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Habitat Selection of "Mad Cocks" of the Western Capercaillies Tetrao urogallus (Galliformes: Phasianidae) from the Fringe of the Range: A Case Study from Rila Mts. (Bulgaria)

Dimitar G. Plachiyski [* 1, 2], ***Georgi S. Popgeorgiev*** [1],
Stefan G. Avramov [2], ***Yurii V. Kornilev*** [1, 3]

1 - National Museum of Natural History, Bulgarian Academy of Sciences,
1 Tsar Osvoboditel Blvd., 1000 Sofia, BULGARIA
2 - Bulgarian Biodiversity Foundation, 39-41 Vesletz Str. fl. 4, ap. 11, 1202 Sofia, BULGARIA
3 - Integrative Zoology, Department of Evolutionary Biology, Faculty of Life Sciences,
University of Vienna, Althanstrasse 14, 1090 Vienna, AUSTRIA
[*]Corresponding author: d.plachiyski@gmail.com

Abstract. We investigated the habitat selection of "mad" Western Capercaillies males from the isolated and threatened Rila-Rhodope population. These "mad" Capercaillies are highly territorially aggressive individuals, that approach and attack people; this abnormal behavior, rarely occurs beyond single individuals in one lek and no studies that we know of have been published on such cases. In 2014–2015, we tagged with GPS transmitters three adult "mad" males associated with one lek. We evaluated the temporal variation in the Capercaillie habitat selection based on three periods ("summer", "winter", and annual). Based on Manly's selection ratios (design III), at the home range scale, males used measured habitat variables non-randomly. Birds selected forests dominated by Scots pine (annually) and Macedonian pine (summer). Males used forest stands in the age class "81 to 120" years more than the availability. They highly avoided stands dominated by Norway spruce, bare rocks and ski slopes, as well as forest stands less than 81 years old (summer and annually). The birds demonstrated significant avoidance of flat and highly slopped terrains as well as those with northern and northwestern exposure. Notwithstanding the abnormal aggressive behavior of Capercaillie males and their affiliation with an edge population, the habitat selection of "mad cocks" in the Rila Mts. is consistent with the principal habitat preference of the species.

Key words: Capercaillie, "mad cocks", GPS devices, habitat utilization, resource selection.

Introduction

The organization of animals in space and time and the resource selection patterns are central questions of ecology. Habitat selection refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (Block & Brennan, 1993; Jones, 2001). Understanding how animals establish their home ranges and how they select and use the resources within the home range is crucial for conservation and wildlife management efforts (Rechetelo et al., 2016).

The Western Capercaillie *Tetrao urogallus* L. (hereafter Capercaillie) is the

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largest and most dimorphic grouse of the boreal and montane forests of Eurasia (Rolstad et al., 1988; Storch, 2002). In the late winter and spring, males establish permanent ranges clumped around lek centers, where they display and interact with females in early spring, when the latter visit the lek to mate (Wegge & Larsen, 1987; Storch, 1997). After the display activity, in early summer, Capercaillie males move to distinct summer ranges and return to their leks in autumn and winter (Rolstad et al., 1988; Storch, 1995; Hjeljord et al., 2000). The Capercaillie requires extensive areas and is regarded as an important indicator of intactness and high structural diverse of mountain forest ecosystems (Grimm & Storch, 2000). The species is habitat specialist with affinity to old conifer forest (Storch, 2002). Due to its broad spatial and specific habitat requirements, the Capercaillie is a popular model species for the analysis of species–habitats interrelationships (Braunisch & Suchant, 2007). The Capercaillie is an anthropophobic species (Boev et al., 2007). However, throughout its range, some male birds might exhibit an abnormal aggressive behavior reaction, resulting in approach and attack of humans during the lekking period. These aggressive Capercaillie males are referred to as "mad cocks" (Storch, 2013). The aggressive abnormal behavior can be regarded as stress-coping responses (Jansen, 1986; Storch, 2013) but there are no indications if it is related to changes in habitat selection of birds.

The Capercaillie is a priority conservation species because much of its population is endangered and protecting Capercaillie habitat will benefit a host of other species of conservation concern (Suter et al., 2002; Pakkala et al., 2003; Storch, 2007; Mikoláš et al., 2016). As other endangered populations, Europe's southernmost Capercaillie's meta-population in the Rila-Rhodope Massif, Bulgaria and Greece, is threatened due to its low population size (709–1185 displaying males in Bulgaria; 350–500 individuals in Greece), isolation, habitat degradation, and decreasing distribution area (Storch, 2007; Boev & Nikolov, 2015; Plachiyski et al., 2018). While the habitat preferences of the Capercaillie are well recognized in Scandinavia (e.g. Rolstad et al., 1988; Rolstad & Wegge, 1989; Gjerde, 1991a, 1991b; Finne et al., 2000; Hjeljord et al., 2000), Scotland (e.g. Moss et al., 1979; Picozzi et al., 1996; Summers et al., 2004), Central Europe (e.g. Storch, 1993a, 1993b, 1995; Saniga, 2002, 2004; Thiel et al., 2007), and the Iberian Peninsula (e.g. Ménoni, 1991; Quevedo et al., 2006; Blanco-Fontao et al., 2010; González et al., 2012), the knowledge of the Rila-Rhodope population is based only on direct observations on the habitat use of the species. Because populations at the edge of a species' distribution use ecologically marginal habitats, observations made in one part of the range are not always applicable at the edge of a species' distribution (Quevedo et al., 2006).

