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Microhabitat utilization of the Tatra marmot (*Marmota marmota latirostris*) in the Western Carpathian Mountains, Europe

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Abstract

The function of Alpine marmot subspecies burrows and factors influencing their distribution were investigated at 17 sites in the Tatra Mountains in Slovakia, Europe. Topographic variables and habitat types expected to influence the location of the Tatra marmot burrows were observed and examined. In the various locations of the studied home ranges (summer, winter and grazing areas, marmot trails) and outside the family territories, we recorded 36 vegetation samples including several reliefs. The collected data were analyzed using multivariate analysis.

The summer areas of the marmot home ranges in the Tatra Mountains are often located within the alpine zone in communities of the Braun-Blanquet alliance *Juncion trifidi* (siliceous short stem grasslands) and in chionophilous communities on stable scree slopes of the alliance *Festucion picturatae* (tall stem grasslands). Marmots usually avoid habitats that have the lowest trophic benefits and the most extreme sites with low-stems or mat-grass communities in the alliance *Nardion strictae*, dense stands of dwarf pine in the alliance *Pinion mugo* (krummholz), and dwarf-shrub and lichen communities in the alliance *Loiseleurio-Vaccinion*. Marmot habitats in summer have suitable grazing areas. The most preferred habitats for foraging are grasslands and tall herb plant communities dominated by *Calamagrostis villosa*, *Trisetum fuscum,* and similar tall grass species.

The most important factor influencing the locations of different parts of home ranges is the gradient of the relief structure. According to their functional differentiation, the location of a marmot burrow is most significantly influenced by the presence of convex geomorphic features and reinforced rock forms.

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Introduction

The Tatra marmot (*Marmota marmota latirostris* Kratochvíl, 1961) is an endemic subspecies of the Alpine marmot, *Marmota marmota* (Linnaeus, 1758), a monogamous species widespread in the Pyrenees, Alps, and Carpathians. The Tatra marmot is restricted to small mountain regions in the Western Carpathian Mountains of Slovakia, where it is considered a threatened taxon. This subspecies occupies habitat from 1500–1660 m a.s.l. to 1900–2300 m a.s.l. in the Tatra Mountains (including the Západné Tatry Mountains and the Východné Tatry Mountains) and the Nízke Tatry Mountains (Kostroň, 1965; Blahout, 1971; Halák, 1984; Chovancová, 1987; Gąsienica-Byrcyn, 1994; Ballo and Sýkora, 2005, 2006, 2007; Karč, 2006; Ballo, 2008, 2009; Bačkor, 2009). This subspecies inhabits only areas in the subalpine and alpine zones. Tatra marmots occupy habitats in the Tatra Mountains that are, except for forest clearings, similar to those occupied by Alpine marmots in the Alps and in the Pyrenees (Herrero et al., 1994; Herrero and García-Serrano, 1994; Herrero and García-González, 2007; López et al., 2010). The altitudinal range of the marmot in the Tatra Mountains seems also to be similar to that in the Alps and in the Pyrenees. The entire range of occurrence of marmots is 56 km long in the Tatra Mountains (Ondruš, 2003) and approximately 26 km in the Nízke Tatry Mountains (Karč, 2006).

The Tatra marmot is a social and territorial subspecies living in family units composed of a resident pair, subordinate adults, yearlings, and juveniles of the year (Blahout, 1971; Halák, 1984). As well as the *M. m. marmota* subspecies, all the individuals in a Tatra marmot family group hibernate together in the same winter burrow and share a common home range (Blahout, 1960, 1971; Barash, 1976; Arnold, 1990; Perrin et al., 1993; Allainé, 2000; Lenti Boero, 2001).

Marmots in the Tatra Mountains are losing suitable habitat due to cessation of livestock grazing above the timberline, which allowed a further increase in dwarf pine cover. In the past, marmot habitats were not always considered when planting dwarf pine in an effort to restore the former timberline vegetation. Changes in timberline dynamics due to climate change also may be adding to a considerable increase in dwarf pine cover in the area. Climate change threatens survival of several marmot species through global warming and extreme weather events. Recent warming resulted in a movement upslope of their lower elevation boundaries (Armitage, 2013).

Until now, research on Tatra marmots has focused on the behavioral ecology of families and colonies (cf. Blahout, 1960, 1971; Novacký, 1978, 1994; Gąsienica-Byrcyn, 2008). Systematic and long-term research on the habitat requirements of the Alpine marmot, including the Tatra marmot subspecies, has not been performed, including studies of species habitat utilization (Allainé et al., 1994; Borgo, 2003). The relationships between marmots and certain habitats in the Tatra Mountains remain unknown. Identifying the main habitat preferences and needs of marmots are critical to understanding, managing, and restoring habitats that can support their populations.

Habitat selection and the process of colonization have not been sufficiently explored for both the Tatra marmot and most other species of marmots. Data on habitat use are often erroneously explained as habitat selection without any analysis of utilization-availability data (Bassano et al., 1992; Macchi et al., 1992; Sala et al., 1992). Until now, the habitat characteristics that marmots prefer have been investigated by examining single variables, which likely do not explain much of the variance in marmot habitat preference (Allainé et al., 1994). Habitat features may interact such that some combinations are preferred over others (Armitage, 2000). As with other animal species, it is necessary to analyze the simultaneous effects of several habitat factors (Borgo, 2003).

Altitude, sun exposure, sunlight duration, slope, human pressure, available food period, and soil composition are known to influence the settlement of marmots (cf. Allainé et al., 1994; Armitage, 2000; Borgo, 2003; Lenti Boero, 2003b). Few studies have addressed the relationship between yellow-bellied (*M. flaviventris*) or hoary marmot (*M. caligata*) colonies and topographic relief or rock features (cf. Floyd, 2004; Karels et al., 2004; Svendsen, 1974, Holmes, 1984). Studies of the ecological niche of the Himalaya marmot, *M. himalayana* (Nikol'skii and Ulak, 2006) suggest that temperature and the presence of glacial and diluvial sediments are key factors influencing their distribution. Snow cover, a major environmental factor, is essential to insulate hibernation burrows from low, stressful temperatures (Armitage, 2013).

Some studies emphasize the importance of temperature for both Alpine marmot distribution and daily activity (Herrero et al., 1994; Turk and Arnold, 1988; Melcher et al., 1990) and thus this factor may limit their habitat utilization. It is also known that food specialization is correlated with marmot distribution in high mountain landscapes (Bibikov, 1996).

Characterizing species habitat using only environmental variables provides a description of the environment in which the animal lives but cannot define the relationship between the species and its habitat (M'Closkey, 1976). Marmot preferences for certain habitat types are based on a combination of environmental factors that interact with the marmots' social systems (Allainé et al., 1994; Lenti Boero, 1995, 1996, 2001, 2003a, 2003b). This interaction is reflected in special organization and activity distribution (Perrin et al., 1993; Lenti Boero, 2003a). The Alpine marmot (including Tatra marmot subspecies) has two different kinds of spatial organization: isolated family groups, and colony, composed of several family groups, with a slight home range overlap (Zelenka, 1965; Blahout, 1971; Mann and Janeau, 1988). Family members occupy a common space and distribute their activities in different parts of their home range area according to the behavior performed and to the hour of the day (Perrin et al., 1993). The mentioned parts of home ranges we called *functional areas*.

Until now, the habitat preferences of the entire marmot genus have been identified by the measures, which are variable during the years of marmot occupation (population density, reproductive output, and the measurement of the home range areas) (Armitage, 2000); therefore, we determined an independent habitat measurement by using the functional areas.

We suggest that patterns of habitat choice are based on functional use of the area. In this paper, we characterize the combinations of selected environmental variables, which determine the location of different parts of the Tatra marmot home ranges. The aim of this study is to contribute to the understanding of marmot ecology and outline the basis for further multivariate analyses of whole marmot home ranges.

Materials and Methods

STUDY AREA

The study area was determined by the occurrence of the Tatra marmot in the mountains of the Western Carpathians (Slovakia), located in the northern part of the Carpathian mountain range (Fig. 1).

Tatra marmots inhabit only a small area of the highest part of the Western Carpathians and represent an endemic subspecies that originated during the Quaternary period (Kratochvíl, 1964). The study area has a cold climate (Lupin et al., 2002), and temperature conditions are determined mainly by increasing altitude, as the temperature decreases by 0.50–0.55 °C every 100 m (Braun-Blanquet, 1964). The precipitation conditions are variable and altitude-dependent. Precipitation increases with increasing altitude, and the average annual precipitation is 1200–1400 mm (Lupin et al., 2002).

Localization, altitude, and aspect of the vegetation plots and marmot burrows were measured using Garmin Oregon 300 equipment (WGS-84 system), and the coordinates were transformed to the S-JTSK system. Slope was measured using a goniometer. Global positioning system (GPS) data and digital maps were prepared using Geographic Resources Analysis Support System Geographic Information System (GRASS GIS). A map of the Slovak republic (M 1:10,000; 1 pixel = 1 m) was used as a base map.

DISTRIBUTION OF SETTLEMENTS

Locations of the investigation were chosen based on previous research concerning the occurrence of the Tatra marmot in the Západné Tatry Mountains, conducted during 2004 to 2010. During that study, in total, 18,368 shelter burrows and 132 maternal burrows were precisely surveyed and GPS-located (Ballo and Sýkora, 2005, 2006, 2007; Ballo, 2008, 2009, 2010; Ballo and Ballová, 2010).

We have GPS-located marmot permanent trails with dug and occasional shelters among family home ranges belonging to the colony. The trails were located outside individual family territories bounded with spotting and marking points. We have suggested that Tatra marmot families share a common colony home range (Ballová and Ballo, 2009).

