Effects of landscape structure and patch characteristics on the density of central populations of the eastern green lizard *Lacerta viridis*

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April 27, 2023

Abstract

A better understanding of the impact of habitat loss on population density can be achieved by evaluating effects of both, parameters within remnant habitat patches and parameters of the landscape surrounding those patches. The integration of predictors at the patch and landscape level is scarce in animal ecological studies, especially for reptiles. In this study, a patchlandscape approach was applied to evaluate the combined effects of within patch habitat quality, patch geometry and landscape configuration and composition on the density of remnant populations of the eastern green lizard, Lacerta viridis, in a highly modified landscape in Bulgaria. Landscape composition variables (proportion of different land covers) were measured at different spatial scales surrounding patches. Single scale models were built to evaluate combined effects of all predictors on density, when including all landscape composition variables at a specific spatial scale. Multiscale models were applied to analyze combined effects when including landscape composition variables at the scale of their strongest effect (scale of effect, SoE). Results showed that the SoE of proportion of cropland and urban areas was small (50 m), while for proportion of habitat was large (1.5 Km). The overall effect of habitat loss was better explained by the multiscale model. Population density increased with patch area and decreased with patch shape irregularity and with the proportion of three land cover types surrounding patches -cropland, urban areas and habitat. Combining patch and landscape parameters is important to identify ecological processes that occur simultaneously at different spatial levels and landscape scales, and which would imply the application of multiscale approaches for the protection of wild animal populations. Results are contrasted with what is known about occupancy patterns of the species in the same region, and approaches to integrate both, occupancy and density, in the field design of animal ecological studies are suggested.

Introduction

Reduced population density and abundance are among the main negative effects of habitat loss on wild animal populations, and can lead to the extirpation of local populations and changes in the distribution of species (Bender, Contreras, & Fahrig, 1998; Tischendorf et al., 2005). Most knowledge about these negative effects and the ecological processes that they trigger resulted from research on birds and mammals (eg. Bender, Contreras & Fahrig, 1998; Thornton, Branch & Sunquist, 2011). However, comparatively lower vagility and higher sensitivity to environmental changes make reptiles more sensitive to landscape modification (Doherty et al., 2020).

The parameters whose effects are most tested on populations density and abundance of reptile species are patch area, isolation and landscape type. Effects of patch area and isolation are highly species- and landscape-dependent. In the case of patch area, several multi-species studies found positive effects on the abundance of some species and no effect on others (Rizkalla & Swihart, 2006; Carvajal-Cogollo & Urbina-Cardona, 2008; Shirk et al., 2014; Delaney et al., 2021), and some authors have reported negative effects (Lion et al., 2016). Such contrasting effects fit meta-analysis findings of Bender et al. (1998) about patch size effects on density

and abundance being negative for edge species, positive for interior species, and negligible for species using both patch edge and interior. Effects of isolation have also been found to be either negative (Carvalho Jr et al., 2008; Williams, Driscoll & Bull, 2012; Sato et al., 2014), positive (Lion et al., 2016) or non-existent (Delaney et al., 2021; Lizana-Ciudad et al., 2021) on population abundance of reptile species. It is known, that isolation effects are dependent from species sensitivity to matrix, which determines immigration and emigration rates affecting density and abundance (Tischendorf et al., 2005).

At the landscape level, most studies testing effects of habitat loss on population density and abundance of reptile species apply categorical approaches comparing between different types of landscapes. Thus, for several species fragmented landscapes have shown lower abundance compared to non-fragmented ones (Leavitt & Fitzgerald, 2013; Walkup, Leavitt, & Fitzgerald, 2017; de Andrade, Dellefrate Franzini, & Mesquita, 2019), while for others, specific landscape management practices have been linked with negative effects on abundance (Biaggini & Corti, 2015; Kaunert & Mcbrayer, 2015; Barrows & Heacox, 2021).

