FORESTRY IDEAS, 2022, vol. 28, No 2 (64): 405–419

Habitat preferences by Western capercaillie (*Tetrao urogallus* L.) on the Lička Plješivica massif (Dinaric Alps)

Krešimir Krapinec[1*], Maja Sabljak[2], Josip Prebanić[3], Ivica Serdar[3], and Dean Konjević[4]

[1]Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Technology, 23 Svetošimunska Str., 10000 Zagreb, Croatia.
[*]E-mail: kkrapinec@sumfak.unizg.hr
[2]Nature Park 'Lonjsko polje', 16 Krapje Str., 44324 Jasenovac, Croatia.
E-mail: sumar@pp-lonjsko-polje.hr
[3]Forest Administration Gospić, Croatian Forests Ltd, 23 Budačka Str., 53000 Gospić, Croatia.
E-mails: josip.prebanic@hrsume.hr, Ivica.Serdar@hrsume.hr
[4]Department of Veterinary Economics and Epidemiology, University of Zagreb, Faculty of Veterinary Medicine, 55 Heinzelova Str., 10000 Zagreb, Croatia.
E-mail: dean.konjevic@vef.unizg.hr

Received: 05 October 2021 / Accepted: 05 December 2022 / Available online: 08 December 2022

Abstract

The Western capercaillie is a large galliform bird whose populations are declining in Europe. By the middle of the 20th century it was present on six massifs of the Dinaric Alps in Croatia. In the meantime, the capercaillie has disappeared from two massifs and lek numbers have fallen by 77 %. The only area where lek numbers have increased is the Lička Plješivica, a massif on the border with Bosnia and Herzegovina. In this study we applied ENFA analysis to evaluate the habitat suitability for capercaillie on the Lička Plješivica massif. The habitat analysis showed that the capercaillie prefers steeper terrain and ridges, forest roads as well as forest associations with higher basal areas, and it avoids grasslands. The capercaillie in general prefers areas with a cold and humid climate. However, compared to the boreal region, the Alps and the Carpathian Mountains, the capercaillie shows a certain habitat preference for the Dinaric Alps. In conclusion, the high suitability of the habitat and its connection to the Bosnia-and-Herzegovinian capercaillie population are probably the causes underlying the increase in the capercaillie population on the Lička Plješivica massif.

Key words: avian habitat suitability, Balkan forest dwelling bird species, Croatia, leks, range decline.

Introduction

Since the middle of the 20th century a population decline has been observed of various species of forest grouse all over the Eurasian area. Currently, two main Eurasian metapopulations of Western capercaillie (*Tetrao urogallus* Linnaeus, 1758) are: boreal (inhabiting the area of northern Europe and Siberia, from Scandinavia to the River Yenisei) and alpine (inhabiting the Central European area) (Segelbacher et al. 2003). Boreal area is non-fragmented habitat with estimated capercaillie population of about 1,000,000 birds. Differently, alpine population is estimated at only 30,000 birds that live in a highly fragmented area, frequently lacking corridors that should connect different populations. Alpine population is therefore divided into small, sometimes isolated, local populations (subpopulations) ranging from 100 to 1000 birds. Beside these areas, capercaillie can also be found on smaller areas of northern Scotland, Cantabria, Ardennes, Jura Mountains, Dinaric Alps, Rhodope Mountains, Rila Mountain, Pirin Mountain and Carpathian area. Though species distribution and still preserved large populations in Scandinavia and Russia prevents it to be declared as highly endangered, its populations in other (out boreal) European habitats are rapidly decreasing (Klaus et al. 1997, Storch 2007).

A similar trend was also observed in the Dinaric Alps. In the middle of the 20th century, the Western capercaillie (*Tetrao urogallus*) was present in the six main massifs in Croatia (Risnjak, Velika Kapela, Mala Kapela, Velebit, Ličko sredogorje and the Lička Plješivica) and almost all the leks were found above 1000 m altitude. The majority of leks were on Risnjak massif (112), while only one was found on Ličko sredogorje massif (Table 1, Fig. 1, Franić 1910, Rucner 1954, Turkalj 1956, Car 1970, Lukač 2004, Frković 2012) mostly in silver fir-beech or sub-mountain beech forests. On most Croatian part of Dinaric Alps populations of the species are composed of boreal lineage and belong to subspecies *Tetrao urogallus major* (Bajc et al. 2011), but some areas are not included in the analysis.

One of the factors behind the population decline is habitat changes. According to Sachot (2002), the decline or even local disappearance of this species has been observed in the following habitat types: a) highly cultivated areas of Western and Central Europe where capercaillie have only survived in smaller, protected areas such as National Parks, b) areas with intensive coniferous production in the Scandinavian region; c) highly-managed forest areas between the River Volga and the Ural Mountains; and d) well-preserved mountain forests on the southern border of its distribution (i.e. the Balkan Peninsula and some parts of the Alps).

In general, the capercaillie prefers habitats that include original spruce-beech-fir stands and a spruce vegetation area (Storch 1993, Saniga 2004). However, the relatively large and dispersed area inhabited by capercaillie has led to the development of certain peculiarities in its habitat preferences. For example, in the Scandinavian area the capercaillie inhabits mostly coniferous forests, while in the Cantabrian region (Spain) it can also be found in predominantly beech (*Fagus sylvatica* L.) forests with few conifers (Rodriguez and Obeso 2000). This suggests that the traditional understanding of the capercaillie's habitat is frequently influenced by the bird's habits, the season, food availability and the bird's sex (Storch 1993, 1994; Miettinen et al. 2008, 2010).

The aim of this study was to give balance of former and recent number of capercaillie leks and to analyse habitat quality from the model of Lička Plješivica, the only massif with an increasing capercaillie population in Croatia, as a prerequisite for the creation of guidelines for preservation of the Dinaric population, and its connection with the population in Bosnia and Herzegovina.

