

## Endangered species' trait responses to environmental variability in agricultural settings

Tijana Nikolić<sup>1,\*</sup>, Maja Arok<sup>2</sup>, Dimitrije Radišić<sup>2</sup>, Marko Mirč<sup>3</sup>, Lea Velaja<sup>1</sup>, Dubravka Milić<sup>1</sup> and Duško Ćirović<sup>4</sup>

<sup>1</sup>University of Novi Sad, Biosense Institute – Research Institute for Information Technologies in Biosystems, Doktora Zorana Đinđića 1, Novi Sad, Serbia

<sup>2</sup>University of Novi Sad, Faculty of Sciences, Department of Biology and Ecology, Trg Dositeja Obradovića 3, Novi Sad, Serbia

<sup>3</sup>Department of Evolutionary Biology, Institute for Biological Research “Siniša Stanković” - National Institute of Republic of Serbia, University of Belgrade, Bulevar despota Stefana 142, Belgrade, Serbia

<sup>4</sup>University of Belgrade, Faculty of Biology, Studentski trg 16, Belgrade, Serbia

\*Corresponding author: [tijana.nikolic@biosense.rs](mailto:tijana.nikolic@biosense.rs)

Received: July 15, 2019; Revised: September 2, 2019; Accepted: September 9, 2019; Published online: September 13, 2019

**Abstract:** Understanding the spatial and temporal effects of variable environmental conditions on demographic characteristics is important in order to stop the decline of endangered-species populations. To capture interactions between a species and its environment, in this work the demographic traits of the European ground squirrel (EGS), *Spermophilus citellus*, were modeled as a function of agricultural landscape structure. The habitat suitability index was determined for 20 localities within the study area based on habitat use, management and type. After mapping the habitat patch occupancy in the field, crop cover maps, the average normalized difference vegetation index (NDVI) and automated water extraction index (AWEI) were obtained from satellite images covering the period 2013-2015. This data was used to develop population-level generalized linear models (GLMs) and individual-level conditional mixed-effects models (GLMMs) in R package lme4, focusing on the key demographic traits of the EGS. The land composition and patch carrying capacity (PCC) are the key determinants of the endangered EGS population size, while system productivity is the main factor influencing individuals' body condition after monitoring for variations across sampling years and age classes. The proposed landscape structural models show that human activities and abiotic factors shape the demographic rates of the EGS. Thus, to conserve threatened species, an appropriate focus on the spatial adaptation strategies should be employed.

**Keywords:** normalized difference vegetation index (NDVI); automated water extraction index (AWEI); demographic traits; *Spermophilus citellus*; habitat

## INTRODUCTION

In agricultural settings, open grassland ecosystems host a significant number of species and have been recognized among the most threatened ecosystems on the planet [1]. The grasslands at the southern edge of the Pannonian Basin (e.g., the region of Vojvodina Province in Serbia) are particularly affected by agricultural intensification and land use degradation as a consequence of adverse local and regional agricultural policies [2]. Increased fragmentation has resulted in the isolation of populations of many species and has reduced habitat availability. Furthermore, the effects of interaction of past and current environmental conditions with species population traits, such as size,

density and sex structure, or with individual traits such as body mass, length and fitness, can be detected through changes in population demographic rates [3,4].

To capture these interactions, as a part of the current investigation, the population traits of an endangered small mammal, the European ground squirrel (EGS), *Spermophilus citellus*, were modeled as a function of landscape structure. The EGS is a ground-dwelling sciurid, obligatory hibernator endemic to central and southeastern Europe [5]. EGS is a grassland specialist, inhabiting a variety of natural, semi-natural and artificial open grassland habitats across its range [6]. Its numbers are in continuous decline, especially in the southern, northern and northwestern parts of

the species' range due to adverse changes in land use practices [7]. A 30% overall population decline has been estimated over the last decade, due to which it is listed on the IUCN Red List as Vulnerable [5]. Most populations of the species in Serbia are situated in Vojvodina, the northernmost region of Serbia [8,9]. Due to land conversion and infrastructural development, these populations are fragmented and their habitats are surrounded by arable land.

To mitigate these negative effects, in 2010 the Institute for Nature Conservation of Vojvodina Province promoted the Regional Eco Network of Habitats [10], comprised of protected areas, eco network elements, corridors and their surroundings. As these elements and their surrounding areas differ in protection status, as well as in temporal, spatial and microclimatic characteristics, revision or evaluation of their individual contributions to specific species protection efforts is required. In order to further support regional biodiversity, a reassessment of the conservation area networks and a better understanding of the magnitude of their dynamics are especially important since empirical evidence indicates that environmental changes have the potential to alter individual traits and population dynamics, as well as increase the vulnerability of many species [11-14]. Most of extant studies in this field have focused on the species inhabiting polar or tropical areas, as well as high altitudes. In this work, the impact of a changing environment on a temperate small mammal species was investigated.

