The Thesis of the Doctoral (Ph.D.) dissertation

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IMPACTS OF UNGULATES ON REPTILES OF HIGH CONSERVATION VALUE AND THEIR HABITATS

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Title: Impacts of ungulates on reptiles of high conservation value and their habitats

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1. Background of the work and its aims

1.1. Ungulate impacts on the Caspian whipsnake in a peri-urban habitat in Hungary

Ungulate herbivory can have significant top-down effects on the density and composition of plant communities in an ecosystem (Carpio et al. 2015). Ungulate activities and behavior; such as wild boar (*Sus scrofa*) rooting and deer browsing can mitigate shrub encroachment and succession processes by decreasing woody vegetation cover in understory layer, which can also be preferential for reptiles benefitting from open sunbathing places or increased insect or lizard prey abundance in some altered habitats. Wild boar-rooted areas may provide good quality open microhabitats for reptiles and other animal species (de Schaetzen et al. 2018), thus they are capable of maintaining and establishing habitats for reptile species. Contrarily, predation on herpetofauna by abundant omnivorous wild boars may be an important reason why reptile populations are deteriorating (Graitson et al. 2019). Therefore, management and regulation of wild boar and other ungulate populations (i.e., deer) are very important for mitigation of losses in reptile populations (Jolley et al. 2010).

The Caspian whipsnake (*Dolichophis caspius*) is primarily found in southern Hungary (Szársomlyó Hill), along the western bank of the Danube River, and on outcrops of dolomite, limestone, and sandstone in and near Budapest (Nagy et al. 2010). In the Carpathian Basin, the populations have become increasingly fragmented owing to habitat alteration (Mahtani-Williams et al. 2020). Although the Caspian whipsnake is a strictly protected species locally, factors threatening it are understudied. However, habitat degradation (Bellaagh et al. 2008), collisions with vehicles (https://herpterkep.mme.hu/), and invasive plants (Babocsay and Vági, 2012) have been previously determined as primary threats to its survival. The spatial ecology of the Caspian whipsnake has not been studied yet, neither in urban nor in natural landscapes. Our study provides the first data on the home ranges and daily movements of this species from a population inhabiting a peri-urban habitat within Budapest. Here an isolated population inhabits a diverse area of hilly dry Rocky Mount with woody vegetation surrounded by shrubby meadows and grasslands and enclosed by extensive forest stands and residential areas. It is important to investigate the possible impacts ungulates may have on strictly protected Caspian whipsnake. In our research study the snake species of interest co-exist with ungulates, which may have direct and indirect impacts on the snake (e.g., predation) or the habitat of the snake by altering vegetation cover. Similarly, as an urban population, those Caspian whipsnakes can suffer from various human effects.

We targeted to determine these impacts, and better understand the aspects of the spatial ecology of the Caspian whipsnake in our study area and relate this information with possible ungulate impacts and that of humans.

1.2. Aim, research objectives and questions

The main aim of the research was to investigate the possible impacts of ungulates on reptiles in general and specifically on the habitat of the strictly protected Caspian whipsnake living in a peri-urban area.

Below are the objectives of the study which were identified based on the research problem; each objective is coupled with one or more research question(s).

(a) To investigate the general impacts of ungulates on reptile species around the World.

a_1- In which geographical ranges and habitat types were ungulate-reptile interactions mainly reported?

a_2 - Which species (ungulate vs. reptile) were involved in these interspecific relationships?

a_3 - What is the nature of revealed effects; direct or indirect and positive or negative for the participants of these interactions?

(b) To investigate the changes in vegetation cover in the study area over time, using field observations and Unmanned Aerial Systems (UAS).

b_1 – How is the shrub density changing in time and space in the study area?

(c) To determine if herbivore browsing pressure may have an impact on the shrub encroachment process.

c_1 – What is the proportion of available and browsed shoots on shrubs of different species as food sources for herbivores?

c_2 – Which shrub species are dominant and mostly preferred by ungulates?

c_3 – What is the extent of browsing pressure on saplings?

(d) To investigate if wild boar rooting activities may have an impact on the shrub encroachment process.

d_1 – What is the proportion and spatiotemporal pattern of wild boar rooting in the study area?

d_2 – What is the relationship between wild boar rooting activity, shrubs and saplings?

(e) To investigate the spatial movements of Caspian whipsnakes in the study area.

e_1 – What is the average daily displacement of Caspian whipsnakes?

e_2 – What is the average seasonal home range size of the snakes?

e_3 – What is the extent of overlap in home ranges between the individuals?

e_4 – What is the extent of variation between home range estimation methods?

e_5 - Which habitat patch type is most likely preferred by Caspian whipsnakes?

(f) To investigate possible direct impacts of wild boar and other wildlife on the Caspian whipsnake using camera trapping.

f_1 - Is there any occurrence of wild boar near Caspian whipsnake burrows?

f_2 - What is the daily emergence pattern of the Caspian whipsnakes from the burrows?

f_3 – What is the duration of exposure of the Caspian whipsnakes around the burrows?

(g) To evaluate possible direct impacts of humans on the Caspian whipsnake – a dummy snake experiment.

g_1 – What is the number of people visiting the area used by Caspian whipsnake?

g_2 - What is the extent of direct human interaction with the dummy snake?

1.3. Hypotheses

In terms of the general impacts of ungulates on reptile species around the World, we hypothesized: $\mathbf{H_a}$ – Ungulates have various effects on reptiles, both beneficial and disadvantageous, and there should be some widely distributed high-impact ungulate species and some highly vulnerable reptile groups involved in these interactions.

We drew several hypotheses from the field-based research: $\mathbf{H_b}$ – Shrub density in the area increases over time due to succession processes and lack of historical management interventions and has already reached a high level. $\mathbf{H_c}$ - Shrub density in cells will decrease if pressure by ungulate activities (i.e., browsing and rooting) increases on the dominant woody species but increase if less pressure is exerted by ungulates, thus ungulate browsing pressure will be exerted more on the dominant woody species and on saplings, $\mathbf{H_d}$ – Grid cells with a high density of shrubs will be highly rooted, due to available hiding place and potentially increased availability of invertebrates and underground plant materials (e.g. roots) under or around shrubs, leading to highly rooted cells and/or areas having fewer saplings. **H_e** - We expected that Caspian whipsnakes might frequently utilize habitat patches consisting of hideouts and hibernacula. As a result, we predicted a relatively high concentration of localization points of snakes on dry, rocky mounts with woody vegetation, especially during the hibernation periods. No extended movements to other habitat patches during activity periods were presumed. We expected high variabilities coming from the methodology of home range estimations, snake individuals, and their sexual differences. **H_f** – Wild boar may be a possible predator of the Caspian whipsnake as they are omnivorous. However, we expected few encounters between them, since wild boar is mainly active during the night; meanwhile whipsnakes should move aboveground during the daytime. **H_g** – Human recreational activities in the area will result in frequent interactions with the Caspian whipsnakes resulting in direct negative impact.

2. MATERIALS AND METHODS

2.1. Broad literature survey: ungulate-reptile interactions

2.1.1. Literature search and paper selection.

We performed a broad literature search on the Web of Science database (Clarivate; https://www.webofknowledge.com), in accordance with the guidelines of Preferred Reporting Items for Systematic Reviews and Meta-Analyses–PRISMA (http://www.prisma-statement.org) for bibliographic surveys (Page et al. 2021). We searched the whole database and retrieved articles published in English from 1990 through 2022 using a combination of keywords/nomenclature, *i.e.*, Total Search = ((impact* OR effect* OR grazing* OR browsing* OR rooting* OR trampling*) AND (reptile* OR snake* OR tortoise* OR alligator* OR crocodile* OR lizard* OR turtle*) AND (ungulate* OR hoofed* OR deer* OR wild boar* OR pig* OR livestock* OR elephant*)) searching in the titles, keywords and abstracts of the potential sources.

We considered only peer-reviewed papers; other reports such as websites, and newspapers, newsletters were excluded. We also utilized additional publications from the references listed in papers obtained from our systematic literature search; we selected these papers when the title of the source suggested it had data or information about the impact of ungulates on reptiles. For articles that were unavailable to the public and we had no direct access to them, we contacted the authors requesting full papers.

We managed to obtain 930 scientific articles from our entire literature search. These scientific articles were read thoroughly in detail, searching for investigations and descriptions of ungulate-reptile interactions. We found 4 review papers that we used to extract additional publications which were not found by our search. Following this screening we found that 69 papers (7.4% of the initial articles) reported clear impacts of ungulates on reptiles, either direct or indirect. Within the 69 papers, some studies reported more than one type of impact; hence, in total we analyzed 75 interactions. Since the reports on this topic were relatively limited, we did not specify or filter the years of publishing during the further analyses.

2.2. Technical field-based research

We established an integrated field-based research method to achieve our objectives (a – g).