During springtime, after marmots have emerged, from 15 April to the beginning of July in 2010 and 2011, we observed 17 sites in the Tatra Mountains (Western Carpathians, Slovakia; coordinates from 49°13′08.43″N and 19°40′01.12″E to 49°10′10.82″N and 20°02′12.86″E), in total 408 hours of observations. Study localities were chosen to represent all habitat types and various marmot settlements (Table 1) in such a way that they were approximately evenly distributed throughout the territory of the Tatra Mountains. The types of marmot burrows, according to their functional differentiation, were identified on the basis of their morphological signatures, presence of mounds of earth, presence of feces, and presence of dry grass, according to personal observations. Functional differentiation of marmot burrows was identified for the study season.

The home range boundaries were estimated on the basis of burrows on digital maps from previous research and by using minimum convex polygon method for calculating boundaries according to the most extreme locations of the burrows and recent personal identification of the most extreme foraging points. The estimates were modified according to family territories by personal identification of spotting places, the marking sites, and the locations where agonistic interactions among individuals of different groups during reproduction period occurred.

We defined home range as the area traversed by members of one family in their normal activities of food gathering, mating, and caring for young (Burt, 1943), burrows dwelling, and scratching. The area bounded by marking points we identified as the territory of the family group (Lenti Boero, 2002). These areas were defended against other family members only during reproduction period in springtime.

In each family home range we distinguished four types of functional area (winter, summer and grazing areas, marmot trails) with appropriate burrow types. For summer areas we identified maternal burrows inhabited by territorial female with

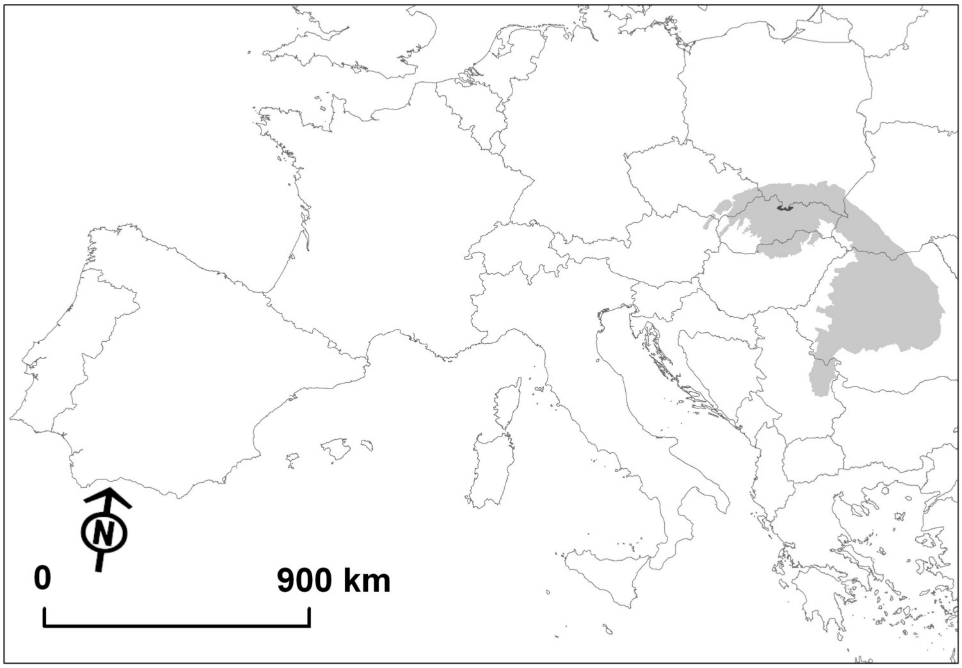

FIGURE 1. Map of the Carpathian chain with displayed Tatra Mountains—the area with the occurrence of Tatra marmots. The Carpathian mountain range represents the most extensive mountain system in Europe, as part of the Alpine-Himalayan system. The mountains cover an area of 210,000 km^2 extending across the territories of Austria, the Czech Republic, Slovakia, Poland, Hungary, Ukraine, Romania, and Serbia.

her litters, burrow feces deposits, and summer burrows. The adult male of each family inhabited a solitary burrow around 20 to 50 m away from the female maternal burrow and usually a few meters above it or a shared burrow with yearlings. The home burrows inhabited by non-maternal group members during summer season we denoted as summer burrows. The winter areas were characterized as sites with hibernacula and their close surroundings. Either hibernaculum or maternal burrow together with feces, multiple entrances (named as auxiliary burrows), underground system of corridors, underground nest, or hibernation chamber are parts of the main burrow system. The next types of functional areas were grazing areas with dug shelter burrows, occasional shelters under stones, and open feces deposited in meadows. Further, we identified marmot trails with dug and occasional shelters (the areas that marmots used for moving within and among home ranges).

The investigation of factors influencing burrow distribution was conducted from summer to autumn 2010 and 2011 at all 17 family home ranges. In each family home range, we chose a sample of several burrows from only one selected functional area. The sampled burrows were localized within a 50 m radius of center of each area. In the certain functional area we defined the appropriate burrow as the center. In grazing areas and trails there were shelters located in the rough middle of the area. Maternal burrows were the center for summer areas, and hibernacula for winter areas. The sampled areas were chosen in order to record all possible habitat types utilized by marmots. Therefore, we selected only one or two functional areas from each family home range. We recorded data from 5 burrow clusters for each type of functional area. In total, we had 20 burrow clusters from four types of area from 17 family sites. The number of burrows in an individual cluster was from 5 to 31. The lowest numbers were on trails and the highest numbers were in the summer territories.

In investigated functional areas we recorded topographic environmental variables expected to influence the location of the Tatra marmot burrows.

VEGETATION SAMPLING

We sampled several locations through the mountain range in order to record as many marmot utilized habitat types as possible. In total, we recorded 36 vegetation samples in 9 locations in the Tatra Mountains (Mount Grapy, Mount Salatín, Bobrovecká dolina Valley, Hlboká dolina Valley, dolina Parichvost Valley, Mount Ráztoka, dolina Kôprovnica Valley, Mount Krížna, Mlynická dolina Valley). All of these locations were used also in the above-mentioned burrows sampling.

We established three positive and one negative 4 × 4 m quadrates (standard size for vegetation sampling of non-forest vegetation; see Chytrý and Otýpková, 2003) in each locality. Positive samples were recorded in selected functional areas (winter, summer and grazing areas, marmot trails) of each family home range (total 9 investigated home ranges with 27 positive samples) and negative plots were located outside each family home range (9 negative samples totally). The locations of these negative samples were selected in areas without obvious present and past marmot utilization.

In each family home range, the locations of positive samples were sampled in various habitats. When we recorded a sample in certain vegetation type from a grazing (or winter, summer, trail) area of one family home range, we did not record the similar sample from a grazing (or winter, summer, trail) area of another family home range. Instead, we went to the next family home range with yet unsampled vegetation. The purpose of this investigation methodology was to find marmot preferred traits of vegetation that are common in our different samples. The positive plots were situated always 50 cm above the entrance of central burrow of the area (from above burrow sampling) and the negative plots were established in a meadow 100 m away from each family home range.

All of the vegetation samples were collected according to the principles of the Zürich-Montpellier school (Braun-Blanquet, 1964; Westhoff and van der Maarel, 1978), with frequent use of the modified 9-degree Braun-Blanquet's sampling scale (Barkman et al., 1964).

TABLE 1

Characteristics of marmot settlements investigated in the Západné Tatry Mountains and in Mlynická dolina Valley (Vysoké Tatry Mountains). From each type of settlement only one family home range was chosen. Samples were recorded from one or two functional areas of each family home range in each settlement.

Settlement	Altitudinal range (m a.s.l.)	Area of the settlement (m²)	Aspect of settlement	Prevailing slope (°)	Location of colony	Relief
[a]Grapy 1	1760–1890	40,100	SW	25	Slope	alpine
[a]Grapy 2	1820–1925	44,900	SW	20	Slope	alpine
[b]Grapy 3	1840–1960	46,700	S	30	Slope	alpine
[a]Podválovce	1790–1930	14,500	SW	30	End of valley	cliff—alpine
[d]Bobrovecká valley	1680–1900	68,300	W	20	Deep gorge	cliff—alpine
[d]Hlboká valley–Vrece	1820–2060	53,100	W	25	Deep gorge	cliff—alpine
[c]Parichvost	1900–1990	24,200	SW	35	Deep gorge	cliff—alpine
[a]Látaná	1600–1770	25,800	N	20	End of valley	cliff—alpine
[a]Ráztoka	1850–1920	21,100	SE	20	Slope	alpine
[c]Jamnická dolina	1760–1830	10,000	SW	30	Slope	cliff—alpine
[e]Račkova dolina–marmot trail	1780–2010	—	SW	30	Slope	alpine
[c]Gáborova valley–Banistá	1700–1930	39,900	S	10	Deep gorge	alpine
[d]Kamenistá valley	1740–2020	310,000	SE	25	Deep gorge	cliff—alpine
[a]Kôprovnica	1610–1860	41,900	SW	10, 20	Deep gorge	cliff—alpine
[d]Krížna	1820–2000	130,200	SW	25	Slope	alpine
[d]Sviština valley (Červené vrchy)	1690–2030	76,100	SE	30	Slope	cliff—alpine
[f]Mlynická valley–two winter areas	1823, 2091	—	EES, SSE	15, 30	Deep gorge	cliff—alpine

Abbreviations: a–unifamily settlement; b–bifamily settlement; c–unifamily home range of the multifamily settlement; d–multifamily settlement; e–marmot trail between summer area with maternal burrow and grazing area; f–two winter areas of two different settlements, altitude is measured for hibernacula).

This methodology is known as a total flora approach, generally used for recording vegetation samples including information about quality and quantity of species composition. Basically the system consists of a few stages: (1) choosing uniform areas of vegetation, (2) describing these areas, (3) recording species composition, and (4) grouping units according to their affinities (Poore, 1955). All phytosociological samples were stored in a TURBOVEG database (Hennekens and Schaminée, 2001; Schaminée et al., 2009). Taxa that were determined only at the genus level were excluded from the numerical analysis; some species were included in more broadly defined aggregates (for general information about methodology, see Jarolímek and Šibík, 2008). All phytosociological samples were consequently transported into the JUICE 7.0 program (Tichý, 2002) for further analyses.

