The Effect of Forest Landscape Structure on the Location and Occupancy of Capercaillie (*Tetrao urogallus* L.) Leks

RYTIS ZIZAS[1]*, GINTAUTAS MOZGERIS[2], VIRGILIJUS BALIUCKAS[1,2], GEDIMINAS BRAZAITIS[2], OLGIRDA BELOVA[1], GINTARĖ GRAŠYTĖ[4] AND PETRAS KURLAVIČIUS[3]

[1] *Institute of Forestry, Lithuanian Research Centre for Agriculture and Forestry, Liepų str. 1, Girionys LT 53101, Kaunas distr., Lithuania*

[2] *Aleksandras Stulginskis University, Studentų str. 11, Akademija, LT-53361 Kaunas district, Lithuania*

[3] *Lithuanian University of Educational Sciences, Studentų str. 39, LT-08106 Vilnius, Lithuania*

[4] *Nature Research Centre, Akademijos 2, LT-08412 Vilnius, Lithuania*

**Corresponding author: r.zizas@gmail.com, phone: +370 670 03271*

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Abstract

Until now, forest characteristics of capercaillie habitats received very little attention in the southeastern Baltic region, including Lithuania. To fill the gap of ecological study of capercaillie we started to reveal the macro habitat characteristics in 2008. Seventy-one capercaillie leks were identified in southeastern Lithuania during about a decade ago, and these visited during the lekking seasons. Lek occupancy level and lek centre were identified by seen/heard capercaillies and/or their activity signs. The leks were divided into ones of the high (≥2 males) and low occupancy (attributed of individual males' leks and abandoned leks). A Geographical Information System technology was used to evaluate the forest landscape in four buffer zones within the radius of 0.25, 0.5, 1.0 and 2.0 km generated around the centres of leks. Random extra points were generated within buffers of 2-5, 5-10 and 10-20 km from each lek centre (same number in total as all leks at all tree buffer zones). In order to reveal the differences between high and low occupancy leks and significant distances, leks were compared at four mentioned radii. In addition, high occupancy leks (n = 41) and low occupancy leks (n = 30) were compared with available landscapes at 1.0 km radius separately. By the results, the proportion of pine stands in high occupancy leks up to 1 km from the lek centre was bigger ($p < 0.05$) if compared with low occupancy leks. High occupancy leks were located about 500 m further from homesteads (the difference $p < 0.0001$) and 180 m further ($p = 0.09$) from the forest edge, if compared with low occupancy leks. Wetland proportions in high occupancy leks at all analysed distances were 2.5-3 times ($p < 0.05$) higher than those in low occupancy leks. The differences of stand areas of different forest types were found only when comparing the areas located 1 km and 2 km in radii from the lek centre. For capercaillies lek selection the distance of 0.5 km from the lek centre was the most significant. Lek selection in Dzūkija and Aukštaitija regions was influenced by the following variables: low (0.5), medium (0.6-0.7) and high (0.8-0.9) stocking level stands, proportion of pine, proportion of middle-age, mature-overmature pine stands, undrained Histosols (wetlands), stands of *Ledo-sphagnosa* and *Vaccinio-myrtillosa* forest vegetation types and core areas. The same forest structure variables influencing lek selection were typical for high and low occupancy leks. Our study shows that (1) capercaillie lek location in Lithuania is influenced by landscape characteristics and (2) that this influence is more pronounced for high occupancy leks compared to low occupancy leks.

Key words: capercaillie, habitat, lek location, forest landscape, high and low occupancy.

Introduction

It is generally recognized that growing economic interests of the public in forest ecosystems caused great losses in biodiversity, especially in Europe (Kostovska et al. 2008). Forestry is largely acknowledged to be the driving force in the population declines of many species of the boreal forest (Esseen et al. 1997) that is one of the most extensive terrestrial ecosystems *(biomes)* in the world (e.g. Haila 1994). In the recent decades, conservationists and foresters are looking for ways to put into practice sustainable forest management and reconcile interests between forest managers, forest owners, conservationists and other stakeholders.

Birds are excellent barometers for the health of the environment. They occur in many habitats and reflect changes in other animal and plant populations; they are sensitive to environmental changes and have great resonance with the public (EBCC 2005, Gregory and Strien 2010). Some conspicuous, well-known, and socially valued species, which are currently under threat and called *umbrella* or *iconic* species, can provide obvious opportunities for establishing forestry-conservation links. One of them is the capercaillie *Tetrao urogallus* (Lohmus et al. 2004), which has specialized habitat preferences (Sjöberg 1996), relatively large home range (in average circa 550 ha, see Storch 1995) and extensive spatial requirements, both making it highly susceptible to habitat and landscape changes.

The capercaillie densities have declined remarkably throughout its entire range, especially in the past several decades (Wegge 1979, Miettinen 2009). The species is at the risk of extinction in the western, central and south-eastern Europe (Storch 2007). For this reason, capercaillie is listed in Annex I of the EC Birds Directive (Council Directive 2009/147/*EC*), and the population trend appears to be decreasing (IUCN 2012, BirdLife International 2015). Capercaillie has been red listed in most of European countries (Brzeziecki et al. 2012). In the Red Data Book of Lithuania, it is listed since 1989 (Rašomavičius 2007) and attributed to the rarity category II (critically endangered species). In accordance with Article 4, the EC Birds Directive, Lithuania has established seven Special Protection Areas (SPAs) for birds of this species.

A good knowledge of the habitat requirements of capercaillie could help to actively protect this species (Brzeziecki et al. 2012). Moreover, Lithuania is at the south-western edge of a contiguous distribution range of capercaillie (see Figure 1 and, e.g. the range map (Snow and Perrins 1998; Figure 2); therefore, it is necessary to ensure the protection of capercaillie habitats in Lithuania avoiding the isolation of its regional populations.

It is indicated that the major reasons of the capercaillie decline in the European range are their habitat destruction and loss caused by cutting of old-growth forests and changes in the stand structure (Storch 2000), and human disturbances (Marchall 2005, Stevenson 2007, Mollet et al. 2008).