Material and Methods

Capercaillie monitoring

The presence of the capercaillie all over the massif was recorded by direct monitoring and by identified signs of their activities (tracks, faeces) tracking during the mating season (March – May), and searching for feathers during the moulting period (summer). Since these traditional methods can have negative impacts on capercaillie, expressed as disturbance during the mating season, or lead to consumption of energy in harsh environmental conditions (flight), we also used 45 camera traps as a non-invasive form of monitoring. The animals were monitored from April 2009 to May 2018. The localities where the presence of capercaillie was confirmed (observed birds, faeces, footprints, feathers, images on cameras) were recorded by GPS (Fujitsu Siemens PDA 560 S coupled with a Navman B-10 antenna magnifier).

Habitat evaluation on the Lička Plješivica massif

The Lička Plješivica massif is the second largest massif in Croatia, partly located in the neighbouring Bosnia and Herzegovina. The area above 1000 m altitude covers a surface of 42,700 m^2. Due to its fragmentation, we have only analysed habitat characteristics in the uninterrupted part that covers a total of 24,205 m^2 (Fig. 1). On this part of the massif the capercaillie is a resident species. According to Köppen climate classification (Šegota and Filipčić 2003), the area belongs to the *Df* climate type (boreal climate). The mean annual temperature varies from 2 to 8 ^{o}C, and mean July temperature from 10 to 17 ^{o}C. Annual precipitation is 1377–2458 mm (Zaninović 2008). The forests are managed. According to stand form the most dominant are European beech (64 %) and mixed silver fir *(Abies alba* Mill.*)* and European beech (33 %) forest stands. The rest of the stands (3 %) belong to management class of oaks (*Quercus petraea* (Matt.) Liebl., *Quercus pubescens* Will. and *Quercus cerris* L.), black pine (*Pinus nigra* J.F. Arnold) and Norvegian spruce (*Picea abies* (L.) H. Karst.). Mixed silver fir-European beech forests are managed in way of selective stand form, while other management class stands are managed as uneven-aged stand forma resident species.

Until now, several habitat suitability models (HSM) frameworks are developed and they can be divided in different techniques (Hirzel and Le Lay 2008), but for wildlife are relatively often in use Habitat Suitability/Selection Models (Guisan and Zimmermann 2000, Ottaviani et al. 2004, Graf et al. 2006, Braunisch and Suchant 2007, Bollmann et al. 2011). The models can use presence/absence or only presence data of focal species. However, when working with rare species, data are often scarce and choosing a wrong absence could significantly reduce the quality of a model. Namely, absence data in particular are often difficult to obtain accurately. A given location may be classified in the 'absence' set because the species could not be detected even though it was present. This problem can exist is situations where absence data are not available (many data banks), when are unreliable (most cryptic or rare species), or they are meaningless (invaders). That's why, in the paper a method was used based only on presence data (Braunisch et al. 2008) – Ecological niche factor analysis (ENFA, Hirzel et al. 2002).

ENFA computes suitability functions by comparing the species distribution in the

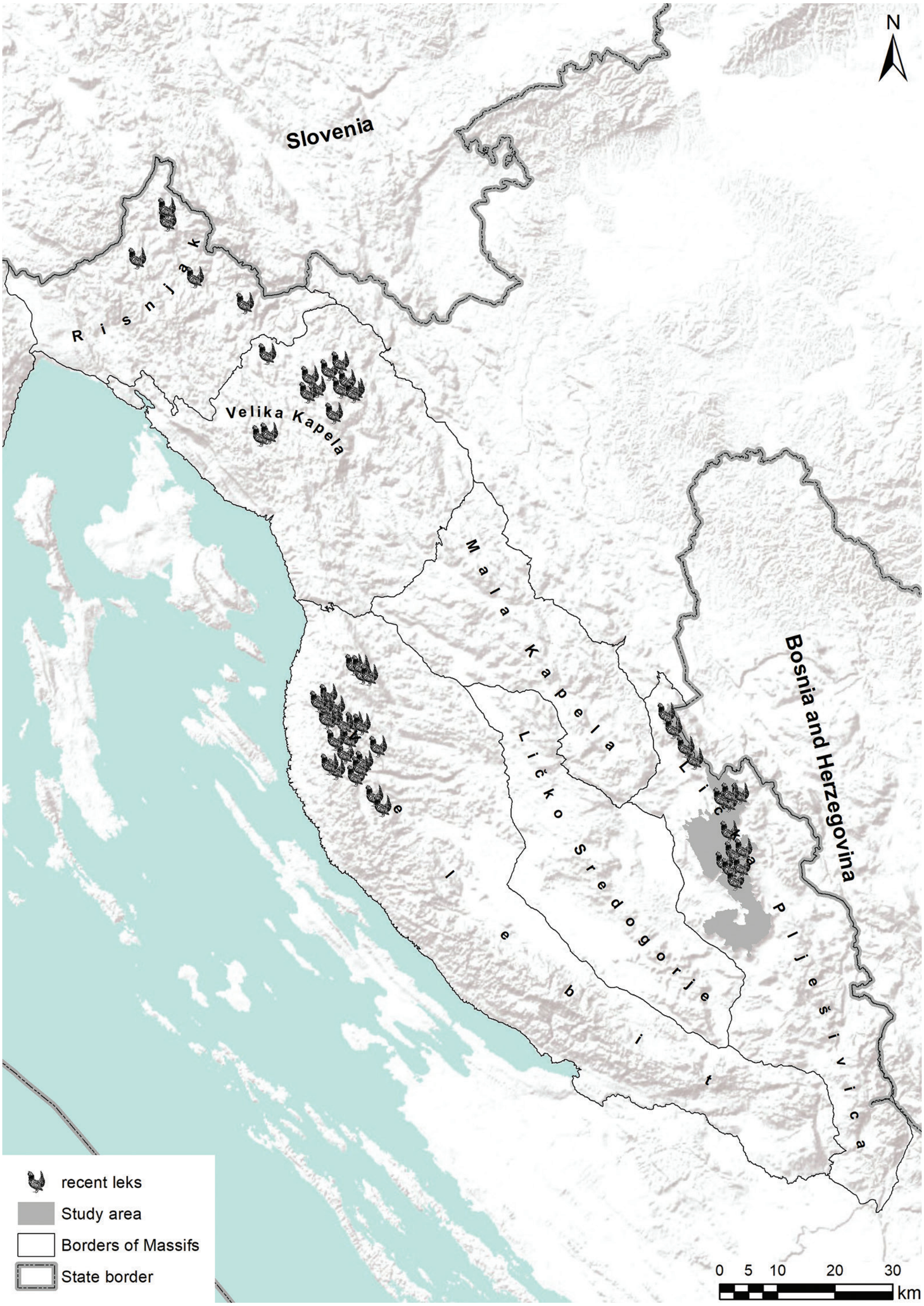

Fig. 1. Current distribution of capercaillie leks with respect to elevations.

ecogeographical space with that of the whole set of cells. The study area is divided in a lattice of adjacent cells (quadrats), each being characterized by a series of N ecogeographical variables (EGV). Thus, EGVs and species distribution are represented as set of raster maps.