Although approaches applied in those studies have allowed to understand the effects of habitat loss on reptiles, two main knowledge gaps remain: First, how do continuous parameters of landscape configuration and composition around remnant habitat patches affect population density and abundance of reptiles? (but see Rizkalla & Swihart, 2006); and second, how do landscape, patch and within-patch parameters affect simultaneously population density and abundance? Only few studies have integrated these different spatial levels (Barrows and Heacox 2021; Sato et al. 2014; Carvalho Jr. et al. 2008). Closing these gaps would allow not only to identify relative effects at different spatial levels (landscape, patch and within-patch), but also those of landscape configuration and composition separately, and the spatial scales around focal habitat patches at which their effects are strongest (eg. Lion et al. 2016), sensu Martin & Fahrig (2012). Moreover, given the effects of isolation and area can depend on the amount of habitat left in the landscape surrounding patches (Andrén, 1994; Fahrig, 2013), integrating spatial levels can give a better understanding of ecological processes.

As for other taxa, despite density and abundance being important population traits to identify possible decline preceding population extirpation, effects of habitat loss have been much more investigated through population persistence indicators like occupancy (eg. van Heezik & Ludwig 2011; Biaggini & Corti 2021; Paterson et al., 2021). Occupancy can be a much more cost-effective parameter in terms of data collection, analysis and interpretation of species distribution (Sewell et al., 2012; Casner et al., 2014). However, factors ruling extinction-colonization processes can differ from those defining the demographic processes that underline abundance (He & Gaston, 2000; Orrock et al., 2000). Such differences have already been reported in the reptile literature (Driscoll, Whitehead, & Lazzari, 2012; Hubbard, Chalfoun, & Gerow, 2016; Lizana-Ciudad et al., 2021), and in cases in which the same environmental factors affect both occupancy and abundance, in opposite directions (Rizkalla & Swihart, 2006; Dibner, Doak, & Murphy, 2017). Some authors argue that these differences can be present due to factors influencing occupancy acting at larger scales compared to those affecting abundance and density (He & Gaston, 2000; Wilson et al., 2016).

In this study, I investigated effects of habitat loss on the density of populations of the eastern green lizard *Lacerta viridis* (Figure 1) inhabiting a modified landscape in central Bulgaria. I applied a patch-landscape approach integrating landscape parameters across spatial scales with patch and within-patch parameters. Effects of habitat loss on occupancy patterns of *L. viridis* have recently been investigated in the same study system (Prieto-Ramirez et al 2020), with occupancy being found to be mostly defined by landscape configuration, with the strongest effect of the overall habitat loss process occurring at the 750 m scale around patches. No negative effect of isolation was found and at the patch level occupancy depended on patches with both, long perimeter and enough core area in the interior, indicating that the species uses both, border and interior of patches. Within-patch habitat quality was not determinant for occupancy but had positive effect. Based on predictions from literature and findings on the species' occupancy patterns I hypothesize: 1) positive effect of within-patch habitat quality on population density, 2) no effect of patch area, 3) no effect of isolation, and 4) an effect at small spatial scales of individual landscape composition parameters, as well as of the overall habitat loss process.

Methods

Study area

The study area was located in the Thracian Plain of Bulgaria, in the surroundings of the city of Plovdiv (Figure 2). This region, which corresponds to part of the current and historical core of the distribution range of the species (Marzahn et al., 2016), is an alluvial plain dominated by the banks of the Maritsa River and its tributary rivers. Here, L. *viridis* inhabits diverse natural and semi-natural habitats, including river banks, shrublands and mesophilic mixed forest (Mollov, 2011). Urban and agricultural expansion in the region have reduced the habitat of the species (Kambourova-Ivanova et al., 2012; Mollov & Georgiev, 2015), which is now composed mostly by habitat patches of variable size separated by a matrix of unsuitable land covers.

Survey design

The present study was carried out in the context of a broader study that included collected and analyzed data on occupancy (Prieto-Ramírez et al.2020). Therefore, the applied survey design corresponds to a mixed designed suitable for both occupancy and density. Data collection was carried out from beginning of April to late May in 2014. Patches to be visited were selected and identified on satellite imagery available in Google earth, based on information regarding species requirements in the region and available information on the species distribution. All selected patches are separated from each other by agricultural landscape, urban areas and/or highways. 42 habitat patches were visited in 2014 (Prieto-Ramirez et al., 2018), from which 24 patches were occupied. Given differences in the factors affecting occupancy and abundance, only data from the 24 occupied patches was used for the present study (Fletcher, MacKenzie, & Villouta, 2005; Dibner, Doak, & Murphy, 2017).