Recently, e.g. in Scandinavia, capercaillie populations are in fact substantially driven by landscape-scale processes (Kurki et al. 2000, Graf 2005). The abundance of this species correlates with several environmental factors, such as ground vegetation, predation, forest structure, forest age or climate (Kurki et al. 2000, Borchtchevski et al. 2003, Baines et al. 2004, Gregersen and Gregersen 2008).

The capercaillie has large spatial requirements and highly specialized habitat preferences (Rolstad et al. 1997, Graf 2005), and it is considered an indicator of structurally rich forest conditions. Protection or wise management of its habitat will benefit other old-growth forest species as well (Pakkala et al. 2003, Suter et al. 2002). Throughout its range, this bird species is found in a variety of conifer and mixed conifer/broadleaf woodlands, comprising oak *Quercus* sp., beech *Fagus sylvatica*, spruce *Picea abies* and Scots pine *Pinus sylvestris* (Dement'ev et al. 1951). However, the association with Scots pine woodland is the strongest (Seiskari 1962), especially in the Baltic region (Hofmanis and Strazds 2004). In a review of habitat use, Rolstad and Wegge (1989) noted that capercaillie is usually associated with forests older than 70 years. This association is explained in terms of the basic needs for food supply and movement considering that males weigh ca. 4 kg (Cramp and Simmons 1980); therefore, stout branches are beneficial (Summers et al. 2004). In addition, the food value of needles from older pines is supposedly better than those from young trees because of their higher energy content (Lindén 1984).

The rapidly advancing GIS-technology and new powerful statistical tools help to address spatial scale questions in species-habitat relationships (Guisan-Zimmermann 2000, Manly et al. 2002). During the last decade, capercaillie habitat preferences were evaluated by an analysis of habitat structure and its key elements at the different spatial scales, most in mountainous areas of Central Europe and Scandinavia (Bollmann et al. 2005, Graf 2005, Braunisch and Suchant 2007). Considering species needs, habitat suitability models (HSM) were developed. HSMs enable to predict the presence or abundance of a population and identify suitable habitats for practical implementation in management providing benefits and attractiveness for birds (e.g. Storch 2002, Brzeziecki et al. 2012, Gret-Regamey et al. 2013). However, the HSM has a limited application. The model can explain well capercaillie preference at the local scale but it is inefficient for explanation of species presence or absence at the larger landscape scale (Storch 2002, Graf 2005, Brzeziecki et al. 2012). Field studies show sometimes opposite behaviour of birds, e.g. less suitable habitats are used more intensively (Gerstgrasser et al. 2002). It can occur because of differences in habitat requirements of population and the certain individual. Moreover, often there are problems of the stability of lek habitats in Lithuania. Despite birds usually use the same leks year after year, location of leks often changes because of one reason or another. Managing forests for timber production, all known capercaillie leks are still protected despite birds have not already used some of them. Changes in the forest structure could cause birds eventually to abandon lek sites resulting in decreased reproductive success. For instance, in Augustów Forest (Poland) near the border with Lithuania, the differences between abandoned and active leks were related to shrub cover in ground vegetation and height of ground vegetation, and the share of bilberry cover (Brzeziecki et al. 2012).

In this study, we analysed the surrounding of capercaillie leks at the stand and landscape scales aimed to: 1) identify the environmental differences between the high and low occupation leks; 2) determine the environmental factors for lek selection in the two separate regions of Lithuania.

Material and Methods

Study area and capercaillie population

The total study area covers the southern and eastern forests of Lithuania (between 53° 59' 43.4", 23° 29' 51.53" and 55° 32' 22.63", 26° 4' 15.33"). Recently, almost all national capercaillie populations are located in the mentioned region. A study area covers two most extensive and partly isolated Dzūkija (the south-eastern region) and Aukštaitija (the north-eastern – eastern region) pine forest areas (Kuliešis and Kasperavičius 1999). In this study, Dzūkija forest area covers territories administrated by Veisiejai, Druskininkai, Varėna, Valkininkai, Šalčininkai and Trakai Forest Enterprises. Respectively, Aukštaitija forest area covers territories administrated by Vilnius, Nemenčinė, Švenčionėliai and Ignalina Forest Enterprises.

This area belongs to the boreal biome and to the zone of temperate continental climate (Rivas-Martinez et al. 2004, Pukelytė 2011). To describe the landscape on the research area, buffer zones of 20 km around randomly generated points within 2-5 km distances from known capercaillie leks (see below) were generated and used to clip out information on the land cover types and forest resources. The data are showed in Table 1.

Recently, it was estimated to be 450 males of capercaillie in Lithuania in 2012 (Kurtinio apsaugos planas 2012). It is supposed that in Lithuania, capercaillie could belong to the two different subspecies. Despite the comprehensive study was not performed yet, the analysis of research data in Belarus (Pavlushchik 2003, Черкас 2008, Pavlushchik and Dzmitranok 2012), which is mostly based on the biomorphological measurement, showed that *T. u. major* Brehm. subspecies could be found in the southern Lithuania (Dzūkija) and *T. u. pleskei* Stegmann subspecies in the Eastern region (Aukštaitija).

Table 1. Types of land cover and forest resources in the research area, %

Land cover type	Dzūkija	Aukštaitija
Peatland	1.6	1.2
Lakes	2.1	4.7
Rivers >30m	0.2	0.1
Forests	58.4	49.6
Agricultural land	33.9	38.9
Orchards	0.3	0.6
Sand, gravel pits, dumps	0.5	0.6
Built-up areas	3.0	4.3
In total	100	100
Forest resources		
Private	54.1	49.8
State owned	45.9	50.2
In total	100	100
Reserve forests	4.2	0.8
Special purpose	9.3	16.5
Protective	19.4	20.3
Commercial	67.1	62.4
In total	100	100
Pine	76.5	60.8
Spruce and other coniferous	7.5	10.7
Hard deciduous	0.4	0.9
Birch	8.9	15.7
Black alder	5.5	4.4
Other soft deciduous	1.2	7.5
In total	100	100
Young	19.2	16.2
Middle-aged	61.6	51.1
Premature	8.6	11.2
Mature	9.4	15.6
Over-mature	1.2	5.9
In total	100	100

Data sampling

Data collection

Before field survey, the data on capercaillie leks were obtained in 2008 conducting a questionnaire survey of employees of state forest enterprises, regional and national parks. The locations, which were indicated by the respondents, were adjusted to the data (in 2009) on the location of capercaillie leks of State Forest Service (SFS). A total seventy-one leks were chosen for further investigation.