DATA ANALYSIS

A data set of 435 marmot burrows, resulting from 4 different functional areas of home ranges (winter, summer and grazing areas, marmot trails) associated with 17 marmot sites, was tested. Marmot burrows were categorized by functional part of the territory and the burrow types (feces deposits in burrows—BF, open feces in meadows—OF, maternal burrows—M, hibernacula—H, summer burrows—SB, occasional shelters under stones—OS, dug shelters—DS) according to its utilization. Different types of functional areas often functionally overlapped; the hibernacula, maternal burrows, and summer burrows also overlapped. Hibernacula were occasionally inhabited in the summer season by marmots as summer or maternal burrows. In this case, one burrow was included in multiple categories.

Collected data were analyzed by indirect and direct multivariate analysis (DCA, CCA) using the CANOCO 4.5 for Windows package (ter Braak, 1988, 1990; ter Braak and Šmilauer, 2002).

Detrended correspondence analysis (DCA) was applied for the ecological interpretation of the main gradients in the studied vegetation plots. Data were transformed by square root transformation to reduce the variance among close values (Lepš and Šmilauer, 2000; ter Braak and Šmilauer, 2002). Average Ellenberg indicator values (Ellenberg et al., 1992) as an indirect assessment of environmental factors such as light, temperature, continentality, moisture, nutrients, and soil reaction for Central European plant species were plotted onto a DCA ordination diagram as supplementary variables to better explain the individual gradients. Considering that data about marmot utilization were collected as supplementary data to sampled vegetation plots, the functional areas of the marmot territories were passively displayed in the DCA ordination diagram.

TABLE 2

Topographic descriptor types.

Variable	Description (units)	Classes or value range	Abbreviation
Relief	General topographic descriptor	Steep slope	R1
		Convex ridge (various cones and ridges in slope)	R2
		Flat ridge (flat ridges in slope)	R3
		Gentle slope	R4
		Flat bottom	R5
		Depression	R6
		Moist depression	R7
		Waterlogged depression	R8
		Avalanche glen	R9
Geomorphic feature	Microtopographic descriptor	Convex geomorphic feature	CGF
		Debris cone	DCO
		Moraine	MOR
		Deep gorge	DEG
		Valley	VAL
		Depression	DEP
		Diluvial sediments	DEL
		Scree	SCR
		Bottom land	BOL
		Dislocation	DIS
		Avalanche glen	AVG
		Slope	SLO
		Edge (mountain ridge)	EDG
		Cavern	CAV
		Erosion	ERO
Biotopes		Siliceous grasslands	al1
		Siliceous snow beds	al2
		Calcareous grasslands	al3
		Siliceous tall-grass communities	al6
		Alpine heaths	al9
		Subalpine deciduous shrubs	kr5
		Siliceous scree	sk3
Geology		Leucocratic granites	kr9
		Porphyritic granitoids to granites	kr38
		Biotitic granodiorites to tonalities with a transition to muscovite-biotite granodiorites	kr55
		Mica schists, mica schistose gneisses, and micaceous gneisses	kr132
		Gneisses, migmatitic gneisses, and migmatites	kr159
		Stromatolites, migmatitic gneiss	kr186
		Reifling limestones	mt97
		Glacial sediments; debris, boulders, and blocks of the retreating moraines	q10
		Diluvial sediments; soil and rocky debris flows	q20
		Diluvial sediments; sediments range from sand and rocks to boulders and blocks (debris cones, block fields, talus screes)	q22
		Diluvial sediments; lithofacially undifferentiated flows and debris sediments	q24
		Glacigenic sediments; gravel, boulders, and moraine blocks	q35

TABLE 3

Plant communities recorded in the studied area of the occurrence of endemic Tatra marmot. Alliances have -ion endings. The alliance is a physiognomically uniform group of plant associations sharing one or more dominant or diagnostic species which, as a rule, are found in the uppermost strata of the vegetation (see Mueller-Dombois and Ellenberg, 1974). Dominant species are often emphasized in the absence of detailed floristic information (such as quantitative plot data), whereas diagnostic species (including characteristic species, dominant, differential, and other species groupings based on constancy) are used where detailed floristic data are available (Moravec, 1993).

Alliances	Number of vegetation samples	Ecological characteristics
Juncion trifidi	8	The alliance comprises species-poor herb and grass communities on siliceous bedrock in the subalpine to subnivale belt usually dominated by one species. Communities of this alliance are regarded all year to strong winds, and that in winter are almost without snow cover. Short grass alpine communities are heliophilous, xero- to mesophilous, chionophobous or slightly chionophobous. They occupy wind-exposed habitats on acid to strongly acid, oligothrophic, shallow and skeleton-rich soils (Dúbravcová and Jarolímek, 2007).
Callamagrostion villosae, *Trisetion fusci*	10	These alliances comprise tall herb and tall grass communities found mainly in mesophilous habitats along mountain streams and on sheltered habitats with a sufficient supply of moisture and nutrients and with thick snow cover in winter (Kliment et al., 2007).
Festucion picturatae, *Salicion herbaceae*	9	Chionophilous grassland communities of fixed screes on siliceous bedrock in the alpine and subalpine belt occupied stable slope screes with long term snow cover, the bases and slopes of deep gashed glens and bottoms of glacial cirques, which are accumulating avalanche areas. These habitats are sheltered from wind and covered by thick layers of snow. Soils are of scree character, with coarse of grained skeleton, that are permeable, medium to strongly acid, humus-rich and relatively moist (Krajina, 1933; Dúbravcová, 2007).
Nardion strictae	3	Alpine and subalpine low-stem, mat-grass communities from this alliance are natural or partly influenced by man grasslands and mountain meadows occupying relatively fresh and deep, nutrient-poor acid soils (Kliment, 2007).
Loiseleurio-Vaccinion, *Pinion mugo*	6	The alliance *Loiseleurio–Vaccinion* comprises mainly natural, partly semi-natural, acidophilous communities of dwarf-shrub heaths dominated by ericaceous species, commonly found in the subalpine to alpine belts. They occupy predominately shallow and strongly skeletal acid soils that are found rarely on basic bedrocks and also in places with a thin layer of litter and raw humus. The communities prefer climatically extreme habitats, slopes exposed to winds, with short duration snow cover (Šibík et al., 2007). The alliance *Pinion mugo* comprises dense stands of krummholz dominated by dwarf pine (*Pinus mugo*) (Šibík et al., 2010).

Direct unimodal gradient analysis–canonical correspondence analysis (CCA) was applied for the examination of the relationship between marmot functional areas and environmental variables. The significance of the first canonical axis and of all canonical axes together was tested by distribution-free Monte Carlo simulation (499 permutations).

To determine the relative importance of the variables, we used forward step-wise selection during the CCA in CANOCO. The most statistically significant variables ($P < 0.05$) were selected among 44 categories of variables (Table 2).

NOMENCLATURE

The nomenclature follows the checklist of Marhold and Hindák (1998) for vascular plants. The names of the taxa have been unified according to Jarolímek et al. (2008). The biotope types and nomenclatural types of vegetation were recorded on the basis of Stanová and Valachovič (2002), Kliment and Valachovič (2007), and Kliment et al. (2010).

Results

The characteristic attributes of the investigated colonies are listed in Table 1.

INDIRECT INFLUENCE OF THE VARIABILITY OF PLANT COMMUNITIES ON THE LOCATION OF DIFFERENT FUNCTIONAL PARTS OF HOME RANGE AREAS

We included recorded plant communities from various functional areas of the studied home ranges and outside the family territories into five groups of alliances based on their common ecological characteristics (Table 3).