Hirzel et al. (2002) created raster maps in 1×1 km (100 ha) lattice of cells. However, the Dinaric massifs in Croatia with altitude of 1000 m a.s.l. are so narrow that usually, neighbouring cells of 100 ha do not enter the researched area. For these reasons, the analysed area was divided into a network of smaller squares, measuring 100×100 m (1 ha). The capercaillie presence map was made in a way that capercaillie observation was recorded by GPS, which represented the centre of their presence (life range). Additionally, the quadrants located within a radius of 500 m from the GPS point were also included in the area. If the quadrants were further from the border of the 1000 m a.s.l. area, they were not considered. With this, the raster network proposed by Hirzel et al. (2002) was partly adjusted. EGVs were calculated for each square. In total, we used 22 EGVs of three categories of data:

a) Topographic (3 EGVs): elevation (01_tu_elev), inclination (02_tu_slope), topographic index (03_tu_topo).

b) Climate (15 EGVs): mean annual number of days with precipitation of at least 1 mm (04_tu_mnd_pr1mm), mean annual number of days with snowfalls above 1 cm (05_tu_mnd_sn1), mean annual number of cold days – $t_{min} < 0$ °C (06_tu_mancd), mean annual precipitation (07_tu_maprec), mean precipitation in spring (08_tu_manprec_spr), summer (09_tu_meanprec_summ), autumn (10_tu_manprec_aut) and winter (11_tu_meeanprec_wint), mean precipitation in vegetation period – 1st May to 31st October (12_tu_meanprec_veget), mean annual air temperature (13_tu_mean_annairtemp), mean air temperature in April (14_tu_meantemp_apr) and July (15_tu_meantemp_july), mean sun exposition per year (16_tu_mean_sunexpos), mean annual humidity (17_tu_mean_humid); and seasonal precipitation amounts, in percentages of multiannual average (in percentiles) in summer (18_tu_percprecip_summ).

c) Landscape variables (4 EGVs): percent of forest area (19_tu_perc_forest), distance of cell to roads (20_tu_dist_road, only forest roads are present in the study area), distance of cell to grasslands (21_tu_dist_grass) and basal area (22_tu_basal_area), Basal area is the common term used to describe the average amount of an area occupied by tree stems (m^2). It is defined as the total cross-sectional area of all stems in a stand measured at breast height (1.3 m), and expressed as per unit of land area – $m^2 \cdot ha^{-1}$ (Sgerm and Pranjić 1987).

Topographic variables were obtained from digitalized topographic maps (1:25,000) and transferred into a digital elevation model (DEM). A topographic index is a variable described by Guisan et al. (1999) and Weiss (2001). The Topographic Position Index (TPI) compares the elevation of each cell in a DEM to the mean elevation of a specified neighbourhood around that cell. Positive TPI values represent locations that are higher than the average of their surroundings, as defined by the neighbourhood (ridges). Negative TPI values represent locations that are lower than their surroundings (valleys). TPI values near zero are either flat areas (where the slope is near zero) or areas of constant slope (where the slope of the point is significantly greater than zero). According to TPI cells were classified in six categories: valleys (1), lower slopes (2), gentle slopes (3), steep slopes (4), upper slopes (5) and ridges.

For TPI we used 'Land Facet Corridor Designer' program for ArcGIS 9.3 (Jenness et al. 2013).

Climate variables were derived by scanning and geocoding meteorological maps (raster maps in 100 ha resolution) (Zaninović 2008). Percentile discrepancies were obtained from the Croatian Meteorological and Hydrological Service, and evaluated using a modified form of Conrad-Chapman's method. Land usage was taken from a map of habitat types in Croatia (Bioportal 2019) and the digitalized forest database (CROATIAN FORESTS 2022) of Croatian Forests Ltd.

Maps were prepared using the ArcGIS 9.3 and Idrisi Selva 17.00 software packages. Prior to the analysis, data were standardized due to the different measuring units.

Data and aerial analysis and preparation of the habitat suitability map were made in the Biomapper 4.0 program (Hirzel et al. 2004), according to following procedure:

1. Testing on discrepancies of EGVs maps.

2. Box-Cox transformation (Box and Cox 1982) and standardisation of EGVs by retrieving means and dividing by standard deviations.

3. Calculation of correlations, making of global correlation tree and calculation of Standardised Levins' niche breadth index (B_{sta}, Krebs 1989). As Standardised Levins' niche breadth index is lower, the focal species are closer to habitat specialist. From this point of view HSM analysis was performed on EGVs with the lowest breadth index in each of three types of data – in total on the basis of 11 EGVs.

4. Calculation of marginality and specialisation. Both of them can be particular (for each EGV) and global (for all EGVs). Marginality represents the absolute difference between global mean and species mean, divided by 1.96 standard deviations of the global distribution. A large value (close to one) means that the species lives in a very particular habitat relative to the reference set. Specialisation represents the ratio of the standard deviation of the global distribution to that of the focal species. Specialization coefficients range from -1 to +1, but only their absolute value is meaningful. A high value indicates a narrow niche breadth in comparison with the available conditions. Global specialization coefficients range from 1 to infinity, but it is important for calculating global tolerance. For ease of interpretation, the global tolerance coefficient is defined as the inverse of the global specialisation and it ranges from 0 to 1. A high tolerance value indicates that within a given study area, the species occupies a relatively wide niche, and vice versa.

