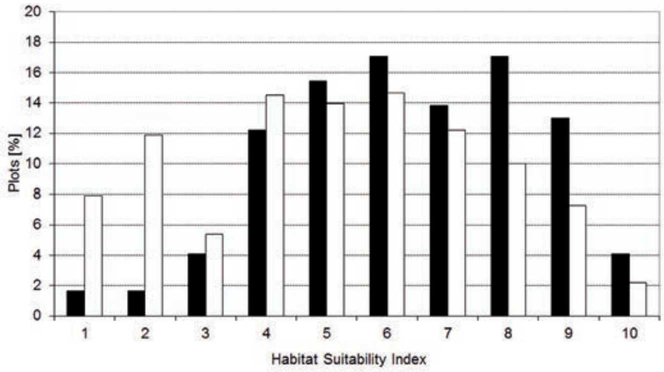

Fig. 3. Percentage of circular plots with (black bars) and without (white bars) Capercaillie signs in the active leks, by the classes of Habitat Suitability Index. 1, 2, 3 – unsuitable habitats, 8, 9, 10 – optimal habitats, 4, 5, 6, 7 – intermediate habitats.

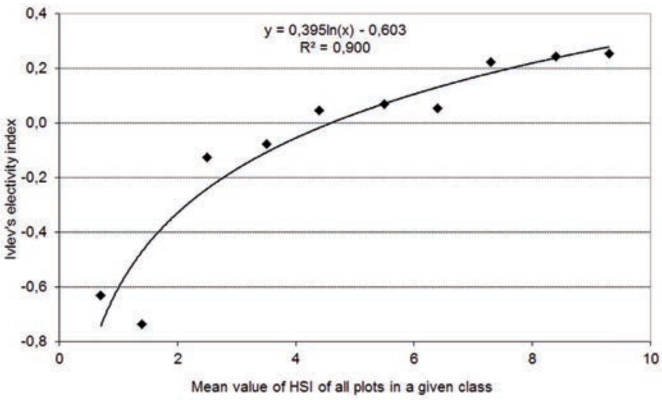

Fig. 4. Validation of the HSI model for Capercaillie (active leks). Correlations between Capercaillie habitat preferences, expressed by the Ivlev's electivity index (I) and HSI, I = 0.395 ln (HSI) – 0.603, n = 10, $R^2 = 0.90$, $P < 0.001$

All plots in active leks (n = 1033) were divided into 10 classes of the HSI values (class 1 being an unsuitable habitat, and class 10 the best habitat). Proportions of plots with Capercaillie signs recorded (n = 123) were lowest in the small HSI classes (from 1 to 3) and clearly increased in the upper classes (Fig. 3). The frequency distributions of plots with and without Capercaillie signs on active leks were significantly different (G = 192.10, df = 4, $P < 0.001$, calculations done for 5 major classes: 1–2, …, 9–10).

The Ivlev's electivity index (I) was positively correlated with HSI (Fig. 4). Thus, habitats with high values of HSI were actually preferred by Capercaillie.

The positive relationship between bird signs and HSI values was also evident in the regression analysis. The probability of finding Capercaillie signs (CS) has grown with the increasing HSI values (Fig. 5).

4.2. Habitat differences between active and non-active leks

The comparison of the HSI values calculated for all circular plots in active versus non-active leks has shown the difference between those two groups. The mean HSI for active leks was 4.8 ± 0.07, and for abandoned leks 4.2 ± 0.08. The difference was statistically significant (Kruskal-Wallis ANOVA, H = 25.31, $P < 0.0001$). The mean HSI values calculated for active leks varied from 4.3 to 5.5, on average 4.8 ± 0.13 (n = 9), while for abandoned leks they varied from 2.7 to 5.1, on average 4.0 ± 0.30 (n = 9).

The comparison of percentage distribution of plots from active and non-active leks in the 10 classes of HSI showed that plots located in active leks were more frequent in the classes from 7 to 10, but the difference between the two distributions was non-significant (G = 2.934, df = 4, *P*> 0.5), (Fig. 6).