To better understand the interaction between the EGS and the environmental conditions characterizing its habitat, the species' colonies were modeled both at the individual and population levels within the predefined landscape structure. This landscape structure is situated in an agricultural area inside a local ecological corridor in Central Banat (Serbia), recognized and labeled by the Institute for Nature Conservation of Vojvodina Province. In order to relate the EGS population dynamics to its environment, population-level generalized linear models (GLMs) as well as individual-level conditional mixed-effects model (GLMMs) were developed. Quantifying this relationship should contribute to a better understanding of the potential effects of changing environmental conditions on further local population changes.

## MATERIALS AND METHODS

### Study area

The area covered by the present study included 20 EGS colonies found within the mosaic landscape of semi-natural and natural open grassland areas in Central Banat, and span across Bočar, Novo Miloševo (NM), Novi Bečej (SK), Kumane, Melenci and Elemir (Supplementary Fig. S1, Supplementary Table S1). The local corridor comprises a mosaic of steppe grasslands, saline soils/depressions and salt steppe ecosystems [2]. This is a highly important conservation area designated for providing protection to certain groups of species, plant communities and host sites recognized as protected areas, Important Bird Areas (IBA) [15], Important Plant Areas (IPA) [16], Emerald [17] and Ramsar [18] sites [10].

### Population data acquisition

To capture the demographic traits of the 20 studied EGS colonies in Central Banat, during the period 2013-2015, the animals were counted annually within 0.25-ha plots [19]. Having an exact area to count the animals in allowed for a high accuracy estimation of the total number of individuals in the habitat patch. As part of this field survey, body weight and length were measured and age and sex determined. To determine the age of individuals, we used morphological characters such as body size and mass as well as molar and premolar wear [20]. The animals from the fourth age class were notably heavier and larger-bodied, with distinguishable marks on their teeth. The body condition coefficient (BCC) was calculated as a regression function of body mass and length [21]. All individuals identified as residing within a particular plot were captured and were kept in cages until the end of the study day, and were subsequently released in the area where they were caught.

To calculate population sizes, the area each colony occupied inside the available fragment was first estimated by mapping of the peripheral burrows at each locality using GPS Garmin eTrex Venture. Based on this information, we drew polygons of the occupied area in QGIS (3.2 Bonn). The number of captured animals was extrapolated to the total area occupied

by one colony and the number of individuals at each locality was estimated.

### Spatial data

For spatial analysis, a buffer zone with a 1-km radius was applied, outlining each mapped occupied area that represents the maximal dispersal capacity of the species (Supplementary Fig. S1) [22]. Within the delineated area, the average seasonal normalized difference vegetation index (NDVI) and the automated water extraction index (AWEI) sourced from the time series of Landsat 8 satellite images were calculated. To further develop the landscape structure within the specified radius, crop maps were used for each consecutive season from 2013 to 2015. The crop maps were developed using a supervised random forest classification algorithm and data obtained from the time series of satellite images generated by the BioSense Institute [23]. Based on habitat use, management and type, the habitat suitability index (HSI) was developed for each of the 20 localities within the study area (further details on this approach are given in Table S1). For each patch included in the analyses, the patch carrying capacity (PCC) was calculated, designating the relationship between habitat suitability, area and average density (i.e.,  $PCC = \text{patch area} \times \text{patch suitability} \times \text{average density}$  in the patch type) [24].

### Model calibration and sensitivity analysis

To analyze the relative relationship between landscape structure (environmental conditions within the buffer zone of 1-km radius) and demographic changes (population size and body condition of individuals), and to account for the year effect, a number of linear regression and linear mixed effect analyses were conducted. Based on the approach presented in [25], population-level GLMs and individual-level conditional mixed effect GLMMs were developed in R package lme4 [26], R version 3.3.2 to study species demographic traits.

To model the relationship between population size and seasonal changes in landscape structure, a GLM was developed, whereas the GLMM captured the relationship between body condition of individuals and seasonal changes in landscape structure. For this pur-

pose, three components of landscape structure were defined: composition, capacity and productivity; and each dependent variable of each category was incorporated into the population GLM and the individual GLMM. The defined landscape categories are presented in Supplementary Fig. S2, whereby Category 1 denotes the composition and accounts for crop percentage (% crop), grassland percentage (% grassland) and the average area covered by water (AWEI); Category 2 pertains to PCC (suitability $\times$ area $\times$ density), and Category 3 relates to system productivity (NDVI). The significance of each dependent variable for predicting the variability in population size and body condition was investigated.