Field works

As capercaillies are difficult to count throughout the year, it is most practicable to count the number of males displaying on leks in spring (Klaus et al. 1986, Saniga 2003). In this study, lek surveys were conducted during the lekking season in March-April 2008-2012. Occupancy level and the location of lek centre were determined as precisely as possible during the visits. Lek occupancy level and lek centre were identified by seen/heard capercaillies, and/or their activity signs. Leks were divided into ones of the **high** (≥2 males) and **low** occupancy (attributed to individual male leks and non-used leks but still stored in the SFS database) (see Discussion). We did not separate capercaillie leks into active and abandoned (e.g. Brzeziecki et al. 2012) considering proposition that because of changes in the forest structure, active leks split into smaller units used by single males (Rolstad and Wegge 2009).

Basing on results of many authors, in this paper, we considered that capercaillie leks have no clear and regular outer boundaries, and they cover a territory of about 400 m from the lek centre (Gjerde and Wegge 1989). With this in mind, a distance was used as the factor to distinguish new leks. The new lek was distinguished, when it was >1,000 m away from the lek, included into the SFS database. If the distance was ≤1,000 m, the decision was made that it is the same (continuous) lek (Rolstad and Wegge 1989). The last concept was used also in our terminology (e.g. lek occupancy and location were analysed, when evaluating the effect of forest landscape structure at 1 km radius from the lek centre). The coordinates of each lek centre were GPS recorded (device GARMIN, the accuracy ±5 m).

Environmental data and habitat measurements

A GIS database of geographical locations of 71 capercaillie leks was created. We used the method of comparison of macrohabitats with control landscapes (e.g. Bielański 2006, Treinys 2009). To compare the forest landscape structure of leks and control landscapes, random points at three buffer zones, keeping a distance of 2-5, 5-10 and 10-20 km around each point indicating the lek, were placed using ArcGIS random point generator. Two criteria were used for generating: 1) the random point cannot hit Lithuanian border and 2) the random point should be in the forest. The number of control landscapes in every buffer zone is equal to the total number of leks. Throughout this paper, control landscapes are named as "available landscapes", since the searching of leks in these areas was not performed.

The variables of the environment describing forest structure at the stand and landscape levels, including human disturbance, were identified in the capercaillie leks and available landscapes: 1) the distribution of stands by the **tree species** (five tree species, the amount more than 0.1% on the analysing areas, were founded i.e. *Pine, Spruce, Birch, Black alder* and *Aspen*); 2) **pine forest age** (pine stands were divided by maturity groups based on pine stand felling age for the commercial forests (forest group IV) (Lithuanian Statistical Yearbook of Forestry 2002)); 3) **stocking level of the stands** (four categories were distinguished as low ≤0.5, medium 0.6-0.7, high 0.8-0.9 and very high ≥1.0 stocking level of stands); 4) **forest vegetation type** (seven types by S. Karazija 1988), the number more than 1% on the analysing areas were distinguished for the following: *Vaccinio-myrtillosa (Vm), Cladoniosa (Cl), Ledo-sphagnosa (Lsp), Carico-sphagnosa (Csp), Myrtillosa (M), Oxalidosa (Ox), Vacciniosa (V)*; 5) **forest land**; 6) **stands**; 7) **core area** (the area located up to 200 metres from forest edge (perimeter)); 8) **undrained Histosols** (very infertile, infertile, fertile and very fertile marked as forest site types Pa, Pb, Pc, Pd, respectively, according to the Lithuanian classification, Vaičys et al. 2006); 9) **drained Histosols** (Pan, Pbn, Pcn, Pdn, respectively); 10) **open areas** (openings, forage areas and forest glades); 11) **density of the surfaced roads** (gravel and asphalt surface); 12) **distance to the nearest surfaced road**; 13) **density of the forest roads** (roads with natural surface); 14) **distance to the nearest forest road**; 15) **distance to the forest edge** and 16) **distance to the nearest homestead**.

GDR10LT information from the Lithuanian Georeference GIS database geographical and attribute data of forest compartment from the Lithuanian Forest Cadastre (2010) were used for this research.

The proportion of all mentioned variables at four radii (0.25 km, represent 19.6 ha, 0.5 km represent 78.5 ha, 1 km represent 314.2 ha and 2 km represent 1,256.6 ha) from centres of the lekking areas and available landscapes were calculated (Figure 1), as well the distance to the landscape objects were measured.

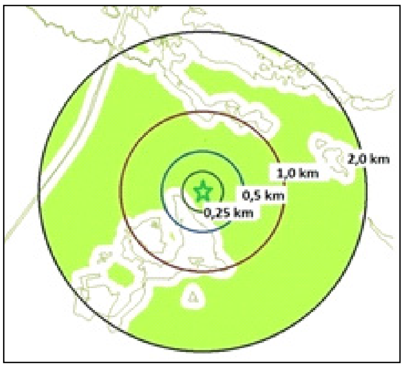

Figure 1. Analysis of forest landscape structure at 0.25 km, 0.5 km, 1 km and 2 km radii from lek (available landscape) centre (star)

Study design

To evaluate the effect of forest landscape structure to the capercaillie lek occupancy, all the leks (n = 71) surrounding of 1 km radius by all aforementioned variables were compared with the available landscapes (n = 71) located at 2-5 km from the centre of leks. In addition, high occupancy leks (n = 41) and low occupancy leks (n = 30) were separately compared with available landscapes. In order to reveal the differences between high and low occupancy leks and significant distances, both group leks were compared at four radii from the centre.