In the last step, we checked which of the 10 habitat features used for HSI calculation, contributed most to the observed differences in the HSI scores between active and abandoned leks. The most important, statistically significant differences were found in the percentage cover of shrubs, the height of ground vegetation, and the share of bilberries in the ground cover (Fig. 7). Capercaillie preferred stands with very small admixture of bushes and young trees (< 10% cover) (G-test, G = 80.098, df = 3, *P* <0.001). The optimal height of ground vegetation on active leks was 21–40 cm and differed from abandoned leks (G = 6.91, df = 2, *P* < 0.05). Active leks often had moderate share (10–40%) of bilberry in the ground vegetation cover (G = 6.806, df = 2, *P* <0.05). The distribution of the other variables: successional stage, the second layer of trees, the canopy closure, share of pine in trees stand, species composition of trees and bushes, the distance from road, and presence of structural elements did not differ significantly between active and abandoned leks (G from 2.546 to 2.868, df from 1 to 3, *P*> 0.1).

5. DISCUSSION

Models of habitat suitability are valuable tools which help to formulate programs of active protection of Capercaillie (Storch 2002, Palahi *et al.* 2004, Bollmann *et al.* 2005, Hurstel 2005). Moreover, HSI may be useful for evaluation of habitat quality in the areas proposed for Capercaillie reintroduction. As shown by our study, HSI model created by Storch (2002) for the Bavarian Alps (Germany), after small modification, have a more universal character and may be used in other geographic regions as well. Validation by the Ivlev's electivity index and significant correlation between calculated HSI scores and frequency of Capercaillie signs indicated that the HSI model constructed for the Augustów Forest adequately reflected habitat preferences of Capercaillie in lowlands of North-Eastern Poland.

The Capercaillie has large spatial requirements and highly specialized habitat preferences (Rolstad *et al.* 1997, Storch 2001, Graf *et al.* 2005). According to Storch (2002) and Graf *et al.* (2005), the HSI model can explain well Capercaillie preference at small, local scale, but is not efficient to explain its presence or absence at the landscape scale. Graf *et al.* (2006), who studied Capercaillie preferences in the Swiss Alps and the Jura Mountain, recommended building more general habitat models using data pooled from several regions, when the aim is to predict Capercaillie distribution in independent regions. Models from only single region have limited application to other geographical regions (Graf *et al.* 2006). In the large spatial scale, the most important variables for determining Capercaillie potential habitat have a more universal character: soil conditions and number of days with snow (Braunisch and Suchant 2007).

Our study provided data to evaluate habitat quality for Capercaillie in the AF. However, although the HSI values for individual

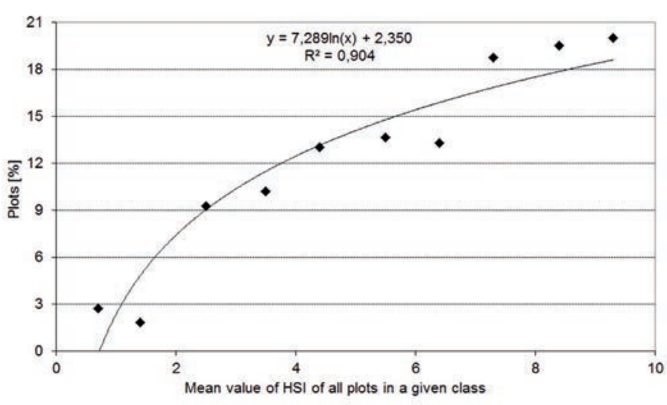

Fig. 5. Relationship between the mean HSI value and the relative occurrence of Capercaillie signs (CS) in active leks: CS = 2.041 + 2.010 HSI, n = 10, R^2 = 0.925, *P* <0.0001