We had the rare chance to identify and to equip with GPS transmitters three "mad" adult Capercaillie males associated with one lek. We used GPS telemetry to understand their habitat selection at home range scale. The main questions asked were: (a) What is the habitat selection in adult Capercaillie males with abnormally aggressive behavior?; (b) Did the habitat selection of adult Capercaillie males with abnormally aggressive behavior differ from the known for the species in general? In addition, the results obtained will indicate potential differences in habitat selection between birds from the southernmost edge and the others populations that will inform conservation-oriented management of the threatened subspecies.

Material and Methods

Study area

The field study was conducted in 2014–2015 in the northeastern part of Rila Mts., southwestern Bulgaria (Fig. 1). The study area (defined precisely as a result of the obtained telemetry data) encompassed 2162 ha of forests and glades from 1430 to 2330 m a.s.l. between the upper wellsprings valleys of the rivers Beli Iskar and Maritsa. The climate is a montane variant of the transitional, with mean temperatures of 0 to 14 °C in July and -7 to -4° C in January, with annual precipitation of 700–900 mm. The ground is usually covered with snow from mid-November to late April or May (depending on altitude and aspect) (Kopralev, 2002). The forest communities are represented by old (mean age 103 yrs. ± 35 SD; authors' unpubl. data), open, mixed and unmixed coniferous communities dominated by Scots pine *Pinus sylvestris* L., Macedonian pine *Pinus peuce* Griseb, Norway spruce *Picea abies* (L.) Karsten, dwarf Mountain pine *Pinus mugo* Turra and European silver fir *Abies alba* Mill (Fig. 2).

The study area was situated predominantly (1491.76 ha) within Rila National Park (IUCN category II), managed with priority on ecosystems diversity maintenance and wildlife protection. Hunting is banned. The remaining territory (670.36 ha) was managed by the ski zone concessionaire and local State Forestry. Forestry activities included predominantly harvesting, afforestation, protection against erosion and floods, and hunting. In the western part of the study area were the infrastructure facilities (ski slopes, lifts, etc.) of the "Borovets" Ski Resort. The resort is located between 1300 and 2560 m a.s.l. The skiing infrastructure included three ski centers with 58 km marked ski trails as well as ski roads, lifts (11.13 km), and roads between the ski centers. In addition, 20 km of mountain bike tracks were marked and used predominantly during the summer (Fig. 1).

Study of individuals and telemetry

In May and August 2014, three displaying "mad" males ("Birds 1–3") associated with one lek were captured at the lek using large fisherman's landing nets and by hand. According to beak depths (Moss et al., 1979; Wegge & Larsen, 1987), all birds were more than three years old. Two young males displaying at the lek's periphery were identified but not captured.

Each of the three adults was equipped on site with a "Bird 2A" backpack GPS tags (e-obs Digital Telemetry, Grünwald, Germany) and released. The devices were fitted to the bird's backs using a 5 mm Teflon ribbon and a 3 mm thick neoprene pad glued to the bottom of the device. The tags weighted 88 g (2.5–2.75% of bird's body mass), provided positional accuracy of about ± 10 m, and could save about 10000 GPS fixes. Timestamped readings were obtained every 1 hour (in the displaying season) and 2 hours otherwise. Data were downloaded wirelessly, with a maximum range of 200–500 m in dense forest, 15 km hilltop to hilltop, and 10 km by use of small plane.

Based on 18241 GPS fixes for the three individuals (for "Bird 1" – 6638 GPS fixes in 428 days; for "Bird 2" – 5678 fixes in 357 days; "Bird 3" – 5925 fixes in 362 days), we obtained the Minimum Convex Polygons utilized by each individual: "Bird 1" - Annual – 735.8 ha; Summer – 604.12 ha; Winter – 110.33 ha; "Bird 2" - Annual – 276.49 ha; Summer – 187.96 ha; Winter – 84.47 ha; "Bird3" - Annual – 1138.95 ha; Summer – 1117.51 ha; Winter – 136.61 ha.

Ethics statement

Strict protocols to minimize stress and potential injury to the birds was followed. Handling was minimal and all procedures were carried on site by a veterinarian. The scientific permit was issued by the Rila National Park Directorate (№ РД–СР–25/10.05.2014). At the end of the study, the tags were removed and the birds were released in good health.

Data analyses

To determine resource selection, we used Manly's selection ratios (w) for habitat selection design III, where individual animals are identified and both utilized and available resources (resource units) are measured at the scale of the individual (Thomas & Taylor, 1990; Manly et al., 2002).