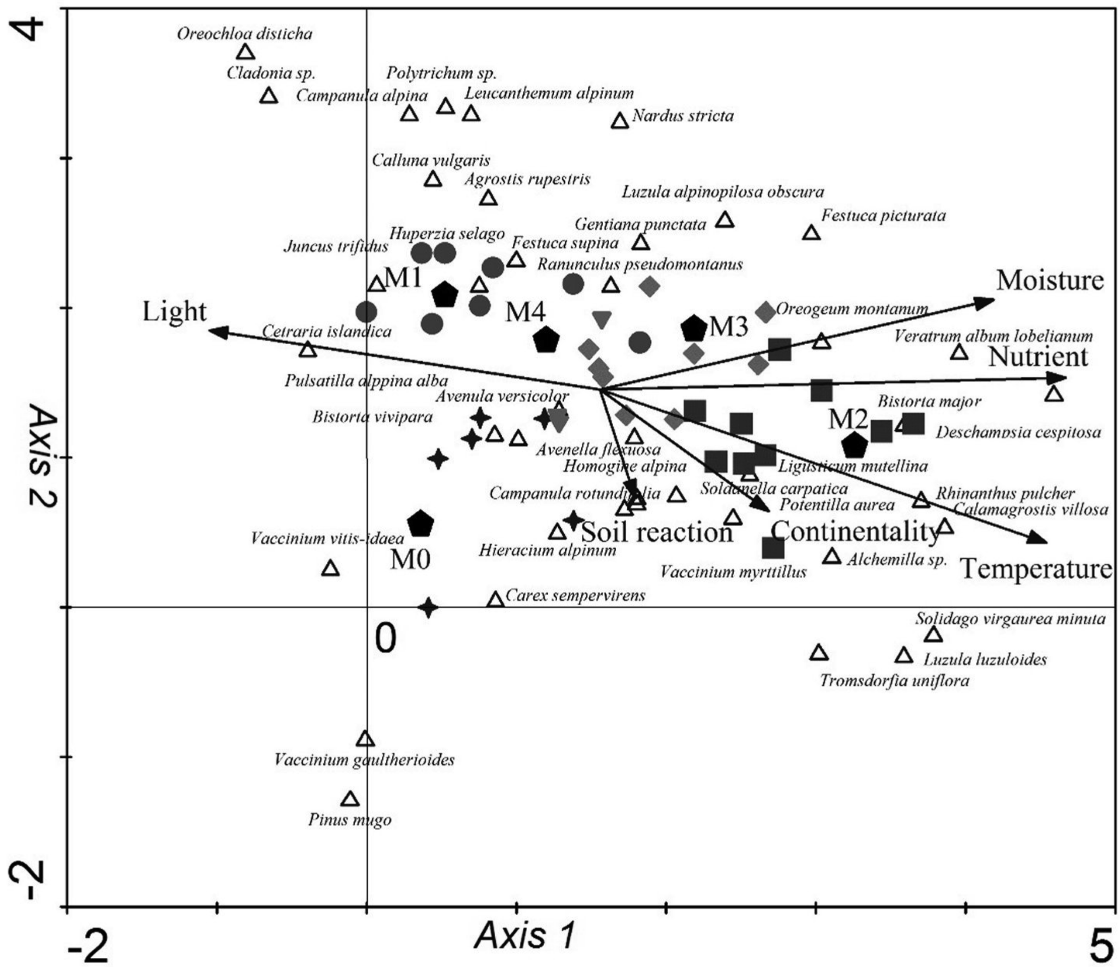

FIGURE 2. Detrended correspondence analysis (DCA) ordination diagram of 36 phytosociological samples in the selected locations in the Tatra Mountains based on average Ellenberg's indicator values. Length of gradients: 3.910 (axis 1), 2.271 (axis 2); eigenvalues: 0.470 (axis 1), 0.247 (axis 2). Legend: Δ species; samples (phytosociological units): ● *Juncion trifidi*; ■ *Callamagrostion villosae*, *Trisetion fusci*; ◆ *Festucion picturatae*, *Salicion herbaceae*; ▼ *Nardion strictae*; ✦ *Loiseleurio-Vaccinion*, *Pinion mugo*; supplementary variables: ⬟ marmot functional areas of home ranges (M0—areas without marmots, M1—marmot trails, M2—grazing areas, M3—summer areas, M4—winter areas); ⟶ Ellenberg's indicator values (estimates of local species ecological optima along main ecological gradients - light, temperature, continentality, moisture, nutrients and soil reaction). The summer areas of the marmot home ranges in the Tatra Mountains are often located in communities of the Braun-Blanquet alliance *Juncion trifidi* (siliceous short grasslands) and in chionophilous communities on stable scree slopes of the alliance *Festucion picturatae* (tall grasslands). Marmots usually avoid habitats that have the lowest trophic benefits and the most extreme sites with low-stems or mat-grass communities in the alliance *Nardion strictae*, dense stands of dwarf pine in the alliance *Pinion mugo* (krummholz), and dwarf-shrub and lichen communities in the alliance *Loiseleurio-Vaccinion*. The most preferred habitats for grazing areas are grasslands and tall herb plant communities in the alliances *Callamagrostion villosae* a *Trisetion fusci* dominated by *Calamagrostis villosa*, *Trisetum fuscum*, and similar tall grass species.

The first two axes of the DCA diagram best explain the cumulative percentage variance of the plant communities. The percentage variance explained by the second axis was low; thus, the second axis was not readily interpretable. Axis 1 in the DCA diagram (Fig. 2) sorted marmot functional areas according to the requirements of the nutritional value of plant species occurring in the plant communities. Nutrients, moisture, and temperature are negatively correlated with light availability (Table 4). This result is due to the higher occurrence of plant species typical for grasslands and tall herb plant communities such as *Bistorta major*, *Deschampsia cespitosa*, *Ligusticum mutellina*, *Luzula alpinopilosa* subsp. *obscura*, *Oreogeum montanum*, and *Veratrum album* subsp. *lobelianum*, and so on, with high requirements for temperature, moisture, and nutrients on the right of Figure 2. The occurrence of summer and grazing areas in plant communities with the above-mentioned plant species is positively correlated with nutrients, moisture, and temperature and negatively correlated with light availability (Table 4). From these results, we can see that marmots have chosen to forage in tall grasslands and tall herb plant communities that are generally well supplied by nutrients.

Vegetation samples from winter areas and trails are found on the left of Figure 2. These samples are dominated by species that grow in nutrient-poor soils from the alliances *Juncion trifidi* and *Nardion strictae* (low-stem grasslands and dense mat-grass communities), such as *Agrostis rupestris*, *Juncus trifidus*, *Nar-*

TABLE 4

Intraset correlations of the first two canonical axes in DCA. The occurrence of summer and grazing areas in plant species typical for grasslands and tall herb plant communities is positively correlated with nutrients, moisture and temperature and negatively correlated with light availability. Trails are negatively correlated with the first ordination axis, temperature, nutrients, and moisture and are positively correlated with light availability. Locations without marmots are negatively correlated with the first ordination axis.

Variable	Axis 1	Axis 2	Light	Temper	Continen	Moist	SoilRea	Nutri	M0	M1	M2	M3	M4
Light	–0.729	0.130	1.000										
Temper	0.770	–0.369	–0.660	1.000									
Contin	0.265	–0.221	–0.403	0.482	1.000								
Moist	0.580	0.116	–0.510	0.633	0.243	1.000							
SoilRea	–0.222	–0.330	0.232	0.133	0.158	0.244	1.000						
Nutri	0.685	–0.098	–0.632	0.742	0.353	0.788	0.345	1.000					
M0	–0.169	–0.199	–0.102	–0.080	–0.128	–0.336	–0.151	–0.223	1.000				
M1	–0.311	0.242	0.140	–0.412	–0.038	–0.105	–0.311	–0.332	–0.231	1.000			
M2	0.569	–0.187	–0.438	0.515	0.371	0.355	0.086	0.471	–0.219	–0.313	1.000		
M3	0.149	0.040	0.122	0.116	–0.177	0.281	0.208	0.252	–0.210	–0.300	–0.284	1.000	
M4	–0.282	0.072	0.291	–0.156	–0.060	–0.274	0.173	–0.214	–0.182	–0.260	–0.246	–0.236	1.000

Ellenberg's indicator values: Light, Temper—temperature, Continen—continentality, Mois—moisture, SoilRea—soil reaction, Nutri—nutrients; M0—areas without marmots; functional parts of marmot home range: M1—marmot trails, M2—grazing areas, M3—summer areas, M4—winter areas.

dus stricta, *Oreochloa disticha*, and others. Trails are negatively correlated with the first ordination axis, temperature, nutrients, and moisture and are positively correlated with light availability. The ordination diagram shows that trails occur mainly in the heliophilous plant communities of the alliance *Juncion trifidi*. Winter areas are also often located within the plant communities of the alliance *Juncion trifidi*. This result can be observed because these communities occupy wind-exposed habitats in acidic to strongly acidic, oligotrophic, shallow, and skeleton-rich soils.

Locations without marmots are negatively correlated with the first ordination axis. This is a result of the occurrence of plant species typical for the most extreme locations for marmot burrowing within the trophically least attractive communities. Marmots avoid low-stem, mat-grass communities (the alliance *Nardion strictae*), dense stands of krummholz dominated by dwarf pine (the alliance *Pinion mugo*), and dwarf shrubs with lichens (the alliance *Loiseleurio-Vaccinion*) (Fig. 2).

THE DIRECT RELATIONSHIP BETWEEN DIFFERENT TYPES OF FUNCTIONAL AREAS AND ENVIRONMENTAL VARIABLES

Of the 44 tested topographic environmental variables (Table 2) included in the CCA, 20 variables were selected by forward selection as the best differentiating habitat preferences of marmot functional areas (Table 5). Permutation tests on the trace value (0.514; $F = 15.707$, $P = 0.002$) and on the value of axis 1 (eigenvalue = 0.365; $F = 181.485$, $P = 0.002$) indicated that the variables included in the model explained a significant amount of the variation in the species data. The inertia in the species data was 1.163. Of this, the first axis explained 31.4%, and the second axis explained 9.5%. Together, the canonical eigenvalues accounted for 51.4% of the total variance. The percentage variance explained by the second axis was low; thus, the second axis was not readily interpretable. The cumulative percentage variance of species-environment relation is 71% (axis 1) and 21.6% (axis 2), and it expresses the amount of inertia explained by our axes as a fraction of the total explainable inertia. Thus, the first two axes taken together display more than half of the variation that could be explained by the variables.

There are two dominant factors (or at least, two factors related to variables we measured) controlling distribution of functional areas: one is related to convex and reinforced rock forms versus surface without sediments and significant curvature, and the other is related to alpine and subalpine meadows conditions. In other words, two dominant factors are good living and good grazing conditions.

The first axis is highly positively related to the edge (mountain ridge) and biotic granodiorites and less positively related to the scree, stromatolites, migmatitic gneiss, and bottomland (there are meadows with possibility of shelter in these conditions). Significant and highly negative correlations ($P < 0.05$) were found between the first axis and the convex geomorphic features, gentle slope, debris cone, and deep gorge (Table 6).

Marmot functional areas were sorted along the first axis according to the reliance on the gradient of the relief structure and the surface curvature. Trails and grazing areas correlated with features suitable only for the building of temporary shelters are on the right of the diagram, and summer and winter areas associated with features suitable for permanent burrows are displayed on the left of the ordination diagram (Fig. 3). The CCA shows that the summer and winter areas with the main burrow systems (maternal, hibernation and summer burrows with auxiliary burrows and burrow feces deposits) are associated with different types of sediment accumulation down the sides of glacial gorges. These features have a stable structure on the aboveground surface and relatively stable microclimatic conditions inside.

TABLE 5

Twenty variables selected by forward selection of the permutation model. Cumulative variance explained by all variables is 0.58.