2.2.1. Study area.

The study took place in a semi-natural habitat complex covering an area of 125 ha surrounded by suburban and forest environments in Pesthidegkút, Budapest, Hungary. Part of the area is included in the Natura 2000 network and forms a part of the landscape protection area of the Buda Hills within Duna-Ipoly National Park. The habitat is a mosaic of grassy, shrubby, rocky patches and forest. In the earlier decades the area was heavily grazed by sheep. The area is now under pressure with proliferating shrubs (shrub encroachment) which are continuously covering the open grasslands.

The center of the area is a rocky elevation consisting of shallow quarries and thick sandstone piles deposed during earlier mining activities (yellow arrow). The shrubby and open grassy areas are characterized by a combination of loess solonetz soil and alluvial meadow soils (see Pasztor et al. 2018); and an old unused grassy airport strip (blue arrow). Recently, shrubby and woody vegetation has been replacing the grassy vegetation creating suitable habitats for wild boar and mammalian predators (e.g., the red fox *Vulpes vulpes*). With observation we can confirm that deer species are also present in the area (evidence: tracks, fecal samples and browsed shoots of shrubs and saplings). The area also serves as a recreational space for residents, which exerts heavy human disturbance (e.g., dog walking, hiking, mountain biking) on the snake population. In 2018, an educational trail (named after Dr. Jane Goodall) was created to inform the lay public about the Caspian whipsnake and other wildlife of the area.

2.2.2. Data collection

2.2.2.1 Drone photography.

To investigate how the woody vegetation occupies the study area, the habitat of Caspian whipsnake, aerial images captured on 26 June 2019 by a DJI Phantom 4 drone with RGB camera (which are stitched together into an ortho-mosaic using DroneDeploy application, and analyzed using standard map grid cells of 20 x 20 m by QGIS (3.10v)).

2.2.2.2. Vegetation density estimation and impacts of ungulates on shrub vegetation.

Different methods were used to measure the impact on vegetation by ungulates, which may ultimately affect the Caspian whipsnake habitat. The measurements included estimation of shrub density and saplings in grid cells and browsing the impact of ungulates on shrubs and saplings.

2.2.2.2.1. Shrub and sapling density estimation.

To estimate the shrub cover and sapling availability, we counted the number of woody individuals within grid cells of 20 m x 20 m size. The surveyed area was assessed and selected based on the concentrations of seasonal wild boar rootings affecting 3.2 hectares (initial phase of the investigation; November 2019 to May 2020 we surveyed 1.32-hectare patch, going forward we increased the surveyed area to 3.2 hectares which represent most the shrubby part of the study area) which is a portion of the study area comprising open grassy patches and shrubby patches. The total surveyed area represents 8.4% of the total area used by the Caspian whipsnakes.

We designated adjacent rows of 20 m x 20 m grid cells parallel to each other covering the whole study area, by which we had a total of 81 grid cells (31 cells in the 1st phase until May 2020). The plant species were not treated separately, but they were distinguished into two categories based on their height: 1) a plant was a sapling, if less than 0,5 meter (and can be dug out completely by rooting) and adult plants (shrubs), more than 0,5 meter (cannot be dug out by rooting).

While in the case of young individuals it was unequivocal, in the case of bigger adult shrub units, the individuals were identified based on the number of their trunks counted just above the ground surface. We also estimated the shrub cover (surface covered by shrubs) in each cell using the following scale: 0%, 1–25%, 26–50%, 51–75% and 76–100%.

2.2.2.2.2. Browsing impacts on shrubs.

To monitor the browsing impact of ungulates on the vegetation, we conducted seasonal (vegetative periods; July 2019, May 2020, August 2020 and June 2021) vegetation surveys in a 6-ha portion of the study area where wild boar rooting is prevalent to evaluate the relationship between ungulate pressure and plant food supply. To achieve this, we designed a 1 km discontinuous transect (330m+340m+340m) around the area occupied by herbaceous vegetation and collected data on 100 sampling points. From this survey we can deduce whether the ungulates maintain or destroy the habitat (their influence on shrub encroachment). Furthermore, we determined which woody species were preferred by ungulates and which ones were avoided. To investigate the actual status of the woody shrub vegetation, we used a special wooden frame of 50x50x30 cm (height x width x depth). This tool functions to count the number of all available and browsed woody shoots (as “food units" for large herbivores) up to 2m in height at all sampling points within this quadrant. The differences in the browsing ratio among different woody species will reflect the selective browsing impact of ungulates (Fehér et. al., 2014).

2.2.2.2.3. Browsing impacts on saplings.

In the area where we surveyed rooting and ungulate browsing activities, we designated random line transects to evaluate the browsing impact on saplings by ungulates. On 6 occasions (between July and August 2022) we walked along six 100m long line transects assessing the browsing impact caused by ungulates on saplings. In total we counted 144 saplings. We distinguished the variety of impact into top-browsed (C), lateral-browsed (O), top and lateral-browsed (CO), entirely over-browsed (T) and intact (NR) categories.

2.2.2.2.4. Wild boar rooting surveys.

For all data collection, transect lines adjacent to surveyed cells of the area along its longer extension were walked such that the two borders at both sides of the investigated cells will be 20m from the transect line. To ensure correct walking direction (without overlapping in other cells) while sampling we used Gaia GPS; v2020.08 (mobile application). Along the full length of the transects, we also recorded by the GPS device the locations of all patches rooted by wild boar. When our transects crossed the rooted areas, we recorded an entry and an exit point. We considered a patch as rooted by wild boar when the disturbed site heavily differed from the undisturbed surroundings. Wild boar rooting often means the disturbance of the top of the soil layer. Thereby litter and soil can mingle. The size of the rooted patch usually varies between 1 and 100 m^2, and the disturbed soil layer can be up to 20 to 40 cm deep.

2.2.2.3. Space use of Caspian whipsnakes.

2.2.2.3.1. Handling the snakes and transmitter implantation.

Radio-tracking the snakes has been carried out in addition to a long-term monitoring programme of the Caspian whipsnake of Hungary by the Amphibian and Reptile Conservation Group of MME BirdLife, Hungary. We searched the area for snakes and caught them by hand. Altogether 79 specimens have been caught and out of these, 68 were identified as separate individuals. Between 2016 and 2019, radio-transmitters were implanted into five individuals (two males, three females). Immediately after capture, the snakes were taken to the veterinary clinic of the Budapest Zoo. They were anaesthetized with injectable (ketamine and midazolam) and inhalant anesthetics (Sevoflurane) to implant VHF radio-transmitters (manufactured by Wildlife Ecology Institute, Vienna, Austria) surgically into the coelomic cavity. The ratio of the transmitter (core body: 17 × 10 × 7 mm, weight = 2.5 g with a flexible antenna of 8 cm) to snake mass was below the 5% threshold value customary in radio-telemetry of snakes (Horning et al. 2017). All surgeries were carried out within 12 hours after capture and all snakes were released after 24 hours of observation care. The lifespan of the transmitters was indicated as a minimum of one year, but they could function a bit longer (less than 18 months). For two individuals (Vali and Lili) we replaced the transmitters once. For a public conservation campaign, the tracked snakes were named (Table 3), and two of them received names honoring Dr. Valery Jane Goodall, who had taken a special interest in the conservation project of this population.

2.2.2.3.2. Radiotelemetry localisations of the snakes.

We localized the snakes with a Televilt RX900 (TVP Positioning AB, Televilt, Sweden) receiver with YAGI-antenna. The snakes were localized at least once a week, but occasionally twice. The frequency of detection during winter was lower than in summer months. We followed each of them for at least a year, but two of them with replaced transmitters were tracked for two and three years, respectively. When a snake was located, the following information was recorded: the coordinates (using a Garmin Map64x handheld GPS with Universal Transverse Mercator [UTM] WGS 84 projection, working with 0-10 meters precision), the date and time, whether the snake was visible above-ground or not (if not it was recorded as being underground) and the vegetation type in which the snake was found.

2.2.2.4. Temporal activity of snakes.

Two Bushnell trail cameras were set out in the field (Vöröskővár, Budapest) for 59 days (for both cameras) to observe and monitor the use of burrows and activity in Caspian whipsnakes to a daily temperature between 13 September 2021 and 14 April 2022. To achieve this, the trail camera was installed at ~1.5m distance from the burrow of the snake and set to capture three images at 1-minute intervals and record temperature data of the surroundings each time an image is captured. Both cameras were placed at fixed locations (two separate burrows) 110m away from each other throughout the survey. Timelapse2 software (Greenberg et al. 2019) was used to count the images and analyze them. The number of pictures of snakes was counted per day and for 30-minute periods within days between sunrise and sunset.