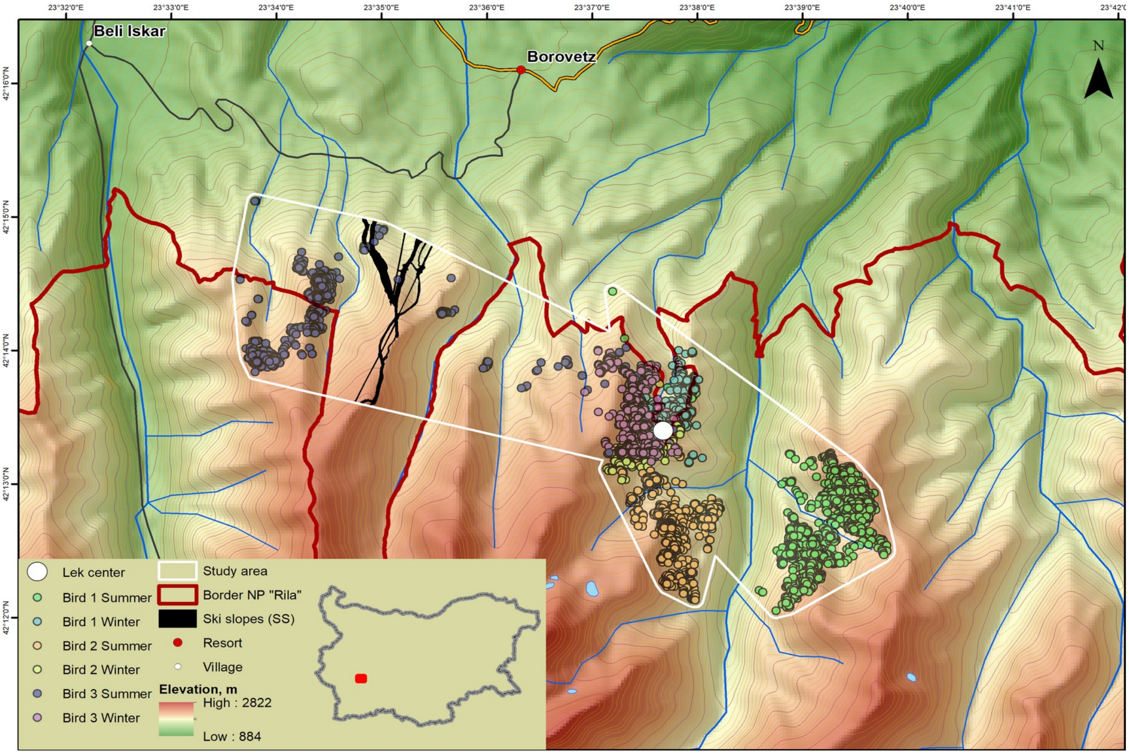

Fig. 1. Study area in Rila Mts., Bulgaria, with temporal distribution of the positions of the three "mad" Capercaillie males.

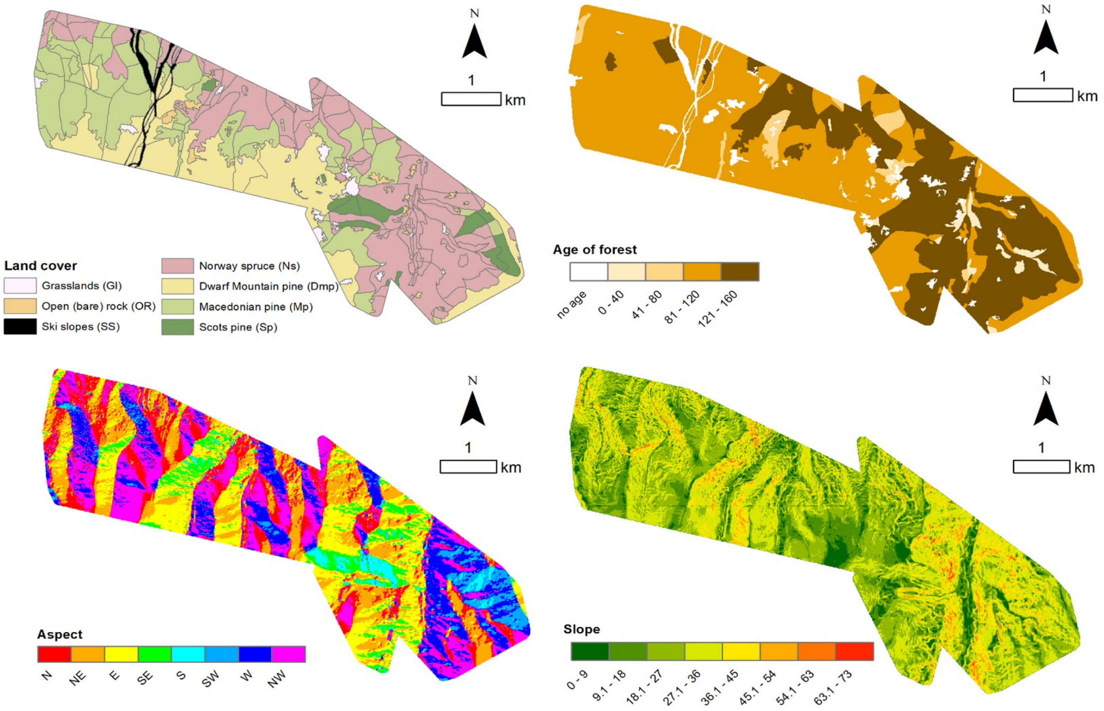

Fig. 2. Distribution of Land cover type, Age of Forest, Aspect and Slope within the study area.