Step of selection	Abbrev.	Variable	*P*-value	*F*-ratio	Cumulative variance explained by the selected variables
1	CGF	Convex geomorphic feature	0.0020	79.13	0.19
2	q35	Glacigenic sediments; gravel, boulders, and moraine blocks	0.0020	22.93	0.24
3	R4	Gentle slope	0.0020	18.29	0.28
4	kr186	Stromatolites, migmatitic gneiss	0.0020	14.61	0.31
5	SCR	Scree	0.0020	14.61	0.33
6	kr9	Leucocratic granites	0.0020	9.34	0.35
7	q24	Diluvial sediments; lithofacially undifferentiated flows, debris sediments	0.0020	11.24	0.37
8	DEG	Deep gorge	0.0020	7.86	0.39
9	mt97	Reifling limestones	0.0020	9.67	0.41
10	kr132	Mica schists, mica schistose gneisses, and micaceous gneisses	0.0020	7.36	0.42
11	VAL	Valley	0.0040	7.03	0.43
12	kr55	Biotitic granodiorites to tonalites	0.0040	6.52	0.44
13	EDG	Edge (mountain ridge)	0.0020	6.42	0.45
14	SLO	Slope	0.0020	8.63	0.47
15	BOL	Bottom land	0.0020	6.59	0.48
16	Al9	Alpine heaths	0.0060	4.73	0.49
17	R5	Flat bottom	0.0100	4.01	0.49
18	DCO	Debris cone	0.0040	5.77	0.50
19	q10	Glacial sediments; debris, boulders, and blocks of the retreating moraines	0.0620	3.07	0.51
20	Al6	Siliceous tall-grass communities	0.0440	2.75	0.51

Discussion

Considering that almost all marmot species except *M. monax* are highly social animals (Armitage, 1996; Armitage and Blumstein, 2000); and all marmot species have the same characteristic pattern of habitat use (Armitage, 2000); and also the capability of the marmots to maintain stable home ranges across years is unique in the genus *Marmota* (Lenti Boero, 2003a), this study contributes to the understanding of the entire marmot genus habitat utilization.

We predict that functional areas of home ranges are associated with distinct habitat types and topography, each of which is linked to a distinct plant community. Different functions imply different characteristics; diverse burrow utilization is a consequence of the variable structure of burrows and of intrinsic characteristics that may be appraised by marmots (Lenti Boero, 2003a).

To study the habitat utilization of Tatra marmots, we focused on microhabitats in their space use. Our objective was to evaluate the influence of combinations of environmental factors on the location of different functional areas of marmot home ranges appraised by the marmot's own utilization and the function of different burrow types.

The microhabitat utilization of Tatra marmots is associated with the interaction of food availability, breeding conditions and hibernation conditions. Thus, the most important parts of home ranges, even in other marmot species, are the foraging areas and main burrow system, especially hibernacula (Bibikov, 1996; Armitage, 1991). The adequate nutritious food (cf. Holmes, 1984; Armitage, 2000) and hibernacula are a limiting factor to the expansion of marmot populations (Svendsen, 1976; Lenti Boero, 1996, 2001; Arnold et al., 1991).

Vegetation is one of the main components of marmot habitats. In addition to food, vegetation provides living conditions for marmots as a protection from predators (Holmes, 1984; Carey, 1985; Carey and Moore, 1986) and a material for stuffing their burrows (cf. Svendsen, 1976; Armitage, 2003). According to our study, the variability of plant communities has an indirect influence on the localization of different functional areas and different burrow types in Tatra marmots (Fig. 3, Table 4). We suggest that plant communities are also an indicator of important ecological factors for building maternal and hibernation burrows and Tatra marmot distribution.

The diet of Tatra marmots is mainly composed of grasses and forbs, which are eaten selectively (Chovancová and Šoltésová, 1988; Karč, 2006). The forbs are a major food of

TABLE 6

Intraset correlations of the first two canonical axes in CCA ordination with 20 significant variables selected by forward selection of the permutation model.

Abbr.	Variable	Intraset correlations Axis 1	Axis 2
R4	Gentle slope	–0.2781	0.1607
R5	Flat bottom	–0.0413	–0.0622
al6	Siliceous tall-grass communities	–0.1042	–0.0228
al9	Alpine heaths	–0.0836	–0.0811
kr132	Mica schists, mica schistose gneisses, and micaceous gneisses	–0.0866	0.2125
kr55	Biotic granodiorites to tonalites	0.2499	0.1357
kr186	Stromatolites, migmatitic gneisses	0.1666	0.2503
kr9	Leucocratic granites	–0.0343	–0.3023
mt97	Reifling limestones	–0.1075	–0.0019
q10	Glacial sediments; debris, boulders and blocks of the retreating moraines	–0.0534	–0.0028
q24	Diluvial sediments; litofacially undifferentiated flows, debris sediments	–0.1235	–0.1573
q35	Glacigenic sediments; gravel, boulders and moraine blocks	–0.1387	–0.1401
CGF	Convex geomorphic feature	–0.5106	0.0602
DCO	Debris cone	–0.2177	–0.0005
DEG	Deep gorge	–0.2073	0.1268
VAL	Valley	–0.1466	0.0562
SCR	Scree	0.1760	–0.0411
BOL	Bottom land	0.1650	–0.0658
SLO	Slope	0.0113	0.0604
EDG	Edge (mountain ridge)	0.2707	–0.0928

choice of marmots, and grasses are eaten in part because of availability (Armitage, 2000). The results of the previous studies of the food selectivity of the *M. marmota latirostris* subspecies (Chovancová and Šoltésová, 1988; Karč, 2006; Table 7) agree with our findings that marmots choose to forage in tall-stem grasslands and tall herb plant communities from the alliances *Calamagrostion villosae* and *Trisetion fusci*. On the contrary to our findings, Carey and Moore (1986) found that the preference for foraging areas in yellow-bellied marmots was negatively correlated with dense, high vegetation. In habitats with tall vegetation, marmots must increase their vigilance time when foraging and reduce the rate of food intake. These results may be interpreted as adaptive behavior integrating the simultaneous demands of food ingestion and predator avoidance (Carey, 1985).

In some marmot species, such as hoary, Olympic, and yellow-bellied marmots, it was found that they cannot simply confine all feeding to small areas near burrows or rock slides (cf. Barash, 1973; Johns and Armitage, 1979; Holmes, 1984). The marmots must move away from these "safe" areas and consequently become more vulnerable to predators (cf. Barash, 1973; Johns and Armitage, 1979). Predation risk and vegetation distribution influenced the location of foraging areas of yellow-bellied marmots (Frase and Armitage, 1984). We found that Tatra marmots forage mainly on pastures that are not the part of the summer or winter area within the main burrow systems. Their grazing areas were mostly situated in periphery of family home ranges. Holmes (1984) verified the direct role of food availability on patch use in hoary marmots. Utilization of habitat patches by *M. flaviventris* in California was explained by high food biomass (Carey, 1985). However, food is not the only determinant of patch use.

Nevertheless, the key for understanding the foraging area pattern might be alimentary choice, which remains poorly understood in the Alpine marmot (Lenti Boero, 2003a). Food choice may be based on protein (Frase and Armitage, 1989) or essential fatty acid (Florant, 1998) content.

Grazing areas have an important role in the localization of the whole Tatra marmot settlements. This fact explains the correlation of locations without marmots with trophically less attractive plant communities from the alliances *Nardion strictae*, *Loiseleurio-Vaccinion,* and *Pinion mugo*.

Food consumption and assimilation may be related to cellulose content. Alpine marmots from the Natural Park Orsiera Rocciavre (Western Alps) were absent from meadows where the predominant plants were *Nardus stricta*, *Carex sempervirens*, *C. curvula,* and *Sesleria* sp. with high cellulose content (Vita, 1992). Similarly, the tarbagans (*M. sibirica*) avoid high cellulose