We also investigated if the snakes emerged aboveground and returned underground using the same burrow. To achieve this, we pinpointed the time of emergence of the snake and time of return within one day. Should this be more than 24 hours, then it implies the snake may have used other existing burrows in the area. We further evaluated the duration of exposure of the snakes on the camera trap. To achieve this objective, we calculated the time difference between the first and the last photograph showing the snake during a visit.

2.2.2.5. Human interactions with the Caspian whipsnake**.**

Part of this work was undertaken by a BSc student Ms. Upendo Nkoma, whom I successfully supervised. As a primary supervisor, I provided oversight of the project and guided data interpretation. This section is included here with Ms. Nkoma's concern.

To investigate human behavior and its possible impact on the Caspian whipsnake, we conducted observational surveys from 3pm to 6 pm every weekend on Saturdays for 8 months (June – August 2021 and 2022), meaning 28 sampling days. A plastic dummy snake of approximately 1.5m was placed on the ground in Vöröskővár on the hiking trail (next to the signage that shows information about Caspian whipsnakes in the area) within the territory of the Caspian whipsnakes. The observer was positioned 15m meters away in such a way that he/she was not noticed but could still see the dummy snake. Here we observed human recreational activities, and noted if one is walking, with or without a dog, cycling, or running; other variables included the interactions with the dummy snake by both humans and their pet dogs; we observed if they noticed the snake or not, or if they ran over the snake and lastly if the dog tries to attack the dummy snake.

2.3. Data analysis.

2.3.1. Literature survey.

From the articles retrieved through our broad literature search, we extracted the following information: the country / continent where the study was carried out, the type of habitat, study approach (*i.e.*, observational (direct observation in the field, *e.g.*,(Antwi et al. 2019), descriptive (short- and long-term correlational studies, *e.g.*, (Petrozzi et al. 2018) or experimental (manipulation of impacting factor, using exclusion and inclusion methods, *e.g.*, (Beever and Brussard, 2004), the ungulate and reptile species of interest of the studied interaction (further grouping ungulates as wild and domestic ones), the conservation status of the affected reptiles according to IUCN Red List (https://www.iucnredlist.org/ ; accessed on 30 June 2022), the nature of impact caused by ungulates (direct or indirect and negative or positive from the point of view of reptiles).

We categorized an impact as positive for reptiles 1) when ungulates are prey to reptiles; 2) when ungulate activities benefit the reptiles either directly or indirectly and this was stated by the results of the source. We further distinguished impact as negative for reptiles 1) when ungulate species intentionally or opportunistically prey on reptiles (*e.g.*, if wild boar predates on snakes during rooting); 2) when ungulate activity significantly modifies the habitat characteristics (*e.g.*, ungulates destroy the habitat of reptile species by rooting or trampling) leading to a decrease in reptile density.

First, we analyzed the spatial and temporal trends in the number of publications that appeared on the studied topic. To describe the different types of effects of ungulates on reptile species, we paired ungulates with reptiles they have impacted based on all reported interactions. Furthermore, we listed the different ungulate-reptile pairs studied and calculated the number of cases of their mentioning. We also analyzed the findings on wild ungulates and livestock and the three digestive/foraging categories separately and compared the relative proportion of their negative and positive; direct and indirect effects on reptile species. The frequency distribution of these categories and impact types were evaluated by Pearson's Chi-squared test with Yates's continuity correction. Additionally, we calculated the odds ratio of the most informative category combinations to quantify the strength of the potential associations (Rita and Konomen, 2008) (e.g., whether wild ungulates tend to exert more direct impacts than livestock). If the value is higher than 1, the event is more likely to occur in the first group (e.g., wild ungulates do have more direct impacts on reptiles) and vice versa (Agresti, 2019).

2.3.2. Field based research

2.3.2.1. Shrub monitoring using drone technology.

Using QGIS software, Madeira, Spain (v3.4.11) we digitized all the visible shrubs at 90% magnification. The shrubs were distinguished from any objects on the orthophoto by their distinct grey coloration as compared to green grass and brown bare soil. We calculated the area covered by the digitized surface in each 20x20m grid cells using the "area" calculation function in the QGIS software.

2.3.2.2. Herbivore browsing pressure on the vegetation and saplings.

Kruskal-Wallis test was used to determine the potentially significant differences in the availability of shoots as food supplied by various woody species in the study area between July 2019 and June 2021.

To determine the types of browsing impact exerted by ungulates on saplings we calculated the proportion and browsing types on saplings by taking into account the ratio of the sum of occasions of browsing type and the total number of occasions browsing occurred on saplings.

Jacobs' selectivity index was used to calculate the browsing preferences toward different woody species (Katona et al. 2013).

2.3.2.3. Wild boar rooting activity and its effects on the shrub encroachment process.

To determine the extent of spatio-temporal wild boar rooting activities in the study area, we calculated the average proportion of rooted and non-rooted 20x20m cells monthly between November 2019 and January 2022. We measured rooting activity in each cell as the proportion (%) of occasions when rooting was found and further determined the extent of wild boar rooting by calculating the sums of total lengths of the rooted surface of each cell. The length was calculated by distance formula using rooting entry and exit points.

To determine the relationship between rooted surface, shrub density and saplings, we performed a Pearson correlation matrix to determine the relationship between rooting activity (proportion of occasions when rooting was found in a cell) sapling and shrub density. We considered a cell more rooted when the average length of the sum of rootings in the area was more than 25m and less rooted if the average length of the sum of rootings was less than 25m. Furthermore, we used Kruskal-Wallis test to investigate the relationship between shrub density in more rooted, >50% and less rooted <50% cells.

2.3.2.4. Spatial ecology of Caspian whipsnake: Radio-telemetry.

Jacobs' selectivity index was calculated and the chi^2-test with Bonferroni correction was conducted to determine the relative availability of different microhabitats and their preference (Katona et al. 2013) by snakes. The analysis was performed separately all year round on individual datasets and the combined dataset (all telemetry locations of five snakes combined). All other datasets were tested for normality using the Shapiro-Wilk test. The average yearly home range sizes of the snakes, as calculated using four estimation methods, and average daily displacements of consecutive months were compared using Friedman ANOVA, followed by Durbin-Conover pairwise comparisons, respectively. To compare the daily displacements among the individuals, the Kruskal-Wallis test, followed by Dwass-Steel-Critchlow-Flinger (DSCF) pairwise comparisons was used. However, due to the small sample size, we could not compare the home range sizes of individuals or sexes for the activity period. We evaluated the relationship between body weight of the tracked snakes and their home range size, estimated using a minimum convex polygon during the activity period, and calculated this using the Spearman correlation test. Similarly, we evaluated the association between body weight and average daily displacements. All statistical analyses were performed using Jamovi v1.1.9.0 (Şahin and Aybek, 2020).

2.3.2.5. Direct impacts of wild boar and other wildlife on the Caspian whipsnake and its activity pattern: Camera trapping.

We counted the number of times wild boar and other predators appeared in the camera trap images. To investigate the pattern of the daily appearance of Caspian whipsnake from the burrows in different periods of the year, we calculated the average number of photos with snakes in them to time. Furthermore, to investigate the duration of exposure on the camera trap (time spent in the vicinity around the burrow) we calculated the average time in minutes spent by the snake around the burrow per day (may be on several occasions, for example, when exiting the burrow and when returning).

2.3.2.6. Possible direct impacts of humans on the Caspian whipsnake – a dummy snake experiment.

We counted the number and proportion of occasions humans (with or without a dog) encountered the snake, either while walking, jogging, cycling and/or running. We also counted the total number and proportion of occasions when the dog attacked the dummy snake.

3. RESULTS

3.1. Literature survey: Ungulates and their impacts on reptiles

The relatively low quantity of original research articles (n=69) shows that studies focusing on ungulate-reptile interactions are scarce**.**

Fifteen ungulate species (13 Artiodactyla, 2 Perissodactyla) were mentioned in the literature and 47 species of reptiles were affected by them (Appendix A); 34% (n = 16) of those reptiles have high conservation value according to IUCN Red List wherein 13% of 47 species (n = 6) are Endangered ones, 11% (n = 5) have a Near Threatened status, 6% (n = 3) are Vulnerable and 4% (n = 2) of the reptiles are Critically Endangered (Appendix 2). *Sus scrofa* was stated as the most problematic species among many other wild ungulates to a variety of reptile species. *Bos taurus* and *Ovis aries* were dominantly studied livestock ungulates according to our results and had more revealed interactions with reptiles than other livestock species.