5. Calculation of habitat suitability (HS) map and it validation. Validation is performed by comparing the habitat suitability value of a validation subset (cross-validation procedure, FAQ 2005). The model quality was quantified using the continuous Boyce index ($B_{cont(W)}$, Hirzel et al. 2006), a threshold independent modification of the Boyce index (Boyce et al. 2002), which quantifies the relationship between the observed and expected number of validation points for different values of the habitat suitability index (HIS). This index varies from -1 to 1. Positive values indicate a model which predictions are consistent with the presences distribution in the evaluation dataset, values close to zero mean that the model is not different from a chance model, negative values indicate an incorrect model, which predicts

poor quality areas where presences are more frequent.

According to ENFA habitat suitability map was developed in a way that area is divided into five categories: a) 0 % of area in net cell is suitable for capercaillie, b) 1–25 % suitability, c) 26–50 % suitability, d) 51–75 %, and e) 76–100 % suitability.

Results

In contrast to other massifs in Croatia, the trend in the capercaillie population on the Lička Plješivica massif shows a 36 % increase in lek numbers. From the previously recorded 11 leks, in this study we found 4 new leks, which gives a total of 15 leks (Table 1). Data for lek numbers of all six massifs in the middle of the 20th century were obtained from literature (Franić 1910, Rucner 1954, Turkalj 1956, Car 1970, Lukač 2004, Frković 2012), game management plans and forest management plans and our direct observations.

The habitat suitability map based on 11 EGV explains 60 % of total variance with the two first factors (marginality and first factor of specialisation, Table 2, Fig. 2). Overall marginality is relatively high, very close to 1 (0.904). It means that capercaillie lives in a very particular habitat relative to the reference set. Positive scores in bold indicate capercaillie preference for microlocalities with higher value than average, while negative scores indicate capercaillie preference for microlocalities with lower value than average in the area.

According to the scores habitat suitability (HS) for capercaillie is most influenced by climatic EGVs. More precisely, HS largely increases with seasonal precipitation in summer (score 0.453), low mean air temperature in July (score -0.391), and during the year (score -0.388), relative air humidity (score 0.374), mean air temperature in April (score -0.367) and mean annual number of days with snowfalls above 1 cm (score 0.031). It means that, capercaillie prefers areas with above average rainfall during summer in regards to long term mean and in general colder microlocalities with more snow days.

The most important land-use variables are distance to roads (score -0.232) and slopes (score 0.189), distance to pasture (score 0.129) and basal area (score 0.121). Negative impact of road distance to capercaillie presence, in fact means that capercaillie prefers microlocalities closer to roads and other EGVs indicate preference of steeper terrains and ridges,

Table 1. Number of capercaillie leks according to the massifs in Croatia.

Massif	Area above 1000 m a.s.l., ha	Area above 900 to 1000 m a.s.l., ha	Numbers of leks in the middle of the 20th century	Current number of leks	Percentage of recent leks in relation to the middle of the 20th century, %
Risnjak	23,232	11,269	112	5	4
Velika Kapela	27,719	19,376	54	14	2
Mala Kapela	6243	13,016	9	0	0
Velebit	65,347	19,038	60	24	40
Ličko sredogorje	6237	11,976	1	0	0
Lička Plješivica	42,697	17,111	11	15	136
Total	171,475	91,787	247	58	23

Table 2. Values of the first four ENFA factors for capercaillie on the Lička Plješivica massif.

Parameter	Marginality factor	Specialization factors		
		Spec. 1	Spec. 2	Spec. 3
	25 %	35 %	9 %	6 %
05_tu_mnd_sn1	**0.310**	-0.045	**0.453**	**-0.656**
14_tu_meantemp_apr	**-0.367**	-0.047	**0.276**	**-0.557**
15_tu_meantemp_july	**-0.391**	**-0.724**	**-0.441**	**0.119**
22_tu_basal_area	**0.121**	-0.008	**0.164**	**0.133**
21_tu_dist_past	**0.129**	-0.018	**0.188**	**0.200**
20_tu_dist_road	**-0.232**	-0.006	**-0.107**	**-0.155**
13_tu_mean_annairtemp	**-0.388**	**0.685**	**0.153**	**0.143**
17_tu_mean_humid	**0.374**	-0.032	**-0.645**	**0.310**
18_tu_percprecip_summ	**0.453**	-0.017	**0.076**	**-0.208**
02_tu_slope	**0.189**	0.002	**-0.072**	0.013
03_tu_topo	-0.016	0.001	-0.005	**0.056**

Note: Numbers in bold indicate statistical significance the level of p<0.05. Percentages refer to explained marginality and specialization.

microlocalities more distant to grasslands and, finally, forest stands of thicker trunks of trees. Topographic index doesn't have significant impact on capercaillie presence.

Eigenvalue attributed to this first factor is relatively low (26.854). It means that randomly chosen cells in Lička Plješivica are about 30 times more dispersed on this axis than are the cells were capercaillie was recorded. In other words, at the Lička Plješivica locality Capercaillie are not very much sensitive to shifts from their optimal conditions on this axis. In addition to that is specialization factor score.

Specialization factor is moderate 1.562 (global tolerance is 0.64). According to the values, capercaillie shows slight tendency toward habitat generalist. It is normally, because we performed analysis of relatively specific area (part of the Lička Plješivica Mountain over 1000 m a.s.l.) which, in *sensu lato*, belong to 'capercaillie areas'. Specialisation scores in bold (Table 2) mean the capercaillie was found occupying a narrower range of values than available. First factor of specialisation explains 35 % of total variance, but only two EGVs significant explain – mean air temperature in July (score 0.724) and mean annual air temperature (score 0.685). Scores of specialisation should be interpreted as unsigned values.

If the suitable area (HS) is divided into the five qualitative classes, then based on the analysis and calibration, the final map of habitat suitability for the capercaillie (Fig. 2) has a relatively high reliability index ($B_{cont(W)}$ = 0.95 ±0.092).