The preference for a given habitat *j*, given by its selection ratio *wj*, is the number of times a Resource Unit (RU) within habitat *j* was used, divided by the available number of RUs for that given habitat. For our study, all the RUs (8 m pixels) within an individual's MCP were defined as available. According to the hypothesis of no particular selection or avoidance, *wj* should approach one, which means that the habitat *j* is used in proportion to its availability (Bengtsson et al., 2014). Habitat selection was defined as the difference in recorded use (distribution of GPS locations) to expected availability of RUs using a log-likelihood chi-square test (Khi2L) for overall habitat selection (Calenge, 2019; Ramesh et al., 2016). Capercaillie habitat preference was computed using Manly's habitat selection ratios combined with 90% Bonferroni simultaneous confidence intervals (Manly et al., 2002). We considered significant habitat preference if the lower *CI* limit was above 1 and significant avoidance if the upper *CI* limit was below 1. Habitat preference analyses were conducted by means of "adehabitatHS" package in R (Calenge, 2007) using a log-likelihood non-random statistic, setting $\alpha = 0.05$. We used software ArcGIS ver. 10.2.1 (ESRI, 2014), in combination with R version 3.5.1. (R Development Core Team, 2013) and R Studio version 1.1.463-2009-2018 (RStudio Team, 2015).

Environment definitions

Dominant tree species and forest stand succession (Table 1, Fig. 2) were based on a digital layer from the Forest Data Base (FDB) (Executive Forest Agency, 2014). Non-forested habitats were added based on CORINE Land Cover level 3 (2012) and by hand-delineating habitats using current high-resolution aerial and satellite imagery (Google Maps Hybrid, Google, 2019; World Imagery Map, ESRI, 2019). The slope and aspect (Table 1, Fig. 2) were derived from a digital elevation model (DEM) with 8-m resolution. The layers were rasterized into 8-m pixels using the "feature to raster" conversion tool and "cubic convulsion" resampling in ArcGIS. All the environment variables were turned into categorical and reclassified either as equal size partitions or using "Jenk's natural breaks" function in ArcGIS. To calculate individual habitat, use and habitat selection, for each GPS location we determined in ArcGIS the respective habitat and surface characteristics.

To study the temporal variation in habitat selection, the data were partitioned conditionally into groups according to distinct movements of tracked birds for occupation of seasonal (winter–spring and summer–autumn) habitats. A distinct movement was defined as a directional movement of 1 km or more within a 5-day period (Rolstad et al., 1988). For each individual, we defined the pre-displaying and displaying period when the male birds inhabit permanently the lek and the territories around it and do not make distinct movements more than 1.5 km from the lek center, as "winter" (usually from December–February to the first week of June). The conditional "summer" (non-breeding) period is then the remainder of the year (usually second week of June to November–January). The annual period then combines the winter and summer.

Results

At the home range scale (using MCP), "mad" males used vegetation cover non-randomly (annual: Khi2L = 5738.89, df = 14, $p < 0.001$; winter: Khi2L = 3773.28, df = 13, $p < 0.001$; summer: Khi2L = 3646.32, df = 14, $p < 0.001$). They significantly selected forests dominated by Scots pine (annually) and Macedonian pine (in summer) (Table 2, Fig. 3). Habitats dominated by Dwarf Mountain pine were used in proportion to its availability, during summer and annually. Forests dominated by Norway spruce, open (bare) rocks and ski slopes were highly avoided (Table 2, Fig. 3). Ski slopes were only present in the summer home range of "Bird 3".

Roosters used forests of different stages non-randomly (annual: Khi2L = 3492.57, df = 8, p < 0.001; winter: Khi2L = 2075.18, df = 8, p < 0.001; summer: Khi2L = 1670.1, df = 6, p < 0.001). They clearly avoided forest stands less than 81 years old in the summer and annually. Males used forest stands in the age class "81–120" years more than the availability but the selection was not significant (Table 2, Fig. 4).

Birds did not use slopes within the class "63.1–73.0" (Table 2). In the summer, males significantly preferred slopes within the class "27.1–36.0" and avoided "0–9", "9.1–18.0" and "54.1–63.0". The birds also demonstrated significant avoidance of flat terrains ("0–9.0") annually (Fig. 5, annual: Khi2L = 608.24, df = 17, p < 0.001; winter: Khi2L = 1148.37, df = 16, p < 0.001; summer: Khi2L = 906.54, df = 17, p < 0.001).

The roosters demonstrated significant preference for southeastern exposure during the winter and annually. They showed significant avoidance of northern exposure overall, as well as avoidance of north-eastern aspect during the winter and southern aspect during the summer (Fig. 6, annual: Khi2L = 4671.87, df = 18, p < 0.001; winter: Khi2L = 3909.04, df = 16, p < 0.001; summer: hi2L = 3095.84, df = 18, p < 0.001). Despite the high availability of northwestern exposures (19.2%, Table 1), the birds did not use them during the year (Table 2).

The large *CI*s for selection of variables indicate individual variation in the preference among the tagged birds.

Table 1. Availability of environmental variables within the study area. pix (n) = the number of the pixels (8×8 m) within the corresponding variable class. ha = variable class area in hectares. % = percent of pix (n) per variable.