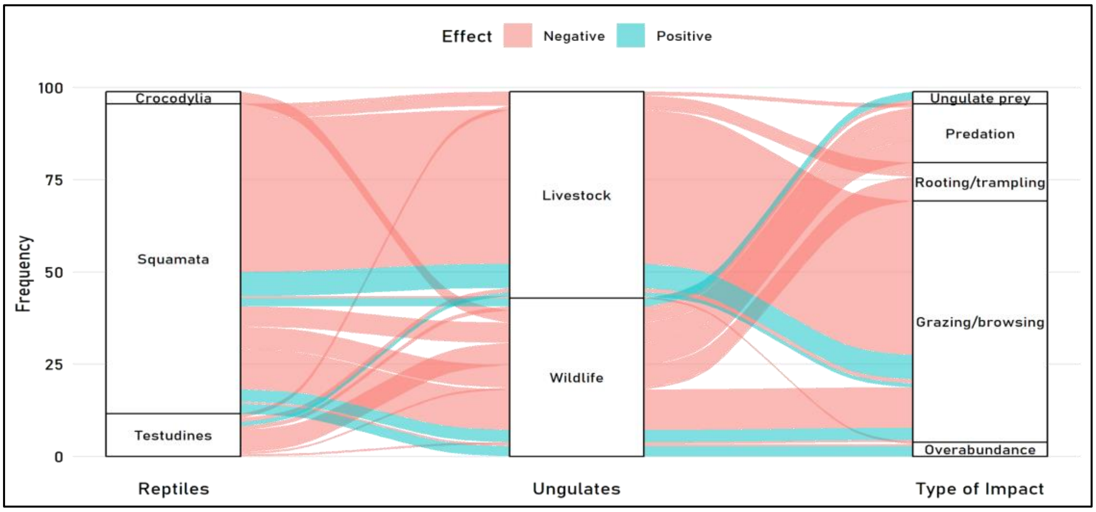

Figure 1: The distribution patterns (frequencies) of publications showing the different types of impacts / interactions of ungulates (wild ones and livestock separately) on / with different orders of reptiles.

Our results show that wild ungulates have one main characteristic type of direct and negative impact on reptiles, which is predation (reported when ungulates directly killed the reptile or remains of reptiles were found in the stomach content) (Fig. 1). Their indirect and negative impacts were mainly related to drastic changes in habitat and vegetation by overgrazing activities causing a decrease in reptile richness. However, the indirect and positive impacts by wild ungulates also included grazing/browsing and in some cases their local overabundance (i.e., overutilization of the area with their combined effects), when high density of ungulates changed the vegetation cover making it suitable for reptiles. Direct positive impacts of wild ungulates were also recorded, these are the situations when wild ungulates are preyed upon by large-bodied reptiles.

Similarly, to wild ungulates, in the case of livestock, the indirect and negative impacts dominantly featured overgrazing, meanwhile their indirect positive impacts comprised of maintaining preferential vegetation characteristics by moderate grazing. However, no statements on domestic ungulates in the role of prey for reptiles or as their predators.

Squamates (i.e., lizards and snakes) were the most negatively affected reptiles by ungulates, variedly impacted by both, wild ungulates and livestock. Occasionally, ungulates had positive impacts on Squamates, when they provided their prey or through grazing effects. In the second case, in highly dense vegetation, ungulates browsing and grazing created open spaces to allow light penetration on the ground, leading to the increase abundance of reptiles. Crocodylia (i.e., alligators) endured only negative impacts, came from wild ungulates; specifically, *Sus scrofa* predation on their nest. Testudines (tortoises and turtles) were affected mainly negatively, primarily by wild ungulates through predation of adults and the nests (destroying eggs and killing hatchlings).

There was a significant difference in the nature of impacts on the reptiles by wild ungulates and livestock (Table 1 and 2). Impacts by wild ungulates tend to be more often direct than in case of livestock. It can be related to the fact, that the proportion of predation on reptiles by wild ungulates was significantly higher than in the case of livestock. However, the proportion of grazing/browsing impacts was higher for livestock than for wild ungulates.

Table 1: The results of Pearson's Chi-square tests with Yates continuity correction on ungulate-reptile interactions. *** $p < .0001$ ** $p < 0.01$ * $p < 0.05$.

	Wild ungulates		*Livestock*		**χ^2 (df)**	**p**
	N	**%**	**N**	**%**		
Effect					0.06 (1)	0.811
Positive	10	13.4	7	9.3		
Negative	30	40	28	37.3		
Nature of impact ***					11.17 (1)	0.000
Direct	23	30.7	6	8		
Indirect	17	22.6	29	38.7		
Impact type						
Ungulate prey	5	6.7	0	0	2.89 (1)	0.089
Grazing/browsing ***	8	10.7	30	40	29.67 (1)	0.000
*Predation*****	16	21.3	1	1.3	12.65 (1)	0.000
Overabundance	4	5.4	1	1.3	0.59 (1)	0.439
Rooting/trampling	6	8	3	4	0.25 (1)	0.618
	Direct		*Indirect*			
Effect					3.03 (1)	0.08
Positive	3	4	14	18.7		
Negative	26	34.7	32	42.6		

Table 2: Odds ratios and their 95% confidence intervals of the specific combinations of ungulate impact type vs. ungulate species groups; the nature (direct or indirect) of ungulate impact vs. positive ungulate effects. Based on the comparison of the odd ratio, ungulate impacts on reptiles are more likely to be direct and positive (r < 1).

Comparison		**Odds ratio (r)**	**95% Confidence interval**
Effect: *Positive*	*Wild ungulates*	1.33	0.4 - 3.9
Impact nature: *Direct*	*Wild ungulates*	6.53	2.2 - 19.3
Impact type: *Ungulate prey*	*Wild ungulates*	11	0.6 - 206.6
Impact type: *Grazing/browsing*	*Livestock*	24	7.1 - 81.6
Impact type: *Predation*	*Wild ungulates*	22.67	2.8 - 182.7
Impact type: *Overabundance*	*Wild ungulates*	3.78	0.4 - 35.5
Impact type: *Rooting/trampling*	*Wild ungulates*	1.88	0.4 - 8.2
Impact nature: *Direct*	Effect: *Positive*	0.26	0.07 - 1.1

3.2.Field – based research

3.2.1. Ungulates food preference

The vegetation structure in the study area is a typical mosaic habitat, comprising of open grassy patches, bushy woody vegetation; ranging from highly dense to less dense shrub covers. Jacobs' index of preference and avoidance revealed that ungulates in the study area avoided (J< 0) most of the available plant species and preferred (J > 0) only *Crataegus monogyna*.

3.2.2. Temporal changes of wild boar rooting in the area and relationship between rooting, shrub cover and sapling availability

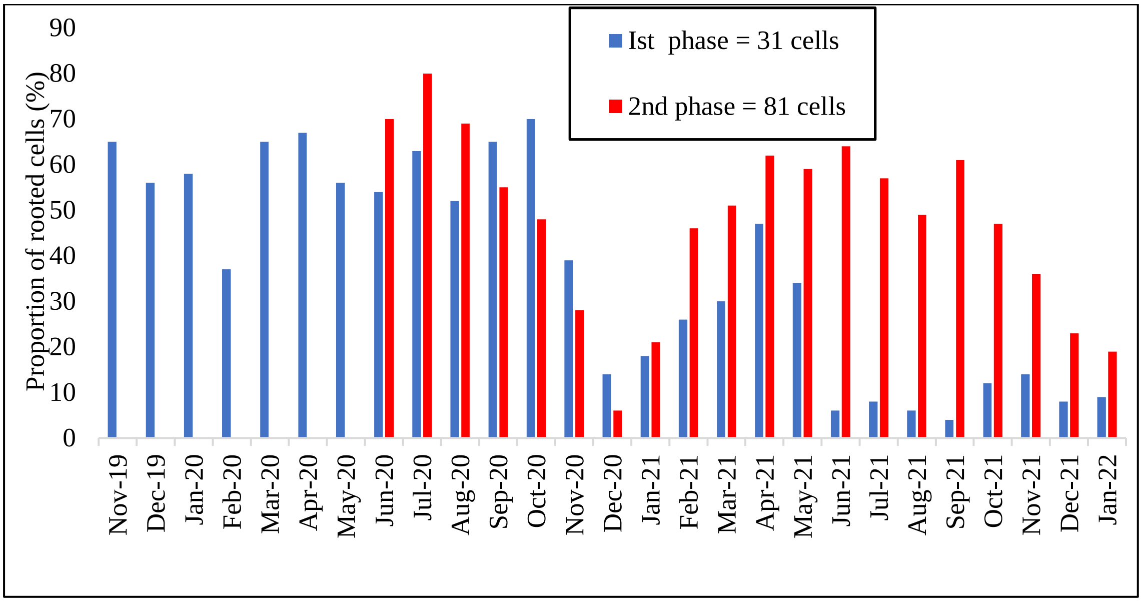

Figure 2: Wild boar rooting disturbance between November 2019 and January 2022.

Our results show that between November 2019 and January 2022 the average proportion of rooted cells in the study area was 41%. The proportion of rooted cells has increased in spring and summer and showed lower values between November and February (Fig. 2).