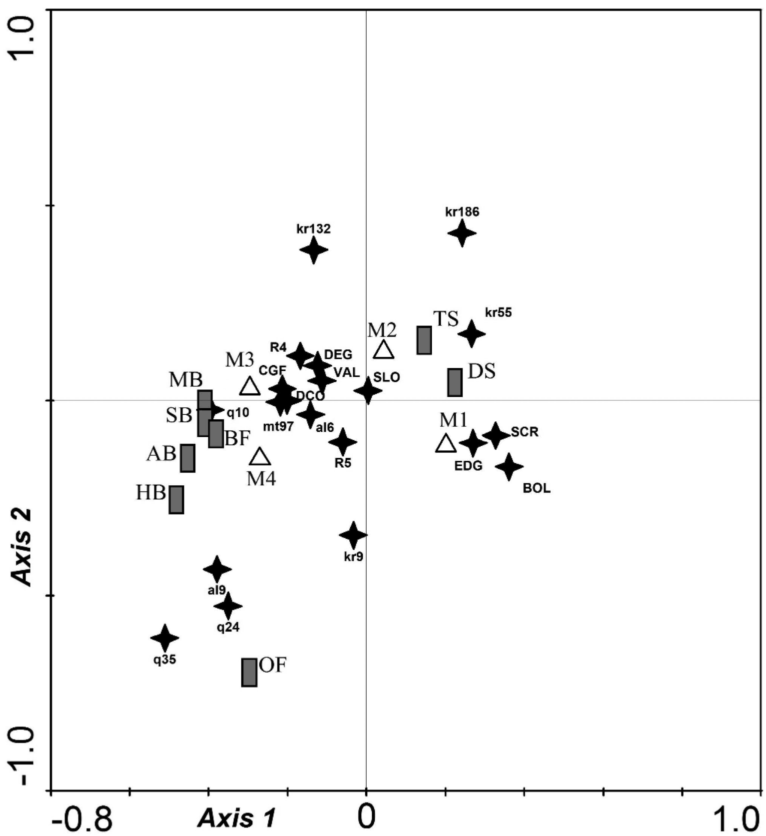

FIGURE 3. CCA ordination diagram of marmot functional areas based on environmental explanatory variables with types of marmot burrows as supplementary variables. Full model of Monte-Carlo permutation test (499 permutations) was performed. Only those variables for which effect was significant ($P < 0.05$) were chosen for analysis as explanatory variables. Eigenvalues: 0.365 (axis 1), 0.111 (axis 2). Cumulative percentage variance of species-environment relation is 71% (axis 1) and 21.6% (axis 2). The summer and winter areas with the main burrow systems (maternal, hibernation, and summer burrows with auxiliary burrows and burrow feces deposits) are associated with different types of sediment accumulation down the sides of glacial gorges (what is expressed in their high correlations with the convex geomorphic features, gentle slope, debris cone, and deep gorge). Trails and grazing areas correlated with features suitable only for the building of temporary shelters (mainly the edge and biotic granodiorites and less positively related to the scree, stromatolites, migmatitic gneiss, and bottomland). Legend: ∆ functional areas of marmot home ranges (M1—marmot trails, M2—grazing areas, M3—summer areas, M4—winter areas); ▮ supplementary variables (types of marmot burrows): AB—auxiliary burrows, BF—burrow feces deposits, MB—maternal burrows, HB—hibernacula, SB—summer burrows, OS—occasional shelters, DS—dug shelters; ✦ nominal environmental variables: Al6—siliceous tall-grass communities, Al9—alpine heaths, BOL—bottom land, CGF—convex geomorphic feature, DCO—debris cone, DEG—deep gorge, EDG—edge (mountain ridge), kr132—mica schists, mica schistose gneisses, and micaceous gneiss, kr186—stromatolites and migmatitic gneiss, kr55—biotitic granodiorites to tonalities, kr9—leucocratic granites, mt97—reifling limestones, q10—glacial sediments (debris, boulders, and blocks of the retreating moraines), q24—diluvial sediments (lithofacially undifferentiated flows and debris sediments), q35—glacigenic sediments (gravel, boulders, and moraine blocks), R4—gentle slope, R5—flat bottom, SCR—scree, SLO—slope, and VAL—valley.

content in plants and thereby in the first half of the active season they eat grasses and some herbs, and in the second half, mainly herbs. Habitats dominated by grasses are less favorable (Seredneva, 1991).

Our results also show that the winter areas in the Západné Tatry Mountains are often located within the plant communities of the alliance *Juncion trifidi* usually dominated by one species (e.g., *Juncus trifidus*, *Agrostis rupestris*, *Oreochloa disticha*, *Festuca supina*). These communities are exposed to strong winds throughout the year, and during winter, they are almost without snow cover (Dúbravcová and Jarolímek, 2007).

The occurrence of hibernacula in the plant communities of the alliance *Juncion trifidi* in the Západné Tatry Mountains is likely linked to both marmot-preferred convex geomorphic features (various cones and ridges of the terrain), which are due to their structure being suitable for the construction of permanent burrows, and the possibility of unrestricted views of the area due to the short grasses. Short-stem herb and grass communities of the alliance *Juncion tri-*

TABLE 7

Plant species frequently consumed by *M. marmota latirostris*.

Author	Plant species	Season
Karč (2006)	*Alchemilla* spec. div. (leaves), *Calamagrostis villosa* (shoot), *Campanula alpina* (flowers), *Carex sempervirens* subsp. *sempervirens*, *Crocus heuffelianus* (leaves), *Luzula luzuloides* (shoot), *Luzula sylvatica*, *Oreochloa disticha* (shoot), *Rhizocarpon geographicum*	May and June
Chovancová and Šoltésová (1988)	*Adenostyles alliariae*, *Bistorta major*, *Calamagrostis villosa*, *Doronicum austriacum*, *Doronicum styriacum, Gentiana punctata*, *Luzula alpinopilosa*, *Ligusticum mutellina*, *Oreogeum montanum*, *Polygonum bistorta*, *Veratrum album* subsp. *lobelianum*	July and August

fidi are rather species poor; despite that fact, they produce a greater biomass of marmot-grazed grass, and include more of the marmots' preferred plant species (Chovancová and Šoltésová, 1988). Compared to the above-mentioned communities, marmot avoided plant communities of the alliance *Loiseleurio-Vaccinion* that are also composed of low-lying plant species and include nonpreferred dwarf shrubs and heaths with lichens. Notwithstanding, all of these communities prefer climatically extreme habitats, slopes exposed to winds, and a short duration of snow cover (Šibík et al., 2007). In accordance with these findings, Herrero et al. (1994) and Lenti Boero (1999) suggested that Alpine marmots avoid woods as well as heaths of *Vaccinium* species. Sites with high percentages of woody species such as *Pinus uncinata* were inhabited by marmots in Pyrenees with the lowest probability (López et al., 2010). Similarly to this study, the most avoided habitats in the Tatra Mountains are dense stands of krummholz dominated by dwarf pine (*Pinus mugo*).

The summer areas of Tatra marmots in the Vysoké Tatry Mountains occur most frequently within the plant communities from the alliances *Festucion picturatae* and *Calamagrostion villosae* (Chovancová and Šoltésová, 1988). According to our results, the summer areas with maternal and summer burrows in the Západné Tatry Mountains are often located near the chionophilous grassland communities of fixed screes on siliceous bedrock (alliance *Festucion picturatae*) and within the chionophilous communities of snow beds and snow fields (alliance *Salicion herbaceae*). These communities grow in habitat conditions that are suitable for building the main burrow systems.

Even relatively common vegetation types in mountain regions are very important for the determination of the locations of different functional areas of the family home range and, thus, for the location of a family home range as a whole.

As previously mentioned, the most important factor influencing the locations of the different functional areas is the gradient of the georelief structure. The presence of geomorphic forms, due to their structure and features suitable for permanent burrows, is important for the localization of family summer and winter areas. The location of Tatra marmot burrows types is significantly influenced by the presence of convex geomorphic features and different types of rocky sediments. Hoary marmots' main burrows are predominantly in talus patches, which provide shelter from predators and weather (Karels et al., 2004). In many cases the lower parts of talus cones constitute "blockfields" of large angular blocks, and there can be cavities among these blocks (Åkerman, 1984). Cavities are characterized by relatively stable climatic conditions suitable for marmot hibernation and maternity chamber. Some marmot species use talus slopes and rocks located in openings with herbaceous vegetation for lookouts, for sunning, and to burrow beneath. The taluses that are composed of rocks of similar size mixed into the soil appear to be used for yellow-bellied marmot burrow support (Svendsen, 1974). Talus slopes are usually susceptible to strong winds all year, and in winter, these slopes are almost without snow cover; thus, in the Západné Tatry Mountains, they are occupied by the communities from the alliance *Juncion trifidi* (Dúbravcová and Jarolímek, 2007). Despite the above fact, the inside climatic conditions are favorable for Tatra marmot utilization throughout the year.

There is little, if any, food within talus patches, and marmots must therefore forage in the adjacent meadows. When aboveground, hoary marmots (*Marmota caligata*) spent 26% of their time on the talus. The rest of their time (74%) was spent in the adjacent meadows (Karels et al., 2004).

Summer and winter areas with permanent burrows are, apart from convex geomorphic features and debris cones, also associated with glacial sediments on the left part of the ordination diagram. The Tatra Mountains are mostly covered with moraine sediments and different rock fragments resulting from slope processes. Moraine accumulations are located only on the bases of valleys. Debris flows can transport a considerable amount of angular fragments released by weathering, which are deposited at the foot of rock walls to form a continuous cover of debris cones (Lukniš, 1973). Due to the preference of reinforced rock forms, the main burrows of Tatra marmots are often found on the surface moraine covering, and it is conceivable that the corridors of their burrows lead inside the moraine accumulations. Rock promontories are apparently important habitat features for surveillance activities in marmots, presumably for the increased field of view that larger rocks provide (Tyser, 1980). Some open meadows with an abundance of large boulders support marmots. At sites where suitable rocks are numerous, yellow-bellied marmots have had excavated burrows beneath nearly every rock (Svendsen, 1974).

Grazing areas are a very important part of Tatra marmot home ranges and have an important role in the localization of all functional areas (Ballová et al., 2012). Thus, marmots in the Tatra Mountains often situate their summer and winter areas (strongly associated with the location of main burrow systems, hibernacula, and feces deposits) in the sites where they can graze. The most preferred areas for grazing (grasslands and tall herb plant communities) also include moist habitats with deeper soils and mountain meadows on exposed slopes prone to soil erosion caused by the avalanches. This environment is suitable for the building of temporary shelters only. Concomitant with increased feeding is the intense construction of shelter burrows in hoary marmot that presumably reduce the risk of feeding (Holmes, 1984).

Conclusions

The output analysis and field observations show that environmental factors do not directly determine the functional differentiation of Tatra marmot burrows but affect the structure and location of burrows in respect to their regular function.

Taken together, the previously mentioned studies confirm that marmots select their habitats according to multi-component strategies in which factors may vary in their importance, as previously mentioned by Allainé et al. (1994). We can conclude that the main factor that determines the Tatra marmot microhabitat utilization is the microtopography of their living area.

This paper presents a study based on a combination of environmental factors that interact with the marmot spatial organization and contributes to the understanding of the marmot microhabitat utilization.

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References Cited

Åkerman, H. J., 1984: Notes on talus morphology and processes in Spitsbergen. *Geografiska Annaler*, 66A (4): 267–284.

Allainé, D., 2000: Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behavioural Processes*, 51: 21–34.

Allainé, D., Rodrigue, I., Le Berre, M., and Ramousse, R., 1994: Habitat preferences of Alpine marmots, *Marmota marmota*. *Canadian Journal of Zoology*, 72: 2193–2198.

Armitage, K. B., 1991: Social and population dynamics of Yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics*, 22: 379–407.

Armitage, K. B., 1996: Social dynamics, kinship, and population dynamics of marmots. *In* Le Berre, M., Ramousse, R., and Le Guelte, L. (eds.), *Biodiversity in Marmots*. Moscow/Lyon: International Marmot Network, 113–128.

Armitage, K. B., 2000: The evolution, ecology, and systematics of marmots. *Oecologia Montana*, 9: 1–18.

Armitage, K. B., 2003: Recovery of a Yellow-bellied Marmot population following a weather-induced decline. *In* Ramousse, D., Allainé, D., and Le Berre, M. (eds.), *Adaptive Strategies and Diversity in Marmots*. Moscow/Lyon: International Marmot Network, 217–224.

Armitage, K. B., 2013: Climate change and the conservation of marmots. *Natural Science*, 5: 36–43.