Variable	Variable class	Available resource units pix (n)	ha	%
Slope (Steepness, °)	0.0–9.0	16633	106.45	4.9
	9.1–18.0	59498	380.79	17.6
	18.1–27.0	108095	691.81	32.0
	27.1–36.0	102046	653.09	30.2
	36.1–45.0	38819	248.44	11.5
	45.1–54.0	10756	68.84	3.2
	54.1–63.0	1811	11.59	0.5
	63.1–73.0	173	1.11	0.1
Aspect (Exposure)	N	46607	298.28	13.8
	NE	63798	408.31	18.9
	E	65909	421.82	19.5
	SE	22878	146.42	6.8
	S	9144	58.52	2.7
	SW	15263	97.68	4.5
	W	49521	316.93	14.7
	NW	64711	414.15	19.2
Forest stand succession (Age, years)	0–40	6217	39.79	1.9
	41–80	9044	57.88	2.8
	81–120	187246	1198.37	58.1
	121–160	119750	766.4	37.2
Land cover: Dominant tree species	Norway spruce (Ns)	134312	859.6	39.8
	Macedonian pine (Mp)	95349	610.23	28.2
	Dwarf Mountain pine (Dmp)	78345	501.41	23.2
	Scots pine (Sp)	14251	91.21	4.2
Non-forest cover	Grasslands (Gl)	6215	39.78	1.8
	Ski slopes (SS)	4896	31.33	1.5
	Open (bare) rock (OR)	4463	28.56	1.3

Table 2. Average selection ratios (*Wi*) at the home range scale for three Capercaillie adult males. *Legend:* Ns = Norway spruce, Mp = Macedonian pine, Dmp = Dwarf Mountain pine, Sp – Scots pine, Gl – Grasslands, Ski slopes (SS), OR – Open (bare) rock, SE = standard error, ± 90% *CI* = confidence interval with lower and upper limits, Use % = habitat use, as % of Capercaillie locations within variable class from total number of locations per variable.

Variable	Variable class	Annual					Winter					Summer				
		Wi	SE	± 90% *CI*		Use %	*Wi*	SE	± 90% *CI*		Use %	*Wi*	SE	± 90% *CI*		Use %
Slope (Steepness, °)	0–9.0	0.45	0.15	0.10	0.81	2.6	0.39	0.27	-0.28	1.06	3.8	0.35	0.11	0.08	0.63	1.8
	9.1–18.0	0.93	0.05	0.80	1.06	16.7	0.95	0.10	0.70	1.20	27.5	0.54	0.11	0.27	0.81	9.4
	18.1–27.0	1.00	0.05	0.88	1.11	32.2	0.81	0.18	0.38	1.24	29.8	1.05	0.08	0.84	1.25	33.9
	27.1–36.0	1.14	0.11	0.88	1.40	33.4	1.44	0.35	0.58	2.29	26.2	1.27	0.07	1.10	1.43	38.3
	36.1–45.0	1.03	0.24	0.45	1.61	11.4	1.65	0.45	0.54	2.76	8.1	1.21	0.49	0.02	2.40	13.6
	45.1–54.0	1.06	0.24	0.48	1.64	3.3	3.81	1.99	-1.06	8.69	4.1	0.86	0.34	0.04	1.68	2.8
	54.1–63.0	0.73	0.25	0.13	1.33	0.4	3.08	1.20	0.14	6.01	0.5	0.52	0.06	0.38	0.65	0.3
	63.1–73.0	NA	NA	NA	NA	0.0	NA	NA	NA	NA	0.0	NA	NA	NA	NA	0.0
Aspect (Exposure)	N	0.48	0.2	0.1	0.9	7.1	0.32	0.3	-0.4	1.0	4.4	0.59	0.1	0.44	0.73	8.9
	NE	0.84	0.4	-0.3	1.9	20.6	0.33	0.2	-0.2	0.9	6.0	1.26	0.6	-0.09	2.61	30.5
	E	0.89	0.3	0.2	1.5	21.9	0.65	0.4	-0.2	1.5	19.8	0.96	0.4	0.07	1.85	23.3
	SE	2.04	0.2	1.6	2.5	22.3	2.45	0.5	1.3	3.6	44.6	0.72	0.3	0.07	1.36	7.2
	S	1.46	0.7	-0.2	3.1	9.5	2.06	1.2	-1.0	5.1	19.9	0.51	0.1	0.27	0.75	2.4
	SW	1.82	0.6	0.3	3.4	8.9	0.40	0.3	-0.4	1.2	0.9	2.58	0.8	0.72	4.44	14.3
	W	0.72	0.5	-0.4	1.9	9.8	0.59	0.4	-0.3	1.5	4.3	0.84	0.6	-0.51	2.20	13.4
	NW	NA	NA	NA	NA	0.0	NA	NA	NA	NA	0.0	NA	NA	NA	NA	0.0
Forest stand succession (Age, years)	0–40	0.41	0.21	-0.06	0.89	1.1	0.78	0.53	-0.42	1.97	1.9	0.26	0.06	0.14	0.39	0.6
	41–80	0.37	0.21	-0.11	0.84	1.1	1.28	0.68	-0.24	2.81	2.5	0.05	0.05	-0.05	0.16	0.1
	81–120	1.26	0.37	0.43	2.09	56.7	1.29	0.53	0.11	2.47	57.2	1.16	0.22	0.66	1.66	56.3
	121–160	0.83	0.38	-0.01	1.68	41.2	0.75	0.45	-0.27	1.77	38.5	0.92	0.33	0.18	1.66	43.0
Land cover:	Norway spruce (Ns)	0.38	0.09	0.16	0.60	16.2	0.21	0.11	-0.06	0.48	5.4	0.54	0.14	0.19	0.89	23.5
Dominant tree species	Macedonian pine (Mp)	1.75	0.40	0.77	2.73	44.9	1.44	0.63	-0.06	2.94	34.6	1.92	0.24	1.34	2.51	51.9
	Dwarf Mountain pine (Dmp)	0.97	0.30	0.23	1.72	16.7	1.06	0.16	0.67	1.45	25.9	0.58	0.31	-0.17	1.32	10.5
	Scots pine (Sp)	2.27	0.31	1.51	3.03	20.1	2.21	1.36	-1.04	5.46	29.4	1.92	1.36	-1.42	5.26	13.8
Non-forest cover	Grasslands (Gl)	0.58	0.51	-0.67	1.83	2.0	0.39	0.32	-0.38	1.15	4.5	0.13	0.07	-0.04	0.29	0.3
	Ski slopes (SS)	0.03	0.00	0.03	0.03	0.0	NA	NA	NA	NA	0.0	0.04	0.00	0.04	0.04	0.0
	Open (bare) rock (OR)	0.08	0.06	-0.08	0.24	0.1	0.19	0.01	0.17	0.21	0.2	0.07	0.05	-0.05	0.18	0.1