There was a significant difference in the lengths of wild boar rooting occurring in cells with different categories of shrub density (Kruskal-Wallis test - X^2 = 35.6; $df = 4$; $p < 0.001$). Dwass-Steel-Critchlow-Flinger pairwise comparisons revealed that intensity of rooting differed significantly between cells at all categories ($p < 0.05$) with the exception that there was no significant difference in the intensity of rooting in cells with 26-50% and 51–75% and 0% and 1–25% ($p > 0.05$). Rooting occurred mainly in more shrubby cells than cells with few shrubs. However, highly dense (>75%) shrubby areas/cells contained fewer saplings than medium/moderate (26-50% and 51-75%) shrubby cells. On the contrary there was no significant difference in the number of saplings recorded in cells with different shrub density categories (Kruskal-Wallis test - $X^2 = 6.85$; $df = 4$; $p = 0.144$).

3.2.3. Spatial ecology of Caspian whipsnake

We obtained 309 location points from the five individuals (Table 3).

Table 3: Length of the tracking period (first and last day), number of aboveground and underground localizations of radio-tracked Caspian whipsnakes and their seasonal distribution. F=female, M=male.

Name	Sex (F/M)	Date	Date	Number of localisation points				
		of first localisation	of last localisation	Total	Above ground	Under-ground	Activity period	Hibernation period
Vali	F	22 May / 2016	19 Jun / 2019	92	37	55	62	30
Jane	F	22 May /2016	07 Jul / 2017	68	29	39	60	8
Lili	F	02 Aug / 2016	19 Oct / 2018	78	42	36	64	14
Lali	M	01 Jun/ 2018	09 Aug / 2019	27	12	15	18	9
Tarzan	M	26 Aug / 2016	06 Jul / 2017	44	6	38	22	22

According to our data, during the entire study period, Caspian whipsnake population used an area of only 40.15 ha (out of the total 125 ha of the study area) characterized by a mosaic of rocky, shrubby, and grassy patches. The snakes aggregated within a small area (1.75 ha) in the central rocky patch during hibernation but their movements covered the whole yearly distribution area during the activity period (Fig. 3).

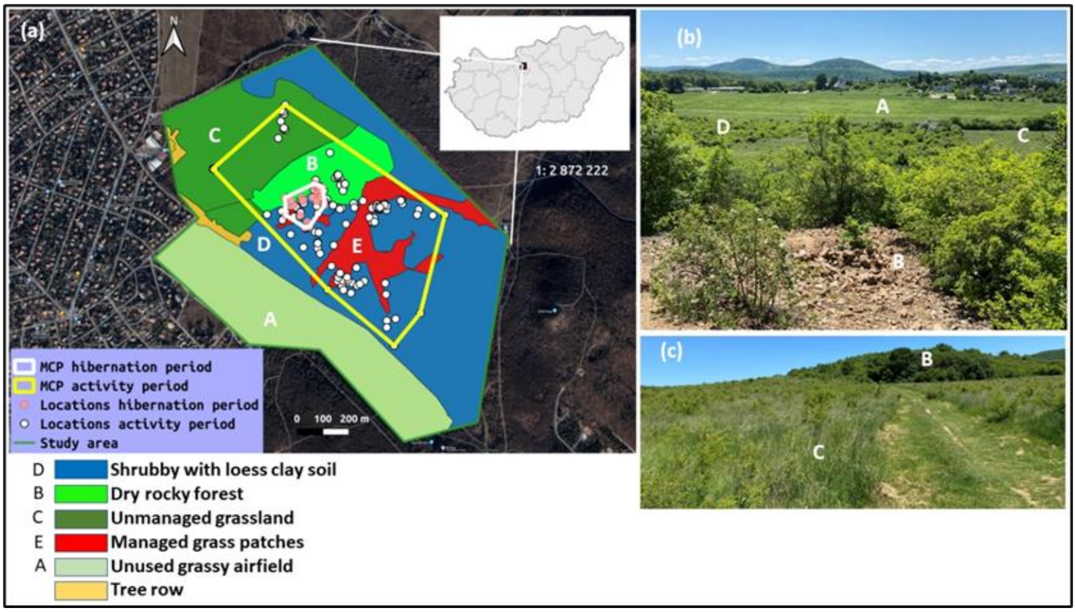

Figure 3: (a); Overall distribution of all localization points during activity period (n=226) and hibernation period (n=83) of five Caspian whipsnakes distributed in various habitat patches estimated by Minimum Convex Polygon (MCP) method: (b) and (c); images from the study area depicting different habitat patches. Capital letters on (a) correspond to those on (b & c) showing some of the habitat types.

The estimated average individual home range sizes calculated using all the (year-round) tracking data of each snake (2016–2019) ranged between 5.19 ha (LoCoH-R) and 13.8 ha (Adaptive KDE). We revealed a significant difference between the mean home range sizes calculated by the four different methods used (Repeated measures ANOVA: $F = 5.342$; $df = 3$; $p = 0.014$). There was a significant difference between adaptive KDE90 and LoCoH-R (Tukey Kramer post-hoc test: $p<0.05$) and no significant difference was found among the estimates of other methods ($p>0.05$) (Fig. 4).

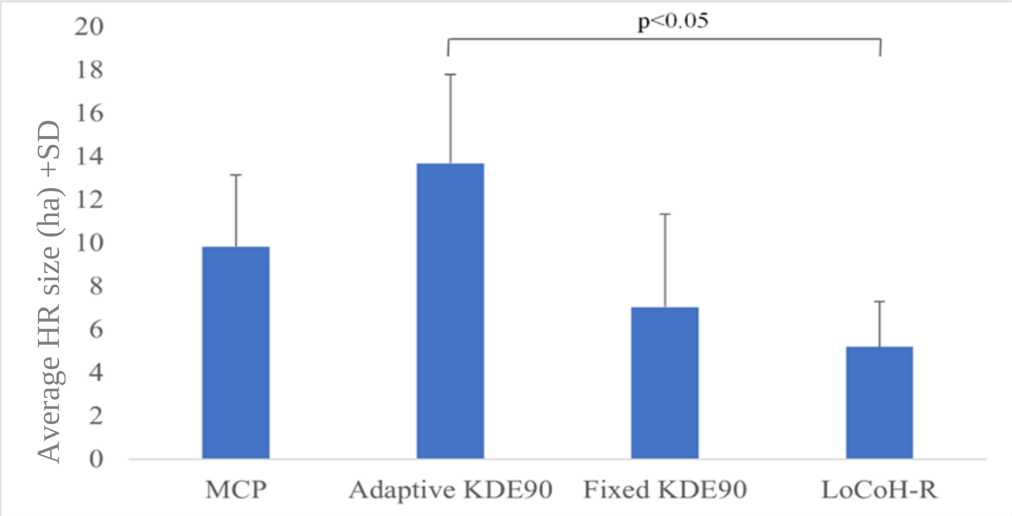

Figure 4: Average home range (HR) sizes calculated using the entire tracking dataset of all the years of tagged Caspian whipsnakes in the study area estimated by four different methods. There was a significant difference between adaptive KDE90 and LoCoH-R ($p < 0.05$).

During the activity periods, individual snakes established home ranges of a size between 6.1 and 15.5 ha calculated by MCP. In this active interval, the home ranges of the two males were larger than those of the three females. During the hibernation periods the individual home ranges were reduced to less than 0.3 ha in the central dry rocky patch with woody vegetation consisting of hibernacula.

There was no significant difference among the individual daily displacements of the five snakes during the activity period (Kruskal-Wallis test: $X^2 = 9.23$; $df = 4$; $p = 0.056$). Jane showed the largest, meanwhile Tarzan the smallest displacements. The maximum absolute value of the daily displacement during the activity period was found to be 226 m by Vali.

3.2.4. Relationship between shrub cover and Caspian whipsnake telemetry points

We determined descriptively the distribution of snake location points (n = 309) among various categories of shrub cover. The distribution of shrub cover in the area shows heterogeneity resulting in a patchy habitat, comprising open grassy patches and various levels of shrub cover.

The results show that 50% (n = 550) of the cells were found to be within the shrub cover category of 0 – 40% in the area utilized by Caspian whipsnakes. During vegetation periods, the snakes also used the moderately open shrubby patches/cells. However, in most cases the snakes used highly dense cells (71 – 100% shrub cover) during vegetation periods. Furthermore, the snakes were found in cells with less shrub cover (0 – 10%). In the hibernation period too, snakes mainly used hugely dense shrubby cells, interestingly they were also detected in much less shrubby cells (0 – 10% and 11 – 20%).

3.2.5. Human impact on the Caspian whipsnake

In total, we managed to survey 225 occasions of human and dogs' encounters with the dummy snake. For the duration of the study 234 persons were seen on the hiking trail at least between 3PM and 6PM. Overall, in 74% of encounters the dummy snake was noticed (seen) whereas in 26% of the occasions the snake was not noticed.