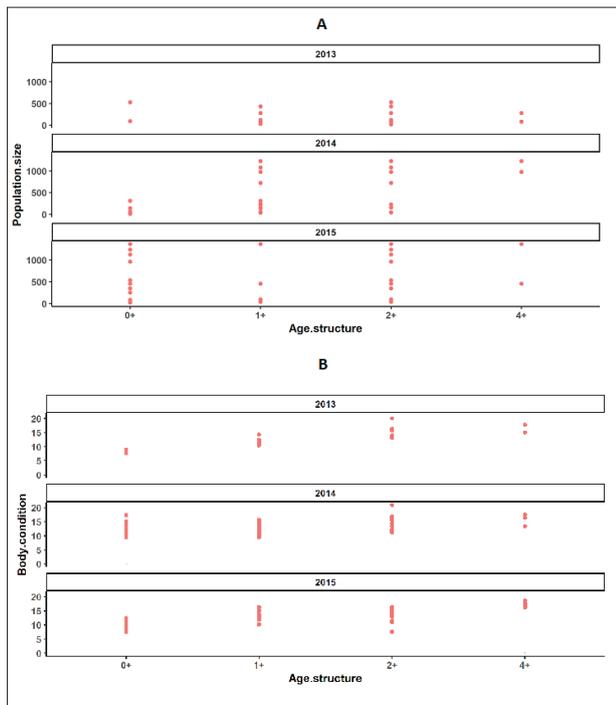
The model pertaining to each category that yielded the best fit to the data was compared to the global model (capturing all variables) as well as the null model. For assessing the body condition changes in the GLMM, crop percentage, grassland percentage, NDVI, AWEI and PCC were included as fixed effects and body condition as the criterion variable (Table 1). Age structure of captured individuals, and locality and year were included in the GLMM as random effects. Local population size served as a criterion variable in the GLM (Table 1). The model that yielded the lowest Akaike information criterion corrected for small sample size score (AICc) was chosen as the best candidate and also the variations within the population or individual models were compared based on the maximum reliability test [27].

## RESULTS

### Population size and body condition

During the 2013-2015 study period, habitat patches in Central Banat on which European ground squirrel colonies were identified, differed in composition, capacity (PCC) and productivity, which affected the population size and body condition of the individuals (Fig. 1).

Global GLM, which includes all three components (Category 1, 2 and 3) of landscape structure, provided the best fit to the data pertaining to population growth (Table 1). Within the population models, the next most supported was the PCC (Category 2) model, followed by the landscape composition model (Category 1), null



**Fig. 1.** **A** – Abundance of different age classes in European ground squirrel populations in central Banat; **B** – Body conditions of individuals of different age classes in populations in central Banat.

model and system productivity (Category 3) (Table 1). On the other hand, based on the findings for the body-condition GLMMs, the system productivity model (Category 3) emerged as the most optimal candidate, followed by the global model (Category 1, 2 and 3), which was found to be more significant than the null model and the PCC model (Category 2; Table 1).

### Environmental variables

For each colony in the study region, the percentage ratio of grasslands, crops and the average area covered by water during the active season of the EGS were identified as the population size-limiting factors. However, PCC, which depends on patch suitability and the area that the patch population occupies, was also significant. A small positive effect on population size was noted for the increase in grassland percentage and crop percentage, while the increase in PCC had a significant positive impact on population growth. Finally, an increase in the average area covered by water exerted a negative impact on population growth.

For capturing individual differences in body condition, system productivity was the most significant variable as it directly related to the average available food quantity during the active season of the species. As expected, within the studied colonies, an increase in productivity had a positive impact on the body condition of the animals in different age classes. Coefficients of the selected variables for the best fitting models on population and individual levels are presented in Table 2.

### DISCUSSION

The findings yielded by the models developed as a part of the present study indicate that land composition and PCC are the main determinants of the population size of endangered EGS. On the other hand, system productivity is positively related to an individual's body condition after monitoring for variations across sampling years and age classes. These results suggest that in agricultural landscape, human-induced conditions (e.g., crop rotation, water impact (irrigation), drainage and general water management or pastoral grazing management), are the main drivers of population-level differences in size, while also indirectly affecting population structure. On the other hand, as environmental abiotic factors (e.g., dry season precipitation or temperature) affect system productivity, they drive individual-level differences in body condition and indirectly influence population dynamic.