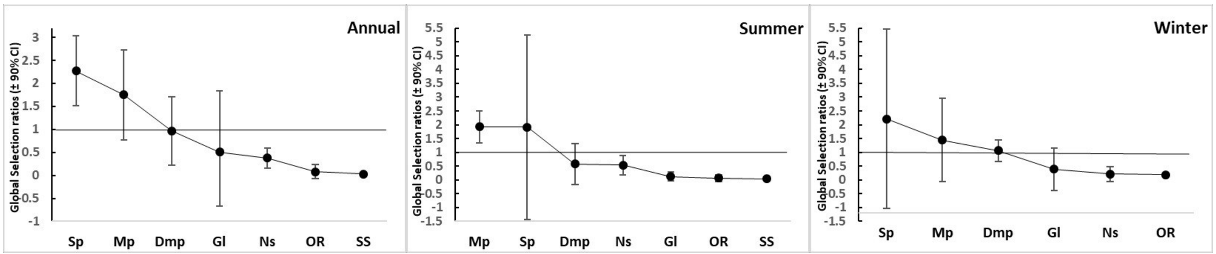

Fig. 3. Vegetation cover selection by Capercaillie males at the home range scale in Rila Mts., Bulgaria. Ns – Norway spruce; Mp – Macedonian pine; Dmp – Dwarf Mountain pine; Sp – Scots pine; Gl – Grasslands; SS – Ski slopes; OR – Open (bare) rock. Circles are Manley's Global Selection ratios' mean selectivity rates; vertical bars are Confidence Intervals. Global Selection ratios values > 1 denote habitats considered positively selected by the birds, while those in the interval 0–1 are considered to be avoided.

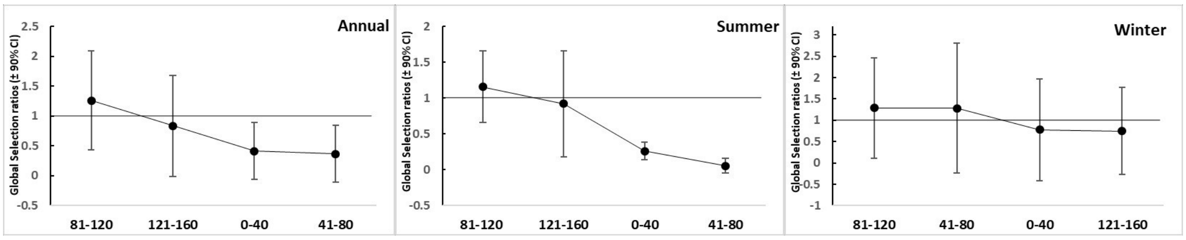

Fig. 4. Forest stage age selection by Capercaillie males at the home range scale in Rila Mts., Bulgaria. See Fig. 3 caption.

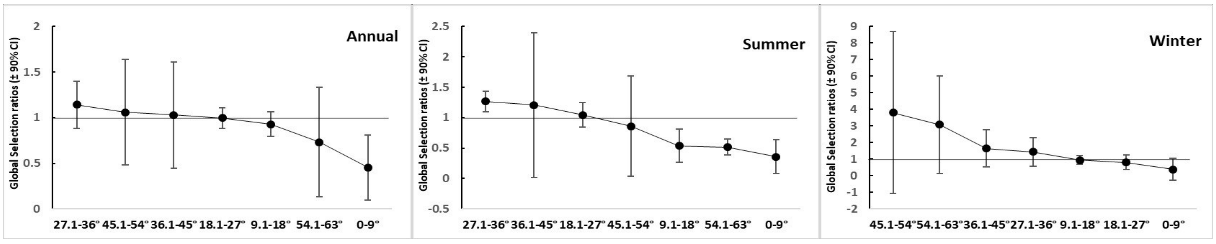

Fig. 5. Slope selection by Capercaillie males at the home range scale in Rila Mts., Bulgaria. See Fig. 3 caption.