There were more walking people on the nature trail than cyclists and jogging individuals. On 144 occasions walkers on the trail were accompanied by dogs, and all dogs were unleashed and freely moving ahead of the handler/owner.

We recorded 40 occasions of cycling activities, 22 jogging activities, and 163 walking occasions. In the event of cycling 77% (n = 31) of the cyclists hit or ran over the snake and 23% (n = 9) missed or swerved at the snake, however they did not stop. Jogging occasions were minimal. The snake was noticed on

36% of the occasions (n = 8) but unnoticed on 64% (n = 14) of the occasions. All joggers who noticed the snake stopped to observe.

Our results show that the most common activity on the nature trail was walking. The dummy snakes were noticed on 91% (n = 152) of the occasions by walkers and 36% (n = 8) by people who were jogging. These 152 people stopped to observe the snake and were not seemed to be afraid of it. However, they were in many cases not aware that it was a dummy snake. On 9% (n = 15) of the occasions the walkers fled when they saw the snake, they were afraid. On occasions (n = 3) when people were walking in a group they hit or stepped on the snakes all the times.

The experiment has proven that dogs off the leash may be an important threat to the Caspian whipsnakes in the area, especially on the hiking trail, considering the high number of people entering the area with dogs either while walking, cycling or running and the very high rate of cases when the dog attacked the dummy snake.

4. DISCUSSION

4.1. Literature survey: ungulates interactions with reptiles

Our results show that ungulates may be significantly problematic to reptiles and their habitat especially if they occur in high densities; Graitson et al. (2019) drew similar conclusions in the case of wild boar. Ungulates may cause more harmful than beneficial impacts on reptiles. The most disruptive ungulate species was found to be the wild boar. Our data showed that wild boar can have tremendous impacts on reptiles due to their rooting/digging behavior which may result in opportunistic feeding of reptiles and change the habitat structure or decrease prey (lizards, amphibians and other invertebrates) for reptiles in the ecosystem. Since many different reptile species were affected by their foraging behavior, it would be hard to state which ones were mostly impacted, as this is also dependent on the effort of scientific research conducted on specific reptile species. However, it is clear that the coexistence of reptiles with ungulate populations, especially with wild boar, and mainly in the case of their high density, will result in several negative effects (Platt et al., 2019). A recent analysis demonstrated that wild pigs threaten 672 taxa in 54 different countries across the globe, most of them being listed as critically endangered or endangered, and some additional ones have been driven to extinction as a direct result of impacts from wild pigs (Risch et al., 2019).

Our results reflect that both direct and indirect ungulate effects can shape the reptile communities but that indirect effects that are less obvious and more difficult to detect are more common. This is consistent with previous studies (Larson and Paine, 2007). We found that the indirect impacts are more dominant by livestock than wild ungulates and mainly related to grazing. Livestock grazing is the most widespread land-use on Earth, and can also have some negative effects on biodiversity (Kay et al., 2017) including reptiles (Schieltz and Rubenstein, 2016). Indirect impacts by livestock and wild ungulates primarily include overgrazing, which often affects the abundance of reptiles (Val et al., 2019).

Positive impacts by ungulates on reptiles were seldom, but we could also reveal some favorable situations (for example, the presence of ungulates may favor some arthropods (Carpio et al., 2017), which can provide prey basis for reptiles). In terms of indirect interactions shaping habitat characteristics by ungulate activities has a special significance and can also lead to favorable conditions. Reider et al (2013) mentioned that collared peccary (*Pecari tajacu*) is an important agent that affects leaf litter structure and promotes the increase in the occurrence of terrestrial reptiles. Even abundant ungulates may also result in positive impacts on reptiles; in abandoned areas, they can contribute to halting forest encroachment and maintaining the required habitat heterogeneity, creating a suitable habitat for reptiles (Zakkak et al., 2015). Similarly, in a recent study in an urban area, it was also demonstrated (Cabon et al. 2022) that wild boar rooting enhanced sand lizard (*Lacerta agilis*) populations in dry grasslands, likely by creating a mosaic of bare ground, litter, sparse and dense vegetation. Positive direct impacts were linked to wild ungulates, being potential prey to large-bodied reptiles such as the Komodo dragon preying on Javan rusa (Ariefiandy et al., 2013) or the African python (*Python sebae*) feeding on kob (*Kobus kob*) (Antwi et al., 2019). Conversely, in such cases reptiles may also cause negative impacts on rare/endangered ungulate species, therefore management of populations or the impact of large-bodied reptiles should also be taken into consideration.

However, the significant number of reptiles with high conservation value affected by ungulates is alarming and should not be ignored. Many of ungulate species are continuously increasing and this proliferation of wild and domestic ungulates may be locally detrimental for reptile species coexisting with them. Effective management should function to monitor the dynamics of ungulates in order to ensure fewer negative impacts on reptile communities. Similarly, close monitoring of ungulates should take place in ecosystems where ungulates such as deer are prey to large-bodied reptiles. Further research and reporting by the scientific communities are encouraged to better understand the diversity of investigated ungulate-reptile interactions. Overgrazing by livestock and wild boar foraging activities tend to be the most problematic impacts on reptiles from ungulates. Therefore, well-planned grazing regimes by livestock and effective control of abundant ungulates, especially wild boar outside its native geographical range, need to be considered in habitats of vulnerable reptile species. Instead of total eradication of ungulate effects, promoting moderate ungulate impact is recommended to maintain their beneficial effects without causing damaging impact on reptile communities.

4.2. Field-based research

4.2.1. Using drone technology to investigate shrub density

Our results show that the area is made up of a mosaic of habitat patches including open grassy patches, central rocky-mount and islands of various levels/densities of shrubs. This habitat is suitable for and selected by reptiles, including snakes (Row et al., 2012). The accumulation of woody vegetation is accelerating in the area, meaning such islands of open patches will soon be replaced and the area will be logged with shrubs. From a methodological point of view, using drones for this purpose, i.e., to describe the status of shrub encroachment, was a relatively cost- and time-efficient solution. It included a one-day field survey; however, the preparation of the orthophoto and its analysis required a longer period.

4.2.2. Shoot availability and browsing on woody species

We found that the area is dominated by *Crataegus monogyna;* almost all shrubby patches in the area are formed by this species. Our results show that *Crataegus monogyna* is the most preferred species by ungulate browsers in the area. These results may be biased as *C. monogyna* is the dominant species, and it is still unclear if it is preferred over other species or if ungulates browse its shoots due to a lack of choice. Although it has ecological benefits as it is a fruit-bearing plant, the existence of such species in an ecosystem may benefit other species, including birds and other ungulates such as wild boar. However, in a normal natural ecosystem deer species may not prefer this species because of its characteristics to defend itself by thorns and having leaves and shoots of small biomass. Its thorns may directly confer the ability to compete with more palatable plants in the vicinity (Fichtner and Wissemann, 2021).

Since ungulate browsing tends to have an impact on one species *Crataegus monogyna,* while it is an important contributor to shrub encroachment in the area, therefore if browsing pressure is exerted on it then browsing ungulates (i.e., deer species) would also contribute to suppression of shrub encroachment in the area.

4.2.3. Spatio-temporal changes of wild boar rooting and the relationship between rooting, shrub cover and saplings

Our results show intensive wild boar rooting in the study area. We can deduce that rooting occurred in the area throughout the years; between November 2019 and January 2022. Current literature has proven that populations of wild boar show an increasing trend in urban areas, such as in Budapest (Sütő et al., 2020) where it was proved that wild boar are not transient species but residents (Csókás et al., 2020). Therefore, their permanent signs in urban areas are expected. However, surprisingly, during two winter months (December 2020 and December 2022) rooting activity seems to have decreased significantly, further research can reveal if this will be a trend going forward. Cells with less or without rooting activity obtained a significant number of saplings as compared to highly rooted cells. More rootings appearing in more shrubby areas may imply that wild boar could play a significant role in mitigating shrub encroachment in this area. Similar results were reported by Cuevas et al. (2012) indicating that wild boar activities such as rooting, may significantly reduce plant cover. If wild boar rooting is intensified in more shrubby areas, understory vegetation and saplings can be removed by rooting, resulting in open patches within the woody shrubs enabling sun penetration into the less dense vegetation which could consequently be a desired habitat for the Caspian whipsnake. However, since more saplings are found in areas with fewer shrubs, this allows for newly emerging shrubs to regenerate in open areas. Moderate wild boar rooting may play a paramount role in maintaining some open spaces in the habitat of the Caspian whipsnake and mitigate against shrub encroachment. Therefore, management needs to monitor and, if necessary, control wild boar densities and their impacts on the vegetation even in such special urban habitats to avoid adverse and enhance the beneficial changes of the vegetation.