Surveys were designed following the protocol proposed by Mackenzie & Royle, 2005 for occupancy, prescribing a specific number of visits depending on the probability of detection of the species. Based on estimates of detection probability for similar species (Janssen & Zuiderwijk, 2006; Sewell et al., 2012), the number of surveys per patch was set to two, one in the morning (9:00–12:00 a.m.) and one in the afternoon (14:00–19:00 p.m.) of the same day or one day later, in accordance with the species' daily activity pattern (Korsós, 1983). Active surveys lasted one hour each, walking along predetermined line transects. With a standard walking speed of 20 m/min, which is slow enough to detect lizards, a one-hour survey corresponds to a total length of 1200m, that were subsequently divided into transects. Because most patches had a heterogenous composition, which might imply non-homogeneous distribution of animals, the number and length of transects was adjusted to represent the different habitat types and the area covered by each into each patch. Nevertheless, all the transects in a patch always summed up 1200 m to assure one hour visit. Satellite imagery was used to define the relative coverage of each habitat type within each patch. Transect lengths varied between 50–400 m, and were randomly located into each within patch habitat type, at least 100 m apart from each other. The total length of each transect was placed in only one habitat type. The number of transects surveyed per patch ranged from three to 12. During transect walking, a width of 2.5 m was scanned at each side of the transect to visually search for L. viridis. Every time a lizard was detected, the perpendicular distance from the transect to the detection point was measured and recorded.

Calculation of patch variables and landscape structure

A patch-landscape approach was applied to analyze the influence landscape structure and patch characteristics on density. Predictors include variables representative of landscape configuration, landscape composition, patch geometry and within patch habitat quality. Landscape configuration is represented by two measures of isolation, the edge-to-edge Euclidean distance to the nearest patch (np_dist) and proximity index (prox). The proximity index (Gustafson & Parker, 1994) is a scale dependent measure of isolation and is calculated as the sum of the ratios patch area /distance to the focal patch for all patches that fall, at least partially, into the buffer of a given distance around the focal patch. Landscape composition variables included the proportion of habitat, cropland and urabn areas surrounding each patch. These variables were calculated using available land cover maps of the region (Prieto-Ramírez et al. 2020), and were measured at various buffer-distances (hereafter, "scales") around each patch. Scales were selected based on reported dispersal distances for *L*. *viridis* (Saint-Girons & Bradshaw, 1989; Mangiacotti et al., 2013; Grimm et al., 2014), and include 50m, 150m, 250m, 500m, 750m, 1km, 1.5km, 2km, 2.5km and 3km.

Patch geometry variables included area, perimeter, perimeter to area ratio (Per_area) and shape index (Shape_index). Within patch habitat quality was defined based on important parameters found for this species, and included vegetation structure and radiation (Böker, 1990; Waitzmann & Sandmaier, 1990; Moser, 1998; Prieto-Ramirez et al., 2018). Vegetation structure was calculated based on available information at the microhabitat scale collected at several 25m2 around several points along transects, as described in Prieto-Ramírez et al. (2020). Radiation was calculated from the digital elevation model (DEM), available from the U.S Geological Survey, with the 'Potential incoming solar radiation' module of SAGA (Conrad et al., 2015). Precise description of the calculation of radiation can be found in Prieto-Ramírez et al., 2020. All other calculation procedures were carried out with ArcMap version 10.3.1 (ESRI, 2018), except for shape_index and prox which were calculated with FRAGSTATS version 4 (McGarigal, Cushman, & Ene, 2012).

Density estimation

As a fixed effort design was applied in the survey, the proportion of area covered by transects was nonhomogeneous across patches. Therefore, estimation was restricted to relative density (density only in the recovered area) instead of abundance. Estimation was using the Distance program (Cassey, 1999; Thomas et al., 2010). First, fitting a detection probability function, and then applying this function to calculate density in each patch.