To evaluate the regional differences, a comparison of all the aforementioned variables of forest landscape structure at 1 km in radius in Dzūkija leks (n = 29), Aukštaitija leks (n = 41) and in available landscapes located at 2-5, 5-10 and 10-20 km from the lek centre was made.

Stepwise discriminant analysis was used to select the variables of forest landscape structure influencing location of high and low occupancy capercaillie leks in two regions (for more details see next section).

Calculations and statistical analysis

Processing of geographic data was implemented using standard functionality of ArcGIS software. The proportion of all the variables constituting forest landscape structure was estimated using statistical software package SAS 9.3. The primary analysis of all the variables was made separately in each region by principal component analysis using SAS/PRINCOMP procedure. Since the values of all variables were displayed on the same scale, covariance analysis method was applied. The results of the principal component analysis of both Aukštaitija and Dzūkija regions showed that the first four components in both regions were significant as indicated by the Broken Stick method (explained variability from 4% to 56%). Having selected the variables, those absolute weights exceeded 0.01 at the axes of principal components, 24% of all variables were present in Aukštaitija region and only 5% in Dzūkija. The average weight of selected variables in four axes was 0.08 and 0.26, respectively. In order to assess the multicollinearity of variables, the correlation matrix between the variables, which was obtained during the principal component analysis, was analysed. The values of correlation coefficients, which were higher than 0.4, showed a close relationship between the variables. We also estimated Pearson correlation coefficients between the variables and correlation reliability. The obtained results were considered while interpreting the influence of individual factors on lek selection. In order to evaluate the influence of separate factor on lek occupancy, data samples were compared with Kolmogorov-Smirnov criterion (Zar 2010), because data samples did not meet normal distribution in most cases (in chapter "Impact of forest landscape structure on the capercaillie leks occupancy" and "Regional differences"). SAS UNIVARIATE procedure was used to test the normality of the data distributions. In order to evaluate the selection of leks, we used a stepwise discriminant analysis SAS STEPDISC and variables, which meet criterion of the significance level less than 0.05 (*alpha*). We have determined the features those best distinguish the location of leks, occupancy and regional groups (in chapter "Regional differences"). Cluster grouping was made using SAS CLUSTER and TREE procedures. MANTEL test (software PAST, version 2.17c; Hammer et al. 2001) with 10,000 permutations were made in order to find out the inter-regional differences between the variables of lek surrounding (in section "Regional differences"). A linear correlation was calculated between habitat similarity matrices for individual radius areas. Distance matrix was obtained after the application of geographical similarity criterion, while similarity was attained by landscape variables using Euclidian distance similarity criterion. Principal component analysis using SAS PRINCOMP procedure was conducted to analyse lek location (with regard to the distance from the centre), lek occupancy and its regional differences (in the section "The influence of forest structure on the capercaillie lek location"). In order to reduce the probability of type I error, conclusions about the differences between sample groups were made only in the cases, when the level of significance of differences was statistically appropriate (<0.01).

Results

The distribution of capercaillie leks in south-eastern Lithuania and their occupancy level

Forty-one leks (58 %) out of the total 71 capercaillie leks were attributed to the high occupancy leks and 30 leks (42 %) were grouped as the low occupancy leks. There were 21 leks of the high occupancy (72 %) and 8 of low occupancy (28 %) in Dzūkija region while 22 leks of high occupancy (52 %) and 20 (48 %) of low occupancy were distinguished in Aukštaitija (Figure 2).

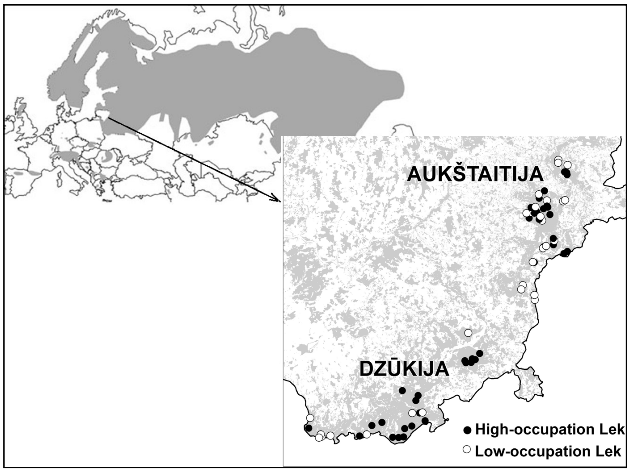

Figure 2. The distribution of high-occupancy (black spots) and low-occupancy (white spots) capercaillie leks in south-eastern Lithuania (Dzūkija and Aukštaitija regions; source of capercaillie distribution range map, see Storch 2007)

Impact of forest landscape structure on the capercaillie leks occupancy

The forest structure characteristics at 1 km radius by separate variables in all analysed capercaillie leks (N = 71), high (N = 41) and low (N = 30) occupancy leks surrounding, equal number available landscapes and their comparison results are shown in Table 2. The results show that in comparison with randomly selected available landscapes at 1 km radius from the capercaillie leks, the forest landscape structure statistically significantly more differ (in bigger numbers of forest structure characteristics) in case of high occupancy leks. For example, in comparison with available landscapes and, differently from the low occupancy leks, on high occupancy leks proportion of pine trees in tree species composition of the stand and part of the middle-aged stands is higher, and the proportion of forest vegetation types "*Oxalidosa*" is less. In cases of high and low occupancy leks, the differences in the stocking level are statistically misleading.