4.2.4. Relationship between shrub cover and Caspian whipsnake location points

Reptiles such as snakes as poikilothermic ectotherms have acclimatized to regulate their body temperature through sun basking (Mukherjee et al., 2018). As a result, they prefer less homogenous habitats but patchy mosaic areas, the latter allows snakes to actively sun bask, and use dense patches to maneuver from predators (Cagle, 2008; Mukherjee et al., 2018). Our results are in agreement with this, as we revealed that Caspian whipsnakes used most patches in the area but avoided open grassy airfields with a less sporadic visit to open grasslands. The snakes used the patches differently between seasons. Our investigations revealed that Caspian whipsnakes entirely avoided some patch types within our study area: the open grassy airfield and the residential area. But they preferred other patches such as the dry rocky outcrops within the woody vegetation for hibernating in the available hibernacula, and shrubby areas including grassy openings for foraging, all of which means a typical habitat structure the Caspian whipsnakes prefer (Bellaagh et al., 2008; Sahlean et al., 2016). Similarly, Reading and Jofré (2009) reported that grass-snakes in Northern England avoided open grazing lands and strongly preferred habitat boundaries and interfaces. Moreover, we tracked one snake (Tarzan) several times on the unmanaged grassland, which was avoided by the others. The open surfaces on the rocks and grassy openings in the shrub land can provide fast-warming basking sites. Additionally, the grass fields on the loess provide substrate for burrowing to the European ground squirrel (*Spermophilus citellus*) and large colonies of the common vole (*Microtus arvalis*) both providing ample biomass of prey for the large-bodied whipsnakes. On the other hand, the snakes may perceive the still regularly mowed airfield and the human residential area as unsuitable or risky with high chances of mortality by mowing machines and direct killing by humans or dogs. During hibernation the snakes were confined in the smaller central rocky area with woody vegetation. We suggest that for this species the woody vegetation was not the priority. Probably, for this large-bodied snake only this part of the habitat ridden with deep-reaching cracks and stone piles or depots left by the former quarry, provide a suitable hibernacula where they find thermally optimal cavities even in harsh cold spells of the winter. Similar findings were reported on the communal hibernaculum use of seven snake species, including Caspian whipsnakes, in Bulgaria (Dyugmedzhiev et al., 2019).

4.2.5. Spatial ecology and habitat patch preference of Caspian whipsnake - Radio-telemetry

We present the first results for spatial activity pattern, home range size and habitat use of the Caspian whipsnakes, obtained in a peri-urban environment. The five radio-tagged Caspian whipsnakes together used only 40.15 ha, 32% of the study area (125 ha), and they appeared to have small home ranges (mean 5.19 to 13.8 ha depending on the home range estimation methods used) as compared to the available habitat. These findings are in agreement with other studies on home ranges of similar temperate zone colubrids such as smooth snakes (*Coronella austriaca*) living in disturbed landscapes (Reading, 2012). Although, studies on the movement ecology of the Caspian whipsnake have been unavailable so far, when we compared to findings on similar large-bodied snakes in natural landscapes, for example; the Coachwhip (*Masticophis flagellum)* tend to establish larger home ranges (~150 ha), making them relatively more prone to fatalities (i.e., predation) in disturbed landscapes than species using less space (Mitrovich et al., 2009). For Caspian whipsnakes, the smaller home ranges may be due to the concentrated locations of shelters in the rocky patches. Bauder et al (2020) found that habitat heterogeneity and low urban intensity resulted in reduced resource dispersion (prey, refuge) leading to smaller home ranges of threatened eastern indigo snakes. Similar findings are observed in our study as the Caspian whipsnake lives in a mosaic habitat in a peri-urban area.

Our results showed that home range sizes were influenced by the analysis method we used. Earlier research stated that home range estimations by MCP may be more accurate than adaptive and fixed kernel when the sample size is small; in that case, the adaptive kernel tends to overestimate home ranges more frequently (Boyle et al., 2009). However, fixed the kernel has shown the best performance in simulation trials of home range estimators (Silva-Opps and Opps, 2011). The LoCoH method underestimates home ranges by identifying "hard boundaries" (sharply separated spots, such as steep slopes, mountains, roads, rivers, etc.) and excluding them from the calculation (Gregory, 2017). At the same time, the method can precisely outline the spatial movements of individuals for which the absence of records indicates real gaps in occurrence. Revealed variability due to the different types of estimates support these trends, as we observe similar trend in our findings in the case of the adaptive kernel and LoCoH-R.

In our study during the activity periods snakes were localized both above and underground, meanwhile during hibernation periods the snakes were found invariably underground, but it is possible that they were moving under or above ground between two consecutive winter localisations. Because of the latter, this kind of separation of the active and hibernation period we performed is somehow arbitrary, potentially leading to the truncation of the active period, but we could decide whether an animal is hibernating or not, based only on the lack of direct visual observations on the emerged individual above ground and the highly reduced length of its daily displacements. During active periods snakes in temperate zones establish larger home ranges owing to hunting and searching for mating partners (*e.g.* Brito, 2009). We found that the snakes showed an average daily displacement of a range of12.6 m to 36.6 m with the longest distance being 226 m established by Vali during the activity period. However, we are aware that with the localization frequency we used we may have missed movements between two localization events (*i.e.*, the snakes could make repeated long-distance movements between two localizations), therefore these averages could be underestimated. During our field work we obtained additional observations on the movements of individuals within a few hours exceeding the above averages.

According to Frank and Dudás (2018), Caspian whipsnake mating peaks in spring (April and May). Although we did not investigate this, during spring periods gravid females are more likely to have small home ranges than males hence we could observe short movements by some females. We found that males used larger home ranges during the activity period as compared to females. Similarly, in Eastern Indigo snakes, males had larger home ranges with a significant increase during the breeding season (Bauder et al., 2016; Breininger et al., 2011). Reading (2012) reported similar findings on smooth snakes in England. The increased spatial use of male Caspian whipsnakes may be due to males actively searching for females as reported on Eastern indigo snakes (Bauder et al., 2016). However, the longest revealed displacement was related to a female (Vali), which may be related to her higher foraging activity after parturition to cover higher reproductive costs (Gregory, 2009)

In the research by Dyugmedzhiev et al. (2019) Caspian whipsnake used the same microhabitats around the hibernacula during the rest of the active period after spring dispersal (pre-hibernation), not moving very far from it. In our research, we found that during the activity period, the areas within which the snakes used underground burrowing places were partly shifted from the rocky area to the neighboring shrubby and grassy areas. This suggests that during summer they use burrows of rodents in the area as temporal hiding places and they may not return to their permanent dens. We have direct observation of Jane, Tarzan and Lili, using these burrows, Jane also spent a whole winter in a rodent burrow in the central hibernation area. Most snakes in temperate zones show syntopic hibernation (Dyugmedzhiev et al., 2019). We could observe Vali and Lili sharing the same burrow over consecutive winters, moreover, Tarzan used the burrow for wintering that Vali was using before.

But the species may aggregate for sheltering due to limited hibernation areas and not because they want to share the hibernacula. In the case of the Caspian whipsnakes, the best hiding places for them could be in the central rocky area (1.75 ha); their cohabitation in this patch during the hibernation period results in aggregation. Therefore, these results suggest that areas used by snakes for burrowing can be seasonally limited, since for hibernation all individuals tend to find shelter in the rocky patches in natural rock fissures, and do not utilize the holes of ground squirrels or other rodents in the grassy areas during winter (except in the abovementioned case of Jane). However, other studies found that small home ranges occurring in altered landscapes may be associated with high-quality habitat (Reading and Jofré, 2009), this may be the case in Caspian whipsnakes and their prioritization of the central dry rock patch.

Our results show that during the activity period, overlaps of individual home ranges were small (<10%), however, for half of the female-male pairs the overlap extended this level and could reach 60%. There were small overlaps especially between snakes of the same sex, suggesting that Caspian whipsnakes may actively avoid conspecifics of the same sex while foraging in the area. Similar findings were reported when investigating the spatial overlap of eastern indigo snakes (Metcalf et al., 2021), as it was found that male home ranges often or completely overlap female home ranges, whereas snakes of the same sex were much less overlapping. However, considering that a large number of individuals were identified (n = 68) in the area the interpretation of these findings calls for caution.

The tagged Caspian whipsnakes were found in a limited area (40.1 ha) relative to the size of the study area potentially occupiable by snakes (125 ha). The individual home ranges were much smaller than the entire available habitat, no matter which estimation method was used. Males tend to establish larger home ranges, but they had somewhat shorter displacements per day than females during the activity period. However, to understand these variations further research should consider spatial patterns for gravid and non-gravid females during mating and non-mating seasons.