Because not all patches had enough data to fit a separate detection function per patch, global detection probability estimation using all data was applied, and then, a stratified density estimation was performed. Two types of models were fitted to find the best detection probability model: conventional distance sampling (CDS) model without covariates influencing detection, and multivariate conventional distance sampling (MCDS) with vegetation structure as a covariate determining detection. For both models, all combinations resulting from three functions (uniform key, half-normal key, hazard rate) and three adjusted terms (cosine, Hermit polynomial and simple polynomial) were tested. Based on Akaike Information Criterion (AIC), the coefficient of variation (%CV), and the Kolmogorov-Smirnov test (K-S test) of goodness of fit (AIC = 1167.2, %CV = 4.02, K-S test: estimate = 0.1199, p = 0.092), the best model for detection probability was a CDS with uniform key function, hermit polynomial adjusted term and encounter rate variance estimated empirically.

To estimate density, data from temporal replicates were pooled together in each transect, only data overlapping within a 5m radius was discarded as it might be the same individual. Detection probability function was applied by adding the estimated global detection probability and standard error as global multipliers. Settings for detection were specified as uniform key function with no adjusted terms for detection not to be computed again. To estimate relative density, area was set to zero and encounter rate settings were defined assuming a poisson distribution with overdisperssion factor set to zero, as applied in other studies on lizard's relative density (de Andrade, Dellefrate Franzini, & Mesquita, 2019).

Statistical analysis

To find the relevant scales at which density is explained I tested whether density is explained at single scale(s) or simultaneously at multiple scales. Single-scale models included all composition variables calculated at the same scale, plus configuration, patch geometry and within patch variables. Multi-scale models included each composition variable at its scale of effect (SoE), together with all other variables. To identify the scale of effect of each landscape composition variable -proportion of habitat, cropland and urban areas-, univariate models with each of these variables were fitted at each scale. The scale with the highest Nagelkerke \mathbb{R}^2 (NR²) was selected as the SoE. In cases when the highest \mathbb{RN}^2 value was present at several scales, the smallest scale was selected. The same procedure was applied to proximity index (Prox).

Data was analyzed applying generalized linear models (GLM) with Gamma error distribution and "logit" link in the program R. To avoid collinearity among variables to be included in the same model, variables

correlations were tested by means of Spearman rank correlation test for each single-scale and multi-scale dataset. If two variables were correlated (rs > 0.60), several global models were built up, each of them including only one of the correlated variables. Additionally, the variance inflation factor (vif) was calculated for each global model, and variables with vif < 10 were retained.

Global models of each single scale and of the multiscale were tested for spatial autocorrelation of residuals by means of Global Moran's I test. Model selection was performed in two steps: first, based on AICc (DeltaAICc<2), and then based on Nagelkerke R2 and on deviance reduction from the null model obtained through a goodness of fit F-test (hereafter deviance change). Comparisons across single scales, and of these with multiscale models were done based on Nagelkerke R2 and deviance change of the F-Test.

Results

Density estimation of the 24 populations studied ranged between 115.31 and 1953.5 individuals/Km2, with a mean of 536.7 individuals/Km2 (see Appendix 1 for complete data on population's density estimates and their specific location). No spatial autocorrelation for residuals was found in any global model.

Scale of effect

SoE of scale dependent variables is shown in Figure 3. Proportion of habitat had a large SoE, with its effect on density being stronger at 1.5km around patches. On the contrary, the scales of effect of proportion of cropland and proportion of urban areas, and of the scale-dependent isolation measure Proxi were small. The strongest effect of both proportion of cropland and proportion of urban areas were at 50m scale, and for Proxi it was found at the 150m.

Multiscale vs. single scale

Results of the best selected models for multi- and single scales are presented in Table 1. Density was better explained by the multiscale approach, including landscape composition variables at their SoE's (Nagelkerke R2=0.745, deviance change=9.845), in comparison with the best model found at any single scale. With this approach, density was better explained at the 500m scale (Nagelkerke R2=0.694, deviance change=9.019).

The variables explaining density in the best multiscale model included two patch geometry variables, area and shape index, and all landscape composition variables -proportion of habitat, cropland and urban areas (Figure 4). Area had a positive effect on the population density of *L. viridis* (β = 0.824, SE=0.194, t-value=4.239), while the effect of shape index (β =-0.768, SE=0.475, t-value=-1.615) and the three landscape composition variables was negative (Proportion of habitat: β =-4.835, SE=1.676, t-value=-2.884; Proportion of cropland: β =-1.481, SE=0.528, t-value=-2.801; Proportion of urban areas: β =-1.25, SE=0.512, t-value=-2.44).