Species' presence in a particular area is likely to be impacted by shifting resource availability due to changes in land use and habitat management [28,29]. Spatial and temporal structures, the amount, suitability and connectivity of habitat define the habitat use [30] and species' responses to changes in spatial gradients reflect local population dynamics and distribution, as well as species' life history traits [31]. In this work, compositional and structural features at the scale of a local patch and its surroundings were integrated to demonstrate the responses of the EGS in terms of habitat occupancy in a lowland area of Vojvodina. The results indicate that habitat occupancy is related to the observed variance in structural heterogeneity, which is in agreement with the findings given at the local [32] and landscape scales [33]. The present study findings further revealed that not only was the pres-

**Table 1.** Results of the multi-model selection based on AICc and log likelihood (LL) values for three categories of models within the population GLM and individual GLMMs.

	<b>K</b>	<b>AICc</b>	<b>ΔAIC</b>	<b>AIC wt</b>	<b>LL</b>
<b>Population level (unconditional) GLM</b>					
<i>Category 1: landscape composition</i>					
AWEI + % crop + % grassland	5	135.18	0.00	0.98	-62.42
AWEI	3	143.64	8.46	0.01	-68.75
AWEI + % grassland	4	145.34	10.16	0.01	-68.56
% crop + % grassland	4	149.15	13.97	0.00	-70.46
% crop	3	150.17	14.99	0.00	-72.02
% grassland	3	150.29	15.11	0.00	-72.08
<i>Category 2: Patch carrying capacity (PCC)</i>					
PCC = Area x patch suitability	2	125.32	NA	NA	NA
<i>Category 3: System productivity</i>					
NDVI	2	148.94	NA	NA	NA
<b>Model ranking (best fitting in each category)</b>					
Global (Composition + Capacity + Productivity)	7	107.83	0.00	1	-46.60
Category 1: AWEI + %crop + %grassland	3	125.45	17.62	0	-59.66
Category 2: PCC		135.18	27.35	0	-62.42
Null model (intercept)	2	148.45	40.61	0	-72.19
Category 3: NDVI	3	149.07	41.24	0	-71.47
<b>Individual level (conditional) GLMM</b>					
<i>Category 1: landscape composition</i>					
AWEI + % crop + % grassland	7	-426.97	0.00	0.67	220.80
% crop + % grassland	6	-425.90	1.07	0.24	219.19
AWEI	5	-425.24	1.73	0.28	217.79
AWEI + % grassland	6	-425.13	1.84	0.16	218.80
% crop	5	-420.84	6.13	0.03	215.59
% grassland	5	-418.53	8.44	0.01	214.43
<i>Category 2: Patch carrying capacity (PCC)</i>					
PCC = Area x patch suitability	5	-419.50	NA	NA	214.74
<i>Category 3: System productivity</i>					
NDVI	5	-430.90	NA	NA	220.45
<b>Model ranking (best fitting in each category)</b>					
Category 3: NDVI	5	-430.57	0.00	0.74	220.45
Global (Composition + Capacity + Productivity)	9	-427.12	3.46	0.13	223.08
Category 1: AWEI + % crop + % grassland	7	-426.97	3.6	0.12	220.8
Null model (age + locality: year)	4	-420.55	10.02	0	214.39
Category 2: PCC	5	-419.15	11.42	0	214.74

\*K – degree of freedom; ΔAIC – delta; AIC – score; AIC wt – weighted AIC score

ence of certain habitat types critical for determining habitat occupancy, but so were the intermediate compositional heterogeneity and the amount of resources. Other authors have reported that habitat suitability and connectivity increase the probability of successful reproduction and facilitate movement among distinct habitat patches [34,35], which is especially important in highly fragmented agricultural landscapes.

Landscape or habitat heterogeneity and spatial scale have been shown to impact site occupancy for various species or groups of species [36] and were found to be more influential on the persistence of specialist species relative to generalists [37]. Findings yielded by ecological studies in protected lowland areas of Vojvodina (e.g. the Special Nature Reserves Slano Kopovo and Okanj Bara, and Nature Park Rusanda)

**Table 2.** Model coefficients of selected variables for population and individual level top models for European ground squirrel habitat use within the Central Banat landscape structure.