Based on the habitat suitability map, Lička Plješivica can be divided into two main zones: northern and middle part, and southern part of the massif. Unsuitable areas (0 %, Table 3) are mostly situated in the southern part of the Lička Plješivica, with relatively low portion (2.49 %). Low suitable areas (1 to 25 %) are situated also in the southern part of the massif and they comprise more than one third of the mountain (37.68 %). Moderate suitable ar-

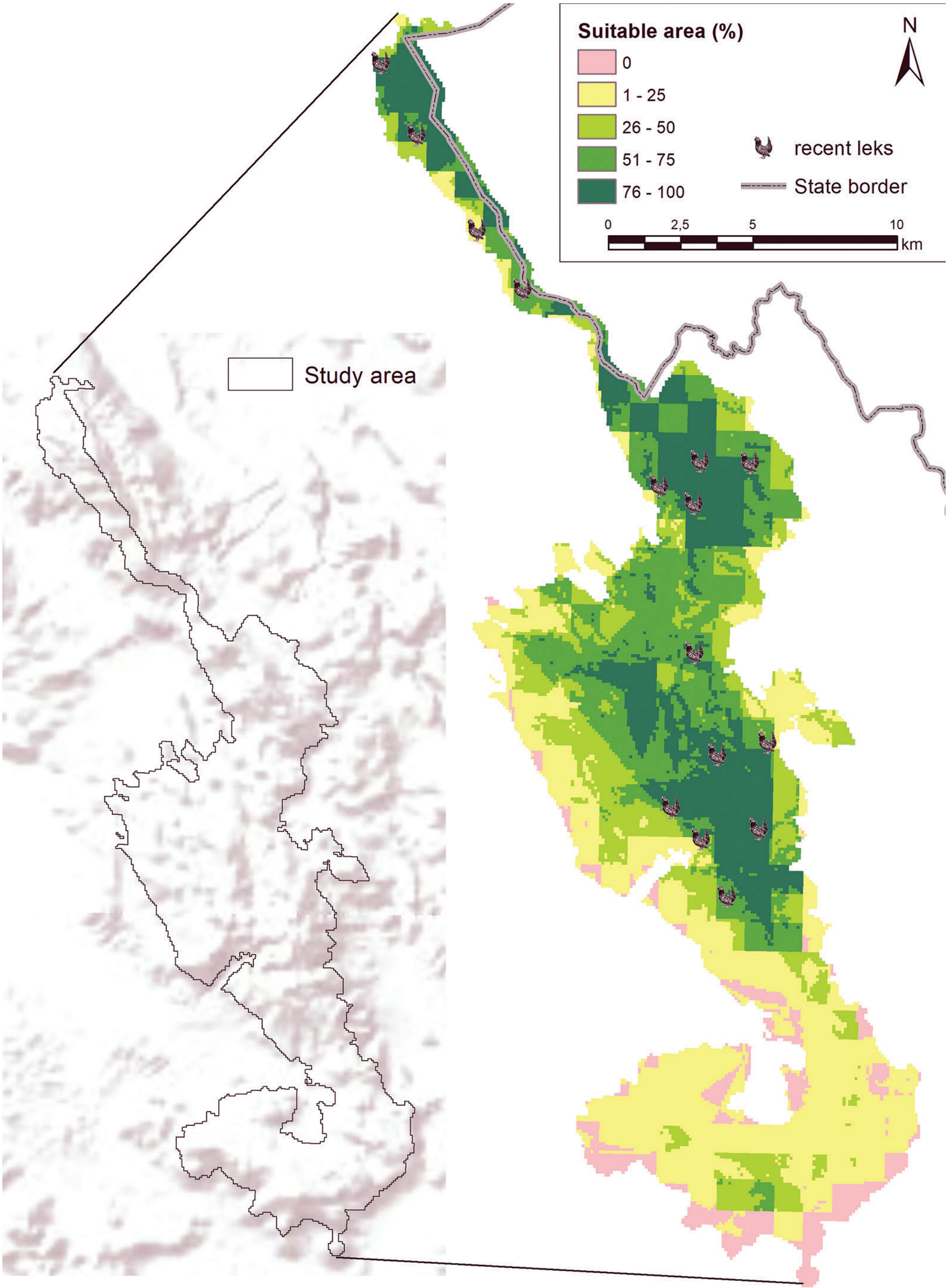

Fig. 2. Relief (left) and habitat suitability map for capercaillie on the Lička Plješivica massif (right).

Table 3. Classes of suitable areas for capercaillie at studied area of the Lička Plješivica massif over 1000 m a.s.l.

Classes of suitable areas	Description	Area, ha	Share in study area, %
0 %	Unsuitable	603	2
1 to 25 %	Low suitable	9121	38
26 to 50 %	Moderate suitable	4125	17
51 to 75 %	Suitable	5246	22
76 to 100 %	Very suitable	5110	21
Total		24,205	100

eas occupied middle part of the mountain with portion of 17.04 %. They surround better capercaillie habitats but some leks are located on this part of the Lička Plješivica. Moderate suitable areas are also placed in the middle part of the study area with some lower share (21.67 %). In this area are also present some leks. Finally, very suitable areas have share of 21.11 %. High quality habitats are located on the ridge of the Plješivica Mountain (Fig. 2), mostly in the northern part of the massif, and less in the midle part. Generally, quality of capercaillie habitats shows some decreasing gradient from north to the south of study area.

Discussion

As capercaillie out from boreal area inhabits high mountains with harsh terrain and is a rather shy species, near-accurate estimation of its population size is related to many difficulties, especially if using classic monitoring methods. Our results support the theses, because capercaillie was present in colder microlocalites, steeper terrain and on the ridges of Lička Plješivica.

Due to the habitat preferences already mentioned, the easiest way of assessing population size is to monitor lek activity. This however complicates habitat evaluation, since males and females have different habitat preferences. For example, while during summer and autumn females use old tree stands and forest clearings (Storch 1993), males only use old tree stands. Saniga (2004) reports that in the Carpathian Mountains males can be found on spruce-beech-fir stands (54 %) after the mating season, while during the summer and autumn they inhabit spruce forests (45 % and 60 % respectively). Similar habitat types, mostly dominated by conifers, prefers the Balkan capercaillie (*Tetrao urogallus rudolfi* Dombrowski, 1912) in Bulgaria (Plachiyski et al. 2018, 2019). This is understandable if known that capercaillie prefers stands where blueberry dominates on the ground floor (Storch 1995), which are strongly related to conifer forests. In our study area patches with blueberry are very rare, but nevertheless capercaillie prefers forest patches with relatively high basal area. More precisely, the patches are presented by groups of old trees in common beech forest stands. Except beech stands, some leks are placed in beech-fir stands. These stands officially have selective structure, but during visiting of leks it seems the stand structure is more uneven-age then selective, which will be more deeply studied in the future.