The variables explaining density in the best single scale model at 500m included area, one variable representative of landscape configuration, distance to river, and one of landscape composition, proportion of urban areas (Figure 5). Distance to river was found to have a negative effect on density (β =-0.152, SE=0.087, t-value=-1.739). For proportion of urban areas, contrary to what was found in the multiscale model, in which this variable was added at its SoE at 50m, at 500m scale it had a positive effect on density (β =1.73, SE=0.489, t-value=3.532).

Area was the only predictor present across all selected single scale models, having a consistent positive effect on density. Other predictors present in selected single scale models show a clear spatial pattern regarding the range of scales at which they exert an effect on density. Shape index, vegetation structure, proportion of habitat and proportion of cropland were present only at small scales, with all of them exerting a negative effect on density. By its side, distance to river was present only from the 250m scale on, and its effect was consistently negative. Finally, proportion of urban areas was present only at medium and large scales and its effect was positive.

Discussion

In this study a patch-landscape approach was applied to evaluate effects of parameters at different spatial

levels on the population density of *L. viridis* in a modified landscape in central Bulgaria. Results do not support the first two hypothesis regarding positive effects of within patch habitat quality and no effect of patch size. On the contrary, only one parameter of habitat quality, vegetation structure, was present at the smallest scale and its effect was negative. By its side, patch area had a consistent positive effect in all models where it was present. The results support the third hypothesis of no effect of isolation on population density. Finally, the prediction of the fourth hypothesis, an effect at small spatial scales of individual landscape composition predictors and of the overall habitat loss process, was partially met. The SoE of both, proportion of cropland and urban areas, was small (50 m), while the SoE of proportion of habitat was large (1.5 Km). The strongest effect of the overall habitat loss process was better described by the multiscale approach, including all composition parameters at their SoE. However, when comparing among single scales only, the strongest overall effect was found at a small-medium scale (500 m).

The best model predicting population density of *L.viridis* in the study system was a multiscale model. It included patch area, shape index, and all landscape composition predictors, with all variables but patch area having a negative effect. Positive effects of patch area on population density were also found in other reptile species (eg. Rizkalla & Swihart, 2006; Shirk et al. 2014), and meta-analysis report positive correlation of area with animal population densities in birds, insects and mammals (Connor, Courtney, & Yoder, 2000). Specially in landscapes with high habitat loss, large patches concentrate resources, like food, refuge and mates, which in turns translate into positive reproduction and survival rates, and lower predation risk in comparison with small fragments.

Moreover, the combined positive effect of patch area and negative effect of shape index (increases with patch irregularity), suggest possible edge effects on population density. Patch interior increases with area and decreases with shape index. therefore, results suggest that population density of the species depends mostly on available patch interior. On the contrary, Prieto Ramirez et al. (2020) concluded that the occupancy of the species depended on both, enough patch interior and patch edge. *L.viridis* is most probably an omnipresent species in this region, using both, edges and patch interior, but patch edge may play a different role for different processes at the population level, being important for population persistence, but not for density. Nevertheless, the importance of patch interior for the species in this region is consistent across processes. In subtropical and tropical regions sufficient interior core area might be very important for reptiles thermoregulation (Nowakowski et al., 2017). Patch edges are known to be hotter and drier than patch interior, given a higher exposure to surrounding open land covers (Chen et al., 1999; Lehtinen, Ramanamanjato, & Raveloarison, 2003); also, habitat loss has been linked to local temperature increment (Laurance, 2004; Arroyo-Rodríguez et al., 2017). Hence, in fragmented landscapes, reptiles rely on the cooler, interior areas of patches to fulfill thermal physiological demands (Todd & Andrews, 2008; Tuff, Tuff, & Davies, 2016).