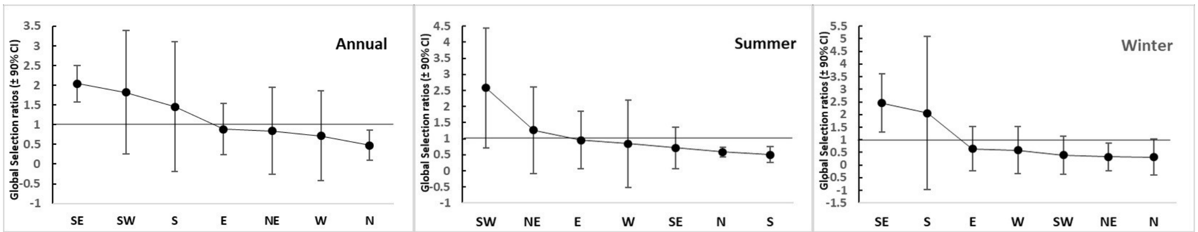

Fig. 6. Aspect selection by Capercaillie males at the home range scale in Rila Mts., Bulgaria. See Fig. 3 caption.

Discussion

Our results are the first to evaluate the habitat selection of "mad" Capercaillie males and the first to report on the Capercaillie habitat selection in the Rila–Rhodope metapopulation.

Land cover selection, forest age, and the importance of old pine forests

The Capercaillie is adapted to climax forests, with leks reportedly confined to such mature, largely undisturbed habitats (Wegge & Rolstad, 1986). Males prefer open-spaced old forests throughout the year (Rolstad et al., 1988; Gjerde & Wegge, 1989; Rolstad & Wegge, 1987; Storch, 1993a, 1993b, 1997; Picozzi et al., 1996; Saniga, 2002) and avoid young forests (Rolstad et al., 1988; Gjerde & Wegge, 1989; Storch, 1993a). Our results agree with the studies from Scandinavia, central Europe and Scotland indicating general preference of old forests (81–120 yrs. old), as well as clear avoidance of forests ≤ 80 yrs. old, both annually and during the summer. The positive selection of forests 41–80 yrs. old and the decreased avoidance of 0–40 yrs. old forests in the winter could be attributed to the territorial behavior of roosters during displaying and the resulting spatial distribution. We suppose that the avoidance of forest patches 121–160 yrs. old is predominantly due to them being dominated by the highly avoided Norway spruce (represented by 65.67% within the age class). The association with old forest fulfils basic needs for food and movement

(Summers et al., 2004) as well as anti-predator behaviors (Finne et al., 2000).

Our results that Capercaillie adult "mad" males habitat selection in winter is principally determined by the strong preference of old and pine-dominated forests agree with previous studies (Wegge & Rolstad, 1986; Rolstad & Wegge, 1987; Gjerde & Wegge, 1989; Summers et al., 2004), whereas continuous, homogenous spruce-dominated stands (Gjerde & Wegge, 1989) as well as open spaces (Finne et al., 2000; Quevedo et al., 2006) are avoided. We confirm the statements of several authors on the habitat use of the species in Bulgaria based on direct observations (Simeonov et al., 1990; Ninov et al., 1994; Botev et al., 1998; Boev et al., 2007).

Due to harsh weather conditions, resource limitation and predators' pressure, the winter habitat selection of the Capercaillie should be evaluated in terms of predator avoidance as well as in an energetic context (Storch, 1993b; Gjerde, 1991a, 1991b). The Scots pine forest are the most common winter habitat for species because the combined availability of staple food and shelter enables the birds to minimize the duration of their activity periods (Lindén, 1981, cited in Thiel et al., 2007), and thereby to minimize heat loss and predation risk (Gjerde & Wegge, 1987; Storch, 1993b). Mature trees' needles have a higher energy content than those of younger (Lindén, 1984). Old forests, such as the Scots and Macedonian pine communities selected by the "mad" males in this study, are distinguished by their open structure (Storch, 1993a). Unlike the avoided spruce trees, old pine forests provide many single trees with broad less dense crowns, with large stout horizontal branches. These trees offer enough space to fly in and are more convenient for displaying, arboreal (day and night) roosting and winter feeding (Moss et al., 1979; Picozzi et al., 1996; Summers et al., 2004). The depredation avoidance strategies of Capercaillie males come down to '*detect predator → escape*' or '*detect predator → self-defense*' (Rolstad et al., 1988). Open forests and open tree structures (typical of old forests) are advantageous to detect predators early on and to assess if defense or escape is the appropriate strategy, as well as facilitate detection of females during the mating period (Moss et al., 1979; Botev et al., 1980; Summers et al., 2004; Finne et al., 2000; Thiel et al., 2007).

Predator avoidance patterns apparently change between day and night (Thiel et al., 2007). The major Capercaillie predators – martens and foxes (Schroth, 1991; Finne et al., 2000; Jahren et al., 2016), hunt mainly during the night. Martens willingly climb trees and move by jumping between tree crowns; thus, the Capercaillie preferred roosting sites, solitary trees or trees in open old stands, are usually isolated enough to prevent this means of access (Thiel et al., 2007). Within the study area the main tree edifiers (Scots pine and Macedonian pine) had a low projective coverage in the mature forests where they dominate; this formed complex communities with the participation of a well-developed Dwarf mountain pine layer and shrub phytocenoses dominated by Common juniper *Juniperus communis* L. During the day, when Capercaillie males spend more time moving on the ground for foraging, courtship and territory defense, this dense understory of Dwarf Mountain pine and Common juniper provides secure shelter against detection by predators.