Regional differences

Complex comparison (Table 3) showed that lek surrounding within different regions differed in about one-third of all the analysed elements. The highest number of differences between the regions was found in available landscapes located 2-5 km from the leks. The number of significant differences in the variables of forest structure in available landscapes located 5-

Table 2. Descriptive statistics of forests (the average ± *SD*, %) in capercaillie leks surrounding (n = 71) and available landscapes (n = 71) at 1 km radius. Also the results of statistical comparison of Kolmogorov-Smirnov (KS) test. Significant differences ($p < 0.05$) are in boldface type; *nd* denotes 'no data available'

Variable		H. Leks (N-41)	Available landscapes (N-41)	*KS test: H. Leks vs AL*	L .Leks (N-30)	Available landscapes (N-30)	*KS test: L.Leks vs AL*
Proportion (%) of:							
Tree species composition	Pine	82.8 ± 9.6	66.9 ± 21.5	**<0.004**	75.7 ± 12.1	69.3 ± 22.9	0.586
	Spruce	2.9 ± 3.4	5.5 ± 5.4	0.105	6.8 ± 7.9	7.8 ± 7.7	0.586
	Birch	7.7 ± 4.6	11.4 ± 8.3	0.105	9.9 ± 4.8	11.5 ± 10.9	0.586
	Black alder	1.5 ± 2.4	3.0 ± 5.4	0.589	1.1 ± 1.3	3.3 ± 6.4	0.134
	Aspen	0.1 ± 0.1	0.4 ± 0.9	0.277	0.1 ± 0.3	0.3 ± 0.6	0.953
Pine-stands age	Clear-cuts	2.0 ± 2.0	4.2 ± 4.8	0.059	4.0 ± 3.2	3.9 ± 3.4	0.953
	Young	12.1 ± 10.7	15.5 ± 14.6	0.589	7.9 ± 7.3	14.7 ± 12.7	0.134
	Middle-aged	47.6 ± 15.1	32.6 ± 15.8	**<0.004**	42.4 ± 15.1	34.4 ± 15.5	0.236
	Premature	20.0 ± 14.1	21.5 ± 16.2	0.920	25.7 ± 16.7	23.0 ± 15.9	0.586
	Mature-overmature	23.1 ± 16.3	18.7 ± 15.2	0.589	25.3 ± 15.1	20.2 ± 13.2	0.388
Stands stocking level							
	Low (≤ 0.5)	4.8 ± 4.5	6.7 ± 5.5	**0.008**	4.7 ± 2.9	5.2 ± 4.4	0.953
	Medium (0.6-0.7)	34.6 ± 16.1	35.0 ± 15.2	0.416	37.4 ± 16.9	37.2 ± 15.4	0.799
	High (0.8-0.9)	54.4 ± 19.0	45.6 ± 18.2	**<0.004**	53.6 ± 18.2	47.9 ± 14.2	**0.035**
	Very high (≥1.0)	3.6 ± 5.1	4.0 ± 5.7	0.589	2.1 ± 1.9	6.7 ± 9.3	**0.035**
Forest vegetation type	*Vaccinio-myrtillosa*	51.5 ± 27.9	52.9 ± 64.1	0.432	65.1 ± 23.2	54.9 ± 29.7	0.134
	Cladoniosa	9.1 ± 15.0	13.6 ± 21.6	0.374	7.4 ± 16.3	14.4 ± 22.6	**0.007**
	Carico-sphagnosa	7.2 ± 9.5	7.0 ± 7.2	0.247	2.6 ± 3.1	3.8 ± 4.6	0.086
	Myrtillosa	4.2 ± 4.7	5.9 ± 7.7	0.422	3.5 ± 5.0	5.2 ± 8.6	0.462
	Oxalidosa	1.9 ± 3.1	3.8 ± 5.1	**0.009**	7.3 ± 10.5	10.1 ± 12.2	0.088
	Vacciniosa	4.1 ± 3.9	5.4 ± 4.3	0.222	2.4 ± 3.3	3.4 ± 3.7	0.069
Forest lands		*nd*	*nd*	*nd*	*nd*	*nd*	*nd*
Stands		*nd*	*nd*	*nd*	*nd*	*nd*	*nd*
Core areas		80.8 ± 20.7	66.4 ± 23.1	**<0.002**	83.2 ± 17.3	66.3 ± 22.7	**<0.003**
Open areas		0.3 ± 1.6	2.7 ± 11.7	0.589	0.3 ± 0.4	0.7 ± 1.3	0.071
Drained Histosols		3.3 ± 4.7	5.2 ± 9.1	0.772	2.7 ± 5.6	5.4 ± 8.6	0.586
Undrained Histosols		21.9 ± 26.5	17.1 ± 20.1	0.920	7.0 ± 9.2	10.1 ± 13.2	0.586
Density of (m/km²):							
Surfaced roads		1276.6 ± 1300.8	1846.3 ± 1562.3	0.277	1621.0 ± 1415.7	2550.2 ± 2239.9	0.134
Forest roads		4110.7 ± 2775.8	5046.0 ± 3094.7	0.589	5563.5 ± 3176.7	5294.9 ± 3496.6	0.799
Distance to the nearest (m):							
Forest edge		1547.2 ± 774.1	542.7 ± 481.9	**<0.0001**	1365.1 ± 640.4	594.4 ± 534.1	**<0.0001**
Surfaced roads		914.9 ± 645.2	623.5 ± 537.4	0.105	680.1 ± 523.3	544.6 ± 434.8	0.799
Forest road		555.6 ± 910.2	469.6 ± 773.1	0.989	637.7 ± 1396.4	495.8 ± 799.5	0.387
Homestead		2159.2 ± 1210.8	1565.6 ± 1129.1	**0.017**	1428.2 ± 692.0	815.0 ± 517.7	**<0.003**

Table 3. Comparison of forest landscape structure at different radii from the capercaillie lek centre (Dzūkija (n = 29) and Aukštaitija (n = 41) regions, Lithuania): leks and their nearest surroundings (1 km from the centre) and available landscapes located at 2-5, 5-10 and 10-20 km from the lek centre. The number of analysed available landscapes is equal to the number of leks. The significance level: *– 0.05> p >0.01, ** – 0.001> p <0.01, ***– <0.001. Blank cells indicate the insignificant differences (Kolmogorov-Smirnov (KS) test)