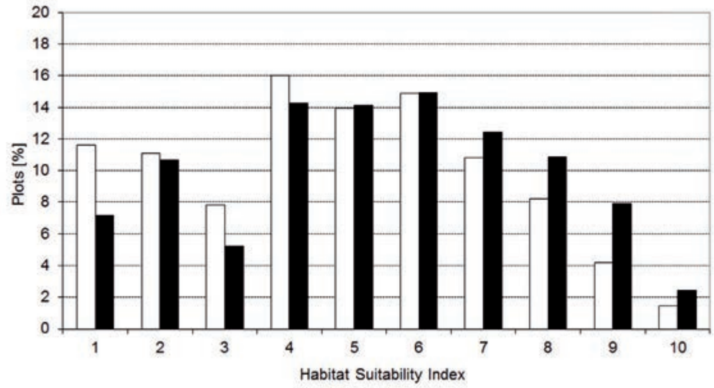

Fig. 6. Frequency distribution of sample plots from active (black bars) and abandoned (white bars) leks of Capercaillie in the HSI classes

plots (covering about 700 m^2 each) ranged from 0 to 10, the average HSI for the lek areas (4 km^2) did not exceed 5.5. It may indicate that in the AF habitats for Capercaillie are moderately suitable, but not optimal. The results also show the lack of excellent habitats on a scale of big forest patches, adequate for needs of a stable population.

Capercaillie is usually defined as a species associated with late successional stages of forest (Klaus *et al.* 1989, Storch 2001). Fragmentation of old forest stands, as a result of long-term, intensive forestry practices, are considered as one of the main reasons of Capercaillie decline in Europe (Storch 2001, 2007, Angelstam 2004, Bollmann *et al.* 2008). Another important habitat feature for this grouse species is the forest structure created by natural processes and forest management (Rolstad and Wegge 1987, Saniga 1996, 2003, Angelstam 2004, Valkeajarvi *et al.* 2007). In the AF, Capercaillie preferred one-layered stands, dominated by Scots pine, with moderate canopy closure, very sparse (< 10% cover) undergrowth, and relatively low ground vegetation, with a substantial share of bilberry. Comparison of active and abandoned leks showed that an increase in the undergrowth cover (shrubs, young trees) is detrimental for Capercaillie. In the AF, the dominant undergrowth species was Norway spruce (83%). Studies by Szczygielski (2007) and Solon and Matuszkiewicz (2008) showed that between 1950s and 2004, forest fertility in the AF increased significantly and this resulted in the expansion of spruce as the second layer of tree stands and dense bush layer in Scot pine-dominated stands. Hence, Scot pine forest preferred by Capercaillie have been changing into mixed coniferous forest, with a significant share of spruce. In the AF, dense undergrowth of spruce that had developed in the areas of abandoned leks, was the most likely reason for their unsuitability for Capercaillie. In addition to a natural process, forest structure is changing in the same direction due to deliberate planting of undergrowth (spruce, oak, and beech *Fagus silvatica*, the last one non-native to the AF). However, the difference between mean HSI values for active and abandoned leks was statistically significant (4.8 *versus* 4.2), but it seems to be too low to fully explain process of abandonment of lek areas. It may suggest that habitat conditions are not the only reason of Capercaillie decline in the AF. In our study, we do not take into account other factors, mainly predation, forest management and other-related human disturbances.

Forest stands occupied by Capercaillie in the AF were younger than those in Norway (Rolstad and Wegge 1987) and in mountains of Central and Western Europe (Saniga 1996, Storch 2001, Bollmann *et al.* 2005), but similar to those in Finland, where densities of Capercaillie were higher in the middle-aged tree stands than in the oldest part of forest (Miettinen *et al.* 2008). However, lek formation in young forest (< 50 years old) is well documented in commercial stands in Norway (Rolstad *et al.* 2007). According to Storch (2000), Capercaillie depend on particular habitat structures, but are rather flexible with regard to conifer species and forest