	Estimate	Std. Error	Adjusted SE	Z value	p (> z )	
Population level GLM						
(Intercept)	-0.3879697	0.8797184	0.8857399	0.438	0.66137	
PCC	0.0050159	0.0009237	0.00093	5.393	1.00E-07	***
% grassland	0.0043888	0.0020513	0.0020654	2.125	0.03359	*
% crop	1.5547895	0.347607	0.3499865	4.442	8.90E-06	***
NDVI	0.4005007	1.2351119	1.2435669	0.322	0.74741	
AWEI	-0.5163714	0.1855644	0.1868347	2.764	0.00571	**
Individual level GLMM						
(Intercept)	-0.8615	0.2519	0.2534	3.399	0.000675	***
NDVI	1.1398	0.3082	0.3103	3.673	0.000239	***

\*  $p$  significant level at  $p < * - 0.05$ ,  $p < ** - 0.001$ ,  $p < *** - 0$

[38-40] highlight the importance of spatial structure within agricultural settings where the continuity of open grassland is interrupted. Every component of landscape structure examined in this study should thus be considered as an additional environmental factor limiting population size. The analyses reported in this work indicate that patch carrying capacity, which entails its management practice, and habitat suitability also influence population size. The population size varies in relation to patch capacity because larger and more heterogeneous sites provide a better chance for population survival [41]. On the other hand, ground-dwelling squirrels act as ecosystem engineers contributing to within-patch heterogeneity by moving soil, modifying local plant distributions and creating annual-dominated assemblages [42-44]. Thus, the EGS plays a significant role in maintaining the diversity and functionality of steppe and open grassland ecosystems, which are amongst the most vulnerable habitats in Europe.

The EGS is predominantly herbivorous, feeding mainly on typical grassland species such as grasses and legumes [45]. A significant difference in grassland vegetation between dry and wet years and its influence on ground squirrel diet have been demonstrated [46]. In this particular study, the proportion of dicots in the field during a wetter year was greater and the animals favored this group of species to monocots. Such climatic effects on food supply are particularly important in spring, just after emergence from hibernation and during the reproductive period. Moreover, results obtained in a study focusing on two sites in Vojvodina showed that the abundance of most grassland plant

species will decline due to the predicted climate change, whereby plants with the highest moisture index will be the most endangered [47]. Therefore, climate change has the potential to alter not only species composition but also system productivity.

High temperatures, but not extreme precipitation events, can be well tolerated by the EGS [48,49]. Based on climate prediction models, in the future, the area covered by the present study will be affected by drought and extreme weather conditions [50], thus increasing the possibility of catastrophic events that could, along with altered ecosystem productivity, affect the species' population survival. Jointly, these findings and forecasts highlight the importance of including reconnection of more suitable habitat environments in future grassland conservation efforts, which should also promote landscape management practices that enable animals to move across landscape unhindered.

The results obtained in the present study demonstrate the importance of evaluating the relationship between species demographic traits and temporal changes in environmental conditions for scaling population changes. To ensure population persistence, there is a need to promote both local remnant open grassland and surrounding area conservation. Such comprehensive strategies would enable individuals to use a wider array of microclimate conditions [51]. The body condition and behavioral traits are closely related to the foraging of small mammal species. As increases in temperatures are forecast for the future, which may lead to uncertain food supply, the flexibility of species traits and their capacity to adapt to

predicted and enhancing weather/climate changes and consequences related to resource availability remain to be elucidated [7].

In terms of land ownership, the grassland fragments containing the colonies are public agricultural land and, therefore, the main task in their conservation is to prevent land use type change of these areas (urbanization, building or industrialization, forestation or infrastructure development), or management change to other agricultural purposes (plowing or turning into vineyards or orchards). Besides maintaining an appropriate land use type, our results show that grassland fragments must cover an area large enough so that its carrying capacity can support viable EGS populations. The habitat quality of the specific grassland patch depends on grazing/mowing intensity, which should be determined for every patch based on vegetation characteristics and productivity. Recent studies [52] have shown that the survival of EGS populations depends to great extent on the landscape characteristics of the area surrounding the colony patches and on enabling (or not) intercolony communication. The appropriate levels of heterogeneity and complexity of the agricultural area surrounding the colonies can be achieved by applying specific measures, such as maintaining field margins, fallow land, etc. These findings point to the need for combining local conservation practices with landscape-level management.

Only a small number of EGS colonies in Vojvodina are located inside protected areas [52] where activities (such as agriculture, tourism, etc.) are monitored and directed by the appropriate authority, the Institute for Nature Conservation of Vojvodina Province. On the other hand, most colonies are a part of the regional eco network, whose legal framework should protect these localities from land management change. Serbia, as non-European Union member state, is in the prepreparation phase of enforcing agri-environment schemes (AES) that will function under the future Common Agricultural Policy. Nevertheless, the proposed local measures promote traditional agricultural practices and local farmers' knowledge and are, thus in concordance with international legislative.