Variable	Leks	Available landscapes 2–5 km	Available landscapes 5–10 km	Available landscapes 10–20 km
Forest land				
Core area				
Stands				
Wetlands				
Drained wetlands	*	*		
Open areas				
Roads with pavement	**	**		
Forest roads	**	***		
Distance to:				
Forest edge				
Road with pavement		*		
Forest road	*	**		
Homestead	*	***	*	
Pine-dominated stands age:				
Clear-cuts				
Young	**	**		
Middle-aged		***		
Premature	*	*		
Mature and overmature		*		
Proportion of tree species				
Pine		*	*	
Spruce	***	**	*	
Birch	*	*		
Black alder				
Aspen				
Proportion of stocking level				
≤0.5		*		
0.6-0.7				
0.8-0.9				
≤1.0				
Proportion of forest vegetation type				
Vaccinio-myrtillosa	**	*		
Cladoniosa	*	*		
Oxalidosa	**	***		
Vacciniosa			*	
Myrtillosa				
Ledo-sphagnosa				
Carico-sphagnosa				

10 km from leks (if compared with the differences in leks) decreased more than twice. No differences were found in available landscapes located 10-20 km from leks. Mantel test results revealed a declining correlation between the geographic distance and all the analysed variables receding from lek centre. The obtained correlation results were significant for leks (R = 0.36) and for available landscapes located 2-5 km from leks (R = 0.22) (Figures 3 A, B). The correlation was not significant for available landscapes located 5-10 km and 10-20 km (R = 0.09 and -0.06, respectively) from leks (Figures 3 C, D).

Regions most differed in the following variables: density of the roads with pavement, density of forest roads, proportion of drained wetlands, distance to a homestead and distance to forest road, proportion of middle-aged pine or spruce stands, *Vm* and *Ox* forest

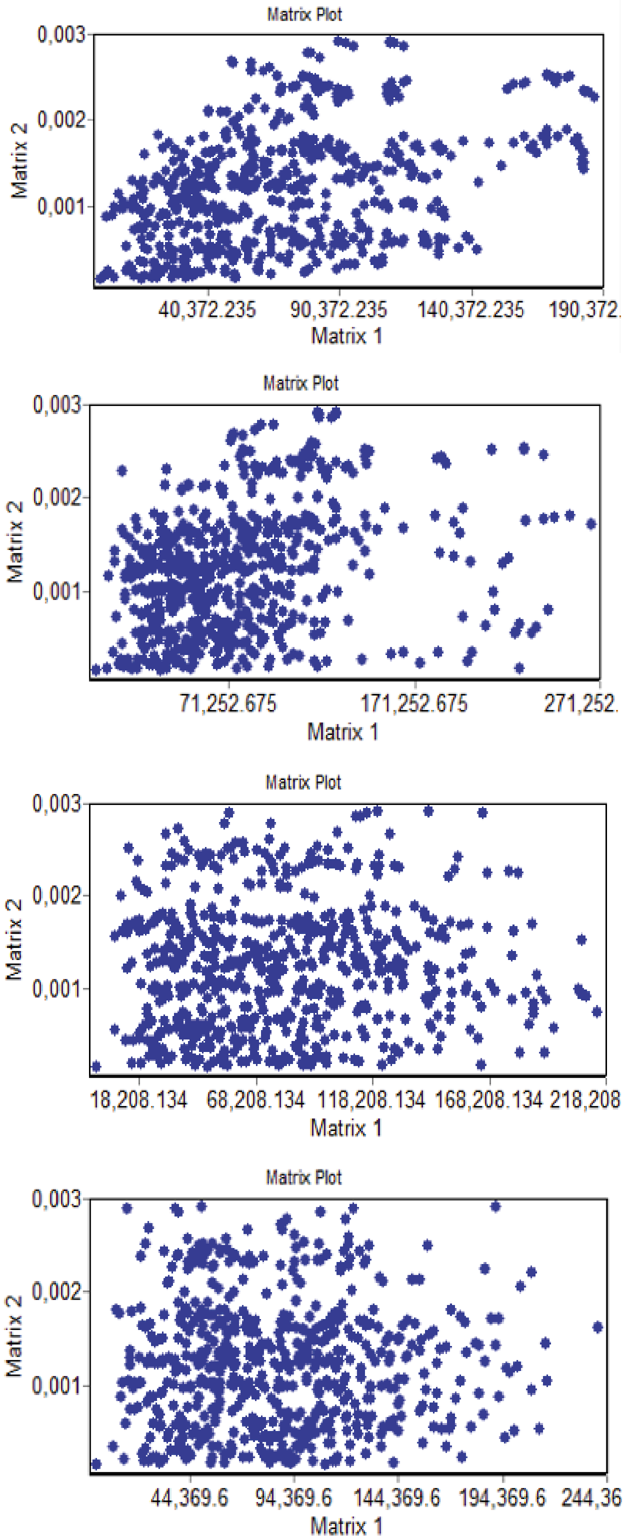

Figure 3. Mantel test for analysis of forest structure variables: at 1 km radius in: leks surrounding (A); available landscapes at 2-5 km distance from leks (B); available landscapes at 5-10 km distance from leks (C); available landscapes at 10-20 km distance from leks (D)

vegetation types. The average canonical correlation coefficient of all these variables was $R = 0.40$.

Lek distribution on the three factorial axes by most disjunctive elements indicated much wider spread of suitable leks over selected gradients in Aukštaitija. Spread of high occupancy leks did not differ much from low occupancy leks, though formed more compact group. Clustering of the leks by similarity of the elements showed that leks in two regions mix only a little bit in between and form quite separate groups (Figure 4).