Habitat utilization in the summer

Capercaillie males face two main problems in the summer – to get enough food to cope with the nutritional cost of the molt, and to avoid predation (Rolstad et al., 1988). In our case, as summer habitats Capercaillie "mad" males strongly selected old (81–120 yrs.) forests dominated by Macedonian and Scots pines, and avoided all other vegetation cover classes. Selected pine communities were characterized by low stocking density, determining availability of well-developed field layer with high abundance of Bilberry *Vaccinium myrtillus* L., Lingonberry *V. vitis-idaea* L., Wild strawberry *Fragaria vesca* L., Common juniper *Juniperus communis* L., Raspberry *Rubus idaeus* L., R. *hirtus* Walds & Kit. (Rusakova, 2015; Dimitrov & Rusakova, 2015) and other plant species, taking significant part in the Capercaillie diet (Cramp, 1985; Simeonov et al., 1990; Storch, 1993a). The presence of a well-developed ground layer provides shelter for birds when they feed and rest on the ground. Due to the dense canopy cover within much of the spruce forests, there is almost no underbrush and, in some cases, even a grass layer (Rusakova & Dimitrov, 2015). In parallel, spruce wood and mixed forests dominated by spruces are the preferred habitat by major Capercaillie predators such as the Pine marten *Martes martes* L. (Sidorovich, 2011; Spassov & Spiridonov, 2015). Therefore, the lack of a rich trophic basis and an increased depredation risk, possibly determine the avoidance of this class of forest stands by Capercaillie males.

Avoidance of open habitats

Avoidance of the open habitat types (bare rocks, grasslands and ski slopes) by the studied "mad cocks" could be considered a predator escape strategy or disturbance avoidance behavior. The Capercaillie is not a permanent inhabitant in stands near centers of human activities (frequented tourist paths, ski slopes, etc.), although these habitats also may fulfill its habitat requirements (Saniga, 2002). The Capercaillie probably use skiing areas only when undisturbed refuges are also available within their home ranges (Thiel et al., 2008). Taking into account the clear avoidance of ski slopes and the negligible presence of "Bird 3" in suitable habitats adjacent to the ski slopes during the summer (Fig. 3), we could speculate that there was no available undisturbed refuge within the ski zone in our study area. The openings within the forest are associated with habitat fragmentation and edge effect. The increase of grass and deciduous shrubs areas trigger higher predator pressure on ground nesting birds such as the Capercaillie (Rolstad & Wegge, 1989). Forest edges and openings are preferred hunting sites of the Northern goshawk *Accipiter gentilis* L. (Storch, 1993a), Pine marten and Red fox *Vulpes vulpes* L. (Clevenger, 1994; Sidorovich, 2011), all important predators of the Capercaillie (Botev et al., 1980; Gjerde & Wegge, 1989; Tornberg, 2001; Wegge & Kastdalen, 2007).

Topographical features

Some authors described preference for upper slopes with NE, E, and SE exposures, due to higher proportions of Bilberry on east-exposed slopes (Botev et al., 1993; Storch, 1993b). According to our results, at the home range scale, Capercaillie males most clearly avoided northern exposed slopes, but excluding the significant selection of SE slopes on annual basis; all other results are difficult to interpret. We consider the avoidance of northern exposures as a consequence of the distribution of the spruce-dominated community, associated with convex relief forms on northern exposures (Rusakova & Dimitrov, 2015). Regarding the exposure of the occupied terrains there is no regularity in the distribution of the *V. myrtillus* associations and it varies according to the area occupied and the habitats specificity (Vitkova & Rusakova, 2015). Therefore, our results are in accordance with the conclusions that the use of the different categories exposure is predestined by the aspect of the hills/valley axis as well as according to the local weather conditions (Saniga, 2002) and Capercaillie select habitats independently of the exposure (Rolstad & Wegge, 1987; Storch, 1993b).

Like Central European and Scandinavian studies, our survey indicates that hills and ridges are attractive Capercaillie display grounds (see Saniga, 2002) but are also preferred terrain features in the summer. Investigations from the Teisenberg Mtn. identified general preference for gentle slopes and avoidance of steep terrains in winter, spring and autumn that were less pronounced in summer (Storch, 1993a, 1993b). In contrast, our results indicate clear avoidance of flat terrains ("0–9.0"), selection of gentle slopes ("27.1–45.0") during summer, as well as preference of wider range ("27.1–63.0") of more steep slopes during winter. However, in general, gentle slopes ("27.1–36") seemed to be preferred, most strongly pronounced in the summer. The flat terrains within the study area were dominated by grasslands and dense Dwarf Mountain pine communities, avoided by Capercaillie males, which could explain why the birds were not utilizing them.

Implications for management

Habitat management for the Capercaillie should aim to provide forests dominated by (or with significant presence of) pines in the late successional stages with open structure, low stocking density, and well-developed understory with shrub and grass communities for foraging and shelter. Extensive cuttings, construction of firebreaks and development of other forest openings within potential Capercaillie habitats should be avoided.

Conclusions

Notwithstanding the abnormal aggressive behaviour of Capercaillie males and their affiliation with an edge population, the habitat selection of "mad cocks" in the Rila Mts. is consistent with the principal habitat preference of the species - old pine dominated forest associations distributed on hills and ridges. The selection of this principal habitat is similar in winter and summer. Thus, future studies can pool results of "mad" and normal individuals, and conservation initiatives should not separate between the two types.

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