In summary, the well-documented decline of the EGS population should not be generalized independently of ongoing changes in weather conditions and

decadal climate prediction. Including demographic traits and behavioral flexibility in analytical models would significantly improve extinction risk assessment for the EGS. Even though the trend that has been observed in phenotype changes of mammals as a response to climate change was mostly attributed to their phenotype plasticity, this was not confirmed for ground squirrel species [53]. Therefore, conservation planning and management actions in agricultural landscape should support ecosystem stability and include spatial adaptation strategies to respond effectively to predicted climate variability.

**Funding:** This work was financially supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia, Grant III 43002, "Biosensing Technologies and Global System for Long-Term Research and Integrated Management of Ecosystems", The Rufford Foundation Grant, "Building a better future for European ground squirrel in Serbia", and the Provincial Secretariat for Science and Technological Development, Grant No. 142-451-2591/2017, "Evaluation of ecological network for more efficient natural protection in AP Vojvodina".

**Acknowledgments:** The authors are grateful to Dr. Branko Brkljač and Predrag Lugonja who kindly prepared and provided us with data on crop classification within the study area for the consecutive sampling years.

**Author contributions:** TN, DR, MA, MM and LV participated in collecting data on European ground squirrel populations in the field. TN prepared the database on the European ground squirrel. TN performed the modeling and prepared the results. The interpretation of the results was done and approved by all authors. TN, MA and DČ wrote the manuscript. DČ and DM supervised the activities and reviewed several drafts of the manuscript.

**Conflict of interest disclosure:** The authors declare no conflict of interest.

## REFERENCES

1. Wolff S, Schrammeijer EA, Schulp CJ, Verburg PH. Meeting global land restoration and protection targets: What would the world look like in 2050? *Glob Environ Change*. 2018;52:259-72.
2. Puzović S, Panjković B, Tucakov M, Stojnić N, Sabadoš K, Stojanović T, Vig L, Marić B, Tešić O, Kiš A, Galamboš L, Pil N, Kicošev V, Stojšić V, Timotić D, Perić R, Bošnjak T, Delić J, Dobretić V, Stanišić J. *Upravljanje prirodnim baštinom u Vojvodini*. Novi Sad: Sekretarijat za urbanizam, graditeljstvo i zaštitu životne sredine, Pokrajinski zavod za zaštitu prirode. 2015. 156 p. Serbian.
3. Benton TG, Plaistow SJ, Coulson TN. Complex population dynamics and complex causation: devils, details and demography. *Proc Biol Sci*. 2006;273(1591):1173-81.