The influence of forest structure on the capercaillie lek location

Analyses of characteristics of forest structure, in relation with the distance from the capercaillie lek centre, revealed that the lek environment most differed in territory up to 0.5 km and in farther surrounding. And in contrary, forest structure was rather similar in territories in the radii of 1 and 2 km as well as in 0.25 and 0.5 km (Table 4). A third part of all analysed variables resulted in the significant differences between

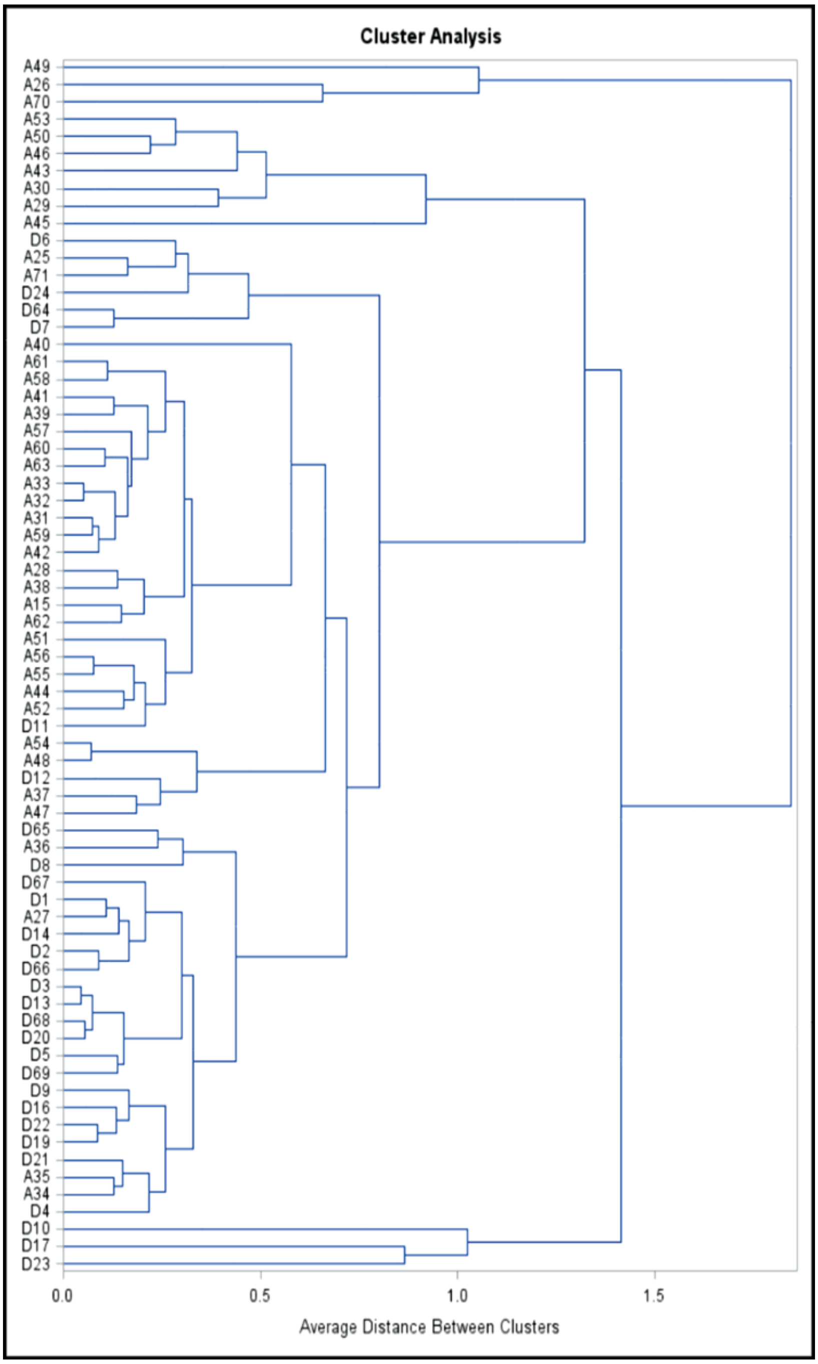

Figure 4. Cluster groups of the capercaillie leks by most disjunctive elements in regions as: the density of the surfaced roads and forest roads, proportion of drained Histosols, distance to a homestead, distance to forest roads, proportion of middle-aged pine or spruce stands, proportion of *Vm* and *Ox* forest vegetation types in stands (A and D symbols with number indicate the lek and its number in Aukštaitija in Dzūkija, respectively)

Table 4. Comparison of forest landscape structure at different radii from the capercaillie lek centre (Dzūkija (n = 29) and Aukštaitija (n = 41) regions, Lithuania): leks (at radii 0.25 km) and their nearest surroundings at 0.5 km, 1 km and 2 km radii from the lek centre. The significance level: *– 0.05> p >0.01, ** – 0.001> p <0.01, ***– <0.001. Blank cells indicate the insignificant differences (Kolmogorov-Smirnov (KS) test)

Variable	0.25 km vs 0.5 km	0.25 km vs 1.0 km	0.25 km vs 2.0 km	0.5 km vs 1.0 km	0.5 km vs 2.0 km	1.0 km vs 2.0 km
Forest land		***	***	*	***	*
Core area	***	***	***	**	***	*
Stands area	***	***	***	**	***	***
Mature stands area			**			
Wetlands		***	***		**	
Drained wetlands		***	***	***	***	
Open areas		***	***	***	***	***
Clear-cuts	***	***	***	***	***	
Roads with pavement	**	***	***	***	***	***
Forest roads	***	***	***	***	***	***
Pine-dominated stands:						
Young	*	***	***		**	
Middle-aged		*	***		**	
Premature			***		**	
Mature and overmature			**		*	
Proportion of tree species						
Pine	*	***	***		***	**
Spruce	**	***	***		***	
Birch	*	***	***		*	
Black alder	**	***	***	***	***	**
Aspen		***	***	**	***	***
Proportion of stocking level						
≤0.5	***	***	***	*	***	
0.6-0.7			**		*	
0.8-0.9		**	***		**	
≥1.0	*	***	***	**	***	
Proportion of forest vegetation type						
Vaccinio-myrtillosa		*	**			
Cladoniosa		***	***		***	
Oxalidosa		***	***	**	***	**
Vacciniosa	*	***	***	**	***	
Myrtillosa		***	***	**	***	
Ledo-sphagnosa			***		***	
Carico-sphagnosa	*	***	***		**	

radii 1 and 2 km, and 47% between radii 0.25 and 0.5 km. All the differences between radii 0.25 and 2 km were significant. As a conclusion, a territory up to 500 m from the capercaillie lek centre is most unique in the forest structure, in comparison with surrounding stands.