Armitage, K. B., and Blumstein, D. T., 2000: Body-mass diversity in marmots. *In* Armitage, K. B., and Rumiantsev, V. Yu. (eds.), *Holarctic Marmots as the Factor of Biodiversity*. Moscow: ABF Publishing House, 22–40.

Arnold, W., 1990: The evolution of marmot sociality. Why disperse late? Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology*, 27: 229–246.

Arnold, W., Heldmaier, G., Ortmann, S., Pohl, H., Ruf, R., and Steinlechner, S., 1991: Ambient temperature in hibernacula and their consequences for Alpine marmots (*Marmota marmota*). *Journal of Thermal Biology*, 16: 223–226.

Bačkor, P., 2009: Current distribution of the Alpine marmot (*Marmota marmota*) in the Nízke Tatry Mts., Slovakia (Rodentia: *Sciuridae*). *Lynx*, 40: 5–13.

Ballo, P., 2008: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách—IV. úsek (2007). *Naturae tutela*, 12: 151–165.

Ballo, P., 2009: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách. V. úsek—Červené vrchy. *Naturae tutela*, 13: 115–137.

Ballo, P., 2010: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách. VI. úsek—Liptovské kopy. *Naturae tutela*, 14: 99–115.

Ballo, P., and Ballová, Z., 2010: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách a migrácie. *In* Adamec, M., and Urban, P. (eds.), *Výskum a ochrana cicavcov na Slovensku IX*. Zborník referátov z konferencie (2009). Banská Bystrica: Štátna ochrana prírody Slovenskej republiky, 59–64.

Ballo, P., and Sýkora, J., 2005: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách—I. úsek (2004). *Naturae tutela*, 9: 169–190.

Ballo, P., and Sýkora, J., 2006: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách—II. úsek (2005). *Naturae tutela*, 10: 156–186.

Ballo, P., and Sýkora, J., 2007: Monitoring kolónií svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Západných Tatrách—III. úsek (2006). *Naturae tutela*, 11: 171–194.

Ballová, Z., and Ballo, P., 2009: Komunikačné prepojenia v osídlení svišt'a vrchovského tatranského (*Marmota marmota latirostris*) v Liptovských kopách. *In* Stloukal, E. (ed.), *Zborník abstraktov z konferencie 15. Feriancove dni 2009*. Bratislava: Faunima, 49.

Ballová, Z., Ballo, P., and Šibík, J., 2012: Factors affecting the location of Tatra marmot communication links. *Naturae tutela*, 16(1): 57–71.

Barash, D. P., 1973: The social biology of the Olympic marmot. *Animal Behaviour Monographs*, 6: 171–249.

Barash, D. P., 1976: Social behaviour and individual differences in free-living Alpine marmots (*Marmota marmota* L.). *Animal Behaviour*, 24: 27–35.

Barkman, J. J., Doing, H., and Segal, S., 1964: Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Botanica Neerlandica*, 13: 394–419.

Bassano, B., Grimod, I., and Peracino, V., 1992: Distribution of Alpine marmot (*Marmota marmota*) in the Aosta Valley and suitability analysis. *In* Bassano, B., Durio, P., Gallo Orsi, U., and Macchi, E. (eds.), *Proceedings of the First International Symposium on Alpine Marmot and genera Marmota*. Aosta: 45–51.

Bibikov, D. I., 1996. Die Murmeltiere der Welt. Heidelberg: Spektrum Akademischer Verlag.

Blahout, M., 1960: Príspevok k bionómii svišt'a horského (*Marmota marmota* L.) v rezervácii Podbanské v Tatranskom národnom parku. *Zborník prác o Tatranskom Národnom parku* 4: 118–150.

Blahout, M., 1971: Príspevok k bionómii svišt'a vrchovského (*Marmota marmota* L.). *Zborník prác o Tatranskom Národnom parku* 13: 243–286.

Borgo, A., 2003: Habitat requirements of the Alpine marmot *Marmota marmota* in reintroduction areas of the Eastern Italian Alps. Formulation and validation of habitat suitability models. *Acta Theriologica*, 48(4): 557–569.

Braun-Blanquet, J., 1964: Pflanzensoziologie. Grundzüge der Vegetationskunde. 3. Aufl. Wien: Springer-Verlag, 865 pp.

Burt, W. H., 1943: Territory and home range concepts as applied to mammals. *Journal of Mammalogy*, 24: 346–352.

Carey, H. V., 1985: Nutritional ecology of Yellow-bellied marmots in the White mountains of California. *Holarctic Ecology*, 8: 259–264.

Carey, H. V., and Moore, P., 1986: Foraging and predation risk in Yellow-bellied marmots (*Marmota flaviventris*). *American Midland Nature*, 116: 267–275.

Chovancová, B., 1987: Výsledky inventarizácie svišt'a vrchovského tatranského (*Marmota marmota latirostris* Kratochvíl, 1961) na území Tatranského národného parku za obdobie rokov 1982–1985. *Folia venatoria*, 17: 137–150.

Chovancová, B., and Šoltésová, A., 1988: Trofická základňa a potravová aktivita svišt'a vrchovského tatranského (Marmota marmota latirostris Kratochvíl, 1961). *Zborník prác o Tatranskom národnom parku*, 28: 71–135.

Chytrý, M., and Otýpková, Z., 2003: Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science,* 14(4): 563–570.

Dúbravcová, Z., 2007: *Salicetea herbaceae*. *In* Kliment, J., and Valachovič, M. (eds.), *Rastlinné spoločenstvá Slovenska, 4. Vysokohorská vegetácia.* Bratislava: Veda, 251–281.

Dúbravcová, Z., and Jarolímek, I., 2007: *Caricetea curvulae*. *In* Kliment, J., and Valachovič, M. (eds.), *Rastlinné spoločenstvá Slovenska,* 4. Vysokohorská vegetácia. Bratislava: Veda, 321–339.

Ellenberg, H., Weber, H. E., Düll, R., Wirth ,W., Werner, W., and Paulißen, D., 1992: Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 2nd edition. Göttingen, 1–258.

Florant, G. L., 1998: Lipid metabolism in hibernators: the importance of essential fatty acids. *American Zoologist*, 38: 331–340.

Floyd, C. H., 2004: Marmot distribution and habitat associations in the Great Basin. *Western North American Naturalist*, 64: 471–481.

Frase, B. A., and Armitage, K. B., 1984: Foraging patterns of yellow-bellied marmots: role of kinship and individual variability. *Behavioral Ecology* and *Sociobiology*, 16: 1–10.

Frase, B. A., and Armitage, K. B., 1989: Yellow-bellied marmots are generalist herbivores. *Ethology Ecology & Evolution*, 1: 353–366.

Gąsienica-Byrcyn, W., 1994: Z ekologii swistaka (*Marmota marmota latirostris* Kratochvíl, 1961). *Rocznik Podhalansky,* 6: 9–121.

Gąsienica-Byrcyn, W., 2008: Chów świstaka tatrzańskiego. *Wierchy*, 72: 163–174.

Halák, K., 1984: Výskyt svišt'a vrchovského (*Marmota marmota latirostris* Kratochvíl, 1961) v Západných Tatrách—Roháčoch. *Zborník prác o Tatranskom národnom parku*, 25: 47–60.

Hennekens, S. M., and Schaminée, J. H. J., 2001: TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science*, 12: 589–591.

Herrero, J., and García-González, R., 2007: Marmota marmota (Linnaeus, 1758). *In* Palomo, L. J., Gisbert, J., and Blanco, J. C. (eds.), *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Madrid: Dirección General para la Biodiversidad–SECEM–SECEMU, 385–386.

Herrero, J., and García-Serrano, A., 1994: La Marmota Alpina en Navarra. Pamplona, Spain: Gobierno de Navarra, 72 pp.

Herrero, J., García-González, R., and García-Serrano, A., 1994: Altitudinal distribution of Alpine marmot (*Marmota marmota*) in the Pyrenees, Spain/France. *Arctic and Alpine Research*, 26(4): 328–331.

Holmes, W. G., 1984: Predation risk and foraging behavior of the hoary marmot in Alaska. *Behavioral Ecology and Sociobiology*, 15: 293–301.

Jarolímek, I., and Šibík, J. (eds.), 2008: Diagnostic, constant and dominant species of the higher vegetation units of Slovakia. Bratislava: Veda, 332 p.

Jarolímek, I., Šibík, J., Hegedüšová, K., Janišová, M., Kliment, J., Kučera, P., Májeková, J., Michálková, D., Sadloňová, J., Šibíkova, I., Škodová, I., Uhlířová, J., Ujházy, K., Ujházyová, M., Valachovič, M., and Zaliberová, M., 2008: A list of vegetation units of Slovakia. *In* Jarolímek, I., and Šibík, J. (eds.), *Diagnostic, constant and dominant species of the higher vegetation units of Slovakia*. Bratislava: Veda, 295–329.

Johns, D. W., and Armitage, K. B., 1979: Behavioral ecology of alpine yellow-bellied marmots. *Behavioral Ecology and Sociobiology*, 5: 133–157.

Karč, P., 2006: Príspevok k poznaniu populácie svišt'a vrchovského (*Marmota marmota* L.) v západnej časti národného parku Nízke Tatry (Prašivá-Ďumbier). *Naturae tutela*, 10: 79–94.

Karels, T., Koppel, L., and Hik, D., 2004: Fecal pellet count as a technique for monitoring an alpine-dwelling social rodent, the hoary marmot (*Marmota caligata*). *Arctic, Antarctic, and Alpine Research*, 36: 490–494.

Kliment, J., 2007: Nardetea strictae Rivas Goday et Borja Carbonell 1961. *In* Kliment, J., and Valachovič, M. (eds.), *Rastlinné spoločenstvá Slovenska*: 4. Vysokohorská vegetácia. Bratislava: Veda, 343–353.