In our research, capercaillie leks were not strictly associated with coniferous forest stands but mixed silver fir and beech or pure sub-mountain beech stands. This indicates the adaptation of the capercaillie to the forest stand composition. Similar findings were recorded in Cantabria (Spain) where the capercaillie inhabits beech forests with a very small ratio of conifers (Rodriguez and Obeso 2000). Furthermore, forest stands in the analysed part of the Dinaric Alps are of uneven age (sub-mountain beech forests), or are selective (beech-fir forests). This makes it difficult to find a relationship between capercaillie presence and forest characteristics on the Dinaric Alps in comparison to the boreal region (Miettinen 2009). ENFA analysis did not confirm any relationship between capercaillie presence and the ratio of coniferous trees, but did confirm a correlation with the size of the trees. This finding confirms previous statements that capercaillie prefer older forests. Another habitat peculiarity is represented by the special type of forest zonality of the Western and Central Dinaric Alps. There the vegetation zones on hilly and mountain areas are initially sessile oak forests and continue with hilly beech forests – beech-fir forests, and end with sub-mountain beech forests (Horvat 1949). This represents the so-called 'Dinaric type of vertical distribution of tree community structure', in which zones of spruce forests do not follow the zones of beech-fir forests as in Central Europe. Therefore, the capercaillie on Dinaric Alps mainly inhabits mixed-aged sub-mountain beech forests. Another important factor in lek establishment is topography. Using the example of the Western Carpathians, Saniga (2002) reported that 27 out of 43 leks were located in the upper half of convex, lateral ridges, in a range of 30 to 300 m from the main ridge. It was hypothesized that these locations are easier to find in conditions of dust and foggy weather. Our results indicate that the capercaillie chooses steeper slopes and ridges (if other habitat requirements are met). Braunisch and Suchant (2007) hypothesize that the capercaillie prefers areas with snow deeper than 10 cm. According to them these areas: i) are more susceptible to the creation of clearances, with the consequent creation of a variety of living conditions, ii) have fewer predators and iii) allow birds to rest in the snow and reduce their energy loss. In our research, marginality analysis has shown similar results, with very high marginality score between capercaillie presence and number of days with snow cover over 1 cm. However, if the analysis goes slightly deeper, it is clear that the capercaillie avoids temperature extremes, both between seasons and years. In general, the capercaillie prefers a colder and humid climate.

Results of analysing capercaillie habitats in Switzerland (Sachot 2002) showed most potential disturbance factors didn't have negative impact on the capercaillie presence. For example, wild boar hunting has a very low influence. But, in Dinaric Alps all three big carnivore species (Brown bear – *Ursus arctos* Linnaeus, 1758, Grey wolf – *Canis lupus* Linnaeus, 1758, Eurasian lynx – *Lynx lynx* Linnaeus, 1758) were present and that's why big game species (Northern chamois – *Rupicapra rupicapra* Linnaeus, 1758; Red deer – *Cervus elaphus* Linnaeus, 1758; Roe deer – *Capreolus capreolus* Linnaeus, 1758; and Wild boar – *Sus scrofa* Linnaeus, 1758) are not abundant. Small game hunting is not present in the study area. Thus, hunting activity is present, but at low level. Moreover, capercaillie tend to be closer to narrow forest roads with soft cover and nordic ski trails (Sachot 2002). In our study, capercaillie presence is more likely close to the roads. Possible explanation lays in the fact that the massif is very depopulated, relatively isolated and human visiting is very rare (foresters and, occassionaly, a few hunters or mountaineers). The situation is the same in most of Croatian part of Dinaric Alps. But, the road network size of study area in the paper is 14.26 m·ha^{-1}. Road network density in out boreal part of the capercaillie distribution area varies from 4 to 5 m·ha^{-1} (Alps respective Jura, Switzerland, Brändli et al. 2016), 6.6 to 6.7 m·ha^{-1} (West Carpathian, Poland, Kroczak et al. 2016), 26.53 m·ha^{-1} (Rhodope and Rila mountains, Bulgaria, Krumov 2019) to 48.6 m·ha^{-1} (Alps, Austria, Toscani et al. 2020). According to these data, it seems forest road network in our study area is moderate and still doesn't show detrimental effect for capercaillie.

The reasons for the population decline in Croatia are still debated, but it seems that the geomorphology of the Dinaric Alps is one of the potential factors. The mountain line from Risnjak massif continues without interruptions via Velika and Mala Kapela massifs to Lička Plješivica, and further to Bosnia, Serbia and Montenegro. This relief enables the spread of capercaillie from Bosnia, where the population is still quite stable (Adamič et al. 2006), to Lička Plješivica, but not further to Mala Kapela massif. This lack of communication with other populations leads to isolation and the consequent local decline. Previous research stated that on Mala Kapela massif the capercaillie inhabits areas from 800 to 1400 m a.s.l. (Turkalj 1934). However, loss of connection with other populations and potential climate and habitat change have resulted in the rapid decline of capercaillie populations on this massif. On the other hand, to the south of the Velebit massif the altitudes are lower, and there are uninterrupted mountain habitats. Müller (1974) claims that the leks are positioned on higher ground as they are usually used as flying corridors for females during the mating season. New leks can be established in areas with a high density of females, or areas where subadult males are visiting females. If they manage to keep them until the mating season, a new lek is established (Gjerde et al. 2000).

From all we observed it is clear that on the Lička Plješivica massif only 6 % of the area above 1000 m a.s.l. is unsuitable for capercaillie, while 31 % is characterized as highly suitable. This, in combination with the connection to the Bosnian capercaillie population, has probably resulted in the gradual population increase.