4. Brooks ME, Mugabo M, Rodgers GM, Benton TG, Ozgul A. How well can body size represent effects of the environment on demographic rates? Disentangling correlated explanatory variables. *J Anim Ecol.* 2016;85(2):318-28.
5. Coroiu C, Kryštufek B, Vohralík V, Zagorodnyuk, I. *Spermophilus citellus*. In: The IUCN Red List of Threatened Species [Internet]. IUCN; 2008 Jun 30. [cited 2019 Feb 10] Available from: <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T20472A9204055.en>
6. Janderková J, Matějů J, Schnitzerová P, Petruš J, Sedláček J, Uhlíková J. Soil characteristics at *Spermophilus citellus* localities in the Czech Republic (Rodentia: Sciuridae). *Lynx.* 2011;42:99-111.
7. Janák M, Marhoul P, Matějů J. Action Plan for the Conservation of the European Ground Squirrel *Spermophilus citellus* in the European Union [Internet]. European Commission; 2013 [cited 2019 Feb 11]. Available from: [https://ec.europa.eu/environment/nature/conservation/species/action\\_plans/pdf/EUSAP\\_EuropeanGround%20Squirrel\\_Final.pdf](https://ec.europa.eu/environment/nature/conservation/species/action_plans/pdf/EUSAP_EuropeanGround%20Squirrel_Final.pdf)
8. Ružić A. Contribution to the knowledge of ecology of the ground squirrel *Citellus citellus* L. *Proc Inst Ecol Biogeogr.* 1950;1:97-140. Serbian.
9. Petrov MB. Mammals of Yugoslavia, insectivores and rodents. Belgrade: Natural history museum of Belgrade. 1992. 186 p.
10. Uredba o ekološkoj mreži. *Offic Gazzete Rep Serb.* 2010;102/2010p. Serbian.
11. Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, Tuljapurkar S, Coulson T. Coupled dynamics of body mass and population growth in response to environmental change. *Nature.* 2010;466(7305):482-7.
12. Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. Ecological responses to recent climate change. *Nature.* 2006;416(6879):389-95.
13. Parmesan C. Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst.* 2006;37:637-69.
14. Toïgo C, Gaillard JM, Van Laere G, Hewison M, Morellet N. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography.* 2006;29(3):301-8.
15. Callaghan D, Heath M, O'Sullivan J, Pritchard D. Important Bird Areas and potential Ramsar Sites in Europe. *Wageningen: BirdLife International;* 2011. 126 p.
16. Anderson S, Darbyshire I, Halski B. Important Plant Areas. In: Willis KJ, Bachman S, editors. RBG Kew, state of the world's plants report-2016. London: Royal Botanical Garden, Kew; 2016. p. 24-7.
17. Sekulić N, Šinžar-Sekulić J, editors. [Emerald Ecological Network in Serbia]. Beograd: Republika Srbija: Ministarstvo životne sredine i prostornog planiranja, Zavod za zaštitu prirode Srbije; 2010. 100 p. Serbian.
18. Ramsar Convention Secretariat. The Ramsar Convention Manual: a guide to the Convention on Wetlands (Ramsar, Iran, 1971). 6<sup>th</sup> ed. Gland, Switzerland: Ramsar Convention Secretariat; 2013. 109 p.
19. Katona K, Váci O, Altbäcker V. Topographic distribution and daily activity of the European ground squirrel population in Bugacpuszta, Hungary. *Acta Theriologica.* 2002;47(1):45-54.
20. Ružić A. Određivanje uzrasnih kategorija u populaciji tekunice *Citellus citellus* L. *Arhiv Biol Nauka.* 1966;18:65-70. Serbian.
21. Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ. Restitution of mass-size residuals: validating body condition indices. *Ecology.* 2005;86(1):155-63.
22. Ramos-Lara N, Koprowski JL, Kryštufek B, Hoffmann IE. *Spermophilus citellus* (Rodentia: Sciuridae). *Mammalian Species.* 2014;46(913):71-87.
23. Crnojević V, Lugonja P, Brkljač BN, Brunet B. Classification of small agricultural fields using combined Landsat-8 and RapidEye imagery: case study of northern Serbia. *J Appl Remote Sens.* 2014;8(1):083512.
24. Verboom J, Pouwels R. Ecological functioning of ecological networks: a species perspective. In: Jongman RHG, Pungetti G, editors. Ecological networks and greenways; concept, design, implementation. Cambridge: Cambridge University Press; 2004. p. 4-72.
25. Merrick MJ, Koprowski JL. Circuit theory to estimate natal dispersal routes and functional landscape connectivity for an endangered small mammal. *Landscape Ecol.* 2017; 32:1163-79.
26. Bates D, Maechler M, Bolker B, Walker S. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.7. *J Stat Softw.* 2014;1(7):1-23.
27. Burnham KP, Anderson DR. Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res.* 2004;33(2):261-304.
28. Fisher JT, Anholt B, Bradbury S, Wheatley M, Volpe JP. Spatial segregation of sympatric marten and fishers: the influence of landscape and species-scapes. *Ecography.* 2013;36(2):240-8.
29. Sozio G, Mortelliti A. Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. *Landscape Ecol.* 2016;31(4):775-89.
30. Hodgson JA, Moilanen A, Wintle BA, Thomas CD. Habitat area, quality and connectivity: striking the balance for efficient conservation. *J Appl Ecol.* 2011;48:148-52.
31. Guo Q, Taper M, Schoenberger M, Brandle J. Spatial-temporal population dynamics across species range: from centre to margin. *Oikos.* 2005;108(1):47-57.
32. Stirnemann I, Mortelliti A, Gibbons P, Lindenmayer DB. Correction: Fine-Scale Habitat Heterogeneity Influences Occupancy in Terrestrial Mammals in a Temperate Region of Australia. *PLoS One.* 2015;10(10):e0140802.
33. Fischer C, Flohre A, Clement LW, Batáry P, Weisser WW, Tscharrntke T, Thies C. Mixed effects of landscape structure and farming practice on bird diversity. *Agr Ecosyst Environ.* 2011;141(1):119-25.
34. Schooley RL, Branch, LC. Habitat quality of source patches and connectivity in fragmented landscapes. *Biodivers Conserv.* 2011;20(8):1611-23.
35. Dickson BG, Roemer GW, McRae BH, Rundall JM. Models of regional habitat quality and connectivity for pumas (*Puma concolor*) in the southwestern United States. *PLoS One.* 2011;8(12):e81898.

36. Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr.* 2004;31(1):79-92.
37. Ye X, Skidmore AK, Wang T. Within-patch habitat quality determines the resilience of specialist species in fragmented landscapes. *Landsc Ecol.* 2013;28(1):135-47.
38. Pavkov G, editor. Specijalni rezervat prirode "Slano Kopovo" – predlog za stavljanje pod zaštitu kao prirodnog dobra od izuzetnog značaja. 1999. Novi Sad: Zavod za zaštitu prirode Srbije, Beograd, Odeljenje Novi Sad. 80 p. Serbian.
39. Panjković B, Kovačev N, editors. Specijalni rezervat prirode "Okanj bara" – predlog za stavljanje pod zaštitu kao zaštićenog područja I kategorije. Novi Sad: Pokrajinski Zavod za zaštitu prirode. 2011. 373p. Serbian.
40. Kicošev V, Tucakov M, Kovačev M. Park prirode "Rusanda" - predlog za stavljanje pod zaštitu kao zaštićenog područja II kategorije. Novi Sad: Pokrajinski Zavod za zaštitu prirode. 2011. 254p. Serbian.
41. Méréš TO, Bocz R, Polyák L, Horváth G, Lengyel S. Local habitat management and landscape-scale restoration influence small-mammal communities in grasslands. *Anim Conserv.* 2015;18(5):442-50.
42. Seabloom EW, Björnstad ON, Bolker BM, Reichman OJ. Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecol Monogr.* 2005;75(2):199-214.
43. Barker OE, Derocher AE. Habitat selection by arctic ground squirrels (*Spermophilus parryii*). *J Mammal.* 2010;91(5):1251-60.
44. Bylo LN, Koper N, Molloy KA. Grazing intensity influences ground squirrel and American badger habitat use in mixed-grass prairies. *Rangel Ecol Manag.* 2014;67(3):247-54.
45. Györi-Koós B, Katona K, Altbäcker V. Diet composition of European Ground Squirrel in grazed or mowed grasslands. *Hung Small Game Bull.* 2013;11:215-25. Hungarian.
46. Györi-Koós B. Diet preference of the European ground squirrel [*Spermophilus citellus* (Linnaeus, 1766)] in Hungarian natural and seminatural grassland habitats investigation by floristic composition and microhistological faeces analysis [dissertation], [Sopron]: Institute of Wildlife Management and Vertebral Zoology, Faculty of Forestry, University of West Hungary; 2015. 16 p.
47. Čavlović D, Beloica J, Obratov-Petković D, Đurđević V, Košanin O. Simulation of long-term changes in environmental factors and grassland composition in three protected areas of Serbia. *Tuexenia.* 2017;37:431-46.
48. Vácz O. The effects of abiotic environmental factors on spatio-temporal activity pattern of the European ground squirrel (*Spermophilus citellus*) [dissertation]. [Budapest]: Eötvös Loránd University. 2005. 131 p. Hungarian.
49. Vácz O, Koós B, Altbäcker V. Modified ambient temperature perception affects daily activity patterns in the European ground squirrel (*Spermophilus citellus*). *J Mammal.* 2006;87(1):54-9.
50. Vuković A, Vujadinović M, Rendulić S, Djurdjević V, Ruml M, Babić V, Popović, D. Global warming impact on climate change in Serbia for the period 1961-2100. *Thermal Science.* 2018;22(6):2267-80.
51. McCain CM, King SR. Body size and activity times mediate mammalian responses to climate change. *Glob Chang Biol.* 2014;20(6):1760-9.
52. Nikolić T, Radišić D, Ćosić N, Díaz-Delgado R, Milić D, Vujić A, Ćirović D. Landscape heterogeneity effects on keystone rodent species: agro-ecological zoning for conservation of open grasslands. *Biodivers Conserv.* 2019;28(12):3139-58.
53. Boutin, S, Lane, JE. Climate change and mammals: evolutionary versus plastic responses. *Evol Appl.* 2014;7(1):29-41.

### Supplementary Material

The Supplementary Material is available at: [http://serbiosoc.org.rs/NewUploads/Uploads/Nikolic%20et%20al\\_4485\\_Supplementary%20Information.pdf](http://serbiosoc.org.rs/NewUploads/Uploads/Nikolic%20et%20al_4485_Supplementary%20Information.pdf)