Kliment, J., and Valachovič, M. (eds.), 2007: *Rastlinné spoločenstvá Slovenska. 4. Vysokohorská vegetácia.* Bratislava: Veda, vydavatel'stvo SAV, 388 pp.

Kliment, J., Jarolímek, I., and Šibík, J. 2007: Mulgedio-Aconitetea Hadač et Klika in Klika 1948. In Kliment, J., and Valachovič, M. (eds.), *Rastlinné spoločenstvá Slovenska*: 4. Vysokohorská vegetácia. Bratislava: Veda, 21–129.

Kliment, J., Šibík, J., Šibíková, I., Dúbravcová, Z., Jarolímek, I. and Uhlířová, J., 2010: High-altitude vegetation of the Western Carpathians—a syntaxonomical review. *Biologia*, 65(6): 965–989.

Kostroň, K., 1965: K histórii rozšíření sviště horského (*Marmota marmota* L.) v oblasti Vysokých Tater. *Zborník prác o Tatranskom národnom parku*, 8: 159–171.

Krajina, V., 1933: Die Pflanzengesellschaften des Mlynica-Tales in den Vysoke Tatry (Hohe Tatra). *Beihefte zum Botanischen Centralblatt*, 2(51): 1–224.

Kratochvíl, J., 1964: Svišť—vzácny cicavec z Vysokých Tatier. *Zborník prác o Tatranskom Národnom parku* 7: 127–133.

Lenti Boero, D., 1995: Scent-deposition behaviour in Alpine Marmots (*Marmota marmota* L.): its role in territorial defense and social communication. *Ethology*, 100: 26–38.

Lenti Boero, D., 1996: Space and resource use in Alpine marmot (*Marmota marmota* L.). *In* Le Berre, M., Ramousse, R., and Le Guelte, L. (eds.), *Biodiversity in Marmots*. Moscow/Lyon: International Marmot Network, 175–180.

Lenti Boero, D., 1999: Population dynamics, mating system and philopatry in a high altitude colony of Alpine marmots (*Marmota marmota* L.). *Ethology Ecology & Evolution*, 11: 105–122.

Lenti Boero, D., 2001: Occupation of hibernacula, seasonal activity, and body size in a high altitude colony of Alpine marmots (*Marmota marmota*). *Ethology Ecology & Evolution,* 13: 209–223.

Lenti Boero, D., 2002: Social interactions in a colony of alpine marmots (*Marmota marmota* L.). *In* Ramousse, R., et al. (eds.), *Abstracts, IV Conférence Mondiale sur les Marmottes.* Montreux: International Marmot Network, 82 pp.

Lenti Boero, D., 2003a: Long-term dynamics of space and summer resource use in the Alpine marmot (*Marmota marmota* L.). *Ethology Ecology & Evolution*, 15: 309–327.

Lenti Boero, D., 2003b: Habitat choice and census techniques in Alpine marmot: a preliminary review. *In* Ramousse, R., Allainé, D., and Le Berre, M. (eds.), *Adaptive strategies and diversity in marmots*. Moscow/Lyon: International Network on Marmots, 177–182.

Lepš, J., and Šmilauer, P., 2000: *Mnohorozměrná analýza ekologických dat*. České Budějovice: Biologická fakulta Jihočeské univerzity v Českých Budějovicích, 102 pp.

López, B. C., Pino, J., and López, A., 2010: Explaining the successful introduction of the alpine marmot in the Pyrenees. *Biological Invasions*, 12: 3205–3217.

Lukniš, M., 1973: Reliéf Tatranského národného parku. *Zborník prác o Tatranskom národnom parku*, 15: 83–132.

Lupin, M., Faško, P., Melo, M., Šťastný, P., and Tomlain, J., 2002: 27. Klimatické oblasti (1:1,000,000). *In* Miklós, L. (ed.), *Atlas krajiny Slovenskej republiky*. Banská Bystrica: Ministerstvo životného prostredia SR, Bratislava & Slovenská agentúra životného prostredia, Banská Bystrica, 344 pp.

Macchi, E., Bassano, B., Durio, P., Tarantola, M., and Vita, A., 1992: Ecological parameters affecting the settlement's choice in Alpine marmot (*Marmota marmota*). *In* Bassano, B., Durio, P., Gallo Orsi, U., and Macchi, E. (eds.), *Proceedings of the First International Symposium on Alpine Marmot and genera Marmota*. Aosta, Italy, 123–127.

Mann, C. S., and Janeau, G., 1988: Occupation de l'éspace, structure sociale, et dynamic d'une population de marmottes des Alpes. *Gibier Faune Sauvage,* 5: 427–445.

Marhold, K., and Hindák, F., 1998: *Zoznam nižších a vyšších rastlín Slovenska*. Bratislava: Veda, 687 pp.

M'Closkey, R. T., 1976: Community structure in sympatric rodents. *Ecology*, 57: 728–739.

Melcher, J. C., Armitage, K. B., and Porter, W. P., 1990: Thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*). *Physiological Zoology*, 63: 803–820.

Moravec, J., 1993: Syntaxonomic and nomenclatural treatment of Scandinavian-type associations and sociations. *Journal of Vegetation Science,* 4: 833–838.

Mueller-Dombois, D., and Ellenberg, H., 1974: *Aims and methods of vegetation ecology*. New York: John Wiley and Sons, 547 pp.

Nikol'skii, A. A., and Ulak, A., 2006: Key factors determining the ecological niche of the Himalayan Marmot, *Marmota himalayana* Hodgson (1841). *Russian Journal of Ecology*, 37(1): 46–52.

Novacký, M., 1978: O etológii svišt'a vrchovského (*Marmota marmota* L. 1758) a o probléme vplyvu civilizačných faktorov na vrodené správanie. *Psychologica. Zborník Filozofickej fakulty Univerzity Komenského*, 25: 132–160.

Novacký, M., 1994: Behavioural changes in flight strategy of the marmot (*Marmota marmota* L.) as indicators of the influence of negative anthropogenous factors. *Acta Environmentalica Universitatis Comenianae*, 2: 33–40.

Ondruš, S., 2003: *Program záchrany svišťa vrchovského* (*Marmota marmota*, Linnaeus, 1758). Banská Bystrica: ŠOP SR Banská Bystrica Správa NP Nízke Tatry, 27 pp.

Perrin, C., Allainé, D., and Le Berre, M., 1993: Socio-spatial organization and activity distribution of the alpine marmot *Marmota marmota*: preliminary results. *Ethology*, 93: 21–30.

Poore, M. E. D., 1955: The use of phytosociological methods in ecological investigations: II. Practical issues involved in an attempt to apply the Braun-Blanquet system. *Journal of Ecology*, 43(1): 245–269.

Sala, L., Sola, C., Spampanato, A., and Tongiorgi, P., 1992: Space and time use in a population of *Marmota marmota*. *In* Le Berre, M., Ramousse, R., and Le Guelte, L. (eds.), *Biodiversity in Marmots*. Moscow/Lyon: International Network on Marmots, 209–216.

Schaminée, J. H. J., Hennekens, S. M., Chytrý, M., and Rodwell, J. S., 2009: Vegetation-plot data and databases in Europe: an overview. *Preslia*, 81: 173–185.

Seredneva, T. A., 1991: Consistent pattern of the tarbagan spatial distribution in the eastern Khangai (Mongolia). *In* Bibikov, D. I., Nikolski, A. A., Rumiantsev, V. Yu., and Seredneva, T. A. (eds.), *Population Structure of the Marmot*. Moscow: USSR Theriological Society, 233–274.

Šibík, J., Kliment, J., Jarolímek, I., and Dúbravcová, Z., 2007: Loiseleurio-Vaccinietea. *In* Kliment, J., and Valachovič, M. (eds.), Rastlinné spoločenstvá Slovenska. 4. Vysokohorská vegetácia. Bratislava: Veda, 283–317.

Šibík, J., Šibíková, I., and Kliment, J., 2010: The subalpine *Pinus mugo*-communities of the Carpathians with a European perspective. *Phytocoenologia*, 40(2-9999993): 155–188.

Stanová, V., and Valachovič, M. (eds.), 2002: *Katalóg Biotopov Slovenska*. Bratislava: DAPHNE–Inštitút aplikovanej ekológie, 225 pp.

Svendsen, G. E., 1974: Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology*, 55: 760–771.

Svendsen, G. E., 1976: Structure and location of burrows of yellow-bellied marmot. *The Southwestern Naturalist*, 20(4): 487–494.

ter Braak, C. J. E., 1988: CANOCO—a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Technical Report LWA-88-02, GLW. Wageningen, Netherlands, 95 pp.

ter Braak, C. J. E., 1990: *Update Notes: Canoco Version 3.10*. Wageningen: Agricultural Mathematics Group, 35 pp.

ter Braak ,C. J. E., and Šmilauer, P., 2002: CANOCO reference manual and CanoDraw for Windows user's guide. Software for canonical community ordination (version 4.5). Wageningen & České Budějovice: Biometris, 500 pp.

Tichý, L., 2002: Juice, software for vegetation classification. *Journal of Vegetation Science*, 13: 451–453.

Turk, A., and Arnold, W., 1988: Thermoregulation as a limit to habitat use in Alpine marmots (*Marmota marmota*). *Oecologia*, 76: 544–548.

Tyser, R. W., 1980: Use of substrate for surveillance behaviors in a community of talus slope mammals. *American Midland Naturalist*, 104(1): 32–38.

Vita, A., 1992: The population of marmot (*Marmota marmota*) in the natural park Orsiera Rocciavrč. *In* Bassano, B., Durio, P., Gallo Orsi, U., and Macchi, E. (eds.), *Proceedings of the 1st International Symposium on Alpine Marmot and genera Marmota*. Torino, Italy, 265–268.

Westhoff, V., and van der Maarel, E., 1978: The Braun-Blanquet approach. *In* Whittaker, R. H. (ed.), *Classification of Plant Communities*. Second edition. The Hague: Junk, 287–297.

Zelenka, G., 1965: Observations sur l'écologie de la marmotte des Alpes. *La Terre et la Vie,* 19: 238–256.

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