Conclusions

Over the last 60 years, capercaillie populations in Croatia have exhibited a 77 % decline. The highest decline was observed on Risnjak massif, were lek numbers dropped from 112 in the middle of the 20th century to the present five. Interestingly, a slight increase in lek numbers was observed on the Lička Plješivica massif (from 11 to 15). The ENFA analysis applied showed that the capercaillie prefers colder areas, steeper terrains and ridges and areas closer to roads where forest stands are comprised with groups of older trees. On the other hand, the capercaillie avoids grasslands (open areas). Compared to boreal areas, the Alps and the Carpathian Mountains, the capercaillie shows certain habitat preferences in the Dinaric Alps. In other words, the ENFA analysis did not confirm a relationship between the presence of capercaillie and the ratio of coniferous trees. This is in accordance with the different zonality of forest vegetation in the Western and Middle Dinaric Alps. The so-called Dinaric type of vertical distribution of tree community structure, in which zones of beech-fir forests are followed again by beech forests, results in the fact that the capercaillie in the Dinaric Alps inhabits mainly uneven-age sub-mountain beech forests. In conclusion, the high suitability of Lička Plješivica as the capercaillie's habitat and its connection to the Bosnian capercaillie population are probably the reasons for the population increase observed on Lička Plješivica.

References

Adamič M., Rapaić Ž., Popović Z., Kunovac S, Koprivica M., Soldo V., Marković B., Maunaga R., Mičević M., Ilkić V. 2006. Endangered Game Species in Bosnia and Herzegovina. Finaly report, Banja luka. 138 p.

Bajc M., Čas M., Ballian D., Kunovac S., Zubić G., Grubešić M., Zhelev P., Paule L., Grebenc T., Kraigher H. 2011. Genetic Differentiation of the Western Capercaillie Highlights the Importance of South-Eastern Europe for Understanding the Species Phylogeography. PLoS ONE 6(8), e23602. doi: 10.1371/journal.pone.0023602.

Bioportal 2019. Web portal of the nature protection information system [Web portal informacijskog sustava zaštite prirode]. Ministry of Economy and Sustainable Development [Ministerstvo gospodarstva i udrživog razvoja]. Web site (in Croatian). http://www.bioportal.hr/gis/

Bollmann K., Graf R.F., Suter W. 2011. Quantitative predictions for patch occupancy of capercaillie in fragmented habitats. Ecography 34: 276–286. http://www.jstor.org/stable/41239320

Box G.E.P., Cox D.R. 1982. An Analysis of Transformation Revisited, Rebutted. Journal of American Statistical Association 77(377): 209–210. doi: 10.1080/01621459.1982.10477788

Boyce M.S., Vernier P.R., Nielsen S.E., Schmiegelow F.K.A. 2002. Evaluating resource selection functions. Ecological Modelling 157(2–3): 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Brändli U.-B., Fischer C., Camin P. 2016. Stand der Walderschliessung mit Lastwagenstrassen in der Schweiz. Schweizerische Zeitschrift für Forstwesen 167(3): 143–151. https://doi. org/10. 3188/szf.2016.0143

Braunisch V., Bollmann K., Graf R.E., Hirzel A.E. 2008. Living on the edge – Modelling habitat suitability for species at the edge of their fundamental niche. Ecological Modelling 214: 153–167. https://doi.org/10.1016/j.ecolmodel.2008.02.001

Braunisch V., Suchant R. 2007. A model for evaluating the 'habitat potential' of a landscape for capercaillie *Tetrao urogallus*: a tool for conservation planning. Wildlife Biology 13(Suppl. 1): 21–33.

Car Z. 1970. Hunting management plan for hunting ground 'Gumance' for time span 1969–1978, Forest office Klana [Lovno privredna osnova za privredno lovište 'Gumance' 1969–1978, područje šumarije Klana]. Delnice. 204 p. (in Croatian).

CROATIAN FORESTS 2022. HRVATSKE ŠUME d.o.o. Headquarters, Zagreb. Web site. http://www.hrsume.hr/

FAQ 2005. Frequently Asked Questions, FAQ version: 02.12.2005. Web site. https://www2.unil.ch/biomapper/faq.html

Franić D. 1910. Plitvice lakes and their surroundings [Plitvička jezera i njihova okolica]. Zagreb. 439 p. (in Croatian).

Frković A. 2012. Capercaillie in Gorski kotar [Tetrijeb gluhan u Gorskom kotaru]. Hunting alliance of Primorsko-goranska County, Zagreb. 208 p. (in Croatian).

Gjerde I., Wegge P., Rolstad J. 2000. Lost hotspots and passive female preference: the dynamic process of lek formation in capercaillie *Tetrao urogallus*. Wildlife Biology 6(4): 291–298. https://doi.org/10.2981/wlb.2000.029

Graf R.F., Bollmann K., Sachot S., Suter W., Bugmann H. 2006. On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. Ecography 29(3): 319–328. https://doi.org/10.1111/j.2006.0906-7590.04328.x

Guisan A., Weiss S.B., Weiss A.D. 1999. GLM versus CCA spatial modelling of plant species distribution. Plant Ecology 143(1): 107–122. https://doi.org/10.1023/A:1009841519580

Guisan A., Zimmermann N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135(2–3): 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Hirzel A.H., Hausser J., Chessel D., Perrin N. 2002. Ecological-niche factor analysis. How to compute habitat-suitability maps without absence data? Ecology 83(7): 2027–2036. https://doi.org/10.1890/0012-9658(2002)083[2027:ENFAHT]2.0.CO;2

Hirzel A.H., Hausser J., Perrin N. 2004. Biomapper 3.1. Lab. of Conservation Biology, Department of Ecology and Evolution, University of Lausanne. http://www.unil.ch/biomapper

Hirzel A.H., Le Lay G. 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology 45(5): 1371–1381. https://doi.org/10.1111/j.1365-2664.2008.01524.x

Hirzel A.H., Le Lay G., Helfer V., Randin Ch., Guisan A. 2006. Evaluating the ability of habitat suitability models to predict species presence. Ecological Modelling 199(2): 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017

Horvat I. 1949. Plant community science [Nauka o biljnim zajednicama]. Nakladni zavod Hrvatske, Zagreb. 434 p. (in Croatian).