The best selected multiscale model also included all landscape composition variables, each of them at its spatial SoE's: 1.5 km for proportion of habitat and 50 m for both, proportion of cropland and of urban areas. All of these variables had a negative effect on the population density of *L. viridis*. Nemitz-Kliemchen et al. (2020) demostrated that the studied populations are not genetically differentiated and might represent a metapopulation with considerable exchange of individuals. Thus, if lizards disperse to use resources, a high proportion of habitat surrounding patches can decrease the density at the interior of patches. Moreover, the scale at which habitat had the strongest effect on density, and that was present in the multiscale model (1.5Km), goes beyond the longest dispersal distance reported for *L. viridis*, which is 1km (Popescu et al., 2013). This supports the idea of dispersal-related processes modulating patch density. My results seem to, at least partly, conform to principles of the Ideal Free Distribution (IFD; Fretwell & Lucas, 1970) theory, which states that individuals are distributed in the space in proportion to the profitability of the available habitat areas. Although the present study cannot judge the profitability or quality of the habitat surrounding the studied patches, based on results it can be expected that individuals into patches seek to exploit resources in the surrounding habitat and that this emigration from patches does decrease the density within patches.

Regarding proportion of cropland and urban area, the strongest effect of these land covers on density was at

the smallest evaluated scale (50m), suggesting that these two parameters affect population density through processes that occur at the direct vicinity of patches, rather than at a large landscape scale. These edge effects would be in line with the discussed importance of core areas for population density and can be related with changes in the local climatic conditions of patches. Urban areas are known to have higher temperatures compared to natural or semi-natural areas (Arnfield, 2003) and cropland could rise the exposure of patches to wind and water fluxes, thus triggering strong shifts in daily temperatures. Both could then affect the quality of patches in terms of lizard's microclimatic necessities for thermoregulation (Tuff, Tuff, & Davies, 2016) and developmental stability (Braña & Ji, 2000; Beasley, Bonisoli-Alquati & Mousseau, 2013; Lazić et al., 2013). Other mechanism through which cropland can negatively affect density is through the reduction of body condition due to exposure to pesticides, as found in *Podarcis bocagei* and *Podarcis muralis* (Amaral et al., 2012; Mingo, Lötters & Wagner, 2017) and to predators, like in populations of *Iberolacerta cyreni* (Amo, López, & Martín, 2007). Low physiological status of individuals produced by either of the mentioned mechanisms can affect vital population rates and lead to population decline (Collinge & Forman, 1998; Henle, Sarre, & Wiegand, 2004).

Across single scales the most important parameters were area, distance to river and percentage of urban areas. Patch area effect is also positive as in multiscale models. In the case of percentage of urban areas, this variable is only present from the 5 00m scale on, and its effect, across scales, contrary to what was found at its SoE, is positive. Urban areas represent a barrier for the species dispersal, which in highly isolated patches surrounded by urban areas, might aggregate individuals within patches, and thus, increase patch population density. By its side, distance to river was not included in the multiscale model, but was present in all selected single scale models from scale 250m on, and had a negative effect on population density. Prieto-Ramírez et al. (2020) found positive effects of distance to river on occupancy probability and suggested riverine vegetation to act as a corridor. As in the case of percentage of habitat, this parameter of landscape configuration can also increase dispersal of individuals, reduce their aggregation and density within patches.

Distance to nearest patch was not found to have an effect on population density. This finding is in concordance with the HAH (Fahrig, 2013), which states that in landscapes with high levels of habitat loss, habitat amount, as composition-based parameter reflecting isolation, affects species distribution much more strongly than lineal, distance-based parameters of isolation (Martin & Fahrig, 2012).

Any of the two evaluated within-patch habitat quality parameters, radiation or vegetation structure, were included in the best selected multiscale and single scale (500m) models. *L. viridis* is a generalist species and in the studied region the species has a bigger realized niche compared to populations in the periphery of its distribution range (Prieto-Ramirez et al. 2018). Also, the occupancy probabilities of the species in this region were found to have a lower dependency on habitat quality compared to the periphery (Prieto-Ramírez et al. 2020). Habitat generalization is known to have a positive relation with capacity to thrive in modified landscapes (Ye, Skidmore & Wang, 2013), and in reptile communities, Swihart et al. (2006) found that niche breadth and proximity to the core of the distribution range positively correlate with tolerance to landscape modification. Therefore, for both, occupancy probability and population density, niche size might be one of the traits ruling the species response to habitat loss.