Discussion and Conclusions

The lek surrounding differed from available landscapes in about one third of all the analysed variables of forest landscape structure. More statistically significant differences were found comparing available landscapes with high occupancy leks than comparing with low occupancy leks of capercaillies (Table 4). This shows the influence of specific variables to the occupancy level of leks. The surrounding of low and high occupancy leks located at different distance from the centre differed in the following variables: stand species composition, forest vegetation type, areas of forest land and wetlands, and distance to forest edge, to a homestead, to the roads with pavement and their density. Different occupancy leks did not differ in the following variables: proportion of the clear-cuts and pine stand age, stocking level of the stands, proportion of the stands, core areas, open areas, drained wetlands, density of the forest roads and distance to them.

The proportion of forest land and core areas in leks was significantly higher if compared with the landscape around random points. This fact showed that leks were spread throughout relatively less fragmented forest areas. This is in full agreement with the opinion of other researchers, who claim that leks are located in continuous forest tracts (e.g. Rolstad and Wegge 1987, Helle et al. 1994). Smaller forest land proportion was found in low occupancy leks at 2 km in radius (the difference was significant; $p = 0.006$), while the distance from low occupancy leks to forest edge was shorter though the difference in this case was insignificant (Zizas 2015). In contrast to the proportion of forest land, stand proportion was smaller in high occupancy leks if compared with low occupancy ones but insignificantly. This shows that a greater forest fragmentation was more characteristic to low occupancy leks than to high occupancy ones. Forest fragmentation is considered to be one of the main factors negatively affecting the abundance of capercaillie populations worldwide (Andrén 1994). However, in order to clarify the obtained results, research should be continued further.

The proportions of undrained Histosols and stands of *Ledo-sphagnosa* forest vegetation type had a tendency to be larger in high occupancy leks than in low occupancy leks at all analysed radii ($p > 0.05$ and $0.002 < p < 0.04$ at 1-2 km distance from the lek centre, respectively). On the contrary, proportions of *Vaccinio-myrtillosa*, *Myrtillosa*, *Vacciniosa*, *Oxalidosa* and other forest vegetation types in stands were larger in the low occupancy leks (in all cases $p < 0.05$). That shows a positive influence of undrained Histosols on the occupancy of leks. Results revealed that in comparison with high occupancy leks, low occupancy ones were located closer to homesteads, surfaced roads and the density of surfaced roads was higher there, but only distance to homesteads was statistically significant ($p = 0.04$). This suggests that anthropogenic disturbance sources are one of the most significant factors to determine lek occupancy level. The obtained results coincide with the results of other authors, who indicate influence of anthropogenic factors to habitat location of capercaillie (Leclercq 1985, Ménoni and Bougerol 1993, Sachot et al. 2003).

Regardless of differences in forest structure between two regions in the surrounding of capercaillie leks and on the area up to 5 km in radius from the leks, lek location was influenced by the same variables as follows: stands of low (≤0.5), medium (0.6-0.7) and high stocking level (0.8-0.9), pine stands proportion, middle-aged, mature-overmature pine stands, undrained

Histosols, *Vaccinio-myrtillosa* and *Ledo-sphagnosa* forest vegetation types and core area. The influence of the aforementioned variables on lek location was obvious at 0.5 km in radius from the centre of leks. This reveals lek uniqueness in the central part that includes male display grounds. The influence of forest structure on the lek location was not revealed within the distance of 1 and 2 km from the centre of leks because these areas were under the boundaries of daily territories of males. The surrounding of these areas was less distinct if compared with display grounds. In addition, the same variables were similar in the both high and low occupancy leks. This tendency shows that the differences in lek surrounding (or, in other words, habitat quality) can explain the occupancy of leks.

Capercaillies prefer pine stands throughout their range (Logminas 1962, Seiskari 1982, Черкас 2008). The results of this analysis revealed an influence of the middle-aged and mature-overmature pine stands (when considering stand age) on lek location. The prior studies emphasized the importance of old forests (e.g. Hjorth 1970, Wegge and Rolstad 1986, Picozzi et al. 1992, Kurki et al. 2000). There is no uniform opinion about the influence of pine stands of different maturity groups on location of the lek site. It shows that mature stands, which grow in the intensive management forests, lose some characteristics typical to natural forests (Miettinen et al. 2009). In order to adapt to the changing conditions (Dzieciolowski and Matuszewski 1981), capercaillies are forced to choose younger forests (Mykrä et al. 2000, Miettinen et al. 2005, Sirkiä et al. 2011). The results of this study as well as the results obtained by Sirkiä et al. (2011) in Finland (leks were analysed at 3,000 m in radius) show that lek occupancy does not depend on the share of old stands. According to the data of the studies performed by Miettinen (2009), even the areas of young pine stands in managed forests in Finland positively correlated with the males' number at the lek.

It is likely that stands of high (0.8-0.9) stocking level had a negative influence, because dense stands reduce the chances of capercaillies to escape from predators (Rolstad and Wegge 1990). However, in the contrary, dense stands could increase cover from potential predators (e.g. Kurki et al. 1997, 1998, Baines et al. 2004, Summers et al. 2004, Hetherington 2006). In this paper, the stands of low (≤0.5) and high (0.6-0.7) stocking level were identified as factors influencing lek location. Other authors also mentioned the preference of capercaillies of the thin stands. I. Storch (1993) argued that approximately 2/3 of middle-aged stands in central Europe are over-dense for capercaillies, especially multi-storey stands (stands with more than one storey). It shows that capercaillies use for lekking forest openings (i.e. "open areas" in the subsection *Environmental data and habitat measurements*), where visibility is 20-50 m (Valkeajärvi and Ijäs 1986, Miettinen 2009, Sirkiä 2010, Wegge et al. 2013). When collecting data, the mating males of capercaillies were often detected on the forest roads, compartment and electrical lines. These findings coincide with the findings of other authors (Dzieciolowski and Matuszewski 1981). When summarising, our results of the effect of the stand stocking level on lek occupancy and location are contradictory.

The results of this study indicated that wetland areas (*Ledo-sphagnosa* forest vegetation type), positively influenced lek location and occupancy. Meanwhile, *Vaccinio-myrtillosa* forest vegetation type stands were very important for after mating period.

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