Jenness J., Brost B., Beier P. 2013. Land Facete Tool Designer. USDA Forest Service Rocky Mountain Research Station, McIntire-Stennis Cooperative Forestry Program Arizona Board of Forest Research. 110 p. www.corridordesign.org

Klaus S., Berger D., Huhn J. 1997. Capercaillie *Tetrao urogallus* decline and emissions from the iron industry. Wildlife Biology 3(3–4): 131–136. doi: 10.2981/wlb.1997.017

Krebs C.J. 1989. Ecological Metodology. Harper & Row, Publishers. New York. 654 p.

Kroczak R., Bryndal T., Bucała A., Fidelus J. 2016. The development, temporal evolution and environmental influence of an unpaved road network on mountain terrain: an example from the Carpathian Mts. (Poland). Environmental Earth Sciences 75, 250. https://doi.org/10.1007/s12665-015-5055-6

Krumov T. 2019. Determination of the optimal density of the forest road network. Journal of Forest Science 65(11): 438–444. https://doi.org/10.17221/101/2019-JFS

Lukač G. 2004. Birds of National park Plitvice lakes [Ptice Nacionalnog parka Plitvička jezera]. Plitvički bilten (radovi) 6: 29–71 (in Croatian).

Miettinen J. 2009. Capercaillie (*Tetrao urogallus* L.) habitats in managed Finnish forests – the current status, threats and possibilities. PhD thesis. Faculty of Forest Sciences, University of Eastern Finland, Joensuu, Finland. 32 p.

Miettinen J., Helle P., Nikula A., Niemelä P. 2008. Large-scale landscape composition and capercaillie (*Tetrao urogallus*) density in Finland. Annales Zoologici Fennici 45(3): 161–173. doi: 10.5735/086.045.0301

Miettinen J., Helle P., Nikula A., Niemelä P. 2010. Capercaillie (*Tetrao urogallus*) habitat characteristics in north-boreal Finland. Silva Fennica 44(2): 235–254. doi: 10.14214/sf.151

Müller F. 1974. Die wichtigsten Ergebnisse zehnjährigen Auerwildforschung im Hessischen Bergland. Allgemeine Forstzeitschrift 29(39): 834–836.

Ottaviani D., Lasinio G.J., Boitani L. 2004. Two statistical methods to validate habitat suitability models using presence-only data. Ecological Modelling 179(4): 417–443. https://doi.org/10.1016/j.ecolmodel.2004.05.016

Plachiyski D., Popgeorgiev G., Avramov S., Boev Z. 2018. The Balkan Capercaillie *Tetrao urogallus rudolfi* Dombrowski, 1912 (Galliformes: Phasianidae): Distribution History and Current Status in Bulgaria. Acta zoologica bulgarica 70(1): 101–111.

Plachiyski D., Popgeorgiev G., Avramov S., Kornilev Y. 2019. Habitat selection of Capercaillie (*Tetrao urogallus*) displaying males: Case from Rila Mountain, Bulgaria. ARPHA

Conference Abstracts 2, e46462. https://doi.org/10.3897/aca.2.e46462

Rodriguez A.E., Obeso J.R. 2000. Diet of the Cantabrian capercaillie: geographic variation and energetic content. Ardeola 47(1): 77–83.

Rucner D. 1954. Birds of National park ‘Plitvice lakes’. Contribution to knowledge of the Lika’s avifauna [Ptice u Nacionalnom parku Plitvička jezera. Prilog poznavanju ornitofaune Like]. Larus 8: 27–65.

Sachot S. 2002. Viability and management of an endangered capercaillie (*Tetrao urogallus*) metapopulation. PhD thesis. University of Lausanne, Lausanne, Switzerland. 117 p.

Saniga M. 2002. Nest loss and chick mortality in capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) in West Carpathians. Folia Zoologica 51(3): 205–214.

Saniga M. 2004. Seasonal differences in habitat use in capercaillie (*Tetrao urogallus*) in the West Carpathians. Biologia, Bratislava 59(5): 627–636.

Segelbacher G., Höglund J., Storch I. 2003. From connectivity to isolation: genetic consequences of population fragmentation in capercaillie across Europe. Molecular Ecology 12(7): 1773–1780. https://doi.org/10.1046/j.1365-294X.2003.01873.x

Sgerm F., Pranjić A. 1987. Basal area. [Temeljnica]. In: Potočić Z. (Ed.). Encyclopaedia of Forest Sciences [Šumarska enciklopedija]. JLZ ‘Miroslav Krleža’, Zagreb: 454–459.

Storch I. 1993. Habitat selection by capercaillie in summer and autumn: Is bilberry important? Oecologia 95(2): 257–265. doi: 10.1007/BF00323498

Storch I. 1994. Habitat and survival of capercaillie nests and broods in the Bavarian Alps. Biological Conservation 70(3): 237–243. https://doi.org/10.1016/0006-3207(94)90168-6

Storch I. 1995. Annual home ranges and spacing patterns of capercaillie in central Europe. Journal of Wildlife Management 59(2): 392–400. https://doi.org/10.2307/3808953

Storch I. 2007. Conservation status of grouse worldwide: an update. Wildlife Biology 13(1): 5–12. https://doi.org/10.2981/0909-6396(2007)13[5:CSOGWA]2.0.CO;2

Toscani P., Sekot W., Holzleitner F. 2020. Forest Roads from the Perspective of Managerial Accounting – Empirical Evidence from Austria. Forests 11, 378. doi:10.3390/f11040378

Turkalj Z. 1934. Biological conditions for capercaillie on the Velika and Mala Kapela habitats [Biološki uslovi za velikog tetrijeba na staništu Velike i Male Kapele]. Lovačko-ribarski vjesnik 43(1): 12–16 (in Croatian).

Turkalj Z. 1956. The big game of the limestone area [Divljač visokog lova na krašu]. Lovačka knjiga, Zagreb. 143 p. (in Croatian).

Weiss A. 2001. Topographic Position and Landforms Analysis. Poster presentation, ESRI User Conference, San Diego, CA. http://www.jennessent.com/downloads/tpi-poster-tnc_18x22.pdf

Zaninović K. (Ed.) 2008. Climate atlas of Croatia 1961–1990, 1971–2000 [Klimatski atlas Hrvatske 1961–1990, 1971–2000]. Državni hidrometeorološki zavod (DHMZ), Zagreb. 200 p. (in Croatian).