However, some differences between occupancy and population density are found when comparing the response of these two parameters to vegetation structure. Although not a determinant factor, vegetation structure did have a positive effect on occupancy probabilities at some few scales (Prieto-Ramírez et al., 2020), while it was not present in almost any model of population density. Vegetation structure is an important thermoregulatory resource for reptiles in subtropical regions, offering shadow and different vegetation levels for basking (Kearney, Shine & Porter, 2009; Muñoz et al., 2016; Grimm-Seyfarth, Mihoub & Henle, 2017), and in the case of *L. viridis*, microhabitats used in the studied region have a higher vegetation structure than those used in the northern periphery (Prieto-Ramírez et al., 2018). What is known about occupancy probability of *L.viridis* in the core region, together with the results of the present study, suggest that a link between individual level processes, like microhabitat use and thermoregulatory behavior, and population level processes is important only for population persistence, but not for the preceding population decline. Other

authors have also reported discrepancies regarding vegetation structure effects in occupancy vs. abudance in other lizard species. For instance, Dibner et al. (2017) found that the occupancy of the greater short-horned lizard (*Phrynosoma hernandesi*) was positively affected by vegetation structure, while on abundance it had a negative effect. By its side, in line with my results, Rizkalla and Swihart (2006) found also no effect of within-patch habitat quality on the abundance of the most common species and with higher ability to adapt to habitat alteration in a turtle community.

Both, population density and patch occupancy reflect important ecological processes, namely population decline and persistence, whose understanding is essential for identifying the best conservation practices to protect species. Therefore, it is very important to analyze effects of habitat loss on both. However, for very few species information on occupancy and density or abundance is available. In the reptile literature, only some authors have integrated both approaches in the same area. For instance, in the Batuecan lizard *Iberolacerta martinezricai* Lizana-Ciudad et al. (2021) found that population persistence depended on connectivity of scree slopes, while abundance of extant population relied on within-patch habitat quality and topography. Also, in the short-horned lizard (*Phrynosoma hernandesi*) analysis of environmental factors on occupancy and abundance showed contrasting effects, with the same factors having opposite effects (Dibner et al. 2017).

Integrating occupancy and abundance/density surveys can be challenging due to specific requirements of the data gathering of each parameter. Occupancy surveys are usually suggested to be uniform, applying the same sampling effort in each patch, in order to not affect detection probability (Krishna, Krishnaswamy, & Kumar, 2008; Cristescu et al., 2019). On the other hand, abundance and density studies are suggested to have a proportional sampling effort, in which the entire area of each patch (which is usually variable) is surveyed (Nufio, McClenahan, & Thurston, 2009). In this study, data to estimate population density was gathered during the same field season in which occupancy data was collected (Prieto-Ramírez et al. 2020), by applying a semi-uniform survey design. All transects within a patch summed up the same total length, and therefore, sampling effort across patches was standardized. However, the number and length of single transects, in which that total length was partitioned within each patch, was proportional to the number and area of habitat types within each single patch. Thus, the survey was "proportional" with respect to how the heterogeneity of each patch was reflected. This is a robust combination of survey design types, which allows to gather relevant ecological information on processes occurring at different stages of the population extirpation process, decline and persistence.

Data Accessibility Statement

Data will be available from the Dryad digital repository once the manuscript be accepted for publication

Conflict of Interest Statement

None declared.

Acknowledgements

Data for this research was not part, but was taken, in the context of a PhD project, carried out with the financial support of the Heinrich Böll Foundation, scholarship P113742. Additional financial support was provided by the Helmholtz Center for Environmental Research (UFZ). I thank Prof. Dr. Klaus Henle for his support as former Head of the Department of Nature Conservation at UFZ, to Pavel Stoev, Georgi Popgeorgiev and Nikolay Tzankov (RIP) for their support during fieldwork and to Roxanne Leberger for comments on the manuscript.

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Figures and Tables

Figure 1. Pair of *Lacerta viridis* (male on the left, female on the right) during the reproduction season.

Figure 2. Study site located in the surroundings of Plovdiv, Bulgaria.