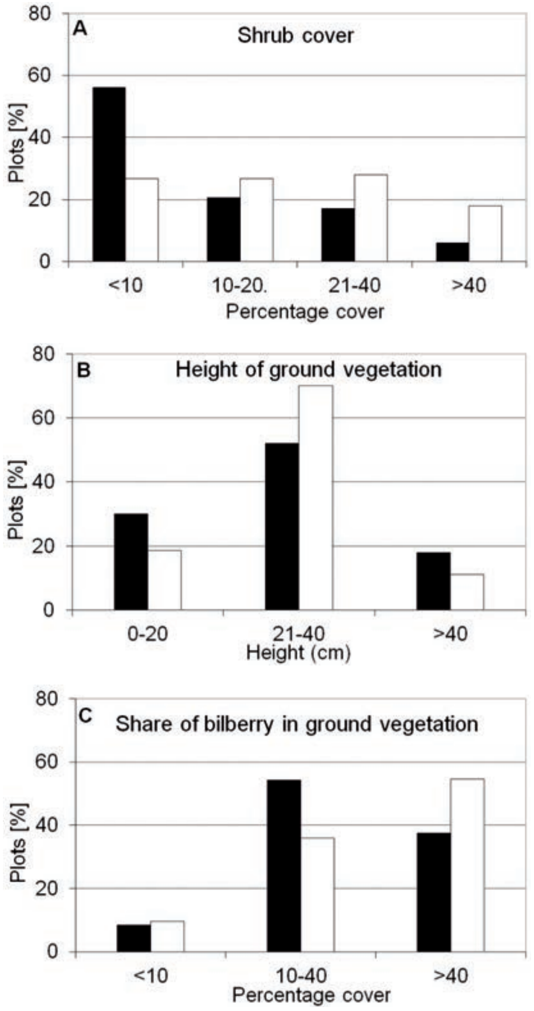

Fig. 7. Differences between active (black bars) and abandoned (white bars) leks in the distribution of shrub cover (A), the height of ground vegetation (B), and the share of bilberry cover in ground vegetation (C)

age. Study in Finland shows, that increasing proportion of younger forest (< 40 years old) does not affect directly Capercaillie density. Other factors associated with forestry, *e.g.* logging, predation, bilberry cover played the main role, responsible for declining in the population number (Sirkiä *et al.* 2010).

In the Augustów Forest, birds occupied dryer forest than in the mounatin and boreal parts of their geographic range in Europe (Storch 2001). Strong domination by Scots pine, the plant species providing winter food and places for roosting, may partly compensate for the lack of food resource plants from wet sites (*e.g. Eriophorum* sp., and cranberry *Oxycoccus palustris*) (Klaus *et al.* 1989, Pavlushchick and Cherkas 1997). Our results confirm the study by Storch (1993) documenting preference of Capercaillie for high cover of bilberries.

Finally, the fact, that Capercaillie signs were recorded on 11.1% of circular plots on the active lek areas in the AF suggests that these areas are used by birds also outside the mating season (the surveys were done in July-September). By comparison, Capercaillie tracks were found on 5.8% of the total number of 414 circular plots in the Vosges (France), mainly on plots with high values of HSI (Hurstel 2005). In the Bavarian Alps (Germany), in 6 study areas covering from 12 to 29 km^2 each, from 1.8% to 9.2% of circular plots contained signs of Capercaillie (Storch 2002).

In conclusion, the HSI model constructed and validated for the Augustów Forest showed that the lowland, pine dominated forests in NE Poland provide only moderately suitable habitats for Capercaillie on a scale required by viable populations. Both human-caused (fragmentation of old stands due to intense forestry practices) and natural processes (expansion of Spruce forming dense undergrowth layer in pine forest) are contributing to deterioration of habitat conditions for Capercaillie. These habitat changes may be an important, but not the only cause of the observed dramatic decline of Capercaillie population in NE Poland.

ACKNOWLEDGMENTS: The study was financed by the grant from the National Found for Environmental Protection and Water Management. We thank Professor Bogumiła Jędrzejewska for her comments on an earlier draft of the manuscript.

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Received after revision May 2012