Our results suggest that in this area the snakes utilize a variety of patches for different reasons: in winter they aggregate in a smaller patch (the central dry rocky mount covered with woody vegetation) primarily due to the high availability of hibernacula, whereas during activity period shrubby vegetation and some open grassy patches are also used for foraging.

Based on our results, we conclude that the population size of Caspian whipsnake in our study area will not expand unless new similar rocky outcrops are freed by thinning the dense forests in nearby areas. Small, protected patches can only support a fewer number of individuals. Therefore, to maintain and increase the population of Caspian whipsnake in this peri-urban area, conservation efforts should be channeled towards habitat management interventions such as clearing dense woody patches on the surrounding dolomite hillsides and opening up grass fields by partially removing shrubby thickets.

4.2.6. Caspian whipsnake activity and possible threats – anthropogenic and natural threats

Snakes spend part of the year in hibernation, by doing so they avoid low temperatures. Furthermore, snakes tend to inhibit congregating behavior around their hideouts. In snakes, the selection of a suitable and appropriate hibernaculum is significantly important as it ensures survival in winter. In our study, Caspian whipsnakes used burrows in an elevated rocky outcrop area; this area may have been selected as suitable winter habitat due to the availability of rocky crevices, shrubby vegetation and a network of burrows existing in the area.

5. CONCLUSIONS AND RECOMMENDATIONS

The predominant woody species, *Crataegus monogyna*, is the main cause of shrub invasion in the study area, which presents serious issues. Deer and other browsing ungulates exacerbate this problem by browsing on buds and saplings, while wild boar rooting, mostly in thickets, may produce the openings that Caspian whipsnakes need. More so than mature shrubs, saplings are impacted by this rooting activity, which could hinder the recruitment of woody species. In order to minimize negative consequences and encourage good vegetation changes for rare reptile species, management must closely monitor and regulate ungulate numbers.

Caspian whipsnakes in the study area have restricted habitats, with smaller individual home ranges compared to the available space. Male snakes establish larger home ranges but travel shorter distances daily than females during the active season. More research is required to understand these variations, especially regarding gravid and nongravid females in different seasons. These snakes utilize different patches for specific purposes, aggregating in smaller areas during winter due to the presence of hibernacula and using shrubby vegetation and open grassy patches for foraging during the active season. To expand the Caspian whipsnake population, it's crucial to create new rocky outcrops by thinning nearby dense forests, as small protected areas can only support a limited number of snakes. Conservation efforts should prioritize habitat management, including clearing woody patches and opening grass fields, while also addressing human activities and disturbances near hibernacula, which could negatively have an impact on the Caspian whipsnake population living in this peri-urban area.

6. NEW SCIENTIFIC RESULTS

- Based on the systematic literature review wild boar (*Sus scrofa*) was found to be the most problematic species on reptiles whereas reptiles which suffered the harshest impacts were Squamates (i.e., lizards, and snakes).
- Shrub density estimation by drone showed a variability in the shrub cover of the cells confirming that the area is indeed a heterogenous habitat for Caspian whipsnake. Cells with 0 – 25% estimated shrub cover were found to be most dominating; meanwhile cells with no shrub cover were the least represented.
- There was a significant difference in the average lengths of wild boar rooting occurring in cells with different categories of shrub density; rooting occurred mainly in more shrubby cells than cells with few shrubs.
- This study provided the first data by radiotelemetry on spatial ecology of *Dolicophis caspius*. The estimated average individual home range sizes calculated using all the (year-round) tracking data of each snake (2016 – 2019) ranged between 5.19 ha (LoCoH-R) and 13.8 ha (Adaptive KDE). During the activity period the individual home range sizes varied between 6.1 and 15.5 ha, estimated using the minimum convex polygon (MCP). We found that the average daily displacement for the different individuals ranged between 12.6 and 36.6 m during their main activity season. The tracked snakes used an area of 40.15 ha during the activity period from spring to autumn, but for the winter, they withdrew to a central area of 1.75 ha, abundant in hibernacula. In the study area, the restricted spatial distribution of hibernacula, which

is mainly available in the central dry rocky forest and partly in the shrubby areas, can limit the extent of the suitable habitat.

- Caspian whipsnakes emerge from their burrows on daily basis. However, snake may not return to the same burrow they have surfaced on, meaning there may exist a connected network of burrows in the area.
- Human recreational activities may be a potential threat to the Caspin whipsnake at least on the rocky outcrop mount where the hiking trail is located. Our results show that the most common activity on the nature trail is walking. People hit the snake on several occasions either while cycling or running, similarly, unleashed dogs attacked frequently the dummy snake.

7. LIST OF PUBLICATIONS

- Publication (Journal Article: Q1 – IF = 3.03) – Peer reviewed

Teffo, T.R.; Katona, K.; Babocsay, G.; Sós, E.; Halpern, B. Home Range of the Caspian Whipsnake *Dolichophis caspius* (Gmelin, 1789) in a Threatened Peri-Urban Population. Animals 2023, 13, 447.

- Publication (Journal Article: Q1 – IF = 3.23) – Peer reviewed

Teffo, T.R.; Fehér, Á.; Katona, K. Ungulates and Their Impact on Reptiles: A Review of Interspecific Relationships. Diversity 2023, 15, 28.

- Publication (Journal Article: Q3 – IF = 1.069) – Peer reviewed

Teffo, T.R.; Fuszonecker, G.; Katona, K. Testing pigeon control efficiency by different methods in urban industrial areas, Hungary. Biologia Futura, 2021

- Publication (Journal Article)

Teffo, T.R., Halpern, B., Katona, K. 2022. Csülkösvad fajok hatásai a kaszpi haragossikló (*Dolichophis caspius*) városközeli élőhelyén. Vadbiológia, 22: 23-29.

- Publication (Journal Article)

Katona K., Lupták, P., Amin, S.S., **Teffo, T.R.**, Csíkvári, D., Sütő, D., Heltai, M. 2022. Vaddisznók szóróhasználata Budapesten. Vadbiológia, 22: 10-15.

- Oral Presentation (Conference Article - Hungarian)

Teffo, T.R.; Halpern, B; Katona K. Csülkösvad fajok hatásai a kaszpi haragossikló (*Dolichophis caspius)* városközeli élőhelyén. Vadbiológia 22: 35th Congress of International Union of Game Biologists (IUGB), 2022. Pg 23 – 29.

- Oral Presentation (Conference Article – Hungarian)

Katona, K.; Lupták P.; Sarkawt S. A.; **Teffo, T.R**.; Csíkvári D.; Sütő D.; Heltai M. Vaddisznók szóróhasználata Budapesten. Vadbiológia 22: 35th Congress of International Union of Game Biologists (IUGB), 2022. Pg 10 – 15.

- Oral Presentation (Conference Abstract)

Teffo T.R., Halpern B., Katona K., 2021. Home range patterns of a strictly protected Caspian Whipsnakes (*Dolichophis caspius,* Gmelin, 1789): A peri-urban population in Vöröskővár, Hungary. 1st International Electronic Conference on Biological Diversity, Ecology and Evolution. 24 – 29 March 2021.

- Oral Presentation (Conference Abstract)

Teffo T.R., Halpern B., Katona K., 2020. Home range and movement patterns of Caspian Whipsnakes (*Dolichophis caspius*) in Vöröskővár, Hungary. 6th Students Conférence on Conservation Science SCCS Europe. 24 – 29 August 2020.

- Oral Presentation (Conference Abstract**)**

Teffo T.R., Halpern B., Katona K., 2021. Ungulates impacts on the vegetation of a peri-urban reptile species. 11th Baltic Theriological Conference. 24 – 29 January, 2021.

- Poster (Conference Abstract)

Teffo, T.R., Halpern,B., Kovács, I., Katona, K., 2022. Investigating possible impacts of wild boar (*Sus scrofa*) in the urban habitat of the strictly protected Caspian whipsnake (*Dolichophis caspius*). 6^{th} European Congress for Conservation Biology. 22 – 26 August 2022.

Other publications

- Conference Article

Nel, L., **Teffo, T.R**., Mfihlakalo, V.M., Kruger, P.J., Munnisunker, S., Nzimande, N., **2020.** Sustainable development of South Africa - An in-country perspective. 26^{th} International Sustainable Development Research Society Conference, Budapest, Hungary.

- Contributing Author: Book Chapter

Waswala, B., Falemara, B.C., Obare, F., Kemboi, J., Luwedde, J.G., Mathe, L., Udenkwere, M., **Dlamini, T., Teffo, T.R**., Maoga, U, et al. 2019**.** GEO-6 for Youth Africa: A Wealth of Green Opportunities. Chapter 5: Our Invaluable Biodiversity - Unlocking Biodiversity's Green Job for Youth in Africa Green Jobs in Nigeria's Forestry Sector. United Nations Environment Programme, *ISBN: 978-92-807-3765-3*.

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