Figure 3. Scale of effect of scale-dependent variables: Proportion of habitat (Habitat), proportion of cropland (Cropland), proportion of urban areas (Urban) and Proximity index (Prox).

Figure 4. Effect of variables present in the best selected model in the multiscale approach on

the density of L. viridis.

Figure 5. Effect of variables present in the best single-scale model at 500m on density of L. viridis.

Table1. Best models explaining density of *L. viridis* with the multi-scale approach and at each single-scale. For each variable present in each selected model the direction of the effect is presented.

| Scale | Nagelkerke R2 | Deviance change | Area | Vegetation structure | Shape index | Distance to river | % Habitat | % Cropland | 9 |
|-------------------|------------------|--------------------|------|-------------------------|----------------|----------------------|-----------|---------------|---|
| Multiscale | 0.7450 | 9.8458 | + | | _ | | - | _ | - |
| $50\mathrm{m}$ | 0.6330 | 8.0883 | + | - | - | | | - | |
| 150m | 0.5740 | 7.1989 | + | | - | | | - | |
| $250\mathrm{m}$ | 0.6460 | 8.2725 | + | | | - | - | - | |
| 500m | 0.6940 | 9.0199 | + | | | - | | | + |
| 750m | 0.6880 | 8.9277 | + | | | - | | | + |
| 1000m | 0.6740 | 8.7131 | + | | | - | | | + |
| 1500m | 0.6540 | 8.4093 | + | | | - | | | + |
| 2000m | 0.6210 | 7.8958 | + | | | - | | | + |
| $2500 \mathrm{m}$ | 0.5910 | 7.4457 | + | | | - | | | + |
| 3000m | 0.5860 | 7.3744 | + | | | - | | | + |

SUPPLEMENTARY MATERIAL

Appendix 1. Location of the studied populations and their density estimation.

| | | Density estimatio | Density estimation | | | |
|---------|----------|-------------------|--------------------|-----------------|--|--|
| Latitud | Longitud | $(ind./Km^2)$ | Upper CI 95% | Lower CI 95% | | |
| 42.1424 | 24.7005 | 1614.3 | 1490.8 | 1748.1 | | |
| 42.1558 | 24.7519 | 115.31 | 106.48 | 124.87 | | |
| 42.1530 | 24.7341 | 576.54 | 532.42 | 624.33 | | |
| 42.1639 | 24.7627 | 230.62 | 212.97 | 249.73 | | |
| 42.1597 | 24.7760 | 345.93 | 319.45 | 374.6 | | |
| 42.1622 | 24.7972 | 461.24 | 425.93 | 499.46 | | |
| 42.1560 | 24.7639 | 1953.5 | 1804 | 2115.4 | | |
| 42.1486 | 24.7074 | 381.71 | 352.5 | 413.35 | | |
| 42.1529 | 24.7065 | 115.31 | 106.48 | 124.87 | | |
| 42.1573 | 24.7179 | 115.31 | 106.48 | 124.87 | | |
| 42.1641 | 24.7708 | 230.62 | 212.97 | 249.73 | | |
| 42.1904 | 24.7691 | 230.62 | 212.97 | 249.73 | | |
| 42.1951 | 24.7754 | 345.93 | 319.45 | 374.6 | | |
| 42.1986 | 24.7590 | 230.62 | 212.97 | 249.73 | | |
| 42.1248 | 24.8670 | 638.63 | 589.75 | 691.57 | | |
| 42.1510 | 24.8828 | 461.24 | 425.93 | 499.46 | | |
| 42.1520 | 24.8169 | 230.62 | 212.97 | 249.73 | | |
| 42.1246 | 24.8686 | 807.16 | 745.38 | 874.06 | | |
| 42.2123 | 24.8676 | 345.93 | 319.45 | 374.6 | | |
| 42.2286 | 24.8579 | 1284.9 | 1186.5 | 1391.4 | | |
| 42.2246 | 24.8831 | 732.55 | 676.48 | 793.27 | | |
| 42.2060 | 24.8987 | 230.62 | 212.97 | 249.73 | | |
| 42.1997 | 24.8894 | 691.85 | 638.9 | 749.2 | | |
| 42.2262 | 24.8482 | 509.79 | 470.77 | 552.04 | | |







Figure 3.



